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ORIGINAL PAPER

Uncertainty in functional response model selection limits ecological interpretation of results in an experimental system

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Abstract Model selection approaches are gaining popularity in biological research due to their utility in evaluating support for multiple candidate hypotheses. However, top-ranked models from a set of candidates do not necessarily describe the underlying processes that give rise to biological phenomena or provide strong predictive ability. The field of invasion ecology is increasingly using comparative functional response (FR) approaches to predict the trophic impacts of invasive species based on the FR model that best fits experimental data. However, noisy experimental data and a variety of, at times, conflicting model selection approaches may limit the ecological interpretation of results. Here, we use experimental (empirical and simulation) and analytical approaches to explore how the ecological interpretation of FR data can be obfuscated by methodologies (i.e., experimental habitat complexity). Finally, we survey the literature and identify which model selection approaches are most common in FR experiments in invasion ecology, and how the resulting model fits are interpreted. The round goby is a prolific invasive fish in North America, responsible for local declines in invertebrate populations through predation. Using round goby as a model predator, we demonstrate that prey-type (mobile versus immobile) can shift the best-fit FR

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from Type III to Type II. In seven out of eight empirical treatments of varying habitat complexity, and eight out of eight corresponding simulated treatments, model selection outcomes differed depending on the analytical approach used. Our results demonstrate the context-dependence of FRs and highlight the limitations of these FR experiments and associated model selection methods. We encourage researchers to critically assess model selection methods and results when identifying and using top-ranked models, and provide recommendations to improve predictive accuracy.

Keywords Consumer-resource dynamics · Functional response models · Model selection

Introduction

Ecological systems are incredibly complex, challenging our mechanistic understanding of biological processes and limiting our predictive ability. In past decades, increasing computational power has allowed researchers to shift their analytical approaches away from null hypothesis significance testing (NHST), towards a model selection framework (Nakagawa and Cuthill 2007; Krausman 2017; Mac Nally et al. 2018). Within the NHST paradigm, researchers use statistical significance tests to determine if the null hypothesis should be rejected based on the observed data and “an arbitrary probability threshold (usually $p < 0.05$)” (Johnson and Omland 2004). However, this approach does not provide the effect size of the parameter of interest (though accompanying quantities, including Pearson’s r or r^2 can be used to estimate variance explained), nor the precision of the estimate (though confidence intervals indicate a range within which the true value of a parameter might sit; Nakagawa and Cuthill 2007). The rejection of the null hypothesis would only lend support for an alternative hypothesis; support that is often overstated as a definitive result rather than an indication that further investigation may be warranted (Krausman 2017). Though not entirely distinct from a NHST testing framework, in a model selection framework, researchers identify multiple hypotheses associated with a set of *a priori* models that represent the processes of interest, and fit each model to data to identify which model best describes the observed phenomenon. In contrast to NHST which evaluates support for one hypothesis, information-theoretic approaches use information criteria (ICs) (e.g., Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), Deviance Information Criterion (DIC), Watanabe-Akaike Information Criterion (WAIC), Leave-One-Out Cross-Validation (LOO-CV)) to rank candidate models (Akaike 1998; Krausman 2017; Mac Nally et al. 2018; Schwarz 1978; Spiegelhalter et al. 2002; Vehtari et al. 2017; Watanabe 2013).

The model selection approach has clear benefits over traditional hypothesis testing, including providing effect sizes and model parameter estimation, summarized by Burnham and Anderson (2004b) and others (e.g., Johnson and Omland 2004; Aho et al. 2014). However, there are potential pitfalls in the application of model selection to ecological systems. Model selection criteria like AIC use within-sample data to approximate and rank competing models’ out-of-sample predictive ability, and thus cannot guarantee that top-ranked models describe the underlying mechanistic processes that give rise to the data (Arif and MacNeil 2022; Tredennick et al. 2021). This is particularly troublesome when within-sample data is captured over a limited timescale, and thus may not be representative of a system’s long-term behaviour (Hastings 2004; Hock et al. 2024). In such a case, a phenomenological or ill-conceived mechanistic model may describe the sample data well and be selected as the top-ranked model, but be unable to predict or explain the long-term behaviour of the system (Arif and MacNeil 2022; Johnson-Bice et al. 2021; Mac Nally et al. 2018). In addition, given that model selection criteria aim to provide relative rather than absolute measures of predictive ability, researchers must be careful in their interpretation of top-ranked models. As argued by Tredennick et al. (2021), researchers often rely on arbitrary cutoffs to differentiate AIC values, which is problematic given that models with high predictive ability are often phenomenological, and may lack the ability to capture explanatory ecological mechanisms.

A recent example of the model selection approach is the increasingly popular use of functional responses (FRs) to make inferences about the *per capita* impacts of invasive species (Faria et al. 2023). FRs characterize a consumer’s intake of resources as a function of the resource density. Predator–prey FRs are most frequently classified as Type I, II, or III

(Papanikolaou et al. 2021; Faria et al. 2023). A Type I FR is characterized by a linear relationship between resource density and consumption rate, and is typical of suspension-feeders such as mussels (Jeshke et al. 2004), but may also arise as an experimental artifact in laboratory studies that provide insufficient low-prey densities (Sarnelle and Wilson 2008). A Type II FR is characterized as a hyperbolic saturating curve and is typical of herbivores and specialist predators (Lundberg 1988; Lundberg and Åström 1990), whereas a Type III FR characterized by low predation rates when a prey species is rare (owing to low encounter rates and a subsequent learning period) but an otherwise positive relationship between consumption rate and resource density towards a saturation point, producing a sigmoidal curve typical of generalist predators (Andersson and Erlinge 1977; Hansson and Henttonen 1985; Holling 1965, 1966; Leeuwen et al. 2007). Both Type II and Type III models include parameters describing the consumer's handling time (the time it takes to process, consume, and digest the resource; Jeschke et al. 2002; Barrios-O'Neill et al. 2016) and attack rate (the rate at which the consumer encounters the resource). While FRs represent general models that can be applied to many consumer-resource systems, the frequent use of FRs to describe invasive species' consumption follows from the hypothesis that highly-impactful invasive species are more efficient resource-consumers than their native counterparts, and therefore may have lower handling times and greater attack rates (Ricciardi et al. 2013). By comparing these parameters across experimental FRs, researchers hope to identify, and prioritize management, for invaders and invasion scenarios with the potential for the greatest consumptive impacts based on individual's *per capita* effects (Ricciardi and MacIsaac 2010; Vander Zanden et al. 2010; Dick et al. 2013).

In addition to the comparisons of FR model parameters between invasive and analogous native species, some have posited that the form of experimentally-derived FR can be used to predict whether the observed consumer-resource relationship is likely to be destabilizing (i.e., Type II FR, leading to resource depletion) or stabilizing (i.e., Type III FR, leading to resource persistence), respectively (e.g., Alexander et al. 2012; Dick et al. 2013; Faria et al. 2023). However, methodological variation in experimental design (e.g., arena size, habitat complexity, consumer starvation, prey replacement, experimental duration, temperature) and noise in the resulting empirical data can influence FR model selection and inference, and mask the inherent quality of consumer-resource dynamics (Alexander et al. 2012; DeLong et al. 2025; Juliano et al. 2022; Kalinkat et al. 2023; Uiterwaal and DeLong 2018). For example, in systems with mobile predators and prey, adding structural complexity to experimental arenas may induce a switch from a Type II FR to a Type III FR, as the predator-free space in which prey can find refugia is increased, slowing the predator's rate of consumption as prey populations become depleted (Alexander et al. 2012; Barrios-O'Neill et al. 2015). In addition, empirical FR data are often highly stochastic and model selection and fitting can be challenging, with multiple, often conflicting, methodologies recommended by different authors (see a description of methods in Pritchard et al. 2017). Although FR metrics have been shown to successfully predict which invaders are likely to have strong trophic impacts (e.g., Dick, et al. 2017a, b), these methodological challenges may impede our ability to predict ecological outcomes of invasions from experimental FRs (Jeschke et al. 2002).

