APPLICATION

FRAIR: an R package for fitting and comparing consumer functional responses

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Summary

1. Consumer-resource interactions (i.e. the functional response) underpin decades of ecological advancements. However, selecting, fitting and comparing functional response models using appropriate methods remains a non-trivial endeavour.

2. The R package FRAIR provides tools for selecting and differentiating various forms of consumer functional response models, a consistent interface for fitting and visualising response curves, and a selection of statistically robust methods for comparing fitted parameters.

3. Using real data from crustacean predator-prey systems, we demonstrate the utility of FRAIR, highlighting best practice and common analytical mistakes.

Key-words: bootstrapping, consumer-resource interactions, maximum likelihood, nonlinear curve fitting, predator–prey, resource use

Introduction

Consumer-resource interactions are at the heart of ecology because all organisms must consume resources of some kind. Functional responses describe how the per capita feeding rates of consumers change systematically with resource availability as a result of the consumer's search for, capture, and handling of resources (Holling 1959, 1966). The ubiquity and simplicity of principles underpinning the functional response continues to resonate with ecologists working at scales ranging from the behaviour of individuals (Toscano & Griffen 2014) to entire food webs (Brose 2010). Across fields – from theoretical explorations of stability and coexistence (Williams & Martinez 2004) to applications in biocontrol, invasions and conservation (Sinclair *et al.* 1998; Twardochleb, Novak & Moore 2012) – functional responses remain central to much ecological research.

THE ANATOMY OF A FUNCTIONAL RESPONSE

Despite decades of refinements (e.g. Real 1977; Hassell 1978; Arditi & Ginzburg 1989; Skalski & Gilliam 2001; Okuyama 2012), the essential components of search, capture and handling outlined by Holling (1959) have remained largely unchanged. A generalised version of the Holling disc equation is (Real 1977):

$$N_e = \frac{aTN^{(q+1)}}{1 + ahN^{(q+1)}} \qquad \text{eqn 1}$$

where N is the resource density or number of prey; T is experimental time (typically hours or days); a is the instantaneous resource capture rate of the consumer, per unit area/volume per unit time; h in practice represents the time spent subjugating, ingesting and digesting each prey item, with the same units as T (Jeschke, Kopp & Tollrian 2002; Sentis, Hemptinne & Brodeur 2013); and q is a scaling exponent defining the extent to which the functional response changes from a decelerating hyperbola (Type II: $q = 0$ and Fig. 1a purple) to a sigmoidal form (Type III: $q > 0$ and Fig. 1a green).

When q is 0, capture rates are constant with resource density, whereas where $q > 0$, capture rates follow a power-law relationship with resource density, often implying that consumers learn as they forage (Real 1977). Type I (linear rather than saturating *sensu*, Holling; Fig. 1a orange) functional responses can be described where $q = 0$ and $h = 0$. Since handling time determines the maximum consumption rate ($1/h$), doubling h suppresses the asymptote for consumers with identical capture rates (Fig. 1c: dashed vs. solid blue curve). In contrast, for consumers with identical handling times, doubling capture rates (a) increases consumption at low resource densities (Fig. 1c: dashed vs. solid purple curves).

An important assumption of eqn 1 is that local resource density does not decline. However, in many experiments,

