1 rdacca.hp: an R package for generalizing hierarchical and variation

2 partitioning in multiple regression and canonical analysis

- 3 Running title: hierarchical partitioning in canonical analysis
- 4 Jiangshan Lai^{1,2*}, Yi Zou³, Jinlong Zhang⁴, Pedro Peres-Neto⁵
- 5 ¹ State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese
- 6 Academy of Sciences, Beijing, 100093, P.R. China
- 7 ² University of Chinese Academy of Sciences, Beijing, 100049, P.R. China
- 8 ³ Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou,
- 9 215123, P.R. China
- ⁴ Flora Conservation Department, Kadoorie Farm and Botanic Garden, Lam Kam Road, Tai Po,
- 11 New Territories, Hong Kong SAR, China
- 12 ⁵ Department of Biology and Canada Research Chair in Biodiversity and Spatial Ecology,
- 13 Concordia University, Montreal, Quebec, Canada
- 14 ^{*}Correspondence:
- 15 Jiangshan Lai (<u>lai@ibcas.ac.cn</u>)
- 16

17 Summary

18	1. Canonical analysis, a generalization of multiple regression to multiple response variables, is
19	widely used in ecology. Because these models often involve large amounts of parameters (one
20	slope per response per predictor), they pose challenges to model interpretation. Currently, multi-
21	response canonical analysis is constrained by two major challenges. Firstly, we lack quantitative
22	frameworks for estimating the overall importance of single predictors. Secondly, although the
23	commonly used variation partitioning framework to estimate the importance of groups of multiple
24	predictors can be used to estimate the importance of single predictors, it is currently
25	computationally constrained to a maximum of four predictor matrices.
26	2. We established that commonality analysis and hierarchical partitioning, widely used for both
27	estimating predictor importance and improving the interpretation of single-response regression
28	models, are related and complementary frameworks that can be expanded for the analysis of
29	multiple-response models.
30	3. In this application, we aim at: a) demonstrating the mathematical links between commonality
31	analysis, variation and hierarchical partitioning; b) generalizing these frameworks to allow the
32	analysis of any number of responses, predictor variables or groups of predictor variables in the
33	case of variation partitioning; and c) introducing and demonstrating the usage of the R package
34	rdacca.hp that implements these generalized frameworks.
35	Key-words: averaging over orderings, CCA, commonality analysis, constrained ordination,
20	and in densities the DDA and the investment

36 explained variation, db-RDA, RDA, relative importance

37 Introduction

38	Canonical analysis (also called "constrained ordination") considering multiple response
39	variables (e.g., species) and multiple predictors (e.g., environmental features, spatial predictors)
40	are widely used as inferential frameworks to determine and contrast the importance of multiple
41	drivers (e.g., environmental conditions, traits) underlying the structure of ecological communities.
42	Redundancy analysis (RDA; Rao 1964), canonical correspondence analysis (CCA; ter Braak
43	1986), and distance-based redundancy analysis (db-RDA; Legendre & Anderson 1999) are the
44	most commonly used ones (Legendre & Legendre 2012). One central challenge in canonical
45	analyses is the estimation of predictor contribution given that the number of regression parameters
46	increase as a function of the number of response variables. For instance, if 200 response variables
47	and 20 predictors are considered, one ends up with 4000 regression slopes.
48	Because canonical analyses are extensions of multiple regression models to multiple response
49	variables (Peres-Neto et al. 2006), we can adapt the existing machinery of multiple regression
50	models to tackle this challenge. The approach we develop here is based on generalizing
51	commonality analysis, a single-response regression framework, to canonical analysis (i.e., multi-
52	response variables). Commonality analysis is often used in psychology and education (Newton &
53	Spurell 1967; Nimon & Reio 2011; see Ray-Mukherjee et al. 2014 for a rare application in
54	ecology) to estimate the relative predictor contributions to the total model's coefficient of
55	determination (R^2). Commonality analysis decomposes the total models' R^2 into unique fractions
56	attributable to individual predictor and the shared fractions among predictors (covariation in the
57	predictive space which can also identify multicollinearity issues). These fractions are semi-partial
58	R^2 s (Peres-Neto <i>et al.</i> 2006) and allow circumventing well-known issues underlying variable

