1 **FRAIR: AN R PACKAGE FOR FITTING AND COMPARING CONSUMER**

2 **FUNCTIONAL RESPONSES**

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14   **SUMMARY**

15   1. Consumer-resource interactions (i.e. the functional response) underpin decades of

16   ecological advancements. However, selecting, fitting and comparing functional

17   response models using appropriate methods remains a non-trivial endeavour.

18   2. The R package *FRAIR* provides tools for selecting and differentiating various forms

19   of consumer functional response models, a consistent interface for fitting and

20   visualising response curves, and a selection of statistically robust methods for

21   comparing fitted parameters.

22   3. Using real data from crustacean predator-prey systems, we demonstrate the utility of

23   *FRAIR*, highlighting best practice and common analytical mistakes.

24

25   Keywords: consumer-resource interactions; predator-prey; resource use; non-linear curve

26   fitting; bootstrapping; maximum likelihood

27

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 —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):

$$N_e = \frac{aTN^{(q+1)}}{1+ahN^{(q+1)}} \tag{1}$$

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 *et al.* 2002; Sentis *et al.* 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).

3

51   When q is 0, capture rates are constant with resource density, whereas where $q > 0$, capture

52   rates follow a power-law relationship with resource density, often implying that consumers

53   learn as they forage (Real 1977). Type I (linear rather than saturating *sensu* Holling; Fig. 1a

54   orange) functional responses can be described where $q = 0$ and $h = 0$. Since handling time

55   determines the maximum consumption rate ($1/h$), doubling h suppresses the asymptote for

56   consumers with identical capture rates (Fig. 1c: dashed *versus* solid blue curve). In contrast,

57   for consumers with identical handling times, doubling capture rates (a) increases

58   consumption at low resource densities (Fig. 1c: dashed *versus* solid purple curves).

59   An important assumption of equation 1 is that local resource density does not decline.

60   However, in many experiments, consumers deplete resources, rendering models in the

61   equation 1 family inappropriate (e.g. Bollache *et al.* 2008). The family of models introduced

62   by Royama (1971) and popularised by Rogers (1972) provide a solution to this problem by

63   integrating instantaneous consumption over time. The modification of equation 1 assuming

64   depletion is:

65   $$N_e = N_0(1 - exp\,(aN_0^q(hN_e - T)))$$ (2)

66   where N_0 is the initial prey density, and other parameters are as in equation 1. Although the

67   number of prey eaten (N_e) appears on both sides of equation 2, it can often be solved using

68   the Lambert-W function (W). The derivation and definition of W is beyond the scope of this

69   manuscript but it is described in detail in Corless *et al.* (1996) and with respect to ecological

70   applications in Lehtonen (2016).

71   <u>APPLICATIONS OF FUNCTIONAL RESPONSES</u>

72   Ecologists often seek objective comparisons between one or more groups; with functional

73   responses this usually necessitates comparisons of fitted model parameters, though the

4

74   particular methods employed remain a subject of confusion and debate (Houck & Strauss

75   1985; Juliano 2001). Renewed interest in consumer functional response models has driven

76   several innovative analytical solutions, at least two of which have been widely adopted. The

77   first involves explicitly modelling the difference fitted parameters between two (or more)

78   groups. This approach – described in Juliano (2001) – whilst computationally simple,

79   requires reparameterisation of the underlying model. It provides a coefficient (the difference

80   between groups of interest) that can be interpreted within a regression-modelling framework,

81   and with proper formulation and sufficient data, can be extended to moderately complex

82   hypotheses (e.g. Paterson *et al.* 2015). A second approach involves bootstrapping (resampling

83   with replacement) of either raw data (e.g. Bovy *et al.* 2015) or modelled residuals (e.g.

84   Médoc *et al.* 2015). This computationally intensive approach explores the likely range of

85   fitted coefficients, and allows for direct comparison of the range of these values (e.g. via

86   confidence intervals).

