1   **partR2: Partitioning R² in generalized linear mixed models**

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31 **Abstract**

32 The coefficient of determination R^2 quantifies the amount of variance explained by regression

33 coefficients in a linear model. It can be seen as the fixed-effects complement to the repeatability R

34 (intra-class correlation) for the variance explained by random effects and thus as a tool for variance

35 decomposition. The R^2 of a model can be further partitioned into the variance explained by a

36 particular predictor or a combination of predictors using semi-partial (part) R^2 and structure

37 coefficients, but this is rarely done due to a lack of software implementing these statistics. Here, we

38 introduce `partR2`, an R package that quantifies part R^2 for fixed effect predictors based on

39 (generalized) linear mixed-effect model fits. The package iteratively removes predictors of interest

40 from the model and monitors the change in the variance of the linear predictor. The difference to

41 the full model gives a measure of the amount of variance explained uniquely by a particular predictor

42 or a set of predictors. `partR2` also estimates structure coefficients as the correlation between a

43 predictor and fitted values, which provide an estimate of the total contribution of a fixed effect to the

44 overall prediction, independent of other predictors. Structure coefficients can be converted to the

45 total variance explained by a predictor, here called 'inclusive' R^2, as the square of the structure

46 coefficients times total R^2. Furthermore, the package reports beta weights (standardized regression

47 coefficients). Finally, `partR2` implements parametric bootstrapping to quantify confidence intervals

48 for each estimate. We illustrate the use of `partR2` with real example datasets for Gaussian and

49 binomial GLMMs and discuss interactions, which pose a specific challenge for partitioning the

50 explained variance among predictors.

51 **Introduction**

52 Coefficients of determination R^2 are of interest in the study of ecology and evolution, because they

53 quantify the amount of variation explained by a linear model (Edwards et al., 2008). By doing so, they

54 go beyond significance testing in putting effects in perspective of the phenotypic variance. R^2 is

55 expressed as a proportion of the total variance in the response, which represents a biologically

56 relevant quantity if the total variation is representative for the total population (de Villemereuil et al.,

57 2018). The total coefficient of determination in a generalised linear mixed model (GLMM) quantifies

58 the variance explained by all fixed effects together (marginal R^2 *sensu* Nakagawa & Schielzeth, 2013,

59 also known as the total correlation coefficient, Watanabe (1960)).

60

61 However, it is often of interest to attribute explained variation to individual predictors. Semi-partial

62 coefficients of determination, also known as part R^2, decompose the variance of R^2 into components

63 uniquely explained by individual predictors (Jaeger et al., 2017; Jaeger, Edwards & Gurka, 2019) or

64 sets of predictors (Figure 1). The set of all predictors in the model yields the total proportion of

65 variance explained by the fixed part of the model (total R^2). With correlations among predictors, it

66 often happens that predictors in univariate regressions explain a large share of the variance, but do

67 not show large part R^2 if other correlated predictors are included in the model. Note that part R^2

68 estimates the proportion of the variance in the response explained by a predictor *while* accounting

69 for covariance between this predictor and the other predictors in the model, whereas the (arguably

70 more familiar) partial R^2 estimates the proportion of the variance that is explained by a predictor of

71 interest *after* accounting for the other predictors from the response as well as the predictor of

72 interest. The difference is subtle, but important (see more below). Therefore, part R^2 represents

73 'variance accounted for' in relation to the total variance, but partial R^2 does not. Consequently, part

74 R^2 will be conceptually easier to compare with (total) R^2.

75

76 Structure coefficients provide a valuable addition to part R^2 in the decomposition of the phenotypic

77 variance (Nimon et al., 2008; Yeatts et al., 2017). Structure coefficients quantify the correlation

78 between individual predictors and the linear predictor. Predictors that correlate well with a

79 response, but are fitted with collinear predictors may show large structure coefficients as they are

80 correlated to the predicted response, but low part R^2 as other predictors explain part of the same

81 variance. Structure coefficients range from -1 to 1 with their absolute value expressing the correlation

82 relative to a perfect correlation if a single predictor explains as much as the total fixed part of the

83 model.

84

85 Structure coefficients are correlations and since the square of a correlation yields the variance

86 explained, we can use structure coefficients to estimate the total variance explained by a predictor

87 (Nimon et al., 2008). We call this the inclusive R^2 of a predictor and calculate it as the squared

88 structure coefficient, i.e. its contribution to the linear predictor independent of other predictors

89 (Nimon et al., 2008) times the proportion of variance explained by the linear predictor (which is the

90 'total' marginal R^2 of the model) (see also Nathans, Oswald & Nimon, 2012). As far as we are aware,

91 inclusive R^2 has not been implemented before, but it provides valuable insights into the structure of

92 the variance explained (Figure 1).