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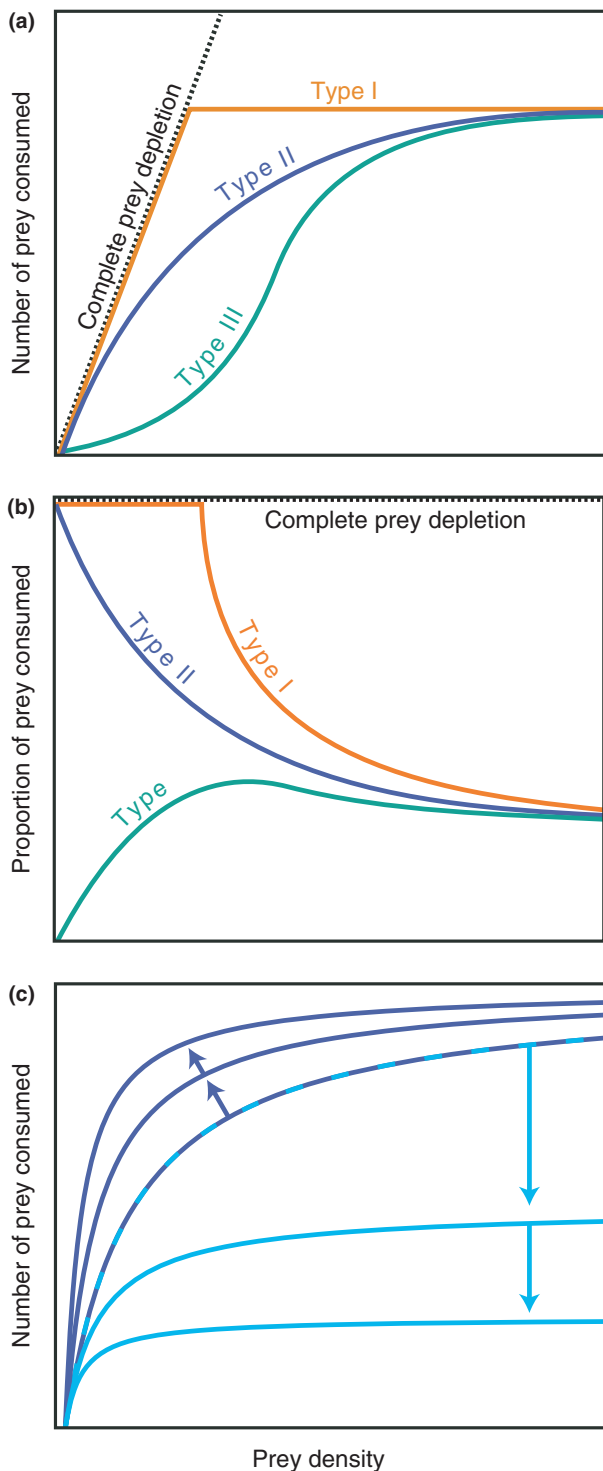
Fig. 1. Categorical forms of functional response curves (Holling 1959) describe relationships between prey density and prey consumption (a), differentiated by corresponding relationships between prey density and proportional consumption (b). For a Type II functional response (c, dashed curve), doubling capture rates (*a* in eqn 1, purple curves) primarily increases consumption at lower prey densities, whilst doubling handling time (*h* eqn 1, blue curves) reduces asymptotic consumption.

consumers deplete resources, rendering models in the eqn 1 family inappropriate (e.g. Bollache *et al.* 2008). The family of models introduced by Royama (1971) and popularised by

Rogers (1972) provide a solution to this problem by integrating instantaneous consumption over time. The modification of eqn 1 assuming depletion is:

$$N_e = N_0(1 - \exp(aN_0^q(hN_e - T))) \qquad \text{eqn 2}$$

where N_0 is the initial prey density, and other parameters are as in eqn 1. Although the number of prey eaten (N_e) appears on both sides of eqn 2, it can be solved using the 'Lambert-W' function (W). The derivation and definition of W is beyond the scope of this manuscript but it is described in detail in Corless *et al.* (1996) and with respect to ecological applications by Lehtonen (2016).