87   Not all analytical approaches in the recent literature are as well advised. For example, some

88   have applied null-hypothesis significance tests to bootstrapped parameter estimates from

89   functional response models (e.g. Dodd *et al.* 2014; Bunke *et al.* 2015) – an approach that is

90   clearly flawed (White *et al.* 2014). We suspect that the lack of a common toolset for non-

91   specialists to fit and examine consumer functional response models has contributed to the

92   propagation of these methods. With research output increasing, it is critical that ecologists

93   working on functional responses can make robust analyses: we anticipate that *FRAIR* can

94   meet this need.

95   **THE FRAIR PACKAGE**

96   *FRAIR* is a package in the R statistical environment for selection, fitting and comparisons

97   among common functional response models and constituent parameters. *FRAIR* is available

98 on CRAN and development is undertaken openly on GitHub

99 (http://github.com/dpritchard/frair).

100 This tutorial is based on *FRAIR* version 0.5 (the most recent version available on CRAN) and

101 outlines key functionalities whilst providing a general introduction to these analyses. The

102 tutorial is based on two experimentally derived datasets included with the package:

103 gammarus, a subset of data from Paterson et al. (2015) and bythotrephes, a previously

104 unpublished dataset.

105 The gammarus dataset describes consumption of dipteran larvae (*Simulium* spp.) by two

106 amphipod species (*Gammarus duebeni celticus* and *Gammarus pulex*). The bythotrephes

107 dataset describes consumption of three size classes of the cladoceran *Polyphemus pediculus*

108 by the cladoceran *Bythotrephes longimanus*. Both datasets concern experimental designs

109 incorporating prey depletion. For further examples, readers are directed to other published

110 studies utilising *FRAIR* (https://github.com/dpritchard/frair/wiki/FRAIR-in-use).

```
111 # Gammarus
112 data("gammarus")
113 str(gammarus)

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

119 levels(gammarus$spp)

120 ## [1] "G.d.celticus" "G.pulex"

121
122 # Bythotrephes
123 data("bythotrephes")
124 str(bythotrephes)

125 ## 'data.frame':    72 obs. of  4 variables:
126 ##  $ density: int  1 1 1 3 3 3 2 2 2 4 ...
127 ##  $ eaten  : int  1 1 0 3 2 3 2 2 2 4 ...
128 ##  $ alive  : int  0 0 1 0 1 0 0 0 0 0 ...
129 ##  $ size   : Factor w/ 3 levels
```

```
130  levels(bythotrephes$size)
131  ## [1] "small" "medium" "large"
132
```

The *FRAIR* workflow involves a three-step process: (1) model selection; (2) model fitting

and; (3) 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 equations 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 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.

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

156  ## FUNCTIONAL RESPONSE TEST
157  ##
158  ## Evidence for type-II response:   Yes
159  ## Evidence for type-III response:  -
160  ##
161  ## Type-II logistic regression output:
162  ##           Estimate Std. Error z value  Pr(>|z|)
163  ## density -0.0792704  0.0044298 -17.895 < 2.2e-16 ***
164  ## ---
165  ## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

166
167  # Bythotrephes
168  frair_test(formula = eaten~density, data = bythotrephes)

169  ## FUNCTIONAL RESPONSE TEST
170  ##
171  ## Evidence for type-II response:   No
172  ## Evidence for type-III response:  Yes
173  ##
174  ## Type-III logistic regression output:
175  ##               Estimate Std. Error z value  Pr(>|z|)
176  ## density        0.3646093  0.1009794  3.6107 0.0003053 ***
177  ## I(density^2) -0.0206557  0.0051263 -4.0293 5.593e-05 ***
178  ## ---
179  ## 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 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 (equation 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:

```
189  # Bythotrephes
190  # Fit a model where q can vary:
191  b_flex <- frair_fit(eaten~density, data=bythotrephes,
192                      response='flexpnr',
```

```
193                     start=list(b = 1, q = 0, h = 0.08),
194                     fixed=list(T = 12/24))
195   # Fit a model where q is fixed to zero:
196   b_II <- frair_fit(eaten~density, data=bythotrephes,
197                   response='flexpnr',
198                   start=list(b = 1, h = 0.08),
199                   fixed=list(T = 12/24, q = 0))
200   summary(b_flex$fit) # q != 0 : Type III preferred
201   AIC(b_flex$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

are 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 non-linear 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).

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