A model invasive consumer—the round goby

The round goby (*Neogobius melanostomus*), is a benthic fish native to the Ponto-Caspian basins of Eurasia and a prolific invader in North America, responsible for declines in native fish and invertebrate populations through competition (Dubs and Corkum 1996; Janssen and Jude 2001; Morissette 2018) and predation (Barton et al. 2005; Lederer et al. 2006; Krakowiak and Pennuto 2008; Paul Leblanc et al. 2020). Management efforts are largely focused on early-detection/rapid-response measures to prevent further spread (Kornis et al. 2012), illustrating the importance of accurately predicting and prioritizing management in areas where impacts will be the greatest. Field observations of round gobies suggest that they prefer rocky substrates (Ray and Corkum 2001; Lapointe et al. 2007; Young et al. 2010), but are often found in similar abundances on soft sediments (Johnson et al. 2005; Taraborelli et al. 2009). The choice of habitat may reflect foraging behaviour; Gebauer et al. (2019) compared FRs of round gobies on sandy substrate and coarse gravel. In both habitats, the gobies exhibited Type II FRs, but had a significantly greater attack rate in sandy habitats, and a greater maximum feeding rate on coarse gravel. Habitat complexity mediates feeding efficiency and behaviour of predators (Gotceitas 1990; Swisher et al. 1998; Alexander et al. 2012; Barrios-O'Neill et al. 2015) in myriad ways (Savino and Stein 1989). Although increased structural complexity can provide predator-free space that serves as a refuge for prey (Alexander et al. 2012; Barrios-O'Neill et al. 2015), this space is only advantageous if prey are able to make use of it (Savino and Stein 1989).

Here, we explore how FR experimental and analytical approaches affect model selection and therefore alter the ecological interpretation of results based on the form of the best-fit FR model. First, we use round gobies to conduct empirical FR experiments, manipulating habitat complexity and prey-type to explore if these variables influence the selection of the best-fit model. We fit Type II and Type III functional response models to the resulting data and use four commonly referenced approaches to select the best-fit model. Next, we perform a simulation experiment to explore variation in outcome by model selection approach. Finally, we present a literature survey of comparative FR studies on invasive species to assess the frequency with which different methods of model selection are employed, and how results are interpreted ecologically.

Methods

Goby collection and care

Round gobies were collected using minnow traps and a beach seine from their invaded range in the St. Lawrence River (45.319180, −73.927180), Québec, Canada in the summers of 2017 and 2018 and transported to a climate-controlled facility at McGill University (Montreal, QC, Canada). The fish were acclimated to established holding tanks held at 16 °C, and a 12:12 hour light:dark regime for at least one month prior to beginning experiments. The holding tanks did not contain any substrate but the gobies were provided with pvc-pipes which served as shelters. Care during holding included feeding ad libitum with sinking shrimp pellets five days per week, weekly water quality monitoring, and weekly 30% water changes.

Habitat complexity experiments (experiments 1 and 2)

FR experiments were conducted using low, intermediate, and high habitat complexities, each repeated with two prey types (six experimental treatments; Fig. 1). Habitat complexity was manipulated by securing river rocks (Exo Terra turtle pebbles, ~ 15–20 mm diameter) to Plexiglas plates (~ 205 mm by 127 mm) using a thin layer of transparent silicone on the bottom of each stone. This approach created a standardized density of hard substrate with interstitial space between stones. Three plates were added to each experimental tank (ten gallon aquariums with opaque dividers between them) in the following layouts: three plates with no rocks (low complexity), two plates with a single layer of rocks and one plate with two layers of rocks (intermediate complexity), or three plates with two layers of rocks each (high complexity; Fig. 1). For each complexity treatment we measured the FRs of round gobies with two common prey types: previously frozen bloodworms (chironomid larvae; Experiment 1), and live amphipods (*Gammarus fasciatus*, collected in the St. Lawrence River; Experiment 2).

Gobies were randomly assigned an experimental treatment and introduced into aquaria held at 16 °C 24 hour prior to the beginning of experiments to allow for acclimation and standardization of hunger levels. Experiments began with the introduction of prey at a randomly selected density (4, 6, 10, 20, 60, 90 or 120 chironomid larvae or 2, 3, 5, 10, 20, 30 or 50 live amphipods) and continued for two hours, without replacing prey as they were consumed. After two hours, the gobies were removed from the experimental arena and the individuals' sex, weight, and length were recorded, and the number of remaining prey were counted. Each prey density was replicated four times for each treatment ($n = 28$ per treatment, $N = 126$). In addition, for trials using live amphipods, predator-free controls were conducted at each density and treatment to account for mortality not attributed to the predator ($n = 21$).

Substrate-type experiments (experiment 3)

Substrate-type experiments were done using the same experimental tanks and temperature-controlled facilities as described above (Fig. 1). Here, FR experiments were conducted with two substrate types

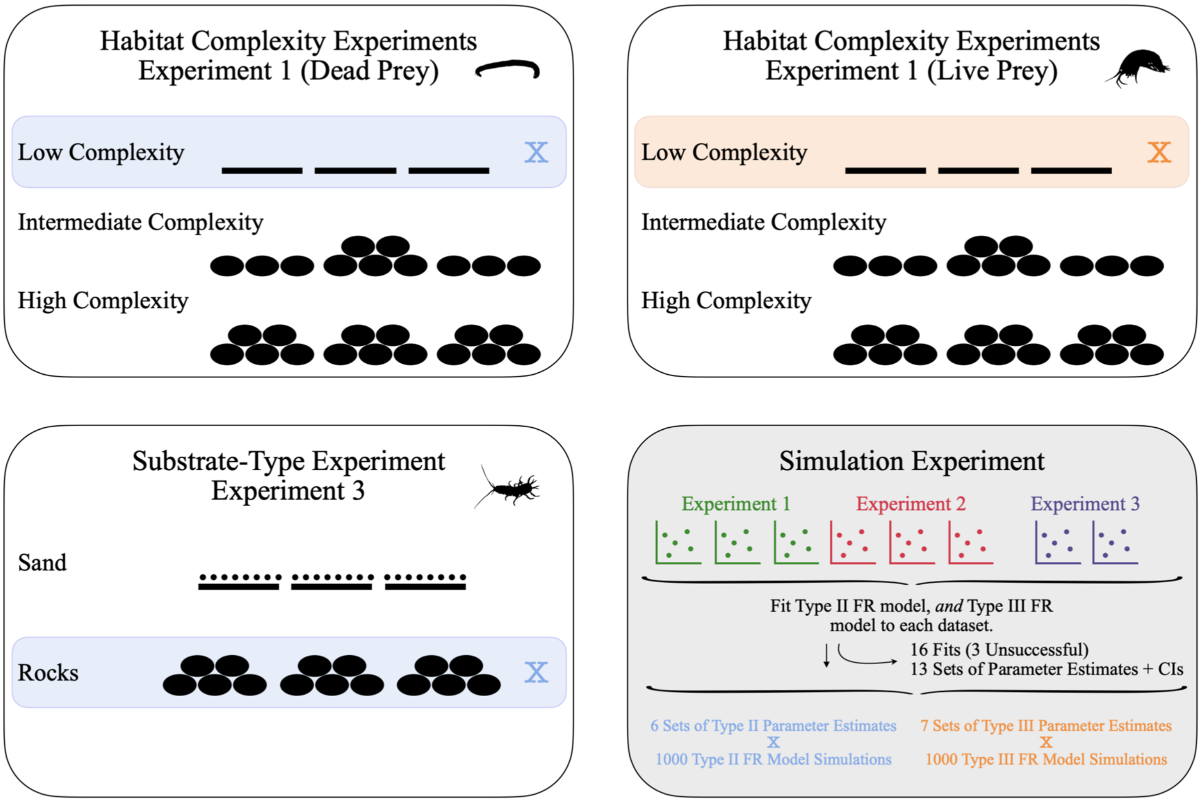

Fig. 1 Schematic detailing experimental designs. In empirical experimental design boxes (white), blue/orange boxes denote cases in which fitting a Type II/III FR model to the empirical data did not produce parameter estimates