APPLICATIONS OF FUNCTIONAL RESPONSES

Ecologists often seek objective comparisons between one or more groups; with functional responses this usually necessitates comparisons of fitted model parameters, though the particular methods employed remain a subject of confusion and debate (Houck & Strauss 1985; Juliano 2001). Renewed interest in consumer functional response models has driven several innovative analytical solutions, at least two of which have been widely adopted. The first involves explicitly modelling the difference fitted parameters between two (or more) groups. This approach – described in Juliano (2001) – is computationally simple, but requires reparameterisation of the underlying model. It provides a coefficient (the difference between groups of interest) that can be interpreted within a regression-modelling frame-work, and with proper formulation and sufficient data, can be extended to moderately complex hypotheses (e.g. Paterson *et al.* 2015). A second approach involves bootstrapping (resampling with replacement) of either raw data (e.g. Bovy *et al.* 2015) or modelled residuals (e.g. Médoc, Albert & Spataro 2015). This computationally intensive approach explores the likely range of fitted coefficients, and allows for direct comparison of the range of these values (e.g. via confidence intervals).

Not all analytical approaches in the recent literature are as well advised. For example, some have applied null hypothesis significance tests to bootstrapped parameter estimates from functional response models (e.g. Dodd *et al.* 2014; Bunke *et al.* 2015) – an approach that is clearly flawed (White *et al.* 2014). We suspect that the lack of a common toolset for non-specialists to fit and examine consumer functional response models has contributed to the propagation of these methods. With research output increasing, it is critical that ecologists working on functional responses make robust analyses: we anticipate that FRAIR can meet this need.

The FRAIR package

FRAIR is a package in the R statistical environment for selection, fitting and comparisons among common functional response models and constituent parameters. FRAIR is available on CRAN and development is undertaken openly on GitHub (https://github.com/dpritchard/frair).

This tutorial is based on FRAIR version 0.5.100 (the most recent version available on CRAN) and outlines key functionalities while providing a general introduction to these analyses. The tutorial is based on two experimentally derived datasets included with the package: `gammarus`, a subset of data from Paterson *et al.* (2015) and `bythotrephes`, a previously unpublished dataset. See Appendix S1 (Supporting Information) for all code used to generate this tutorial.

The `gammarus` dataset describes consumption of dipteran larvae (*Simulium* spp.) by two amphipod species (*Gammarus duebeni celticus* and *Gammarus pulex*). The `bythotrephes` dataset describes consumption of three size classes of the cladoceran *Polyphemus pediculus* by the cladoceran *Bythotrephes longimanus*. Both datasets concern experimental designs incorporating prey depletion. For further examples, readers are directed to other published studies utilising FRAIR (https://github.com/dpritchard/frair/wiki/FRAIR-in-use).

```
# Gammarus
data("gammarus")
str(gammarus)

## 'data.frame':   224 obs. of  4 variables:
## $ density:int  2 2 2 2 2 2 2 2 2 ...
## $ eaten  :int  0 2 2 2 2 2 2 2 2 ...
## $ alive  :int  2 0 0 0 0 0 0 0 0 ...
## $ spp    :Factor w/ 2 levels

levels(gammarus$spp)

## [1] "G.d.celticus" "G.pulex"


# Bythotrephes
data("bythotrephes")
str(bythotrephes)

## 'data.frame':   72 obs. of  4 variables:
## $ density:int  1 1 1 3 3 3 2 2 2 4 ...
## $ eaten  :int  1 1 0 3 2 3 2 2 2 4 ...
## $ alive  :int  0 0 1 0 1 0 0 0 0 0 ...
## $ size   :Factor w/ 3 levels
levels(bythotrephes$size)

## [1] "small" "medium" "large"
```

The FRAIR workflow involves a three-step process: (i) model selection; (ii) model fitting and; (iii) comparison of fits and coefficients. An essential step in this process is to visually inspect the raw plotted data (Fig. 2).

MODEL SELECTION

FRAIR offers a range of commonly used functional response models that can be viewed using `frair_responses()`. Basic models assume constant resource density throughout experimental trials (resources are replaced). For experiments where resources are depleted (so-called non-replacement experiments), models are provided (suffixed with `nr`) with Rogers (1972) modifications and solved using the 'lambertW' function (Bolker 2008).