```
225
226     # Bythotrephes
227     with(bythotrephes, plot(density, eaten, xlab="Prey Density",
228                             ylab="No. Prey Eaten"))
229     x <- with(bythotrephes, seq(from = min(density), to = max(density),
230                             by = 0.1))
231     lines(x, flexpnr(X = x, b = 1, h = 0.04, q = 1, T = 12/24),
232           col='grey50', lty=2)
233     lines(x, flexpnr(X = x, b = 2.4, h = 0.04, q = 0, T = 12/24),
234           col='grey50', lty=2)
235
```

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. For example, with the `gammarus` dataset:

```
239     # The role of T in modifying fitted coefficients.
240     g_T1 <- frair_fit(formula = eaten~density, data = gammarus,
241                       response = "rogersII",
242                       start = list(a = 2, h = 0.1), fixed = list(T = 1))
243     g_Td <- frair_fit(formula = eaten~density, data = gammarus,
244                       response = "rogersII",
245                       start = list(a = 1, h = 0.1), fixed = list(T = 40/24))
246     g_Th <- frair_fit(formula = eaten~density, data = gammarus,
247                       response = "rogersII",
248                       start = list(a = 0.05, h = 4), fixed = list(T = 40))
249     diff_t <- round(rbind(coef(g_T1), coef(g_Td), coef(g_Th)), 2)
250     row.names(diff_t) <- c("g_T1 (Time)", "g_Td (Days)", "g_Th (Hours)")
251     print(diff_t)

252     ##                    a    h     T
253     ## g_T1 (Time)   2.37 0.11  1.00
254     ## g_Td (Days)   1.42 0.18  1.67
255     ## g_Th (Hours)  0.06 4.33 40.00
```

Many authors implicitly accept units of experimental time" by setting $T = 1$. Unless the raw

data is 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).

262   This robust approach to fitting non-linear models (Bolker 2008) allows for optimisation on

263   the basis of arbitrary probability distributions. Internally, all *FRAIR* models use a binomial

264   likelihood function, which imposes an upper (all prey eaten) and lower (no prey eaten) limit

265   on the response. A practical limitation of this likelihood specification is that *FRAIR* can only

266   fit curves when the density (x-axis) is specified as whole integer values (the most common

267   situation for individual prey items).

268   In *FRAIR*, optimisation by MLE is provided by `frair_fit` and is implemented using

269   `bbmle::mle2` (Bolker 2008). The resulting output (of class `frair_fit`) provides information

270   on the fit and the maximum likelihood estimators (fitted coefficients) and a `lines` method to

271   plot the fitted curve (Fig. 2). `frair_fit` also returns the raw output from the maximum

272   likelihood optimisation, which provides typical regression output including asymptotic

273   standard errors, *z*-statistics and *p*-values.

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

283    ## FUNCTIONAL RESPONSE FIT
284    ##
285    ## Response:            rogersII
286    ## Description:         Roger's type II decreasing prey function
287    ## Optimised variables: a, h
288    ## Fixed variables:     T
289    ##
290    ## Coefficients:
291    ##     a     h     T
292    ## 1.423 0.180 1.667
293    ##
294    ## NOTE: It is recommended you inspect the raw fit too (see: ?frair_fit)

295    summary(g_fit$fit)

296    ## Coefficients:
297    ##    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 non-parametric bootstrapping of the raw data, provided by

`frair_boot`. Both functions operating on objects produced by `frair_fit` (i.e. class `frfit`).

338 Comparisons between constituent parameters require that those parameters are equivalent.

339 Comparisons of handling times, h, and maximum feeding rates ($1/hT$) are possible between

340 all models in *FRAIR* (assuming consumers are handling limited), but comparisons of capture

341 rates are often problematic. For example, there is no equivalence between capture rates as

342 defined in `hassIIInr` and `rogersII`, which respectively describe Type III and Type II

343 responses (e.g. Alexander *et al.* 2012). Indeed, a Type II model assumes a prey density-

344 independent capture rate, whilst for a Type III model capture rates typically follow a power

345 law with prey density. Where comparing Type II and Type III models it is common to resort

346 to comparisons of maximal capture rates, usually the steepest part of the curve (Englund *et al.*

347 2011). Often, however, responses in a dataset are of the same categorical form, making

348 comparisons straightforward.

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

359   ## FUNCTIONAL RESPONSE COEFFICIENT TEST
360   ##
361   ## Response:           rogersII
362   ## Optimised variables: a,h
363   ## Fixed variables:    T
364   ##
365   ## Original coefficients:
366   ##           a         h
367   ## p_fit 1.47748 0.14268
368   ## c_fit 1.41745 0.23381
369   ##
370   ## Test: p_fit - c_fit
371   ##
372   ##    Estimate Std. Error z value  Pr(z)
373   ## Da  0.05961    0.27132  0.2197 0.8261
374   ## Dh -0.09115    0.02087 -4.3681  1e-05
```

