

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

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13

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

28 INTRODUCTION

29 Consumer-resource interactions are at the heart of ecology because all organisms must
30 consume resources of some kind. Functional responses describe how the per capita feeding
31 rates of consumers change systematically with resource availability as a result of the
32 consumer's search for, capture, and handling of resources (Holling 1959, 1966). The ubiquity
33 and simplicity of principles underpinning the functional response continues to resonate with
34 ecologists working at scales ranging from the behaviour of individuals (Toscano & Griffen
35 2014) to entire food webs (Brose 2010). Across fields—from theoretical explorations of
36 stability and coexistence (Williams & Martinez 2004) to applications in biocontrol, invasions
37 and conservation —functional responses remain central to much ecological research.

38 THE ANATOMY OF A FUNCTIONAL RESPONSE

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

$$43 \quad N_e = \frac{aTN^{(q+1)}}{1+ahN^{(q+1)}} \quad (1)$$

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

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:

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

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 APPLICATIONS OF FUNCTIONAL RESPONSES

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

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
```

133 The *FRAIR* workflow involves a three-step process: (1) model selection; (2) model fitting
134 and; (3) comparison of fits and coefficients. An essential step in this process is to visually
135 inspect the raw plotted data (Fig. 2).

136 MODEL SELECTION

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

142 Although equations 1 and 2 imply consumer functional responses can be described on a
143 linear (Type I) to sigmoidal (Type III) continuum, the original categorical descriptions of
144 Holling remain prominent (e.g. Denny 2014). This is likely because deviations from Type II
145 towards Type III functional responses can stabilise otherwise chaotic consumer-resource
146 dynamics (Williams & Martinez 2004; Barrios-O’Neill *et al.* 2016).

147 Juliano (2001) advocates fitting polynomial logistic functions to proportional consumption
148 data to determine functional response Type. Type II is characterised by a negative first-order
149 term (declining proportional consumption with increasing resource density; Fig. 1b), in
150 contrast to a positive first-order term of Type III (initial increase and subsequent decrease in
151 proportional consumption; Fig. 1b). Using this logic, the `frair_test` function uses forward
152 selection based on the sign and significance of first-order (`density`) and second-order
153 (`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

```

180

181 Although this approach provides a statistical test to distinguish between Type II and Type III,
182 it is considered phenomenological in that describes only the general shape of the response,
183 without determining whether a particular mechanistic model is appropriate. An alternative
184 approach involves fitting a generalised form of the functional response model with a scaling
185 exponent (q) parameterised such that $q = 0$ represents a Type II response (equation 1 or 2),
186 thus exposing a useful null-hypothesis test (i.e. $q \neq 0$) via a regression output and allowing
187 for comparison of models using information criteria (e.g. AIC, BIC, AICc). For example,
188 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

```

202

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

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

210 MODEL FITTING

211 Essential to the optimisation of non-linear models is the provision of reasonable starting
212 values for free parameters. There are some rules of thumb, for example, for Type II models, h
213 can be approximated as the inverse of the maximum number eaten where T is set to 1 (Bolker
214 2008). An equally reliable method is a visual assessment of the data, plotting of putative
215 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

236 Note that all *FRAIR* functional response models take at least one fixed parameter (T), which
237 is experimental time. Although not optimised, this value will change the units of the fitted
238 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

```

256

257 Many authors implicitly accept units of experimental time” by setting $T = 1$. Unless the raw
258 data is made available this limits the use of parameter estimates in subsequent studies (e.g.
259 meta-analyses, food-web models). Therefore, we recommend users adopt units of either hour
260 or day and have adopted units of day in this manuscript. Once starting estimates and fixed
261 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)
```

```

298 ## a 1.4228013 0.1314562 10.823 < 2.2e-16
299 ## h 0.1802657 0.0098583 18.286 < 2.2e-16
300 ##
301 ## -2 log L: 1129.631

302
303 # A fit to the entire bythotrephes dataset
304 b_fit <- frair_fit(formula = eaten~density, data = bythotrephes,
305                   response = "flexpnr",
306                   start = list(b = 1.5, h = 0.04, q = 1),
307                   fixed = list(T = 12/24))
308 with(bythotrephes, plot(density, eaten, xlab="Prey Density",
309                        ylab="No. Prey Eaten"))
310 lines(b_fit, lty = 1, col = "grey25")
311 print(b_fit)

312 ## FUNCTIONAL RESPONSE FIT
313 ##
314 ## Response:          flexpnr
315 ## Description:      Flexible exponent, not assuming replacement
316 ## Optimised variables: b, h, q
317 ## Fixed variables:  T
318 ##
319 ## Coefficients:
320 ##      b      q      h      T
321 ## 0.652 1.215 0.053 0.500
322 ##
323 ## NOTE: It is recommended you inspect the raw fit too (see: ?frair_fit)