covering the bottom of the tank: fine sandy sediment or river rocks (~ 19–38 mm in diameter), and used live isopods (*Caecidotea* spp. collected in the St. Lawrence River) as prey. The difference between types of live prey used in experiments 2 and 3 were on account of seasonal availability of wild-caught invertebrates. As previously described, gobies were introduced into arenas 24 hours before experimentation for a randomly selected substrate, and experiments were initiated with the introduction of prey at a randomly selected density of 2, 3, 5, 10, 20, or 30 individuals. Gobies were allowed to consume the prey (without prey replacement) for a period of four hours (the time it took for the number of prey consumed to plateau at high prey densities in pilot studies), after which the gobies were removed and the individuals' sex, weight, and length were recorded. The remaining number of live prey were counted. Each prey density was replicated in triplicate ($n = 18$ per treatment), plus predator-free controls.

Gobies used in each experiment were subject to reuse, but never at same treatment and prey density to avoid pseudoreplication, and always with at least a two-week rest period between uses.

Model selection

FRs were modeled using Rogers' Type II model (Rogers 1972; Eq. (1)) and Hassell's Type III model (Hassell et al. 1977; Eq. (2)). Per Hassell et al. 1977, attack rate, a, in Rogers' Type II model can be substituted with $\frac{bN_0}{1+cN_0}$ to represent a Type III FR (Pritchard et al. 2017):

$$N_e = N_0(1 - exp(a(N_e h - T))) \tag{1}$$

$$N_e = N_0(1 - exp(bN_0 \frac{N_e h - T}{1 + cN_0})) \tag{2}$$

where N_e is the number of prey consumed, N_0 is the initial prey density, a is the attack rate (the rate at which the predator encounters the prey, at a given density), h is the handling time (the time it takes for the predator to process and consume the prey), T is the experimental duration in hours, and b and c are free parameters. Both models account for the depletion of prey, and therefore are appropriate for experiments without prey replacement (Alexander et al. 2012). We omit Type I FRs from the candidate models as Type I FRs are generally considered to be mechanistically constrained to filter feeders and thus are inappropriate for describing goby predation (Jeschke et al. 2004).

Model fitting and selection were completed using the FRAIR package in R (Pritchard et al. 2017). There are multiple techniques commonly reported in the literature for the selection of best-fit models for FR data (Alexander et al. 2012; Paterson et al. 2015; Pritchard et al. 2017); here, we used four model-selection methods described in Pritchard et al. (2017):

1. Juliano's method (Juliano 2001) fits a polynomial logistic function to the proportion of prey consumed by density. A Type II curve is characterized by declining proportional consumption with increasing density, while a Type III curve follows an initial increase followed by a decrease in the proportional consumption with increasing prey density. Juliano's method was achieved using the "frair_test" function in FRAIR (Pritchard et al. 2017), which uses forward selection step-wise regression to statistically test for support of Type II and Type III FRs.
2. Fitting a generalized FR model with a scaling exponent q on the attack rate (a). When $q = 0$ the model represents a strict Type II curve, whereas $q > 0$ progressively represents stronger support for a Type III curve, up to a maximum value of $q = 1$ (Real 1977; Rosenbaum and Rall 2018; Pritchard 2025). This generalized form allows for prey depletion:

$$a = bN_0^q \tag{3}$$

$$N_e = N_0(1 - exp^{(a(N_e h - T))}) \tag{4}$$

We allowed q to vary and used a regression to test the null hypothesis that $q = 0$.

3. AIC comparison. We fit Type II (Eq. 1) and Type III (Eq. 2) models to the data and used AICc to calculate AIC differences and Akaike weights to determine which was a better fit. AIC differences of ~2 points were considered to have differing levels of support, and the model with the lower AIC score was considered the best-fit model (Burnham and Anderson 2004a).
4. Visual inspection. We inspected the relationship between proportional prey consumption and initial prey density fit with a locally-weighted regression. Type II curves are diagnosed by a declining proportional consumption with increasing density, while Type III curves are suggested when there is an initial increase in the proportional consumption followed by a decline with increasing prey density.

The best-fit model (Rogers' Type II or Hassel's Type III) identified using each approach was recorded and further analyses were conducted using the model that had the most agreement amongst the methods above (i.e., the "consensus model").

Model fitting and comparisons

The best-fit model (as determined by consensus by the model selection approaches above) was fit to each empirical dataset using the "frair_fit" function from the FRAIR package in R. This function employs a maximum likelihood estimation using the "mle2" function from the bbmle package in R, and the default Nelder-Mead optimization algorithm (Nelder and Mead 1965). We used reasonable starting parameter estimates ($a = 1$, $h = 0.1$ for Rogers' Type II, and $b = 1$, $c = 1$, $h = 0.1$ for Hassel's Type III). Resulting parameter estimates are stated in Table S3, and a full description of the model-fitting procedure can be found in the online repository (https://github.com/JaimeGrimm/GobyFunctionalResponse).

Overall model fits to empirical data were compared by bootstrapping the data ($n = 999$) to produce 95% CIs on the fit (Table S3; Pritchard et al. 2017). Comparisons of attack rates and maximum feeding rates are available in the supplementary materials (e.g., Fig. S1 and Fig. S2).

Influence of Goby size and sex

We did not attempt to size match round gobies collected for experiments because of challenges collecting a minimum quantity for sample sizes. Instead, all gobies collected were used in experiments regardless of size or sex, and the gobies collected likely represent a limited size selection of the actual population due to sampling techniques. For this reason, we assessed what, if any, influence goby size and sex had on experimental results by measuring weight, length and sex after each trial. Weight and length were analyzed against the proportion of prey consumed across all treatments using Pearson's *r* correlation test. The effect of sex on the proportion of prey consumption was assessed using a 2-group Mann–Whitney U Test.

Simulation experiment

After using the described methods (Juliano's method, fitting a generalized FR model with a scaling exponent, AIC comparison, and visual inspection) to fit Type II and Type III FR models to the empirical data and identifying the best-fit model, we performed a simulation experiment to explore variation in model selection outcomes (Fig. 1). We began by using experimentally-derived parameter estimates (i.e., from models fit to empirical data; Table S3) to simulate Type II and Type III FR models (Eqns. (1) and (2), as described in Bolker (2008); Fig. S3). Per experiment ((1) Habitat Complexity with Dead Prey, (2) Habitat Complexity with Live Prey, and (3) Substrate) and treatment ((1) Low, Intermediate, High; (2) Low, Intermediate, High; (3) Rocks, Sand), we drew one thousand sets of parameter values from a uniform distribution bounded by the 95% confidence interval and conducted one thousand simulations of the Type II and/or Type III model(s) (Figs. S4–S6). Given three cases in which fitting an FR model to the empirical data did not produce parameter estimates ((1) Experiment 1, Low Complexity Treatment, Type III FR, (2) Experiment 2, Intermediate Complexity Treatment, Type II FR, (3) Experiment 3, Rocks Treatments, Type III FR; Table S3), we conducted a total of thirteen sets of simulations. We then used the described methods (Juliano's method, fitting a generalized FR model with a scaling exponent, AIC comparison, and visual inspection) to fit Type II and Type III FR models to the simulated data. Per treatment (set of one thousand simulations) and model selection method, we determined how often each FR model was identified as the best-fit model, and summarised our findings by calculating how often a given model selection method identified the "correct" data-generating model as the best-fit model.