375

376 `frair_compare` implements a difference test with the null hypothesis that fitted parameters

377 do not differ. The fitted parameters *Da* and *Dh* estimate the differences between the capture

378 rates and handling times of the two predators respectively. Here, we have evidence that

379 capture rates do not differ ($Da = 0.06$, $z = 0.22$, $p = 0.826$), but that the handling time of

380 *G. pulex* is shorter than that of *G. d. celticus* ($Dh = -0.02$, $z = -4.36$, $p < 0.001$).

381 Unfortunately the difference method does not allow for direct comparisons between predicted

382 consumption a across the range of resource densities and because consumers can switch

383 between Type II and Type III responses (Barrios-O'Neill *et al.* 2016) objective comparisons

384 using this approach are often impossible. Therefore, *FRAIR* also provides `frair_boot`,

385 which implements non-parametric bootstrapping and leverages `boot::boot` (Canty & Ripley

386 2016). This method generates multiple estimates of curves and constituent parameters (based

387 on a default minimum of 999 samples; Dixon 2001) and reports 95% confidence intervals

388 (CIs) by default. We recommend using bias corrected and accelerated intervals – BCa – to

389 account for bias, skew and bounded parameters (a and h > 0). It is expected that the

390 underlying maximum likelihood estimation will sometimes fail, even with reasonable starting

391 values, therefore `frair_boot` warns if > 10% of all bootstrapped fits fail and returns an error

392 if >50% of the fits fail. Because bootstrapping generates population metrics, the equivalent of

393 a null hypothesis test is simply a lack of overlap between the CIs of model parameters.

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

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

400
401   # Bootstrap the Gammarus duebeni celticus fit
402   c_fitb <- frair_boot(c_fit)
403   confint(c_fitb, citypes = 'bca')
```