Although eqns 1 and 2 imply consumer functional responses can be described on a linear (Type I) to sigmoidal (Type III) continuum, the original categorical descriptions of Holling remain prominent (e.g. Denny 2014). This is likely because deviations from Type II towards Type III functional
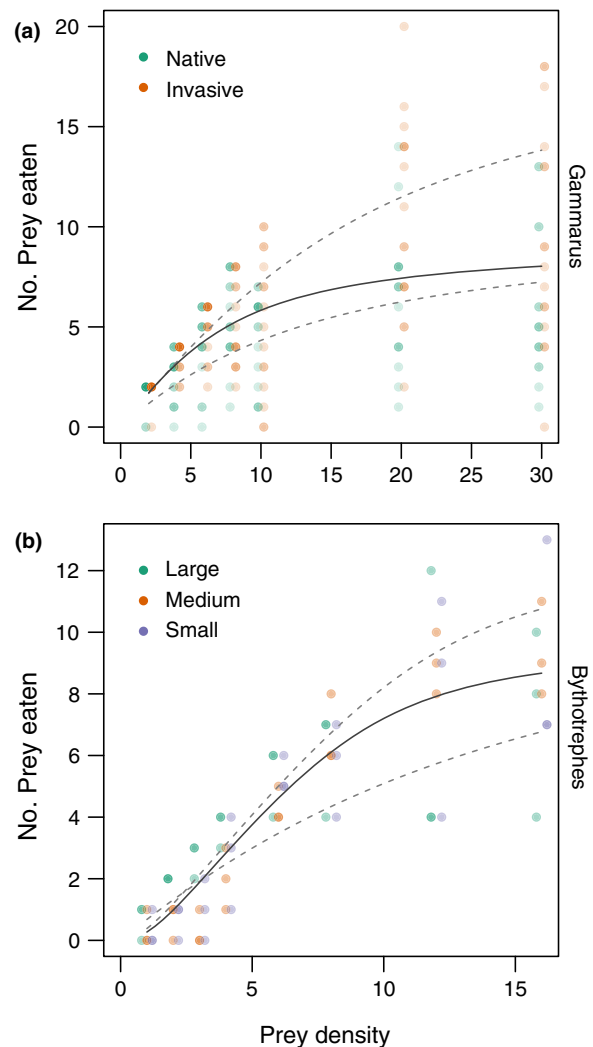
Fig. 2. Visualisation of the datasets included with the *FRAIR* package. (a) Consumption of dipteran larvae (*Simulium* spp.) by native *Gammarus duebeni celticus* and invasive *Gammarus pulex* and (b) The consumption of three size classes of *Polyphemus pediculus* by *Bythotrephes longimanus*. Dashed lines represent plausible starting values for MLE optimisation and solid lines represent optimised fits for Rogers (Type II, Gammarus) or Flexible Exponent (Bythotrephes) models.

responses can stabilise otherwise chaotic consumer-resource dynamics (Williams & Martinez 2004; Barrios-O'Neill *et al.* 2016).

Juliano (2001) advocates fitting polynomial logistic functions to proportional consumption data to determine functional response Type. Type II is characterised by a negative first-order term (declining proportional consumption with increasing resource density; Fig. 1b), in contrast to a positive first-order term of Type III (initial increase and subsequent decrease in proportional consumption; Fig. 1b). Using this logic, the `frair_test` function uses forward selection based on the sign and significance of first-order (`density`) and second-order (`density^2`) terms in logistic regressions.

```
# Gammarus
frair_test(formula = eaten~density, data = gammarus)

## FUNCTIONAL RESPONSE TEST
##
## Evidence for type-II response:  Yes
## Evidence for type-III response: -
##
## Type-II logistic regression output:
##          Estimate Std. Error z value Pr(>|z|)
## density -0.0792704 0.0044298 -17.895 < 2.2e-16 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
# Bythotrephes
frair_test(formula = eaten~density, data = bythotrephes)

## FUNCTIONAL RESPONSE TEST
##
## Evidence for type-II response:  No
## Evidence for type-III response: Yes
##
## Type-III logistic regression output:
##               Estimate Std. Error z value Pr(>|z|)
## density        0.3646093 0.1009794  3.6107 0.0003053 ***
## I(density^2)  -0.0206557 0.0051263 -4.0293 5.593e-05 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Although this approach provides a statistical test to distinguish between Type II and Type III, it is considered phenomenological in that it describes only the general shape of the response, without determining whether a particular mechanistic model is appropriate. An alternative approach involves fitting a generalised form of the functional response model with a scaling exponent (q) parameterised such that $q = 0$ represents a Type II response (eqns 1 or 2), thus exposing a useful null hypothesis test (i.e. $q \neq 0$) via a regression output and allowing for comparison of models using information criteria (e.g. AIC, BIC, AICc). For example, with the bythotrephes dataset:

```
# Bythotrephes
# Fit a model where q can vary:
b_flex <- frair_fit(eaten~density, data=bythotrephes,
                response='flexpnr',
                start=list(b = 1, q = 0, h = 0.08),
                fixed=list(T = 12/24))
# Fit a model where q is fixed to zero:
b_II <- frair_fit(eaten~density, data=bythotrephes,
                response='flexpnr',
                start=list(b = 1, h = 0.08),
                fixed=list(T = 12/24, q = 0))
summary(b_flex$fit) # q != 0 : Type III preferred
AIC(b_flex$fit, b_II$fit)
# The model including q is preferred
```

The usefulness of these tests depends on the quality of data at low resource densities (Barrios-O'Neill *et al.* 2015) and some authors recommend that proportional relationships are visually inspected with locally weighted regression (Juliano 2001).

The experimental designs of our datasets indicate that depletion models are required as prey is not replaced during the experiment. Plots of the raw data and these analyses suggest that for the gammarus dataset, a Type II model is sufficient; however, a Type III – or flexible model – may be most appropriate for the bythotrephes data.

MODEL FITTING

Essential to the optimisation of nonlinear models is the provision of reasonable starting values for free parameters. There are some rules of thumb, for example, for Type II models, h can be approximated as the inverse of the maximum number eaten where T is set to 1 (Bolker 2008). An equally reliable method is a visual assessment of the data, plotting of putative starting values and trial and error (Fig. 2).

```
# Gammarus
with(gammarus, plot(density, eaten, xlab = "Prey Density",
                ylab = "No. Prey Eaten"))
x <- with(gammarus, seq(from = min(density),
                    to = max(density), by = 0.1))
lines(x, rogersII(X = x, a = 1.2, h = 0.08, T = 40/24),
    col='grey50', lty=2)
lines(x, rogersII(X = x, a = 0.6, h = 0.16, T = 40/24),
    col='grey50', lty=2)
```

```
# Bythotrepes
with(bythotrephes, plot(density, eaten, xlab = "Prey Density",
                ylab = "No. Prey Eaten"))
x <- with(bythotrephes, seq(from = min(density),to = max(density),
                    by = 0.1))
lines(x, flexpnr(X = x, b = 1, h = 0.04, q = 1, T = 12/24),
    col='grey50', lty=2)
lines(x, flexpnr(X = x, b = 2.4, h = 0.04, q = 0, T = 12/24),
    col='grey50', lty=2)
```

Note that all FRAIR functional response models take at least one fixed parameter (T), which is experimental time. Although not optimised, this value will change the units of the fitted coefficients. Many authors implicitly accept units of 'experimental time' by setting $T = 1$. Unless the raw data are made available, this limits the use of parameter estimates in subsequent studies (e.g. meta-analyses, food web models). Therefore, we recommend users adopt units of either 'hour' or 'day' and have adopted units of 'day' in this manuscript.

Once starting estimates and fixed values are provided, the model is optimised using maximum likelihood estimation (MLE). This robust approach to fitting nonlinear models (Bolker 2008) allows for optimisation on the basis of arbitrary probability distributions. Internally, all FRAIR models use a binomial likelihood function, which imposes an upper (all prey eaten) and lower (no prey eaten) limit on the response. A practical limitation of this likelihood specification is that FRAIR can only fit curves when the density (x-axis) is specified as whole integer values (the most common situation for individual prey items).

In FRAIR, optimisation by MLE is provided by frair_fit and is implemented using bbmle::mle2 (Bolker 2008). The resulting output (of class frair_fit) provides information on the fit and the maximum likelihood estimators (fitted coefficients) and a lines method to plot the fitted curve (Fig. 2). frair_fit also returns the raw output from the maximum likelihood optimisation, which provides typical regression output including asymptotic standard errors, *Z*-statistics and *P*-values.