93

94 Here, we introduce `partR2`, a versatile package for estimating part R^2, inclusive R^2, structure

95 coefficients and beta weights from mixed-effects models. Figure 1 gives an overview of how

96 variances are calculated and how they relate to partial R^2 and to commonality analysis (Ray-

97 Mukherjee et al., 2014; Seibold & McPhee, 1979; Zientek & Thompson, 2006). We illustrate how to

98 use `partR2` with real example datasets for Gaussian and binomial GLMMs, discuss how to estimate

99 part R^2 in the presence of interactions and discuss some challenges and limitations.

100

101
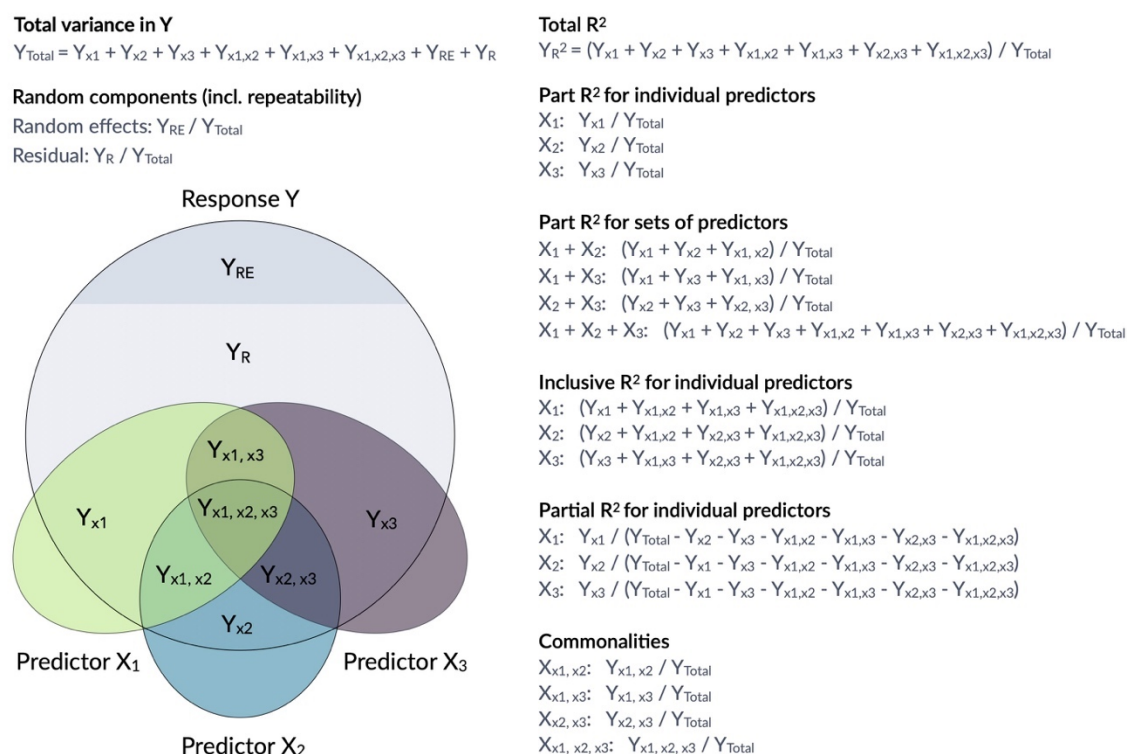
102 **Figure 1: Conceptual framework for the estimation of proportions of variance components in a mixed**
103 **model.** The large grey circle symbolizes the variance in a response Y, the dark grey area on the top indicates
104 the share explained by random effects and the coloured ellipses symbolize variance in covariates with

105 intersections indicating jointly explained variances. `partR2` calculates total R^2, part R^2 for individual predictors
106 and sets of predictors as well as inclusive R^2. The package does not report partial R^2 and commonalities,
107 although they could be calculated from the `partR2` output.
108

109 **Mathematical representation**

110 **Part R^2**

111

112 A Gaussian mixed-effects model can be written as:

113 $$\mathbf{y} = \mathbf{X\beta} + \sum \mathbf{\alpha}_k + \mathbf{\varepsilon} \qquad \text{(Eq. 1)}$$

114 $$\alpha_k \sim N(0, \sigma^2_{\alpha_k})$$

115 $$\varepsilon \sim N(0, \sigma^2_\varepsilon)$$

116 Where $\mathbf{y}$ is a vector of response values (outcomes), $\mathbf{X}$ is the design matrix of fixed effects, $\mathbf{\beta}$ is a

117 vector of regression coefficients, $\sum \mathbf{\alpha}_k$ is the random part of the model that might contain multiple

118 random effects and $\mathbf{\varepsilon}$ is a vector of residual deviations. The linear predictor $\mathbf{\eta}$ represents the vector

119 of predicted values from the fixed part of the model as $\mathbf{\eta} = \mathbf{X\beta}$. Note that we dealing with estimates

120 of regression coefficients and variance components throughout (hence all $\mathbf{\beta}$ should be read as $\hat{\mathbf{\beta}}$).