```
404   ## Coefficient  CI Type        Lower   Upper
405   ## a            BCa            0.94    2.133
406   ## h            BCa            0.183   0.286
```

408   Bootstrapping outputs for the `gammarus` dataset concur with the difference method for

409   capture rates: the 95% CIs clearly overlap. In contrast to the difference method `frair_boot`

410   suggests no difference between consumer handling times (95% CIs for h fractionally

411   overlap). While both methods are sensitive to underlying data quality and quantity, the

412   difference method makes assumptions about the error structure of the fitted parameters,

413   whilst bootstrapping reflects the likely range of values given the data provided, whilst

414   accounting for the bounded (e.g. non-negative) nature of handling times.

415   Based on the output from bootstrapped fits, *FRAIR* provides visual comparisons of entire

416   functional response curves using `drawpoly` (Fig. 3). This function plots empirical

417   approximations of the confidence intervals using the desired quantile predictions (0.025 and

418   0.975 for 95% CIs). Even where estimates of 95% CIs for all fitted parameters overlap (as in

419   this example), parameters can combine to yield differences in predicted consumption as a

420   function of prey density (Fig. 3). Such differences cannot be addressed using the delta

421   method, and `drawpoly` provides a means to identify where predicted consumption may differ

422   along an axis of resource density.

423   **LIMITATIONS**

424   Fitting non-linear models to ecological data can be a challenging and frustrating process

425   (Bolker *et al.* 2013), resulting from highly variable data, low replication, use of an overly

426   complex model, a desire to test many hypotheses, or a combination of these. Although there

427   have been computational improvements, the challenges are as real now as they were in 1988,

428   when Trexler *et al.* noted that it may be impossible to fit a curve to data, even with 11

429   resource densities and 10 replicates per resource density – a quantity of data rarely attained in

430   experimental functional response analyses (Trexler *et al.* 1988). Even after many days of

431   laboratory work, it may be impossible to fit the desired functional response model, or

432   distinguish between the subtleties of a Type II and Type III response. This may be an

433   unavoidable problem that no software can solve, but accessible tools for analysis will

434   improve understanding of the strengths and limitations of consumer functional responses.

435   Nevertheless, even with these tools, it seems clear that there is nothing straightforward about

436   application or interpretation.

437   *FRAIR* has been designed with the non-specialist in mind. However, for those seeking