Literature survey

To gain insight into model selection methods and interpretations of FR results in the literature of invasion ecology, we conducted a publication search in summer 2023 using the Web of Science database with the search terms "functional response" AND "invas*". Our initial search yielded 404 results with publications between the years of 1992 and 2023, and 402 of those articles were available online in full. We limited our survey to FR literature that is used in the context of invasive species because we are interested in which studies apply ecological meaning to the form of FR models best fit to their data. In addition, we excluded review papers and theoretical papers, focusing only on research that presented novel empirical data. After screening publications that met those criteria, we were left with 144 studies. For each, we summarized the data on which model selection methods were used, whether model goodness-of-fit was reported and whether ecological conclusions were attributed to the type of curve.

Results

Model selection

The best-fit model identified by the four model selection approaches differed for seven of eight treatments across experiments (Table 1). In most cases of disagreement, only one of the four methods yielded a different preferred model, but the model selection approach that yielded a differing candidate FR differed across treatments. The "consensus" model was selected as the FR form that was determined to be the best fit by the majority of approaches, with the exception of the low complexity with live prey treatment, for which the model selection approaches did not have a majority agreement on the best fit. For this treatment, we chose to report model fits from a Type III FR for ease of comparison between habitat complexity treatments.

Table 1 The best-fit model (Roger's Type II or Hassel's Type III FR) for each experimental treatment using four methods of model selection

Model selection method:	Habitat complexity experiments						Substrate type experiments	
	High/Live	Int/Live	Low/Live	High/Dead	Int/Dead	Low/Dead	Rocks	Sand
Julianos	No preference	III	II	II	II	II	II	II
Generalized FR	II	III	II	III	III	II	II	III
AIC	III	No preference	III	II	II	III	No preference	II
Visual inspection	III	III	III	II	II	II	III	II
Consensus	**III**	**III**	**No consensus**	**II**	**II**	**II**	**II**	**II**

Experimental treatments are: high, intermediate and low structural complexity with live and dead prey, and pebble versus sand substrate types. The "consensus" model was chosen by agreement by the majority of selection methods and is shown in bold. AIC values and weights reported in Table S1

Habitat complexity and substrate-type FR forms

In the habitat complexity experiments, all round goby FRs to dead prey (chironomid larvae) were best fit by a Type II FR, while FRs to live prey (amphipods) were best fit by a Type III FR regardless of habitat complexity (except the low prey treatment, for which there was no consensus amongst model selection approaches; Table 1). In the substrate-type experiments, FRs to both treatments (i.e., pebble and sandy substrates) were best fit by Type II curves. Within experiments, we saw the highest FRs (i.e., asymptotic maximum feeding rates; see supplementary materials) in less complex habitats (with amphipod prey) and on sandy versus rocky substrates (Figs. 2A and 3). There were no significant differences in overall FRs in habitat complexity with dead chironomid prey (Fig. 2B). In predator-free controls, amphipod survival rate was 99.7% across all densities and treatments, therefore we treated all mortalities as being attributed to the predator. Across all treatments, there was no correlation between the proportion of prey consumed and goby length (Pearson's r; $t_{215} = 1.38$, $p = 0.17$, $r = 0.11$), weight (Pearson's r; $t_{200} = -0.76$,

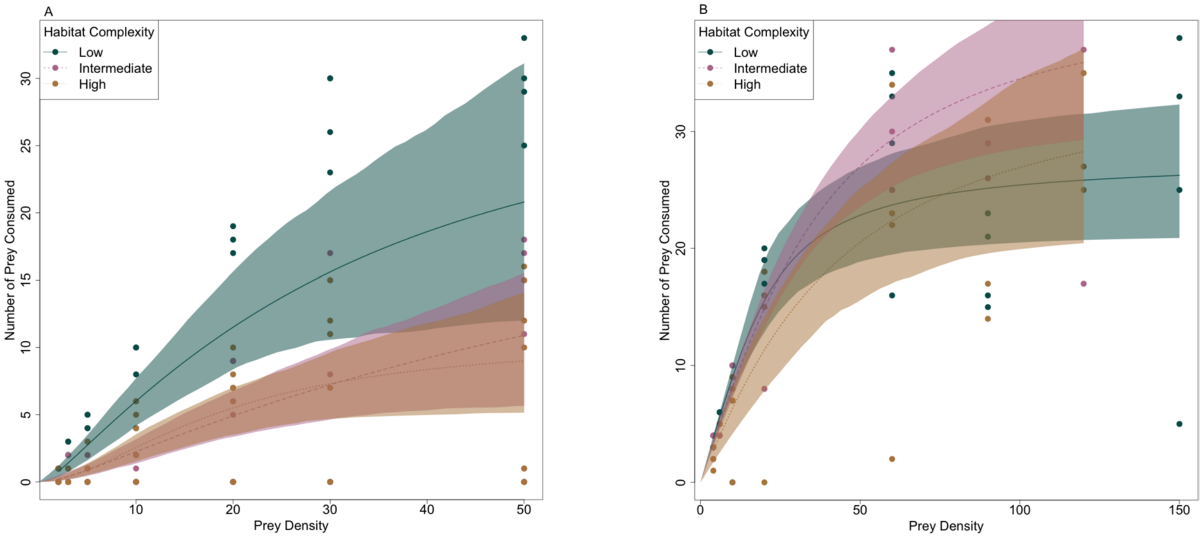

Fig. 2 FRs of invasive round gobies with high, intermediate and low habitat complexity. (A) with live amphipod prey and (B) dead (previously frozen) chironomid larvae prey. Lines are the best-fit model for each treatment: Roger's Random Predator equation (Type II) for dead prey and Hassel's equation (Type III) for live prey. Shaded regions are the 95% confidence intervals on the model fit, generated by bootstrapping (n = 999)

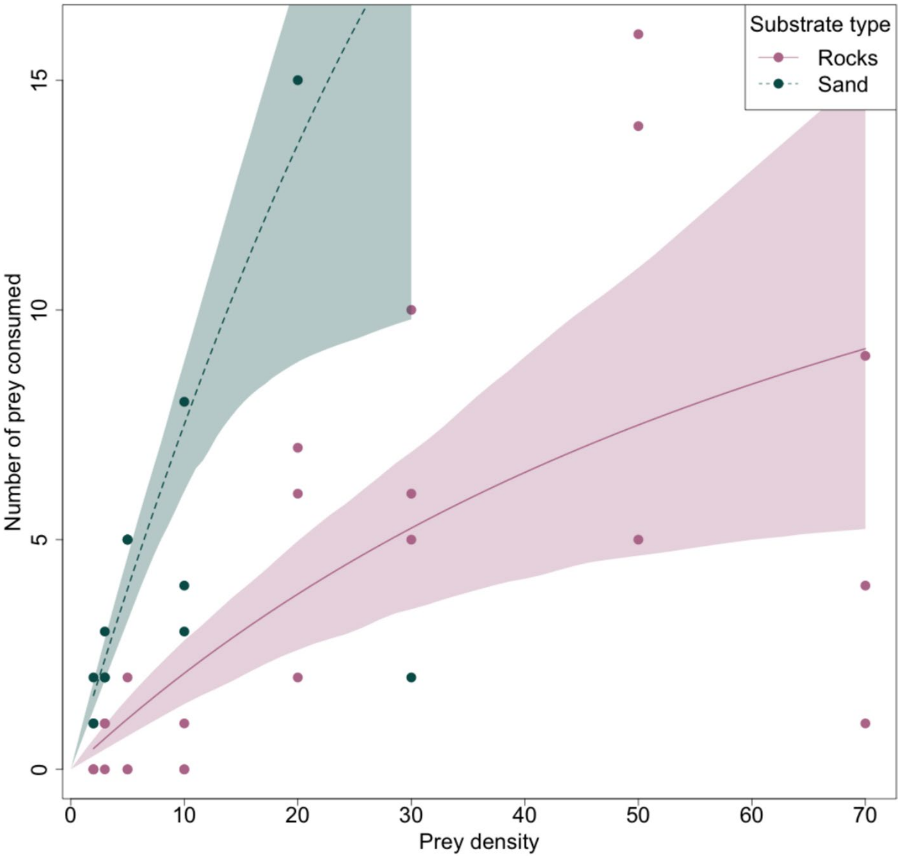

Fig. 3 FRs of invasive round gobies on rocky and sandy substrate types. Lines are the fitted Roger's Random Predator equation (Type II). Shaded regions are the 95% confidence intervals on the model fit, generated by bootstrapping (n = 999)

$p = 0.45$, $r = -0.061$), or sex (Mann–Whitney U; $W = 2663$, $p = 0.47$).