121

122 Since we are interested in the proportion of the phenotypic variance explained, we symbolize

123 variance components by upper case Y and index by the source of variance (als in Figure 1). While

124 variances are frequently represented as V with the source of variance as an index, this leads to

125 ambiguity for V_X which might represent variance in y explained by x or variance in x itself, which is

126 why we use this alternative notation. The total variance in the response is $Y_{Total} = \mathrm{var}(y)$ and is

127 estimated from the raw data or from the model (see below). The variance of the residuals is estimated

128 by the model as $Y_R = \mathrm{var}(\varepsilon)$. The variance of the (sum of) random effects is estimated by the model

129 as $Y_{RE} = \mathrm{var}(\sum \mathbf{\alpha}_k)$ and the variance explained by fixed effects can be estimated as the variance

130 in the linear predictor $Y_X = \mathrm{var}(\mathbf{X\beta})$.

131

132 The coefficient of determination R^2 estimates the proportion of variance in the response that is

133 explained by fixed effects. The coefficient of determination R^2 for the total fixed part of the model is

134 thus:

135 $$R^2_X = \frac{Y_X}{Y_X + Y_{RE} + Y_R} = \frac{Y_X}{Y_{Total}} \qquad \text{(Eq. 2)}$$

136   Note that the sum of the components in the denominator might deviate numerically from the total

137   outcome variance in the raw data. However, conceptually they are the same in that they represent

138   the population-level outcome variance. The variance in the outcome is an estimate from the specific

139   sample, while the sum of components of the mixed model represents a population-level estimate

140   given the data and the model.

141

142   A reduced model with a (set of) fixed effect predictors X^* removed but the same random effect

143   structure can be fitted as (now using the tilde to highlight the differences from Eq. 1):

144    $$\mathbf{y} = \widetilde{\mathbf{X}}\widetilde{\boldsymbol{\beta}} + \sum \widetilde{\boldsymbol{\alpha}}_k + \widetilde{\boldsymbol{\varepsilon}} \qquad\qquad\qquad\text{(Eq. 3)}$$

145    $$\widetilde{\alpha}_k \sim N(0, \sigma_{\widetilde{\alpha}_k}^2)$$

146    $$\widetilde{\varepsilon} \sim N(0, \sigma_{\widetilde{\varepsilon}}^2)$$

147   with the variance in the linear predictor of the reduced model being $Y_{\widetilde{X}} = \mathrm{var}(\widetilde{\mathbf{X}}\widetilde{\boldsymbol{\beta}})$.

148

149   The variance uniquely explained by X^* is then the difference between the variance explained by

150   fixed effects in the full and the reduced model $Y_{X^*} = Y_X - Y_{\widetilde{X}}$. Part R^2 sets this variance in proportion

151   to the total outcome variance:

152    $$R_{X^*}^2 = \frac{Y_X - Y_{\widetilde{X}}}{Y_X + Y_{RE} + Y_R} = \frac{Y_X - Y_{\widetilde{X}}}{Y_{Total}} \qquad\qquad\text{(Eq. 4)}$$

153   The process of fitting a reduced model, estimation of Y_{X^*} and estimation of $R_{X^*}^2$ can be repeated

154   for all predictors and combinations of predictors. At the limit for a model with all fixed effects

155   removed, $R_{X^*}^2 = R_X^2$.

156

157   **Side-note on partial R^2**

158

159   For completeness we note that the partial R^2 could be calculated as:

160    $$R_{X^*}^2 = \frac{Y_X - Y_{\widetilde{X}}}{Y_{Total} - Y_{\widetilde{X}}} \qquad\qquad\qquad\text{(Eq. 5)}$$

161   However, this estimate does not put the explained variance in perspective of the total variance in the

162   response. It has the major disadvantage that the denominator depends on $Y_{\widetilde{X}}$. The same effect in

163   terms of Y_{X^*} thus appears larger if the reduced model explains more variance (larger $Y_{\widetilde{X}}$). Even in

164   the case of independent additive predictors, the contributions of the different fixed effects do not

165   sum up to R_X^2, because of the change in the denominator that different Y_{X^*} are compared to.

166   Finally, since we are interested in explaining phenotypic variation in some biological response (the

167   phenomenon to be explained), we think that part R^2 is the more relevant quantity, as it represents

168   the proportion of variance in the response uniquely explained by X^*.

169

170   **Inclusive R^2**

171

172   Structure coefficients are the Pearson correlations between a particular predictor of interest x^* and

173   the linear predictor η . Note that we now use a lower case x^* to indicate that we are dealing with a

174   single predictor. Structure coefficients are quantified from the full model as:

175    $SC_{x^*} = \mathrm{cor}(\eta, x^*)$ (Eq. 6)

176

177   The squared correlation between two variables *a* and *b* gives the variance explained for these

178   variables $\mathrm{cor}(a,b)^2 = R_a^2$. The squared structure correlations thus quantify the proportion of

179   variance in the linear predictor Y_X that is explained by a the predictor of interest x^*. Since the

180   proportion of outcome variance explained by the linear predictor in the full model is R_x^2, the

181   inclusive variance explained by predictor x^* is:

182    $IR_{x^*}^2 = SC^2 \cdot R_x^2$ (Eq. 7)

183

184   Inclusive R^2 as we define it here, complements part R^2 by giving additional insights. While part R^2

185   quantifies the variance uniquely explained by a predictor (or set of predictors), inclusive R^2 quantifies

186   the total proportion of variance explained in the model, both uniquely and jointly with other

187   predictors. In the special case of a single predictor in a model $SC_{x^*} = \mathrm{cor}(\eta, x^*) = 1$, such that

188    $IR_{x^*}^2 = R_x^2$.