324 summary(b_fit$fit)

325 ## Coefficients:
326 ## Estimate Std. Error z value Pr(z)
327 ## b 0.651730 0.258996 2.5164 0.01186
328 ## q 1.215357 0.296077 4.1049 4.045e-05
329 ## h 0.052912 0.005112 10.3509 < 2.2e-16
330 ##
331 ## -2 log L: 241.1805

```

332

333 MODEL COMPARISON

334 The third step in the *FRAIR* workflow includes comparisons of fitted coefficients. The two
335 approaches currently implemented are the delta or difference method of Juliano (2001),
336 provided by `frair_compare` and non-parametric bootstrapping of the raw data, provided by
337 `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 `hassIIIInr` 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 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')
```

##	Coefficient	CI Type	Lower	Upper
##	a	BCa	0.94	2.133
##	h	BCa	0.183	0.286

407

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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467 **REFERENCES**

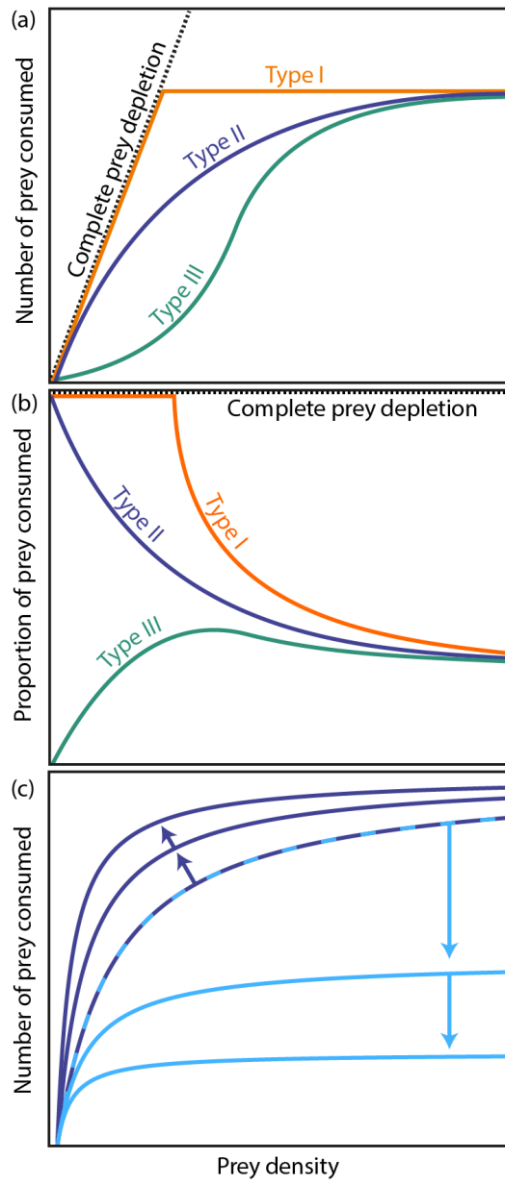
- 468 Alexander, M.E., Dick, J.T., O'Connor, N.E., Haddaway, N.R. & Farnsworth, K.D. (2012).
469 Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of
470 prey supply, model selection and habitat complexity. *Marine Ecology Progress*
471 *Series*, **468**, 191–202.
- 472 Arditi, R. & Ginzburg, L.R. (1989). Coupling in predator-prey dynamics: ratio-dependence.
473 *Journal of theoretical biology*, **139**, 311–326.
- 474 Barrios-O'Neill, D., Dick, J.T., Emmerson, M.C., Ricciardi, A. & MacIsaac, H.J. (2015).
475 Predator-free space, functional responses and biological invasions. *Functional*
476 *Ecology*, **29**, 377–384.
- 477 Barrios-O'Neill, D., Kelly, R., Dick, J.T., Ricciardi, A., MacIsaac, H.J. & Emmerson, M.C.
478 (2016). On the context-dependent scaling of consumer feeding rates. *Ecology letters*,
479 **19**, 668–678.
- 480 Beddington, J.R. (1975). Mutual interference between parasites or predators and its effect on
481 searching efficiency. *The Journal of Animal Ecology*, 331–340.
- 482 Bolker, B.M. (2008). *Ecological models and data in R*. Princeton University Press.
- 483 Bolker, B.M., Gardner, B., Maunder, M., Berg, C.W., Brooks, M., Comita, L., Crone, E.,
484 Cubaynes, S., Davies, T., de Valpine, P., Ford, J., Gimenez, O., Kéry, M., Kim, E.J.,
485 Lennert-Cody, C., Magnusson, A., Martell, S., Nash, J., Nielsen, A., Regetz, J.,
486 Skaug, H. & Zipkin, E. (2013). Strategies for fitting nonlinear ecological models in R,
487 AD Model Builder, and BUGS (S. Ramula, Ed.). *Methods in Ecology and Evolution*,
488 **4**, 501–512.
- 489 Bollache, L., Dick, J.T., Farnsworth, K.D. & Montgomery, W.I. (2008). Comparison of the
490 functional responses of invasive and native amphipods. *Biology letters*, **4**, 166–169.
- 491 Bovy, H.C., Barrios-O'Neill, D., Emmerson, M.C., Aldridge, D.C. & Dick, J.T.A. (2015).
492 Predicting the predatory impacts of the 'demon shrimp' *Dikerogammarus*
493 *haemobaphes*, on native and previously introduced species. *Biological Invasions*, **17**,
494 597–607.
- 495 Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and
496 food-web dynamics. *Functional Ecology*, **24**, 28–34.
- 497 Bunke, M., Alexander, M.E., Dick, J.T., Hatcher, M.J., Paterson, R. & Dunn, A.M. (2015).
498 Eaten alive: cannibalism is enhanced by parasites. *Open Science*, **2**, 140369.
- 499 Canty, A. & Ripley, B.D. (2016). *boot: Bootstrap R (S-Plus) Functions*.
- 500 Corless, R.M., Gonnet, G.H., Hare, D.E.G., Jeffrey, D.J. & Knuth, D.E. (1996). On the
501 LambertW function. *Advances in Computational Mathematics*, **5**, 329–359.
- 502 Denny, M. (2014). Buzz Holling and the Functional Response. *The Bulletin of the Ecological*
503 *Society of America*, **95**, 200–203.