Simulation experiment

Across thirteen cumulative treatments and a majority (over five hundred of one thousand) of simulated datasets, Juliano's method identified the "correct" FR in four cases, mis-identified the FR in three cases, and failed to support one model over another in six cases (Tables S4, Table S5). Fitting a generalized FR model with a scaling exponent resulted in the identification of the "correct" FR in six cases, and in the identification of the "incorrect" FR in seven cases (Tables S4, Table S5). AIC comparison identified the "correct" FR in seven cases, mis-identified the FR in five cases, and failed to support one model over another in one case (Tables S4, Table S5). More generally, Juliano's method and AIC comparison favoured the selection of Rogers' Type II model, while fitting a generalized FR model favoured the selection of Hassell's Type III model (Table 2). Visual inspection resulted in the identification of the "correct" FR in nine cases, and in the identification of the "incorrect" FR in four cases (Tables S4, Table S5). While we were easily able to visually identify Rogers' Type II FR, we experienced difficulty in identifying Hassell's Type III FR (Table 2).

Literature survey

Of the 144 studies that met our criteria for inclusion, model selection was done in 119 (83%) studies using the methods outlined above. Juliano's method was the most ubiquitous (72%), followed by AIC (16%) (Table S2). 20 studies used multiple methods of model selection, and of those, methods agreed in 45% of cases. In an additional 20% of studies, the authors do not report all results of selection methods described in the methods Sect. 16% of studies explicitly acknowledged that models were applied phenomenologically rather than mechanistically, and of those

Table 2 The best-fit model (Roger's Type II or Hassel's Type III FR) for each simulation treatment using four methods of model selection

Experiment Category	Experiment	Treatment	**Juliano's**	**Generalized FR**	**AIC**	**Visual Inspection**
Habitat Complexity Experiments	Experiment 1 (Dead Prey)	Low, Type II	II	III	II	II
		Int., Type II	II	III	II	II
		Int., Type III	II	III	II	II
		High, Type II	II	III	II	II
		High, Type III	II	III	II	II
	Experiment 2 (Live Prey)	Low, Type II	No Preference	III	II	II
		Low, Type III	No Preference	III	II	II
		Int., Type III	No Preference	III	II	III
		High, Type II	No Preference	III	II	II
		High, Type III	No Preference	III	NA	III
Substrate Experiment	Experiment 3	Rocks, Type II	No Preference	III	II	II
		Sand, Type II	II	III	II	II
		Sand, Type III	II	No Preference	II	II

As above, simulation treatments are: high, intermediate and low structural complexity with live and dead prey, and pebble versus sand substrate types. The stated best-fit model is the model selected in an absolute majority of fits to one thousand datasets per treatment (Table S5). When choosing the best-fit model via "Visual Inspection", per treatment, we used Lowess smoothing to combine simulated datasets into groups of fifty and evaluated the resulting twenty curves manually. Blue and orange text indicate Type II and Type III data-generating models, respectively

that acknowledged phenomenological use, 65% still posited mechanistic and/or predictive ability of the FR model.

Discussion

In the habitat complexity experiments, only prey type (i.e., mobile versus immobile), influenced the type of FR best fit given our experimental data. Increasing complexity and switching the substrate type from sand to pebbles had no effect on the best-fit FR model. However, we found that the model selection approach employed in the analysis of empirical FR data altered the determination of the best-fit model in seven out eight cases, demonstrating the need for careful consideration of model selection methods and results when identifying and using top-ranked models. Model selection approaches reported in the literature to identify top FR models are variable. In studies that used more than one approach, the methods agreed on the top model in only 45% of cases. We have demonstrated that the type of FR model that best describes empirical data is context-dependent and highly influenced by the model selection approaches used. We suggest that model selection could be improved through careful experimental design, and by considering the biology of the system of interest to inform the inclusion of candidate models and expected outcomes, assessing goodness-of-fit, and comparing different model selection approaches and employing robust model selection methods, like cross-validation.

Substrate-type, habitat-complexity, and simulation experiments

When considering the consensus model (i.e., the FR form that was determined to be the best fit to the data by the majority of model selection approaches), we did not observe the expected switch from Type II to Type III FRs with increased structural complexity that has been reported in other studies (e.g., Alexander et al. 2012; Barrios-O'Neill et al. 2015). The results did indicate a preference for Type III FRs for data generated with live prey in habitat-complexity experiments, but this preference was consistent between intermediate and high complexity treatments, and there was no model consensus for the low complexity treatment (Table 1). Increased complexity is expected to provide predator-free space (i.e., interstices between rocks that can be accessed by prey, but not the predator) reducing the slope of the curve at low densities (Barrios-O'Neill et al. 2015), resulting in data best fit by Type III models. This effect should be greater for prey that have the ability to actively seek out the predator-free space than for dead prey that only enter interstitial spaces by chance, as seen here. This observation is consistent with similar results comparing FRs of topmouth gudgeon (*Pseudorasbora parva*; another invasive fish) on live prey (*Daphnia*) and frozen chironomids (Boets et al. 2019). However, this result is contingent on which model selection approach is used. Further, as this study (and the study reported by Boets et al. 2019), used different prey species to represent live and dead treatments, it is impossible to disentangle the effect of prey mobility with biomass or the predators' detection and processing of different prey types. Future studies are needed to disentangle this effect.

Following the assertion that Type III FRs represent stabilizing predator–prey dynamics, our findings could suggest that invasive round goby *per capita* consumptive impacts are less pronounced on complex substrates than on simple ones, and should be less disruptive to prey populations in these habitats. Several studies point to invasive round goby abundances being greater on rocky substrates (Ray and Corkum 2001; Lapointe et al. 2007; Young et al. 2010), and that these substrates may protect the eggs of broadcast spawners from goby consumption (Miano et al. 2019). However, field observations show that round gobies exclude native logperch (*Percina caprodes*) on coarse but not sandy substrates (Leino and Mensinger 2017). Given these observations, it is logical to conclude that any advantage observed for round gobies on coarse substrate likely has very little to do with their adaptation for feeding efficiently on such a substrate, and more to do with escaping predators by using interstitial spaces themselves, or more adequate hard substrate required for building nests which increases their recruitment (Kornis et al. 2012). It is also likely that the aggressive behaviour of the round goby excludes other species like logperch from complex habitat even if their predation efficiency is lower in such habitats. Nonetheless, the ecological interpretation of the results presented here and in other studies—with regards to the stability of predator–prey dynamics— is contingent on the model selection approach used.

Per treatment and across one thousand simulated datasets, each model selection method consistently favoured one model over another (Table S4). However, regardless of the identity of the data-generating model, different model selection methods exhibited strong biases towards the selection of one model over another (Table 2). For example, the application of Juliano's method produced minimal variation in model selection within treatment groups, but overwhelmingly selected Rogers' Type II model as the best-fit model across treatment groups. While consistency in model selection within treatment groups may inspire confidence, rigidity in selection among treatment groups suggests that methodological biases may undermine the reliability of these methods.