189

190   **Part R^2 in non-Gaussian models**

191

192   For Gaussian models there is a single residual error term ε with variance $Y_R = \mathrm{var}(\varepsilon)$. For non-

193   Gaussian models, however, there is additional error that arises from the link function that translates

194   latent-level predictions to observed outcomes. This variance can be approximated for a variety of

195   link functions and error distributions (Nakagawa & Schielzeth, 2010; Nakagawa, Johnson &

196   Schielzeth, 2017). Our R package currently implements distribution-specific variances for Poisson

197   models with log and square root link functions and binomial models with logit and probit link

198   functions. For Poisson models and non-binary binomial models (proportion models), `partR2` also

199   fits an observational level random effect (if none is fitted already) to estimate variance due to

200   overdispersion (Harrison, 2014). Both the overdispersion variance, now denoted Y_R and the

201   distribution-specific variance Y_D are included in the denominator of the part R2 calculation:

202

203    $$R^2_{X*} = \frac{Y_X - Y_{\widetilde{X}}}{Y_X + Y_{RE} + Y_D + Y_R}$$ (Eq. 8).

204

205

206   Notably, there are other estimation methods for R^2 for non-Gaussian models or GLMM (Jaeger et

   al., 2017; Piepho, 2019). Currently, `partR2` only implements the method based on Nakagawa &

207   Schielzeth (2013) and Nakagawa, Johnson & Schielzeth (2017).

Other implementations in R packages

209   There are a few R packages that calculate part R^2 for linear models (lm), for example

210   `rockchalk::getDeltaRsquare` (Johnson & Grothendieck, 2019). Other packages calculate

211   partial R^2 (not part R^2) such as `asbio::partial.R2` (Aho, 2020) and `rr2::R2` (Ives & Li, 2018) for

212   lms and `rsq::rsq.partial` (Zhang, 2020) for linear models and generalized linear models (glm).

213   Note that partial R^2 is different from part (semi-partial) R^2 (partial R^2 > part R^2), since it represents the

214   unique variance explained by a particular predictor but after removing ('partialling out') the variance

215   explained by the other predictors (Yeatts et al., 2017, Figure 1). The ppcor package calculates semi-

216   partial and partial correlations, but does not work on fitted GLM or GLMM models (Kim, 2015). The

217   package `yhat` features functions for commonality analyses in glms (Nimon, Oswald & Roberts,

218   2020). None of these packages estimates part R^2 for mixed-effects models that we focus on here.

219   Several packages estimate (marginal) R^2 as the variance explained by all fixed effects in linear mixed-

220   effects models. This includes `performance::r2_nakagawa` (Lüdecke et al., 2020),

221   `MuMIn::r.squaredGLMM` (Bartoń, 2019), and `rptR::rpt` (Stoffel, Nakagawa & Schielzeth, 2017).

222   These packages do not allow to estimate part R^2. The only versatile package to estimate part R^2 from

223   linear mixed-models is `r2glmm` (Jaeger, 2017). The function `r2glmm::r2beta` computes part R^2

224   from lmer, lme and glmmPQL model fits (also for linear models lm and glm) based on Wald statistics.

225   However, it does neither support `lme4::glmer` for generalized linear model fits nor does it allow

226   to estimate R^2 for combinations of predictors. Furthermore, it does not estimate structure

227   coefficients, inclusive R^2 or part R^2 for multilevel factors as a unit.

228

Features of `partR2`

229

230   `partR2` takes a fitted (generalized) linear mixed-model (GLMM), from the popular mixed model

231   package `lme4` (Bates et al., 2015) and estimates part R^2 by iteratively removing fixed effects (Nimon

232   et al., 2008). The specific fixed effects of interest are specified by the `partvars` and/or by the

233   `partbatch` argument. The package estimates part R^2 for all predictors specified in `partvars`

234   individually and in all possible combinations (the maximum level of combinations can be set by the

235   `max_level` argument). A custom specification of fixed effects of interest saves computation time as

236   compared to an all-subset specification and is therefore required in `partR2`.

237   The central function `partR2` will work for Gaussian, Poisson and binomial GLMMs. Since the model

238   fit is done externally, there is no need to supply a family argument. For non-Gaussian GLMMs, the

239   package estimates link-scale R^2 *(sensu* Nakagawa & Schielzeth, 2013*)*. We implement parametric

240   bootstrapping to quantify sampling variance and thus uncertainty in the estimates. Parametric

241   bootstrapping works through repeated model fitting on simulated data based on fitted values

242   (Faraway, 2015). The number of bootstrap iterations is controlled by the `nboot` argument. We

243   recommend a low number of `nboot` for testing purposes and a large number (e.g. `nboot = 1000`)

244   for the final analysis.

