partR2: Partitioning R^2 in generalized linear mixed models

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Abstract

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

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

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

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

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

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

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

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

and monitors the change in R^2 as a measure of the amount of variance explained uniquely by a

particular predictor or a set of predictors. `partR2` also estimates structure coefficients as the

correlation between a predictor and fitted values, which provide an estimate of the total contribution

of a fixed effect to the overall prediction, independent of other predictors. Structure coefficients are

converted to the total variance explained by a predictor, termed 'inclusive' R^2, as the square of the

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

regression coefficients). Finally, `partR2` implements parametric bootstrapping to quantify

confidence intervals for each estimate. We illustrate the use of `partR2` with real example datasets

for Gaussian and binomials GLMMs and discuss interactions, which pose a specific challenge for

partitioning the explained variance among predictors.

Introduction

Introduction

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

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

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

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

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

2018). The total coefficient of determination quantifies the variance explained by all fixed effects

together (marginal R^2 *sensu* Nakagawa & Schielzeth (2013), also known as the total correlation

coefficient, Watanabe (1960)).

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

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

uniquely explained by individual predictors (Jaeger et al., 2017) or sets of predictors (Figure 1). The

set of all predictors in the model yields the total proportion of variance explained by the fixed part

of the model (total R^2). With correlations among predictors, it often happens that predictors in

univariate regressions explain a large share of the variance, but do not show large part R^2 if other

correlated predictors are included in the model.

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

variance (Nimon et al., 2008). Structure coefficients quantify the correlation between individual

predictors and the linear predictor ($\eta = \mathbf{X}\boldsymbol{\beta}$, where $\mathbf{X}$ is the design matrix for fixed effects and $\boldsymbol{\beta}$

is a vector of regression coefficients). Predictors that correlate well with a response, but are fitted

with collinear predictors may show large structure coefficients as they are correlated to the predicted

response, but low part R^2 as other predictors explain part of the same variance. Structure coefficients

range from -1 to 1 with their absolute value expressing the correlation relative to a perfect correlation

if a single predictor explains as much as the total fixed part of the model.

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

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

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

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

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

'total' marginal R^2 of the model). As far as we are aware, inclusive R^2 has not been implemented

before, but it provides valuable insights into the structure of the variance explained (Figure 1).

Figure 1: Conceptual framework for the estimation of proportions of variance components in a mixed
model. The large grey circle symbolizes the variance in a response Y, the dark grey area on the top indicates
the share explained by random effects and the coloured ellipses symbolize variance in covariates with
intersections indicating jointly explained variances. `partR2` calculates total R^2, part R^2 for individual predictors
and sets of predictors as well as inclusive R^2. The package does not report partial R^2 and commonalities,
although they could be calculated from the `partR2` output.

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

coefficients and beta weights from mixed-effects models. The analysis is similar to, but not identical,

to commonality analysis (Ray-Mukherjee et al., 2014; Seibold & McPhee, 1979; Zientek & Thompson,

2006, Figure 1). We illustrate how to use `partR2` with real example datasets for Gaussian and

binomial GLMMs, discuss how to estimate part R^2 in the presence of interactions and discuss some

challenges and limitations.

Other implementations in R packages

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

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

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

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

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

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

explained by the other predictors (Yeatts et al., 2017, Figure 1). The package `yhat` features a suite

of functions for full communality analyses in glms (Nimon, Oswald & Roberts, 2020). None of these

packages estimates part R^2 for mixed-effects models that we focus on here.

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

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

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

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

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

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

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

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

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

Features of `partR2`

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

package `lme4` (Bates et al., 2015) and estimates part R^2 by iterative removal of fixed effects (Nimon

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

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

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

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

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

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

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

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

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

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

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

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

for the final analysis.