```
# A fit to the entire gammarus dataset
g_fit <- frair_fit(formula = eaten~density, data = gammarus,
                   response = "rogersII",
                   start = list(a = 1, h = 0.1),
                   fixed = list(T = 40/24))
with(gammarus, plot(density, eaten, xlab="Prey Density",
                    ylab="No. Prey Eaten"))
lines(g_fit, lty = 1, col = "grey25")
print(g_fit)

## FUNCTIONAL RESPONSE FIT
##
## Response:         rogersII
## Description:      Roger's type II decreasing prey function
## Optimised variables: a, h
## Fixed variables:   T
##
## Coefficients:
##    a     h     T
## 1.423 0.180 1.667
##
## NOTE: It is recommended you inspect the raw fit too
   (see: ?frair_fit)

summary(g_fit$fit)

## Coefficients:
##   Estimate Std. Error z value    Pr(z)
## a 1.4228013  0.1314562 10.823 < 2.2e-16
## h 0.1802657  0.0098583 18.286 < 2.2e-16
##
## -2 log L: 1129.631
```

```
# A fit to the entire bythotrephes dataset
b_fit <- frair_fit(formula = eaten~density,
                   data = bythotrephes, response = "flexpnr",
                   start = list(b = 1.5, h = 0.04, q = 1),
                   fixed = list(T = 12/24))
with(bythotrephes, plot(density, eaten, xlab="Prey Density",
                        ylab="No. Prey Eaten"))
lines(b_fit, lty = 1, col = "grey25")
print(b_fit)

## FUNCTIONAL RESPONSE FIT
##
## Response:         flexpnr
## Description:      Flexible exponent,
                    not assuming replacement
## Optimised variables: b, h, q
## Fixed variables:   T
##
## Coefficients:
##    b     q     h     T
## 0.652 1.215 0.053 0.500
##
## NOTE: It is recommended you inspect the raw fit too
   (see: ?frair_fit)

summary(b_fit$fit)

## Coefficients:
##   Estimate Std. Error z value    Pr(z)
## b 0.651730  0.258996 2.5164   0.01186
## q 1.215357  0.296077 4.1049 4.045e-05
## h 0.052912  0.005112 10.3509 < 2.2e-16
##
## -2 log L: 241.1805
```

MODEL COMPARISON

The third step in the FRAIR workflow includes comparisons of fitted coefficients. The two approaches currently implemented are the delta or difference method of Juliano (2001), provided by `frair_compare` and nonparametric bootstrapping of the raw data, provided by `frair_boot`. Both functions operate on objects produced by `frair_fit` (i.e. class frfit).

Comparisons between constituent parameters require that those parameters are equivalent. Comparisons of handling times, h, and maximum feeding rates $(1/hT)$ are possible between all models in FRAIR (assuming consumers are handling limited), but comparisons of capture rates are often

problematic. For example, there is no equivalence between capture rates as defined in `hassIIInr` and `rogersII`, which respectively describe Type III and Type II responses (e.g. Alexander *et al.* 2012). Indeed, a Type II model assumes a prey density-independent capture rate, while for a Type III model capture rates typically follow a power-law with prey density. Where comparing Type II and Type III models it is common to resort to comparisons of maximal capture rates, usually the steepest part of the curve (Englund *et al.* 2011). Often, however, responses in a dataset are of the same categorical form, making comparisons straightforward.