245   The package returns an object of class `partR2` that contains elements for part R^2, inclusive R^2,

246   structure coefficients, beta weights (standardized regression slopes), bootstrapping iterations and

247   some other information. An extended summary, that includes inclusive R^2, structure coefficients and

248   beta weights can be viewed using the `summary` function. The `forestplot` function shows a

249   graphical representation of the variance explained by individual predictors and sets of predictors

250   along with their bootstrapping uncertainties. All computations can be parallelized across many cores

251   based on the `future` and `furrr` packages (Vaughan & Dancho, 2018; Bengtsson, 2020). An

252   extended vignette with details on the complete functionality accompanies the package.

253

Example with Gaussian data

254

255   We use an example dataset with hormone data collected from a population of captive guinea pigs

256   to illustrate the features of `partR2`. The dataset contains testosterone measurements of 31 male

257   guinea pigs, each measured at 5 time points (age between 120 and 240 days at 30-day intervals).

258   We analyze log-transformed testosterone titers and fit male identity as a random effect. As covariates

259   the dataset contains the time point of measurement and a rank index derived from behavioral

260   observations around the time of measurement (Mutwill et al., in prep.).

261   *Rank* and *Time* are correlated in the dataset ($r = 0.40$), since young individuals are typically low rank,

262   while older individuals tend to hold a high rank. *Time* might be fitted as a continuous predictor or as

263   a factor with five levels. Here we present the version of a factorial predictor to illustrate the estimation

264   of part R^2 for interactions terms. Hence, an interaction between time and rank will also be fitted.

265   First, the package needs to be loaded (after successful installation) in an R session (R Core Team,

266   2019). The package comes with the guinea pig dataset that also needs to be loaded using the data

267   function.

268

269   ```
library(partR2)
```

270    ```
data(GuineaPigs)
```

271

272   A single record contains missing values for testosterone measurements. Missing records can be

273   problematic to handle in `partR2` and are better removed prior to the analysis. We also log-transform

274   the response and convert *Time* to a factor and filter for the first three time points to simplify the

275   output.

276
277   ```
GuineaPigs <- subset(GuineaPigs,
```

278    ```
               !is.na(Testo) & !is.na(Rank) & (Time %in% c(1,3,5)))
```

279   ```
GuineaPigs$TestoTrans <- log(GuineaPigs$Testo)
```

280    ```
GuineaPigs$Time <- factor(GuineaPigs$Time)
```

281

282   We then fit a linear mixed effects model using `lmer` from the `lme4` package (Bates et al., 2015).

283   Further exploration of the data and model checks are omitted here for simplicity, but are advisable

284   in real data analysis.

285

286   ```
library(lme4)
```

287    ```
mod <- lmer(TestoTrans ~ Rank * Time + (1|MaleID), data=GuineaPigs)
```

288

289   The `partR2` analysis takes the `lmer` model fit (an `merMod` object) and a character vector `partvars`

290   indicating the fixed effects to be evaluated. Interactions are specified with the colon syntax (see the

291   package's vignette for further details).

292

```
293   res <- partR2(mod, partvars = c("Rank", "Time", "Rank:Time"),
294                    nboot=100)
295
```

296 The function returns a `partR2` object. The `print` function reports the part coefficients of
297 determination and a more extensive summary can be viewed with the `summary` function which also
298 shows inclusive R^2, structure coefficients and beta weights (standardized slopes) (Figure 2).

```
299
300   print(res)
301   summary(res, round_to = 2)
```

```
        R2 (marginal) and 95% CI for the full model:
         R2   CI_lower CI_upper ndf
         0.17 0.09      0.36     6

         ----------

        Part (semi-partial) R2:
         Predictor(s)        R2    CI_lower CI_upper ndf
         Model               0.17 0.09      0.36     6
         Rank                0.00 0.00      0.18     6
         Time                0.02 0.00      0.20     4
         Rank:Time           0.04 0.00      0.21     4
         Rank+Time           0.02 0.00      0.20     4
         Rank+Rank:Time      0.16 0.08      0.34     3
         Time+Rank:Time      0.04 0.00      0.22     2
         Rank+Time+Rank:Time 0.17 0.09      0.36     1

         ----------

        Inclusive R2 (SC^2 * R2):
         Predictor   IR2  CI_lower CI_upper
         Rank        0.13 0.03      0.26
         Time3       0.00 0.00      0.04
         Time5       0.00 0.00      0.04
         Rank:Time3  0.05 0.01      0.13
         Rank:Time5  0.01 0.00      0.07

         ----------

        Structure coefficients r(Yhat,x):
         Predictor  SC    CI_lower CI_upper
         Rank       0.87  0.56     0.94
         Time3      0.14 -0.18     0.43
         Time5      0.16 -0.26     0.48
         Rank:Time3 0.56  0.22     0.75
         Rank:Time5 0.28 -0.14     0.57

         ----------

        Beta weights (standardised estimates)
         Predictor  BW    CI_lower CI_upper
         Rank        0.50 -0.08     0.94
         Time3      -0.19 -0.53     0.14
         Time5       0.17 -0.20     0.55
         Rank:Time3  0.17 -0.36     0.83
         Rank:Time5 -0.36 -0.95     0.38

         ----------
```
302