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

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

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

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

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

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

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

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

Example with Gaussian data

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

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

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

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

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

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

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

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

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

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

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

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

function.

```
library(partR2)
```

159   ```
data(GuineaPigs)
```

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

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

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

164   output.

165
166   ```
GuineaPigs <- subset(GuineaPigs,
```

```
167                    !is.na(Testo) & !is.na(Rank) & (Time %in% c(1,3,5)))
168    GuineaPigs$TestoTrans <- log(GuineaPigs$Testo)
169    GuineaPigs$Time <- factor(GuineaPigs$Time)
170
```

171 We then fit a linear mixed effects model using `lmer` from the `lme4` package (Bates et al., 2015).
172 Further exploration of the data and model checks are omitted here for simplicity, but are advisable
173 in real data analysis.
174

```
175    library(lme4)
176    mod <- lmer(TestoTrans ~ Rank * Time + (1|MaleID), data=GuineaPigs)
177
```

178 The `partR2` analysis takes the `lmer` model fit (an `merMod` object) and a character vector `partvars`
179 indicating the fixed effects to be evaluated. Interactions are specified with the colon syntax (see the
180 package's vignette for further details).
181

```
182    res <- partR2(mod, partvars = c("Rank", "Time", "Rank:Time"),
183        data=GuineaPigs, nboot=100)
184
```

185 The function returns a `partR2` object. The `print` function reports the part coefficients of
186 determination and a more extensive summary can be viewed with the `summary` function which also
187 shows inclusive R^2, structure coefficients and beta weights (standardized slopes) (Figure 2).
188

```
189    print(res)
190    summary(res, round_to = 2)
```

```
R2 (marginal) and 95% CI for the full model:
 R2   CI_lower CI_upper nboot ndf
 0.17 0.1      0.31     100   6

----------

Part (semi-partial) R2:
 Predictor(s)        R2   CI_lower CI_upper nboot ndf
 Model               0.17 0.10     0.31     100   6
 Rank                0.00 0.00     0.14     100   6
 Time                0.02 0.00     0.16     100   4
 Rank:Time           0.03 0.00     0.17     100   4
 Rank+Time           0.02 0.00     0.16     100   4
 Rank+Rank:Time      0.15 0.08     0.29     100   3
 Time+Rank:Time      0.04 0.00     0.17     100   2
 Rank+Time+Rank:Time 0.17 0.10     0.31     100   1

----------

Inclusive R2 (SC^2 * R2):
 Predictor  IR2  CI_lower CI_upper
 Rank       0.13 0.06     0.22
 Time3      0.00 0.00     0.04
 Time5      0.00 0.00     0.05
 Rank:Time3 0.05 0.01     0.14
 Rank:Time5 0.01 0.00     0.07

----------

Structure coefficients r(Yhat,x):
 Predictor  SC   CI_lower CI_upper
 Rank       0.87  0.61    0.97
 Time3      0.14 -0.20    0.46
 Time5      0.16 -0.13    0.55
 Rank:Time3 0.56  0.21    0.78
 Rank:Time5 0.28 -0.03    0.64

----------

Beta weights (standardised estimates)
 Predictor  BW    CI_lower CI_upper
 Rank        0.50  0.08    0.98
 Time3      -0.19 -0.55    0.17
 Time5       0.17 -0.14    0.55
 Rank:Time3  0.17 -0.48    0.75
 Rank:Time5 -0.36 -1.00    0.24

----------

Parametric bootstrapping resulted in warnings or messages:
Check r2obj$boot_warnings and r2obj$boot_messages.
```

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

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

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

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

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

Dealing with interactions

200 Models with interaction are problematic, because the variance explained by a main factor can be

201 estimated in multiple ways (Figure 3) and because of internal parametrization of the model matrix.

(A) Main effect and interaction alone

Generic syntax

```
mod <- lmer(Y ~ X1 * X2 + (1|RE),
            data)
partR2(mod, partvars = c('X1',
       'X2', 'X1:X2'), data)
```

Components estimated

X_1

X_2

$X_1 : X_2$

(B) Main effects with their interaction

Generic syntax

```
mod <- lmer(Y ~ X1 * X2 + (1|RE),
            data)
partR2(mod, partbatch =
       list(X1 = c('X1', 'X1:X2'),
       X2 = c('X2', 'X1:X2')),
       data)
```

Components estimated

X_1

X_2

(C) Main effect priority

Generic syntax

```
mod1  <- lmer(Y ~ X1 * X2 + (1|RE),
            data)
part1 <- partR2(mod, partvars =
            c('X1:X2'), data)
mod2  <- lmer(Y ~ X1 + X2 + (1|RE),
            data)
part2 <- partR2(mod2, partvars =
            c('X1','X2'), data)
mergeR2(part1, part2)
```

Components estimated

X_1

X_2

$X_1 : X_2$

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.