When fitting a generalized model to select between Type II and Type III models, FRAIR's "fair_fit" function estimates parameter estimates for the specified model (e.g., Eq. 1 or Eq. 2) using a maximum likelihood approach. By fitting Eq. 4, which allows q to vary, we use this function to test the null hypothesis that $q = 0$, and thus assess support for a Type II FR (Pritchard et al. 2017). The NHST paradigm suggests the rejection of the null hypothesis when $p < 0.05$ (Johnson and Omland 2004), and as such, when $p > 0.05$, a lack of support for a Type II FR is often interpreted as support for a Type III FR (Pritchard et al. 2017). As such, while small shifts in the value of q can transfer support for a Type II FR to support for a Type III FR (Rosenbaum and Rall 2018), interpreting a lack of statistical support for a Type II FR as implicit support for a Type III FR may result in the undue selection of a Type III FR, as we observed (Table 2, "Generalized FR"). Similarly, to discourage overfitting, AIC applies larger penalties to more parametrically complex models. While the prevention of overfitting often serves to improve predictive accuracy, when multiple competing models provide an adequate fit to the data, mechanism-independent model selection may preferentially select for simpler models (Symonds and Moussalli 2011). While this phenomenon can result in bias towards the selection of the simpler Type I FR (when included in the set of candidate models), here, this phenomenon results in the undue selection of a Type II FR (Table 2, "AIC") (though recent work identifies bias toward the selection of a Type III FR (DeLong et al. 2025) when data are sparse and noisy).

Relative to other model selection methods, visual inspection of the simulated curves produced more within-treatment variation, likely owing to the fact that this method, while established in the literature (Table S2), relies on the subjective judgement of the researcher.

Model selection

Model selection can be challenging in ecological studies due to high variability in data. For FRs, there is no one method that is widely recommended by methodological papers (e.g., Pritchard et al. 2017) or that is consistently applied across studies (Table S2). Some studies have foregone model selection all together, and instead fit only one type of FR model to their data, but still make predictions about the stability of population dynamics from their results (Table S2). The FoRAGE database (Functional Responses from Around the Globe in all Ecosystems; a global database of standardized functional responses) attempts to address these issues by refitting FR models to published data using a standardized approach, and reporting resulting functional responses and parameter estimates, along with experimental designs and conditions (Uiterwaal et al. 2022). Even when model selection is attempted, most empirically-derived FRs are classified as Type II (Faria et al. 2023). It is unclear whether this trend is driven by simplified experimental arenas limiting prey refuges, a lack of prey replacement in experimental settings, the absence of alternative resources, or because Type II curves are the simplest model to fit to data (Jeschke et al. 2002; Faria et al. 2023). Empirical FR data, even in highly controlled experiments, are often not clearly best described by one model or another (Barrios-O'Neill et al. 2015; Faria et al. 2023). In reality, the fit of Type II versus Type III curves is often not binary. Rosenbaum and Rall (2018) used simulation experiments allowing the scaling exponent q (Eq. 3) to be estimated as a free parameter, and demonstrated that a small shift (e.g., from $q=0$ to $q=0.2$) can significantly increase the stability of trophic interactions. By estimating q in a generalized FR model, researchers can avoid the temptation to provide a binary assertion of whether populations' predator–prey dynamics are stabilizing or destabilizing. However, existing methods of model selection via the estimation of q assume that data are best described by Type II ($q=0$) or Type III ($q>0$) FRs and do not identify cases in which data are not well described by either FR, introducing bias towards the selection of a Type III FR and against the consideration of an alternative FR. As such, the estimated value of q should be interpreted carefully, and within the biological context of the observed or experimental system.

Although AIC explicitly takes into account the number of parameters included in a model, it may favour complex (or, overfit) models, especially in scenarios where none of the models presented are a particularly good fit for the data (Symonds and Moussalli 2011). Variation in environmental and ecological conditions in the field additionally challenge the application of these predictions to wild populations (e.g., increases in temperature can shift the type of FR best fit to the data; Avlijaš et al. 2022). Further, AIC aims to compare the predictive accuracy of competing models, which is distinct from causal inference, but uses within-sample data to do so (Arif and MacNeil 2022). We may improve our confidence in the selection and predictive accuracy of an FR model by (1) incorporating low resource densities in the experimental design and space resource density levels logarithmically (Kalinkat et al. 2023), (2) considering the biology of a system and how system-specific mechanisms inform the inclusion of candidate models and expected outcomes (e.g., omitting Type I FR models when handling time is a biological reality for the predator), (3) empirically assessing goodness-of-fit (χ^2 or r^2), and (4) employing more robust model selection methods, like cross-validation, which involve fitting a model to a "training" dataset, and evaluating its predictive accuracy using a "holdout" or "testing" dataset (Gelman et al. 2014) (though the reliability of both traditional information criteria and cross-validation may be case-dependent; Wor et al. 2025). Regardless, models that are appropriate for predictive inference are not necessarily appropriate for causal inference, and as such, should not be presented using causal language (Arif and MacNeil 2022; Johnson-Bice et al. 2021; Mac Nally et al. 2018; Symonds and Moussalli 2011). When multiple candidate models are assigned similar ranks, model averaging may constitute an attractive way forward (Burnham and Anderson 2004b; Grueber et al. 2011; Johnson and Omland 2004). Model averaging allows researchers to develop multimodel inferences by using assigned rankings to weight competing model estimates (Cade 2015). However, averaging parameter estimates across candidate models relies on candidate models being structurally comparable. When candidate models do not share the same structure, parameter estimates are not comparable, and thus, should not be averaged (Banner and Higgs 2017; Cade 2015; Dormann et al. 2018). Alternatively, one may resolve model uncertainty by averaging predictions across candidate models, as detailed by Dormann et al. (2018), and empirically demonstrated by Meller et al. (2014).

Conclusions

A shift from the paradigm of null hypothesis testing and the reliance on *p*-values to model selection, associated model ranking, and goodness-of-fit estimates can unearth a greater understanding of biological phenomena. However, ecologists must be cognizant and upfront about the limitations of whatever tools we are using. Comparative FR experiments are a robust experimental approach for comparing the relative impact of species or populations in a controlled setting, while accounting for potential context dependencies (Dick et al. 2013, 2017a, b; Faria et al. 2023). In this application, and recognizing its limitations, model selection may be unnecessary as choosing to fit one a priori model can be sufficient if the goal is only to understand the *relative per capita* effects between two groups. In this case, researchers should be upfront that their approach is *phenomenological* rather than *mechanistic* so the conclusions are not extrapolated beyond their limitations (i.e., their predictive power). However, if the goal is to be able to apply the results from comparative FR studies to make predictions about patterns in the field, we advise undergoing careful model selection and consideration of limitations, including the limited predictive ability to out-sample data. Studies using this mechanistic approach should incorporate realistic conditions into their experimental designs to closely approximate field conditions (e.g., habitat structural complexity, multiple prey types, prey replacement, multiple trophic levels). Ecological predictions derived from FR experiments should be tested in the field (e.g., O'Neil 1989; Shenk and Bacher 2002) or in very carefully designed experiments that capture the context-dependent nature of invasion impacts.

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Data availability Data and scripts to replicate this study are available from GitHub at https://github.com/JaimeGrimm/GobyFunctionalResponse.