303 **Figure 2: Summary output for example data analysis with Gaussian data (guinea pig analysis).**
304

305   The variances appear largely additive, since combinations of predictors explain about the sum of the

306   variance explained by individual predictors. The main components of the `partR2` object can be

307   accessed for further processing as `res$R2` for part R^2 (with point estimates and confidence intervals),

308   `res$SC` for structure coefficients, `res$IR2` for inclusive R^2 and `res$BW` for beta weights.

309

Dealing with interactions

311   Models with interactions are problematic, because the variance explained by a main factor can be

312   estimated in multiple ways (Figure 3) and because of the internal parametrization of the model

313   matrix.

314
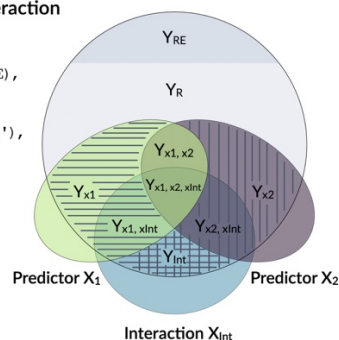
Figure 3: Conceptual framework for dealing with interactions. An interaction is the product of two main effects and thus often correlated with each of the main effects. The figure shows three options for estimating the part R^2 for main effects that are involved in an interaction.

318 The model output above shows the number of parameters fitted in each model (Figure 2, each row

319 in the R2 part refers to a reduced model). In the `print` and `summary` output this is visible as a column

320 labelled 'ndf'. A close inspection shows that the removal of rank did not change the number of

321 parameters (6 for the full model, 6 for the model excluding rank). This is because the model matrix

322 is reparametrized in the reduced model and `lmer` will fit three terms for the interaction (here

323 `Time1:Rank, Time3:Rank, Time5:Rank`) rather than just two for the interaction in the full model.

324 Dummy coding of the factor can be usefully combined with centering of dummy coded variables

325 (Schielzeth, 2010) and gives more control over this re-parametrisation. It allows for example to

326 estimate the part R^2 for the average effect of *Rank* by constraining the average *Rank* effect to zero,

327 so that only the two contrasts are fitted (here `Time3:Rank, Time5:Rank`):

328
329 ```
GuineaPigs <- cbind(GuineaPigs, model.matrix(~ 0 + Time,
```

330 ```
    data=GuineaPigs))
```

331 ```
GuineaPigs$Time3 <- GuineaPigs$Time3 - mean(GuineaPigs$Time3)
```

332 ```
GuineaPigs$Time5 <- GuineaPigs$Time5 - mean(GuineaPigs$Time5)
```

333

334 The model can then be fitted with dummy predictors. Since the usual specification in `partR2` via

335 `partvars` would fit all possible combinations, including combinations of the different *Time* terms,

336 such a run can take a long time. However we are mostly interested in fitting and removing all dummy

337 predictors at a time. The package therefore features an additional argument `partbatch` to specify

338 a list of character vectors containing the sets of predictors that should always be kept together. In

339 the example, the list has two elements, a character vector for the dummy-coded main effects and a

340 character vector for the interaction terms. The analysis yields part R^2 for two batches of predictors as

341 well as *Rank* and their combinations.

342
343 ```
mod <- lmer(TestoTrans ~ (Time3 + Time5) * Rank + (1|MaleID),
```

344 ```
    data=GuineaPigs)
```

345 ```
batch <- c("Time3", "Time5")
```

346 ```
partR2(mod, partvars=c("Rank"), partbatch=list(Time=batch,
```

347 ```
    `Time:Rank`= paste0(batch, ":Rank")), nboot=100)
```

348

349     This, however, is only one way of dealing with interactions (Option A in Figure 3). It represents the

350     variance uniquely explained by main effects even in the presence of an interaction. Since interactions

351     are the products of main effects, interaction terms are typically correlated with main effects and the

352     part $R^2$ calculated above might not represent a biologically relevant quantity. There are two

353     alternative ways of how to deal with interactions. Both are possible in `partR2`, but since

354     requirements differ between applications, we do not implement one with priority.

355     One way to think about variance explained by main effects and their interactions is to pool the

356     variance explained by a main effect with the variance explained by interactions that the term is

357     involved in (Option B in Figure 3). In the guinea pig example, for instance, *Rank* might be considered

358     important either as a main effect or in interaction with time and we might want to estimate the total

359     effect of rank. This can be done for the guinea pig dataset by using `partbatch`:

360
361     ```
mod <- lmer(Testo ~ Time * Rank + (1|MaleID), data=GuineaPigs)
```