59	importance and model interpretation based solely on standardized partial slopes (see Ray-
60	Mukherjee et al. 2014 for a review of the issues). This is an interesting property because
61	canonical analyses produce estimates of total models' R^2 and semi-partial R^2 s that are unbiased
62	(Peres-Neto et al. 2006).
63	Although commonality analysis is applied to single-response regression models, ecologists
64	are widely familiar with the parallel framework of variation partitioning applied to canonical, with
65	thousands of studies published using it (Borcard, Legendre & Drapeau 1992; Peres-Neto et al.
66	2006; see Fig. 1). Variation partitioning is employed by grouping predictors together into matrices
67	and estimating the unique and shared semi-partial R^2 s of each matrix compounded across all
68	response variables (Peres-Neto et al. 2006). Indeed, the algebra involved in commonality analysis
69	and variation partitioning are equivalent even though they are often used in different situations.
70	Notwithstanding, packages conducting commonality analysis are restrained to single response
71	variables, e.g., R package yhat (Nimon, Oswald & Roberts 2013); and packages conducting
72	variation partitioning (i.e., multi-response), such as the widely used R package vegan (Oksanen
73	et al. 2006), are restrained to a maximum of four predictor matrices. These constraints are either
74	implementational or computational. In particular, variation partitioning has not been generalized to
75	multiple predictor matrices (but see Økland 2003) and commonality analysis has not been
76	generalized to multi-response models.
77	Beyond variation partitioning, estimating the relative importance of predictor in multiple
78	regression (e.g., multicollinearity being an extreme case) is an old and very active research (see
79	the reviews in Bi 2012; Nathans, Oswald & Nimon 2012; Grömping 2015). Among them, the
80	"averaging over orderings" approach proposed independently by Lindeman, Merenda & Gold

81	(1980), Cox (1985) and Kruskal (1987) in the 1980s has been considered as a breakthrough (Bi
82	2012). These methods are generally referred as to the LMG metric and are based on all model
83	subsets, and are also equal to methods described independently such as hierarchical partitioning
84	(Chevan & Sutherland 1991) and dominance analysis (Budescu 1993). Because the calculations
85	described in these papers are overly complicated, one is led to think that they differ. In the next
86	section, we simplify the presentation of "averaging over orderings" so that others can take full
87	advantage of its simplicity while describing model complexity. Our computational presentation
88	also makes a clear link between commonality analysis, and variation and hierarchical partitioning.
89	Because we were particularly inspired by the very popular paper by Chevan & Sutherland (1991),
90	we used the term "hierarchical partitioning" (HP) to relate to these equivalent methods. HP
91	produces all possible combinations of predictors to determine the order in which a predictor
92	dominates over the others (hence the name dominance analysis used by Badescu 1993) across all
93	subset models, and it has been widely used and recommended to access the relative importance of
94	predictors in multiple regression (Soofi 1992; Mac Nally & Walsh 2004; Walsh et al. 2004;
95	Grömping 2006; 2007; 2009; 2015). Corresponding R packages are relaimpo for LMG
96	(Grömping 2006), hier.part for HP (Walsh & Mac Nally 2013) and dominanceanalysis
97	(Navarrete & Soares 2020). We show that analytical results from these packages are identical for
98	multiple regression (see Appendix S1). However, unlike variation partitioning, HP is not
99	currently available for multi-response models (i.e., canonical analysis) and is implemented in
100	our package: rdacca.hp. By doing so, we also extend HP to consider matrices of predictors
101	in variation partitioning.

102 The overall goal of this application paper is to unify commonality analysis, variation and

100	1 1 1 1	1	1 1 6 1 1 1
103	hierarchical partitioning	generalizing them to unlimited	l number of responses and predictor
100	moruronnour purtitioning	, generalizing them to annihited	indiffeet of responses and predictor

- 104 variables (or matrices of predictors as in variation partitioning). These analyses are implemented
- 105 in our package rdacca.hp which is presented and illustrated in the next sections.
- 106 Unifying commonality analysis, and variation and hierarchical partitioning
- 107 Assuming a multi-response matrix Y and three correlated predictors (Fig. 1). The fractions
- 108 of variation [a], [b] and [c] correspond to the variation in Y that are uniquely explained by
- 109 predictors X_1 , X_2 , X_3 , respectively (i.e., unique semi-partial R^2). Fractions [d], [e], [f] are the
- shared semi-partial R^2 s by combinations of their two respective predictors accounting for the third,
- 111 Fraction [g] is the shared semi-partial R^2 among all predictors, and [h] is the fraction
- 112 corresponding to residuals. All fractions summed totalize 100%. Shared fractions are the variation
- in the response data that is explained by the correlation of the predictors involved. The larger this
- 114 fraction is, the more multicollinearity is present in the model. While model selection reduces the
- shared variation among predictors (collinearity), it also reduces our ability to improve model
- 116 interpretability. The calculations involved in variation partitioning are well described elsewhere
- 117 (e.g., Peres-Neto et al. 2006) and our package: rdacca.hp generalizes it for any number of
- 118 predictors (or matrices of predictors).