The model output above shows the number of parameters fitted in each model (Figure 2, each row in the R2 part refers to a reduced model). In the `print` and `summary` output this is visible as a column labelled 'ndf'. A close inspection shows that the removal of rank did not change the number of parameters (6 for the full model, 6 for the model excluding rank). This is because the model matrix is reparametrized in the reduced model and `lmer` will fit three terms for the interaction (here `Time1:Rank`, `Time3:Rank`, `Time5:Rank`) rather than just two for the interaction in the full model. Dummy coding of the factor can be usefully combined with centering of dummy coded variables

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

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

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

218
219
```
GuineaPigs <- cbind(GuineaPigs, model.matrix(~ 0 + Time,
220      data=GuineaPigs))
221 GuineaPigs$Time3 <- GuineaPigs$Time3 - mean(GuineaPigs$Time3)
222 GuineaPigs$Time5 <- GuineaPigs$Time5 - mean(GuineaPigs$Time5)
223
```

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

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

226 such a run can take a long time, while we are mostly interested in fitting and removing all dummy

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

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

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

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

231 well as *Rank* and their combinations.

232
233
```
mod <- lmer(TestoTrans ~ (Time3 + Time5) * Rank + (1|MaleID),
234      data=GuineaPigs)
235 batch <- c("Time3", "Time5")
236 partR2(mod, partvars=c("Rank"), partbatch=list(Time=batch,
237      `Time:Rank`= paste0(batch, ":Rank")), data=GuineaPigs,
238      nboot=100)
239
```

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

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

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

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

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

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

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

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

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

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

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

251
252
```
mod <- lmer(Testo ~ Time * Rank + (1|MaleID), data=GuineaPigs)
```

253
```
      partR2(mod, partbatch = list(Time=c("Time", "Time:Rank"),
```

254
```
      Rank=c("Rank", "Time:Rank")), data=GuineaPigs, nboot=100)
```

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

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

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

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

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

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

262
263
```
mod1 <- lmer(Testo ~ Time * Rank + (1|MaleID), data=GuineaPigs)
```

264
```
part1 <- partR2(mod1, partvars = c("Time:Rank"), data=GuineaPigs,
```

265
```
    nboot=100)
```

266
```
mod2 <- lmer(Testo ~ Time + Rank + (1|MaleID), data=GuineaPigs)
```

267
```
part2 <- partR2(mod2, partvars = c("Time", "Rank"), data=GuineaPigs,
```

268
```
    nboot=100)
```

269
```
mergeR2(part1, part2)
```

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

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

274   **An example with proportion data**

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

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

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

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

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

280 various aspects of ecologically relevant climatic conditions (see Karger *et al*. 2017). The aim is to

281 identify the climatic conditions that favour one or the other colour variant.

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

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

284 to account for overdispersion (Harrison, 2014).

286 `data(Grasshoppers)`

287 `for (i in which(substr(colnames(Grasshoppers),1,3)=="Bio")){`

288 `        Grasshoppers[,i] <- scale(Grasshoppers[,i])`

289 `}`

290 `Grasshoppers$OLRE <- 1:nrow(Grasshoppers)`

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

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

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

295 2018). For illustration, we use the four Bioclim variables that show a loading of more than 0.30 on

296 the first principle component.

298 `mod <- glmer(cbind(nGreen, nBrown) ~ Bio7 + Bio14 + Bio17 + Bio19 +`

299 `        (1|SiteID) + (1|OLRE), data=Grasshoppers, family="binomial")`

300 `res <- partR2(mod, partvars=c("Bio7", "Bio14", "Bio17", "Bio19"),`

301 `        data=Grasshoppers, max_level = 1, nboot=100)`

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

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

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

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

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

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

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

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

311 `"BW"`.