```
# Compare two species in the gammarus dataset
pulex <- gammarus[gammarus$spp=='G.pulex', ]
celt <- gammarus[gammarus$spp=='G.d.celticus', ]
st <- list(a = 1, h = 0.1)
fx <- list(T = 40/24)
p_fit <- frair_fit(eaten~density, data = pulex,
                   response = 'rogersII',
                   start = st, fixed = fx)
c_fit <- frair_fit(eaten~density, data=celt,
                   response='rogersII',
                   start = st, fixed = fx)
frair_compare(p_fit, c_fit)

## FUNCTIONAL RESPONSE COEFFICIENT TEST
##
## Response:         rogersII
## Optimised variables: a,h
## Fixed variables:   T


##
## Original coefficients:
##           a       h
## p_fit 1.47748 0.14268
## c_fit 1.41745 0.23381
##
## Test: p_fit - c_fit
##
##    Estimate Std. Error z value Pr(z)
## Da  0.05961  0.27132 0.2197 0.8261
## Dh -0.09115  0.02087 -4.3681 1e-05
```

`frair_compare` implements a difference test with the null hypothesis that fitted parameters do not differ. The fitted parameters *Da* and *Dh* estimate the differences between the capture rates and handling times of the two predators respectively. Here, we have evidence that capture rates do not differ $(Da = 0.06, z = 0.22, P = 0.826)$, but that the handling time of *G. pulex* is shorter than that of *G. d. celticus* $(Dh = -0.02, z = -4.36, P < 0.001)$.

Unfortunately, the difference method does not allow for direct comparisons between predicted consumption across the range of resource densities and, because consumers can switch between Type II and Type III responses (Barrios-O'Neill *et al.* 2016), objective comparisons using this approach are often impossible. Therefore, FRAIR also provides `frair_boot`, which implements nonparametric bootstrapping and leverages `boot::boot` (Canty & Ripley 2016). This method generates multiple estimates of curves and constituent parameters (based on a default minimum of 999 samples; Dixon 2001) and reports 95% confidence intervals (CIs) by default. We recommend using bias corrected and accelerated intervals – BCa – to account for bias, skew and bounded parameters (a and $h > 0$). It is expected that the underlying MLE will sometimes fail, even with reasonable starting values, therefore

`frair_boot` warns if >10% of all bootstrapped fits fail and returns an error if >50% of the fits fail. Because bootstrapping generates population metrics, the equivalent of a null hypothesis test is simply a lack of overlap between the CIs of model parameters.

```
# Bootstrap the Gammarus pulex fit
p_fitb <- frair_boot(p_fit)
confint(p_fitb, citypes = 'bca')