- 504 Dixon, P.M. (2001). The Bootstrap and the Jackknife. *Design and Analysis of Ecological*
505 *Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 267–288. Oxford University
506 Press, Oxford, UK.
- 507 Dodd, J.A., Dick, J.T., Alexander, M.E., MacNeil, C., Dunn, A.M. & Aldridge, D.C. (2014).
508 Predicting the ecological impacts of a new freshwater invader: functional responses
509 and prey selectivity of the ‘killer shrimp’, *Dikerogammarus villosus*, compared to the
510 native *Gammarus pulex*. *Freshwater Biology*, **59**, 337–352.
- 511 Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011). Temperature dependence of the
512 functional response. *Ecology letters*, **14**, 914–921.
- 513 Hassell, M.P. (1978). *The dynamics of arthropod predator-prey systems*. Princeton
514 University Press.
- 515 Hassell, M.P. & Varley, G.C. (1969). New Inductive Population Model for Insect Parasites
516 and its Bearing on Biological Control. *Nature*, **223**, 1133–1137.
- 517 Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *The*
518 *Canadian Entomologist*, **91**, 385–398.
- 519 Holling, C.S. (1966). The functional response of invertebrate predators to prey density.
520 *Memoirs of the Entomological Society of Canada*, **98**, 5–86.
- 521 Houck, M.A. & Strauss, R.E. (1985). The comparative study of functional responses:
522 experimental design and statistical interpretation. *The Canadian Entomologist*, **117**,
523 617–629.
- 524 Jeschke, J.M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: discriminating
525 between handling and digesting prey. *Ecological Monographs*, **72**, 95–112.
- 526 Juliano, S.A. (2001). Nonlinear curve fitting. Design and analysis of ecological experiments.
527 *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch),
528 pp. 178–196. Oxford University Press, Oxford, UK.
- 529 Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013). Body
530 masses, functional responses and predator–prey stability. *Ecology Letters*, **16**, 1126–
531 1134.
- 532 Lehtonen, J. (2016). The Lambert W function in ecological and evolutionary models (M.
533 Rees, Ed.). *Methods in Ecology and Evolution*, **7**, 1110–1118.
- 534 Médoc, V., Albert, H. & Spataro, T. (2015). Functional response comparisons among
535 freshwater amphipods: ratio-dependence and higher predation for *Gammarus pulex*
536 compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus*
537 *berilloni*. *Biological Invasions*, **17**, 3625–3637.
- 538 Okuyama, T. (2012). Flexible components of functional responses. *Journal of Animal*
539 *Ecology*, **81**, 185–189.
- 540 Paterson, R.A., Dick, J.T.A., Pritchard, D.W., Ennis, M., Hatcher, M.J. & Dunn, A.M.
541 (2015). Predicting invasive species impacts: a community module functional response