Declarations

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References

Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. Ecology 95(3):631–636. https://doi.org/10.1890/13-1452.1

Akaike H (1998) Information theory and an extension of the maximum likelihood principle. In: Parzen E, Tanabe K, Kitagawa G (eds) Selected papers of Hirotugu Akaike. Springer, New York, pp 199–213. https://doi.org/10.1007/978-1-4612-1694-0_15

Alexander M, Dick J, O'Connor N, Haddaway N, Farnsworth K (2012) Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. Mar Ecol Prog Ser 468:191–202. https://doi.org/10.3354/meps09978

Andersson M, Erlinge S (1977) Influence of predation on rodent populations. Oikos 29(3):591. https://doi.org/10.2307/3543597

Arif S, MacNeil MA (2022) Predictive models aren't for causal inference. Ecol Lett 25(8):1741–1745. https://doi.org/10.1111/ele.14033

Avlijaš S, Mandrak NE, Ricciardi A (2022) Effects of substrate and elevated temperature on the growth and feeding efficiency of an invasive cyprinid fish, Tench (*Tinca tinca*). Biol Invasions 24(8):2383–2397. https://doi.org/10.1007/s10530-022-02778-7

Banner KM, Higgs MD (2017) Considerations for assessing model averaging of regression coefficients. Ecol Appl 27(1):78–93. https://doi.org/10.1002/eap.1419

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ (2015) Predator-free space, functional responses and biological invasions. Funct Ecol 29(3):377–384. https://doi.org/10.1111/1365-2435.12347

Barrios-O'Neill D, Kelly R, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2016) On the context-dependent scaling of consumer feeding rates. Ecol Lett 19(6):668–678. https://doi.org/10.1111/ele.12605

Barton DR, Johnson RA, Campbell L, Petruniak J, Patterson M (2005) Effects of Round Gobies (*Neogobius melanostomus*) on Dreissenid Mussels and Other Invertebrates in Eastern Lake Erie, 2002–2004. J Great Lakes Res 31:252–261. https://doi.org/10.1016/S0380-1330(05)70318-X

Boets P, Laverty C, Fukuda S, Verreycken H, Green K, Britton RJ, Caffrey J, Goethals PLM, Pegg J, Médoc V, Dick JTA (2019) Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. Biol Invasions 21(5):1751–1762. https://doi.org/10.1007/s10530-019-01932-y

Bolker BM (2008) Ecological models and data in R. Princeton University Press

Burnham KP, Anderson DR (Eds.) (2004a) Model Selection and Multimodel Inference. SpringerNew York. https://doi.org/10.1007/b97636

Burnham KP, Anderson DR (2004b) Multimodel Inference: Understanding AIC and BIC in ModelSelection. Sociological Methods Research 33(2): 261–304. https://doi.org/10.1177/0049124104268644

Cade BS (2015) Model averaging and muddled multimodel inferences. Ecology 96(9):2370–2382. https://doi.org/10.1890/14-1639.1

DeLong JP, Coblentz KE, Uiterwaal SF (2025) Are type 3 functional responses just statistical apparitions? Ecosphere 16(4):e70247. https://doi.org/10.1002/ecs2.70247

Dick JTA, Gallagher K, Avlijas S, Clarke HC, Lewis SE, Leung S, Minchin D, Caffrey J, Alexander ME, Maguire C, Harrod C, Reid N, Haddaway NR, Farnsworth KD, Penk M, Ricciardi A (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biol Invasions 15(4):837–846. https://doi.org/10.1007/s10530-012-0332-8

Dick JTA, Alexander ME, Ricciardi A, Laverty C, Downey PO, Xu M, Jeschke JM, Saul W-C, Hill MP, Wasserman R, Barrios-O'Neill D, Weyl OLF, Shaw RH (2017a) Functional responses can unify invasion ecology. Biol Invasions 19(5):1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Robert Britton J, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Caffrey JM (2017b) Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J Appl Ecol 54(4):1259–1267. https://doi.org/10.1111/1365-2664.12849

Dormann CF, Calabrese JM, Guillera-Arroita G, Matechou E, Bahn V, Bartoń K, Beale CM, Ciuti S, Elith J, Gerstner K, Guelat J, Keil P, Lahoz-Monfort JJ, Pollock LJ, Reineking B, Roberts DR, Schröder B, Thuiller W, Warton DI, Hartig F (2018) Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecol Monogr 88(4):485–504. https://doi.org/10.1002/ecm.1309

Dubs DOL, Corkum LD (1996) Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J Great Lakes Res 22(4):838–844. https://doi.org/10.1016/S0380-1330(96)71005-5

Faria L, Cuthbert RN, Dickey JWE, Jeschke JM, Ricciardi A, Dick JTA, Vitule JRS (2023) The rise of the functional response in invasion science: a systematic review. NeoBiota 85:43–79. https://doi.org/10.3897/neobiota.85.98902

Gebauer R, Veselý L, Vanina T, Buřič M, Kouba A, Drozd B (2019) Prediction of ecological impact of two alien gobiids in habitat structures of differing complexity. Can J Fish Aquat Sci 76(11):1954–1961. https://doi.org/10.1139/cjfas-2018-0346

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2014) Bayesian data analysis, 3rd edn. CRC Press, Taylor and Francis Group

Gotceitas V (1990) Variation in plant stem density and its effects on foraging success of juvenile bluegill sunfish. Environ Biol Fishes 27(1):63. https://doi.org/10.1007/BF00004905

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions: Multimodel inference. J Evol Biol 24(4):699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hansson L, Henttonen H (1985) Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67(3):394–402. https://doi.org/10.1007/BF00384946

Hassell MP, Lawton JH, Beddington JR (1977) Sigmoid functional responses by invertebrate predators and parasitoids. J Anim Ecol 46(1):249. https://doi.org/10.2307/3959

Hastings A (2004) Transients: the key to long-term ecological understanding? Trends Ecol Evol 19(1):39–45. https://doi.org/10.1016/j.tree.2003.09.007

Hock K, Hastings A, Doropoulos C, Babcock RC, Ortiz JC, Thompson A, Mumby PJ (2024) Transient dynamics mask the resilience of coral reefs. Theor Ecol 17(1):1–12. https://doi.org/10.1007/s12080-023-00570-4

Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. Mem Entomol Soc Can 97(S45):5–60. https://doi.org/10.4039/entm9745fv

Holling CS (1966) The functional response of invertebrate predators to prey density. Mem Entomol Soc Can 98(S48):5–86. https://doi.org/10.4039/entm9848fv

Janssen J, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby

Neogobius melanostomus. J Great Lakes Res 27(3):319–328. https://doi.org/10.1016/S0380-1330(01)70647-8

Jeschke JM, Kopp M, Tollrian R (2002) PREDATOR functional responses: discriminating between handling and digesting prey. Ecol Monogr 72(1):95–112. https://doi.org/10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2

Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol Rev 79(2):337–349. https://doi.org/10.1017/S1464793103006286

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19(2):101–108. https://doi.org/10.1016/j.tree.2003.10.013

Johnson TB, Allen M, Corkum LD, Lee VA (2005) Comparison of methods needed to estimate population size of round gobies (*Neogobius melanostomus*) in Western Lake Erie. J Great Lakes Res 31(1):78–86. https://doi.org/10.1016/S0380-1330(05)70239-2

Johnson-Bice SM, Ferguson JM, Erb JD, Gable TD, Windels SK (2021) Ecological forecasts reveal limitations of common model selection methods: predicting changes in beaver colony densities. Ecol Appl 31(1):e02198. https://doi.org/10.1002/eap.2198

Juliano SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, 2nd edn. Oxford University Press, New York, pp 178–196. https://doi.org/10.1093/oso/9780195131871.003.0010

Juliano SA, Goughnour JA, Ower GD (2022) Predation in many dimensions: spatial context is important for meaningful functional response experiments. Front Ecol Evol 10:845560. https://doi.org/10.3389/fevo.2022.845560

Kalinkat G, Rall BC, Uiterwaal SF, Uszko W (2023) Empirical evidence of type III functional responses and why it remains rare. Front Ecol Evol 11:1033818. https://doi.org/10.3389/fevo.2023.1033818

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. J Fish Biol 80(2):235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x

Krakowiak PJ, Pennuto CM (2008) Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). J Great Lakes Res 34(4):675–689. https://doi.org/10.1016/S0380-1330(08)71610-1