## Coefficient CI Type    Lower  Upper
## a          BCa         0.998  2.295
## h          BCa         0.102  0.203

# Bootstrap the Gammarus duebeni celticus fit
c_fitb <- frair_boot(c_fit)
confint(c_fitb, citypes = 'bca')

## Coefficient CI Type    Lower  Upper
## a          BCa         0.94   2.133
## h          BCa         0.183  0.286
```
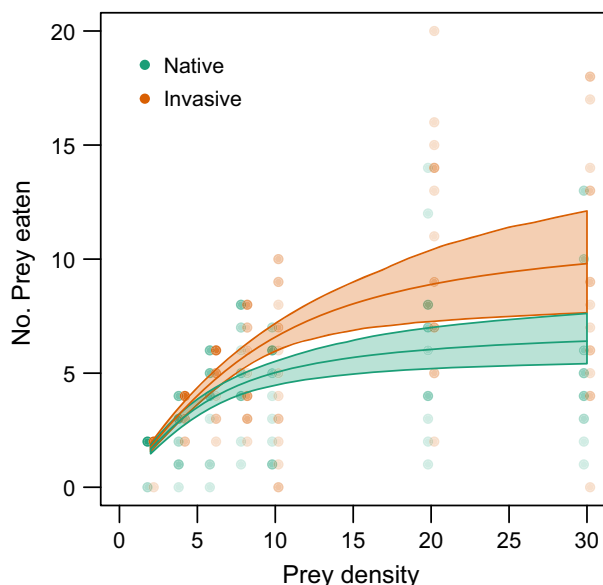
Bootstrapping outputs for the `gammarus` dataset concur with the difference method for capture rates: the 95% CIs clearly overlap. In contrast to the difference method, `frair_boot` suggests no difference between consumer handling times (95% CIs for *h* fractionally overlap). While both methods are sensitive to underlying data quality and quantity, the difference method makes assumptions about the error structure of the fitted parameters, while bootstrapping reflects the likely range of values given the data provided, while accounting for the bounded (i.e. non-negative) nature of handling times.

Based on the output from bootstrapped fits, FRAIR provides visual comparisons of entire functional response curves using `drawpoly` (Fig. 3). This function plots empirical approximations of the confidence intervals using the desired quantile predictions (0·025 and 0·975 for 95% CIs). Even where estimates of 95% CIs for all fitted

parameters overlap (as in this example), parameters can combine to yield differences in predicted consumption as a function of prey density (Fig. 3). Such differences cannot be addressed using the delta method, and `drawpoly` provides a means to identify where predicted consumption may differ along an axis of resource density.

Limitations

Fitting nonlinear models to ecological data can be a challenging and frustrating process (Bolker *et al.* 2013), resulting from highly variable data, low replication, use of an overly complex model, a desire to test many hypotheses, or a combination of these. Although there have been computational improvements, the challenges are as real now as they were in 1988, when Trexler, McCulloch & Travis (1988) noted that it may be impossible to fit a curve to data, even with 11 resource densities and 10 replicates per resource density – a quantity of data rarely attained in experimental functional response analyses. Even after many days of laboratory work, it may be impossible to fit the desired functional response model, or distinguish between the subtleties of a Type II and Type III response. This may be an unavoidable problem that no software can solve, but accessible tools for analysis will improve understanding of the strengths and limitations of consumer functional responses. Still, even with these tools, it seems clear that there is nothing straightforward about the application or interpretation of these models.

FRAIR has been designed with the non-specialist in mind; however, for those seeking advanced analyses, FRAIR has some practical limitations. For example, currently FRAIR does not provide ratio- or predator-dependent models (e.g. Hassell & Varley 1969; Beddington 1975), body size-dependent models (e.g. Kalinkat *et al.* 2013) or convenience functions to explore and avoid local optima, or the capacity to specify user-defined models (e.g. those with arbitrary probability distributions). We aim to add these features to FRAIR in the future and welcome third party participation in package development (https://github.com/dpritchard/frair). We encourage those seeking to work outside the structure provided by FRAIR to consider the details provided by Bolker (2008), as well as guidance in the FRAIR help manual (e.g. `?frair_fit`).

Conclusion

We have presented the FRAIR package and demonstrated how it provides a reproducible framework for the selection, fitting and comparison of functional response models. We anticipate that FRAIR will help to consolidate functional response analysis methods for non-specialists by ensuring that common mistakes are not perpetuated, and by exemplifying the current best practice for nonlinear curve fitting and comparison. Consumer-resource interactions are fundamental to many aspects of contemporary ecological research and thus, we anticipate that in providing an accessible open source package for functional response analysis, FRAIR will provide a useful tool for many ecologists.

Fig. 3. Empirical approximations of 95% confidence intervals based on bootstrapped model fits for the number of prey eaten by native *Gammarus duebeni celticus* and invasive *Gammarus pulex* (Gammarus dataset).

Authors' contributions

Acknowledgements

Data accessibility

All data used in this manuscript are included in the FRAIR package, which is available on the CRAN repository at: https://cran.r-project.org/web/packages/frair

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. The R Markdown document contains all code and examples used in this manuscript.