362   ```
partR2(mod, partbatch = list(Time=c("Time", "Time:Rank"),
```

363     ```
    Rank=c("Rank", "Time:Rank")), nboot=100)
```

364

365   A third, which we think usually preferable option is to prioritize main effects by assigning the

366   proportion of variance that is explained by a main effect together with the variance jointly explained

367   with its interaction to the main effect (Option C in Figure 3). This implies that part R^2 for a main effect

368   is estimated when its own interaction is excluded from the model (`mod1` and `part1` below). The

369   variance explained by the interaction is then estimated in a separate model (`mod2` and `part2` below).

370   We have implemented a helper function `mergeR2` that allows to merge two `partR2` runs.

371
372   ```
mod1 <- lmer(Testo ~ Time * Rank + (1|MaleID), data=GuineaPigs)
```

373     ```
part1 <- partR2(mod1, partvars = c("Time:Rank"), nboot=100)
```

374   ```
mod2 <- lmer(Testo ~ Time + Rank + (1|MaleID), data=GuineaPigs)
```

375     ```
part2 <- partR2(mod2, partvars = c("Time", "Rank"), nboot=100)
```

376   ```
mergeR2(part1, part2)
```

377

378     All these results can be viewed by `print`, `summary` and plotted by `forestplot`. It is important to

379     bear in mind the differences in the interpretation as illustrated in Figure 3.

380

**An example with proportion data**

381

382 As an example for proportion data, we analyze a dataset on spatial variation in color morph ratios in

383 a color-polymorphic species of grasshopper. Individuals of this species occur either in a green or a

384 brown color variant and the dataset contains counts of brown and green individuals (separated for

385 females and males) from 42 sites sampled in the field (Dieker et al., 2018). Site identity will be fitted

386 as a random effect. As covariates the dataset contains a range of Bioclim variable that describe

387 various aspects of ecologically relevant climatic conditions (Karger et al., 2017). The aim is to identify

388 the climatic conditions that favour one or the other colour variant.

389 We first load the grasshopper dataset. We standardise all Bioclim variables using the `scale` function

390 and add an observation-level counter that will be used as an observation-level random effect (OLRE)

391 to account for overdispersion (Harrison, 2014).

392

```
data(Grasshoppers)
for (i in which(substr(colnames(Grasshoppers),1,3)=="Bio")){
        Grasshoppers[,i] <- scale(Grasshoppers[,i])
}
Grasshoppers$OLRE <- 1:nrow(Grasshoppers)
```

398

399 We first fit a GLMM with binomial error structure and logit link using the `glmer` function from the

400 `lme4` package (Bates et al., 2015). A previous analysis has shown that the first principle component

401 of the Bioclim data explains a small, but significant part of variation in morph ratios (Dieker et al.,

402 2018). For illustration, we use the four Bioclim variables that show a loading of more than 0.30 on

403 the first principle component.

404

```
mod <- glmer(cbind(nGreen, nBrown) ~ Bio7 + Bio14 + Bio17 + Bio19 +
        (1|SiteID) + (1|OLRE), data=Grasshoppers, family="binomial")
res <- partR2(mod, partvars=c("Bio7", "Bio14", "Bio17", "Bio19"),
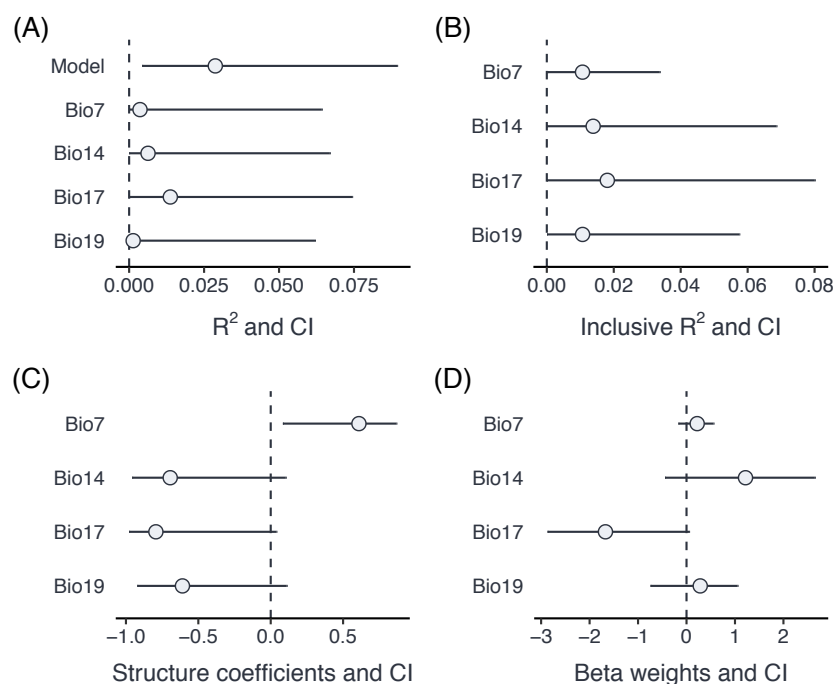        max_level = 1, nboot=100)
```

409

410 The `summary` output informs us (at the bottom) that there have been warnings in the bootstrapping

411 processes. This is not unusual since bootstrapping frequently generates data, for which one of the

412 parameters is estimated at the boundary (in particular if one of the variance components is very

413 small). The results can be visualised using the `forestplot` function (Figure 4). Plotting is based on

414 `ggplot2` (Wickham, 2016), and multiple forest plots can easily be assembled using the `patchwork`

415 package (Pedersen, 2020). Forest plots show the effect sizes graphically and can be set to either

416 show part R^2 when `type = "R2"` (the default), inclusive R^2 when `type = "IR2"`, structure

417 coefficients when `type = "SC"`, and beta weights (standardized model estimates) with `type =`

418 `"BW"`.

419