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

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

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

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

317

318   library(patchwork)

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

320   "(", tag_suffix = ")")

321
```

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

A comparison of part R^2, inclusive R^2, structure coefficients beta weights shows the different insights that can be gained from these different summaries of the model fit (Figure 3). In this case, three of the Bioclim variables (*Bio14*, *Bio17*, *Bio19*) are highly positively correlated (r ≥ 0.93), while a fourth one (*Bio7*) is moderately negatively correlated to all three of them (r ≤ -0.63). Part R^2 are thus low, because none of the parameters uniquely explains a large share of the variance. *Bio17* seems to be the best predictor of morph ratios, with the largest (negative) beta weight, largest part R^2, largest structure coefficients and largest inclusive R^2. Beta weights for the two positively correlated (but slightly weaker) predictors, *Bio14* and *Bio19*, switch sign as is not unusual for collinear predictors.

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

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

336   does *Bio17*.

Challenges

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

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

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

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

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

344   complications and renaming can offer an easy solution.

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

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

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

348   posterior predictive model checks (Gelman & Hill, 2007). If generating new data from the fitted

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Code and data availability

The development version of `partR2` can be obtained from GitHub (https://github.com/mastoffel/partR2) and includes the data used in the examples. The package will be uploaded to CRAN after peer-review.

Author contributions

SN and HS conceived the idea. HS and MAS wrote the manuscript with contributions from SN. MAS wrote the package and the vignette, supervised by HS. All authors contributed critically to the manuscript, package and vignette and gave final approval for publication.

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References

Aho K. 2020.asbio: A Collection of Statistical Tools for Biologists. *Available at https://CRAN.R-project.org/package=asbio* (accessed July 25, 2020).

Bartoń K. 2019.MuMIn: Multi-Model Inference. *Available at https://CRAN.R-project.org/package=MuMIn* (accessed July 25, 2020).

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

Bengtsson H. 2020.future: Unified Parallel and Distributed Processing in R for Everyone. *Available at https://CRAN.R-project.org/package=future* (accessed July 25, 2020).

Dieker P, Beckmann L, Teckentrup J, Schielzeth H. 2018. Spatial analyses of two colour polymorphisms in an alpine grasshopper reveal a role of small-scale heterogeneity. *Ecology and Evolution* 8:7273–7284. DOI: 10.1002/ece3.4156.

392   Edwards LJ, Muller KE, Wolfinger RD, Qaqish BF, Schabenberger O. 2008. An R2 statistic for fixed

393   effects in the linear mixed model. *Statistics in Medicine* 27:6137–6157. DOI:

394   10.1002/Sim.3429.

395   Faraway JJ. 2015. *Linear models with R*. Boca Raton: CRC Press, Taylor & Francis Group.

396   Gelman A, Hill J. 2007. *Data analysis using regression and multilevel/hierarchical models*.

397   Cambridge; New York: Cambridge University Press.

398   Harrison XA. 2014. Using observation-level random effects to model overdispersion in count data

399   in ecology and evolution. *PeerJ* 2:e616. DOI: 10.7717/peerj.616.

400   Ives A, Li D. 2018. rr2: An R package to calculate R2s for regression models. *Journal of Open*

401   *Source Software* 3:1028.

402   Jaeger B. 2017.r2glmm: Computes R Squared for Mixed (Multilevel) Models. *Available at*