Krausman PR (2017) *P* -values and reality. J Wildlife Manage 81(4):562–563. https://doi.org/10.1002/jwmg.21253

Lapointe NWR, Corkum LD, Mandrak NE (2007) Seasonal and ontogenic shifts in microhabitat selection by fishes in the shallow waters of the Detroit River, a Large Connecting Channel. Trans Am Fish Soc 136(1):155–166. https://doi.org/10.1577/T05-235.1

Lederer A, Massart J, Janssen J (2006) Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. J Great Lakes Res 32(1):1–10. https://doi.org/10.3394/0380-1330(2006)32[1:IORGNM]2.0.CO;2

Leeuwen EV, Jansen VAA, Bright PW (2007) How population dynamics shape the functional response in a one-predator–two-prey system. Ecology 88(6):1571–1581. https://doi.org/10.1890/06-1335

Leino JR, Mensinger AF (2017) Interspecific competition between the round goby, *Neogobius melanostomus,* and the logperch, *Percina caprodes,* in the Duluth-Superior Harbour. Ecol Freshw Fish 26(1):34–41. https://doi.org/10.1111/eff.12247

Lundberg P (1988) Functional response of a small mammalian herbivore: the disc equation revisited. J Anim Ecol 57(3):999. https://doi.org/10.2307/5107

Lundberg P, Åström M (1990) Functional response of optimally foraging herbivores. J Theor Biol 144(3):367–377. https://doi.org/10.1016/S0022-5193(05)80081-5

Mac Nally R, Duncan RP, Thomson JR, Yen JDL (2018) Model selection using information criteria, but is the “best” model any good? J Appl Ecol 55(3):1441–1444. https://doi.org/10.1111/1365-2664.13060

Meller L, Cabeza M, Pironon S, Barbet-Massin M, Maiorano L, Georges D and Thuiller W (2014) Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. Divers Distrib 20:309–321. https://doi.org/10.1111/ddi.12162

Miano AJ, Leblanc JP, Farrell JM (2019) Laboratory evaluation of spawning substrate type on potential egg predation by round goby (*Neogobius melanostomus*). J Great Lakes Res 45(2):390–393. https://doi.org/10.1016/j.jglr.2019.02.002

Morissette O (2018) Spatio-temporal changes in littoral fish community structure along the St. Lawrence River (Québec, Canada) following round goby (*Neogobius melanostomus*) invasion. Aquat Invasions 13(4):501–512. https://doi.org/10.3391/ai.2018.13.4.08

Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev 82(4):591–605. https://doi.org/10.1111/j.1469-185X.2007.00027.x

Nelder JA, Mead R (1965) A simplex method for function minimization. Comput J 7(4):308–313. https://doi.org/10.1093/comjnl/7.4.308

O’Neil RJ (1989) Comparison of laboratory and field measurements of the functional response of *podisus maculiventris* (Heteroptera: Pentatomidae). J Kansas Entomol Soc 62(2):148–155

Papanikolaou NE, Kypraios T, Moffat H, Fantinou A, Perdikis DP, Drovandi C (2021) Predators’ functional response: statistical inference, experimental design, and biological interpretation of the handling time. Front Ecol Evolut. https://doi.org/10.3389/fevo.2021.740848

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. J Anim Ecol 84(2):453–463. https://doi.org/10.1111/1365-2656.12292

Paul Leblanc J, Killourhy CC, Farrell JM (2020) Round goby (*Neogobius melanostomus*) and native fishes as potential nest predators of centrarchid species in the upper St. Lawrence River. J Great Lakes Res 46(1):216–224. https://doi.org/10.1016/j.jglr.2019.12.001

Pritchard DW, Paterson RA, Bovy HC, Barrios-O'Neill D (2017) Frair: an R package for fitting and comparing consumer functional responses. Methods Ecol Evol 8(11):1528–1534. https://doi.org/10.1111/2041-210X.12784

Pritchard D (2025) frair: tools for functional response analysis. https://doi.org/10.32614/CRAN.package.frair, R package version 0.5.203

Ray WJ, Corkum LD (2001) Habitat and site affinity of the round goby. J Great Lakes Res 27(3):329–334. https://doi.org/10.1016/S0380-1330(01)70648-X

Real LA (1977) The kinetics of functional response. Am Nat 111(978):289–300

Ricciardi A, MacIsaac HJ (2010) Impacts of biological invasions on freshwater ecosystems. In: Richardson DM (ed) Fifty years of invasion ecology: the legacy of Charles Elton, 1st edn. Wiley, pp 211–224. https://doi.org/10.1002/9781444329988

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83(3):263–282. https://doi.org/10.1890/13-0183.1

Rogers D (1972) Random search and insect population models. J Anim Ecol 41(2):369. https://doi.org/10.2307/3474

Rosenbaum B, Rall BC (2018) Fitting functional responses: direct parameter estimation by simulating differential equations. Methods Ecol Evol 9(10):2076–2090. https://doi.org/10.1111/2041-210X.13039

Sarnelle O Wilson AE (2008) Type iii functional response in daphnia. Eco 89:1723–1732. https://doi.org/10.1890/07-0935.1

Savino JF, Stein RA (1989) Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environ Biol Fishes 24(4):287–293. https://doi.org/10.1007/BF00001402

Schenk D, Bacher S (2002) Functional response of a generalist insect predator to one of its prey species in the field. J Anim Ecol 71(3):524–531. https://doi.org/10.1046/j.1365-2656.2002.00620.x

Schwarz G (1978) Estimating the dimension of a model. Ann Stat. https://doi.org/10.1214/aos/1176344136

Spiegelhalter DJ, Best NG, Carlin BP, Van Der Linde A (2002) Bayesian measures of model complexity and fit. J R Stat Soc Ser B Stat Methodol 64(4):583–639. https://doi.org/10.1111/1467-9868.00353

Swisher BJ, Soluk DA, Wahl DH (1998) Non-additive predation in littoral habitats: influences of habitat complexity. Oikos 81(1):30. https://doi.org/10.2307/3546464

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65(1):13–21. https://doi.org/10.1007/s00265-010-1037-6

Taraborelli AC, Fox MG, Schaner T, Johnson TB (2009) Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. J Great Lakes Res 35(2):266–271. https://doi.org/10.1016/j.jglr.2008.12.004

Tredennick AT, Hooker G, Ellner SP, Adler PB (2021) A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology 102(6):e03336. https://doi.org/10.1002/ecy.3336

Uiterwaal SF, DeLong JP (2018) Multiple factors, including arena size, shape the functional responses of ladybird beetles. J Appl Ecol 55(5):2429–2438. https://doi.org/10.1111/1365-2664.13159

Uiterwaal SF, Lagerstrom IT, Lyon SR, DeLong JP (2022) FoRAGE database: a compilation of functional responses for consumers and parasitoids. Ecology 103(7):e3706. https://doi.org/10.1002/ecy.3706

Vander Zanden MJ, Hansen GJA, Higgins SN, Kornis MS (2010) A pound of prevention, plus a pound of cure: Early detection and eradication of invasive species in the Laurentian Great Lakes. J Great Lakes Res 36(1):199–205. https://doi.org/10.1016/j.jglr.2009.11.002

Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 27(5):1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Watanabe S (2013) A widely applicable Bayesian information criterion. J Mach Learn Res 14(1):867–897

Wor C, Greenberg DA, Holt CA, Connors B, Feddern ML, Freshwater C, Britten GL, Mazur M (2025) Recommendations for estimating and detecting time-varying spawner-recruit dynamics in fish populations. Ecol Modell 507:111159. https://doi.org/10.1016/j.ecolmodel.2025.111159

Young JAM, Marentette JR, Gross C, McDonald JI, Verma A, Marsh-Rollo SE, Macdonald PDM, Earn DJD, Balshine S (2010) Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. J Great Lakes Res 36(1):115–122. https://doi.org/10.1016/j.jglr.2009.11.001