```
420  p1 <- forestplot(res, type = "R2")

421  p2 <- forestplot(res, type = "IR2")

422  p3 <- forestplot(res, type = "SC")

423  p4 <- forestplot(res, type = "BW")

424

425  library(patchwork)

426  (p1 + p2) / (p3 + p4) + plot_annotation(tag_levels = "A",

427       tag_prefix = "(", tag_suffix = ")")
```

428

429

430 **Figure 4:** Comparison of part R^2 for individual predictors (A), inclusive R^2 (B), structure coefficients
431 (C) and beta weights (D) for an example dataset with proportion data from grasshoppers.

432   A comparison of part R^2, inclusive R^2, structure coefficients beta weights shows the different insights

433   that can be gained from these different summaries of the model fit (Figure 3). In this case, three of

434   the Bioclim variables (*Bio14*, *Bio17*, *Bio19*) are highly positively correlated (r ≥ 0.93), while a fourth

435   one (*Bio7*) is moderately negatively correlated to all three of them (r ≤ -0.63). Part R^2 are thus low,

436   because none of the parameters uniquely explains a large share of the variance. *Bio17* seems to be

437   the best predictor of morph ratios, with the largest (negative) beta weight, largest part R^2, largest

438   structure coefficients and largest inclusive R^2. Beta weights for the two positively correlated (but

439   slightly weaker) predictors, *Bio14* and *Bio19*, switch sign as is not unusual for collinear predictors.

440   This means that after accounting for the effect of *Bio17*, they contribute positively to prediction.

441   However, structure coefficients show that both variables load negatively on the linear predictor, as

442   does *Bio17*.

443

444   **Challenges**

445   Using transformation or functions in the formula argument can lead to issues with matching the terms

446   of the model with the `partvars` argument of `partR2`. It is therefore important that the names in

447   `partvars` match exactly the terms in the `merMod` object. However, any complications are easily

448   circumvented by implementing the transformations before fitting the model and storing them in the

449   data frame used in the analysis. It is also worth to be aware that unusual names may cause

450   complications and renaming can offer an easy solution.

451   We have repeatedly seen model outputs where the point estimate does not fall within the confidence

452   interval. This might seem like in the bug in the package, but in our experience usually indicates issues

453   with the data and/or the model. In fact, parametric bootstrapping can be seen as a limited form of

454   posterior predictive model checks (Gelman & Hill, 2006). If generating new data from the fitted

455   model (as done with parametric bootstrapping) results in data that are dissimilar to the original data,

456   then the model is probably not a good fit to the data.

457   Bootstrap iterations can sometimes yield slightly negative estimates of part R^2, in particular if the

458   variance explained by a predictor is low. These negative estimates happen in mixed-effects models,

459   because estimates of random-effect variance might change when a predictor is removed and this

460   can lead to a slight decrease in the residual variance, and hence a proportional increase in R^2 (see

461   also Rights & Sterba, 2019). By default, partR2 sets negative R^2 values to 0, but this can be changed

462   by setting `allow_neg_r2` to `TRUE`. It also happens that inclusive R^2 is estimated slightly lower than

463   part R^2 when the contribution of a particular predictor is very large. We consider both cases as

464 sampling error that should serve as a reminder that variance components are estimated with

465 relatively large uncertainly and minor differences should not be over-interpreted.

466 A warning needs to be added for the estimation of R^2 (and, in fact, also repeatability R) from small

467 datasets. In particular if the number of levels of random effect is low, variance components might be

468 slightly overestimated (Xu, 2003). This issue applies similarly to the variance explained by fixed

469 effects, in particular if the number of predictors is large relative to the number of data points.

470

471 **Code and data availability**

472 The current stable version of `partR2` can be downloaded from CRAN (https://cran.r-

473 project.org/web/packages/partR2/index.html) and the development version can be obtained from

474 GitHub (https://github.com/mastoffel/partR2). The data used in the examples is part of the package.

475

476

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479

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