403   *https://CRAN.R-project.org/package=r2glmm* (accessed July 25, 2020).

404   Jaeger BC, Edwards LJ, Das K, Sen PK. 2017. An R2 statistic for fixed effects in the generalized

405   linear mixed model. *Journal of Applied Statistics* 44:1086–1105. DOI:

406   10.1080/02664763.2016.1193725.

407   Johnson PE, Grothendieck G. 2019.rockchalk: Regression Estimation and Presentation. *Available at*

408   *https://CRAN.R-project.org/package=rockchalk* (accessed July 25, 2020).

409   Lüdecke D, Makowski D, Waggoner P, Patil I. 2020.performance: Assessment of Regression

410   Models Performance. *Available at https://CRAN.R-project.org/package=performance*

411   (accessed July 25, 2020).

412   Mutwill AM, Schielzeth H, Zimmermann TD, Richter H, Kaiser S, Sachser N. in prep. Endocrine

413   mechanisms underlying dominance rank acquisition in males: individuality meets plasticity

414   in a complex social environment.

415   Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized

416   linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142. DOI:

417   10.1111/j.2041-210x.2012.00261.x.

418   Nimon K, Lewis M, Kane R, Haynes RM. 2008. An R package to compute commonality coefficients

419   in the multiple regression case: an introduction to the package and a practical example.

420   *Behavior Research Methods* 40:457–66. DOI: 10.3758/brm.40.2.457.

421   Nimon K, Oswald F, Roberts JK. 2020.yhat: Interpreting Regression Effects. *Available at*

422   *https://CRAN.R-project.org/package=yhat* (accessed July 25, 2020).

423   Pedersen TL. 2020.patchwork: The Composer of Plots. *Available at https://CRAN.R-*

424   *project.org/package=patchwork* (accessed July 25, 2020).

425   R Core Team. 2019. *R: A language and environment for statistical computing. R Foundation for*

426   *Statistical Computing*. Vienna, Austria.

427   Ray-Mukherjee J, Nimon K, Mukherjee S, Morris DW, Slotow R, Hamer M. 2014. Using commonality

428   analysis in multiple regressions: a tool to decompose regression effects in the face of

429   multicollinearity. *Methods in Ecology and Evolution* 5:320–328. DOI: Doi 10.1111/2041-

430   210x.12166.

431   Rights JD, Sterba SK. 2019. New recommendations on the Use of R-squared differences in

432   multilevel model comparisons. *Multivariate Behavioral Research*:1–32. DOI:

433   10.1080/00273171.2019.1660605.

434   Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients.

435   *Methods in Ecology and Evolution* 1:103–113. DOI: 10.1111/j.2041-210X.2010.00012.x.

436   Seibold DR, McPhee RD. 1979. Commonality analysis: a method for decomposing explained

437   variance in multiple regression analyses. *Human Communication Research* 5:355–365.

438   Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance

439   decomposition by generalized linear mixed-effects models. *Methods in Ecology and*

440   *Evolution* 8:1639–1644. DOI: 10.1111/2041-210X.12797.

441   Vaughan D, Dancho M. 2018.furrr: Apply Mapping Functions in Parallel using Futures. *Available at*

442   *https://CRAN.R-project.org/package=furrr* (accessed July 25, 2020).

443   de Villemereuil P, Morrissey M, Nakagawa S, Schielzeth H. 2018. Fixed effect variance and the

444   estimation of repeatabilities and heritabilities: Issues and solutions. *Journal of Evolutionary*

445   *Biology* 31:621–632. DOI: 10.1111/jeb.13232.

446   Watanabe S. 1960. Information theoretical analysis of multivariate correlation. *IBM Journal of*

447   *Research and Development* 4:66–82. DOI: DOI 10.1147/rd.41.0066.

448   Xu RH. 2003. Measuring explained variation in linear mixed effects models. *Statistics in Medicine*

449   22:3527–3541. DOI: Doi 10.1002/Sim.1572.

450   Yeatts PE, Barton M, Henson RK, Martin SB. 2017. The use of structure coefficients to address

451   multicollinearity in sport and exercise science. *Measurement in Physical Education and*

452   *Exercise Science* 21:83–91.

453   Zhang D. 2020.rsq: R-Squared and Related Measures. *Available at https://CRAN.R-*

454   *project.org/package=rsq* (accessed July 25, 2020).

455   Zientek LR, Thompson B. 2006. Commonality analysis: Partitioning variance to facilitate better

456   understanding of data. *Journal of Early Intervention* 28:299–307.

457