- 542 approach reveals context dependencies (B. Woodcock, Ed.). *Journal of Animal*
543 *Ecology*, **84**, 453–463.
- 544 Real, L.A. (1977). The kinetics of functional response. *American Naturalist*, 289–300.
- 545 Rogers, D. (1972). Random search and insect population models. *The Journal of Animal*
546 *Ecology*, 369–383.
- 547 Royama, T. (1971). A comparative study of models for predation and parasitism. *Researches*
548 *on Population Ecology*, **13**, 1–91.
- 549 Sentis, A., Hemptinne, J.-L. & Brodeur, J. (2013). Parsing handling time into its components:
550 implications for responses to a temperature gradient. *Ecology*, **94**, 1675–1680.
- 551 Skalski, G.T. & Gilliam, J.F. (2001). Functional responses with predator interference: viable
552 alternatives to the Holling type II model. *Ecology*, **82**, 3083–3092.
- 553 Toscano, B.J. & Griffen, B.D. (2014). Trait-mediated functional responses: predator
554 behavioural type mediates prey consumption. *Journal of Animal Ecology*, **83**, 1469–
555 1477.
- 556 Trexler, J.C., McCulloch, C.E. & Travis, J. (1988). How can the functional response best be
557 determined? *Oecologia*, **76**, 206–214.
- 558 Uszko, W., Diehl, S., Pitsch, N., Lengfellner, K. & Müller, T. (2015). When is a type III
559 functional response stabilizing? Theory and practice of predicting plankton dynamics
560 under enrichment. *Ecology*, **96**, 3243–3256.
- 561 White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C. & White, C. (2014). Ecologists
562 should not use statistical significance tests to interpret simulation model results.
563 *Oikos*, **123**, 385–388.
- 564 Williams, R.J. & Martinez, N.D. (2004). Stabilization of chaotic and non-permanent food-
565 web dynamics. *The European Physical Journal B-Condensed Matter and Complex*
566 *Systems*, **38**, 297–303.

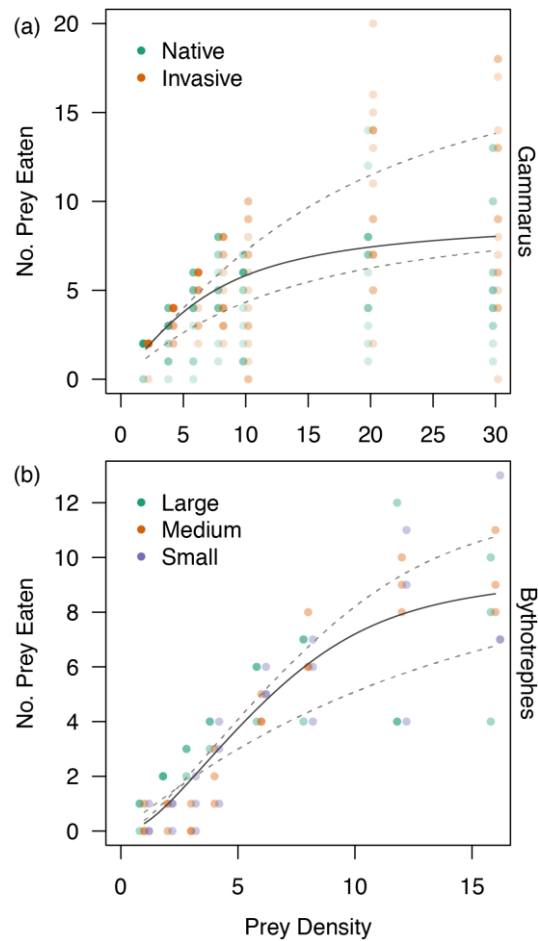
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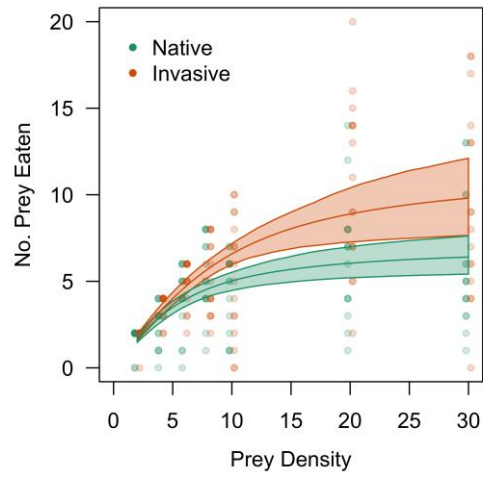
570 Figure 1. Categorical forms of functional response curves (Holling 1959) describe
 571 relationships between prey density and prey consumption (a), differentiated by corresponding
 572 relationships between prey density and proportional consumption (b). For a Type II
 573 functional response (c,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



576

577 Figure 2. Visualisation of the datasets included with the *FRAIR* package. (a) Consumption of
 578 dipteran larvae (*Simulium* spp.) by native *Gammarus duebeni celticus* and invasive *G. pulex*
 579 and (b) The consumption of three size classes of *Polyphemus pediculus* by *Bythotrephes*
 580 *longimanus*. Dashed lines represent plausible starting values for MLE optimisation and solid
 581 lines represent optimised fits for Rogers (Type II, Gammarus) or Flexible Exponent
 582 (Bythotrephes) models.

583



584

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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589