438   advanced analyses, *FRAIR* has some practical limitations. For example, currently *FRAIR*

439   does not provide ratio- or predator-dependent models (e.g. Hassell & Varley 1969;

440   Beddington 1975) or body size-dependent models (e.g. Kalinkat *et al.* 2013) and FRAIR

441   does not include some convenience functions (e.g. to explore and avoid local optima) or the

442   capacity specify user defined models (e.g. those with arbitrary probability distributions). We

443   aim to add these features to *FRAIR* in the future and welcome third party participation in

444   package development (https://github.com/dpritchard/frair). Those seeking to work outside the

445   structure provided by *FRAIR* should consider the details provided by Bolker (2008) and can

446   find some guidance in the *FRAIR* help manual (e.g. `?frair_fit`).

447

448   **CONCLUSION**

449   We have presented the *FRAIR* package and demonstrated how it provides a reproducible

450   framework for the selection, fitting and comparison of functional response models. We

451   anticipate that *FRAIR* will help to consolidate functional response analysis methods for non-

452   specialists by ensuring that common mistakes are not perpetuated, and by exemplifying the

453   current best practice for non-linear curve fitting and comparison. Consumer-resource

454   interactions are fundamental to many aspects of contemporary ecological research and thus,

455   we anticipate that in providing an accessible open source package for functional response

456   analysis, *FRAIR* will provide a useful tool for many ecologists.

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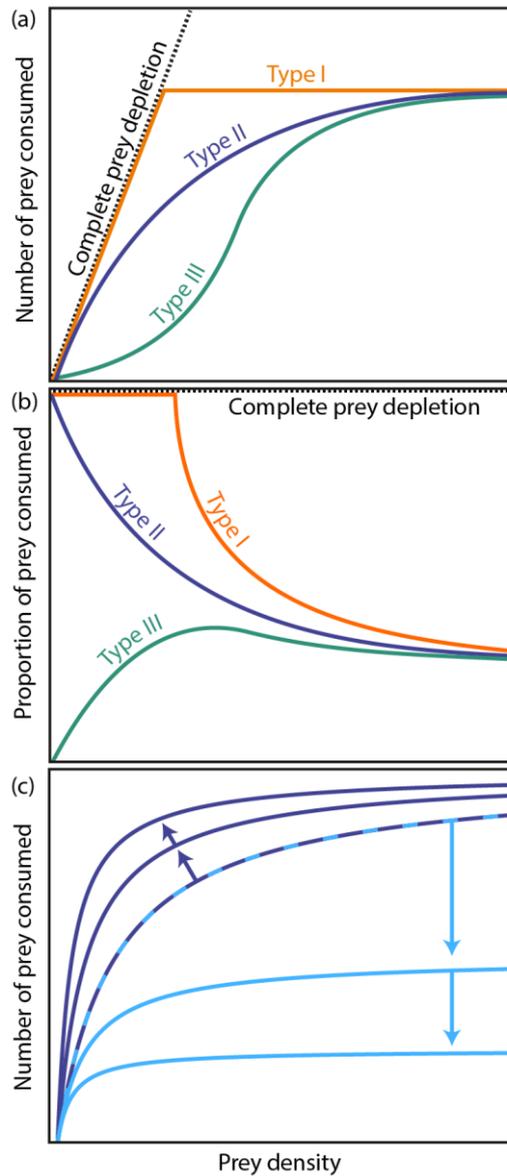
Figure 1. Categorical forms of functional response curves (Holling 1959) describe relationships between prey density and prey consumption (a), differentiated by corresponding relationships between prey density and proportional consumption (b). For a Type II functional response (c, dashed curve), doubling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

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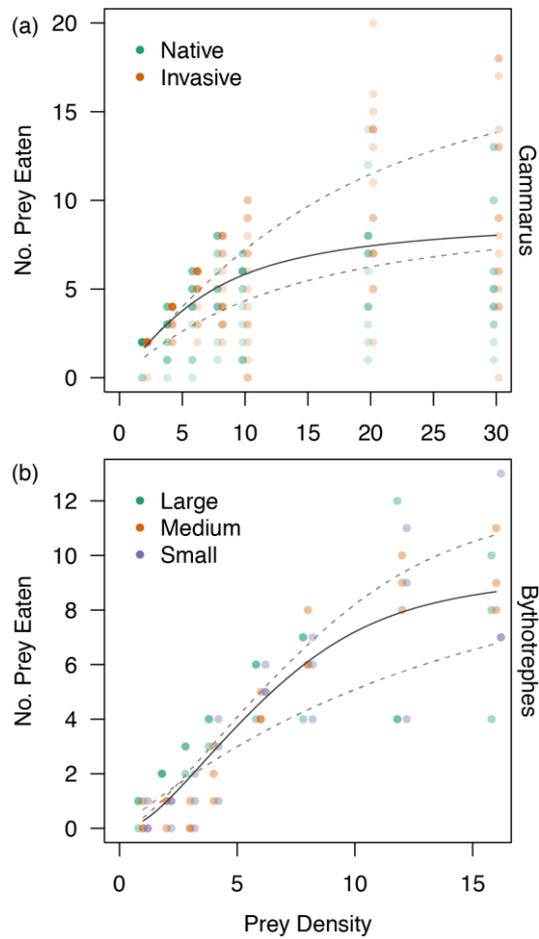
Figure 2. Visualisation of the datasets included with the *FRAIR* package. (a) Consumption of

dipteran larvae (*Simulium* spp.) by native *Gammarus duebeni celticus* and invasive *G. 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.

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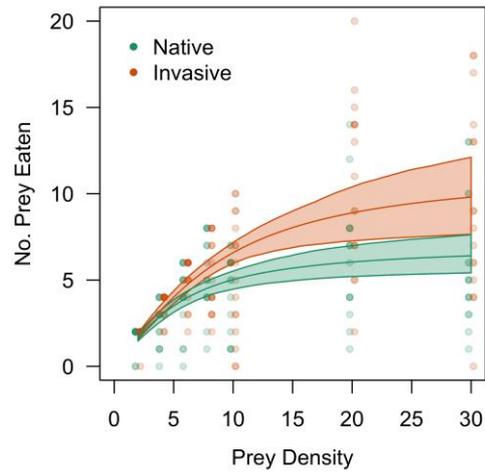
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585   Figure 3. Empirical approximations of 95% confidence intervals based on bootstrapped

586   model fits for the number of prey eaten by native *Gammarus duebeni celticus* and invasive *G.*

587   *pulex* (Gammarus dataset).

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