119 Individual predictor contribution in HP (also called "independent contribution") can be

- 120 simply estimated as its unique contribution to the total model R^2 plus its average shared
- 121 contributions with the other predictors, simplifying its presentation dramatically. The independent
- 122 contribution across all possible models derived from combinations of predictors can be derived
- 123 directly from variation partitioning (Fig. 1). For example, the independent contribution of X₁
- 124 (I_{X_1}) can be calculated by its unique contribution [a] and its respective shared contributions by

125 the number of predictors involved in each of:

126
$$I_{X_1} = a + \frac{d}{2} + \frac{f}{2} + \frac{g}{3} \tag{1}$$

127 For completion, the contributions of X₂ and X₃ are calculated as follows:

128
$$I_{X_2} = b + \frac{d}{2} + \frac{e}{2} + \frac{g}{3}$$
(2)

129
$$I_{X_3} = c + \frac{f}{2} + \frac{e}{2} + \frac{g}{3}$$
(3)

130 and:

131
$$I_{X_1} + I_{X_2} + I_{X_3} = R_{Total}^2$$
 (4)

132 Generalizing, the independent contribution of any predictor $i(I_{X_i})$ can be computed as:

133
$$I_{X_i} = \sum_{k=1}^{n} \sum_{j=1}^{m} \frac{R_{SX_{ik,j}}^2}{k}$$
(5)

where *n* is the number of predictors, $R_{SX_{ik,i}}^2$ is semi-partial R² of the *j*th fraction shared between X_i 134 135 and the other k predictors, and m is the number of combinations that X_i shared with other k predictors, with $m = \binom{k-1}{n-1}$. Note that as the number of predictor increases, the number of 136 fractions including shared and unique R^2 s increases exponentially (2^N-1 fractions). The above 137 138 computation only uses individual predictors to illustrate the process. It is also applicable to 139 matrices of predictors as in routine ecological applications applying variation partitioning. In general, we find variation partitioning should be the starting point prior to hierarchical 140 141 partitioning. While the former emphasizes unique and common variation among predictors, the 142 latter emphasizes the overall importance of each predictor (or group of predictors). Our package rdacca.hp synchronously implements variation and hierarchical partitioning for single- and 143 144 multiple-response models without limits in the number of predictors / matrices of predictors 145 Package description

146 The rdacca.hp package is written in R (R Development Core Team 2019) and can be

147 installed from CRAN (<u>http://cran.r-project.org/web/packages/rdacca.hp/</u>) or Github

148	(https://github.com/laijiangshan/rdacca.hp). The package contains one key homonymous function:
149	rdacca.hp that conducts both variation and hierarchical partitioning in single- and multiple-
150	response multiple regression (canonical analysis). The internal function: Canonical.Rsq,
151	calculates R^2 and adjusted R^2 (hereafter R ² adj) of RDA, db-RDA and CCA, which are called by
152	rdacca.hp. For canonical analysis, the R^2adj is used given that the contribution of null
153	predictors can differ quite a lot from zero due to sampling variation related to large number of
154	predictors and small number of observations (Peres-Neto et al. 2006). The R ² adj is calculated
155	using Ezekiel's formula (Ezekiel 1930) for RDA and db-RDA, while permutation procedure be
156	used for CCA (Peres-Neto et al. 2006). The interpretation of arguments and some key notes in
157	function rdacca.hp are described briefly here.
158	rdacca.hp(dv, iv, method, type, n.perm, trace, plot.perc)
159	In this usage, both a variation partitioning and hierarchical partitioning are performed in which the
160	unique, shared (referred as to "common") and independent contributions of each predictor
161	(columns in iv) to the global \mathbb{R}^2 canonical model are computed. In the section below (working
162	examples), we show how the function can conduct the analysis based on blocks of variables as in
163	routine ecological applications of variation partitioning. Response variables (columns in dv) must
164	be numerical, while the predictors (iv) can be either numerical or categorical. method is the type
165	of canonical analysis set as either RDA (default), dbRDA, or CCA. If method="dbRDA", dv
166	should be a distance matrix (i.e., dist class). If dv is imputed as one numerical vector, RDA
167	would be equivalent to the classic (single response) multiple regression (see Appendix S1). An
168	additional advantage of our package in relation to relaimpo, hier.part and

169	dominanceanalysis is that it also decomposes R^2adj for multiple regression, so this package
170	is also useful across many other ecological applications and research fields. \mathtt{type} is the type of
171	total explained variation: "adjR2" is for R ² adj and "R2" for unadjusted R^2 , by default is
172	"adjR2". n.perm is the number of permutations when computing R^2adj for CCA and default is
173	1000 to get a relatively stable value. trace is a logical argument indicating whether the output of
174	variation partitioning should be printed (see the example below). It is set by default as FALSE to
175	save screen space, as this output will increase exponentially with the number of predictors. If
176	focusing on variation partitioning, then trace=TRUE should be set. plot.perc is a logical
177	argument indicating whether a bar plot of the relative independent contribution of predictors is
178	plotted; the default is FALSE. The output of rdacca.hp is explained in the example below.
179	A working example
180	We illustrate the usage of rdacca.hp by using the Doubs River fish data readily available
180 181	We illustrate the usage of rdacca.hp by using the Doubs River fish data readily available in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally
181	in the ade4 package (Thioulouse et al. 2018). The dataset is a subset of the data originally
181 182	in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors
181 182 183	in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see
181 182 183 184	in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see Verneaux <i>et al.</i> 2003). This dataset contains 27 fish species with abundance classes (ranging from
181 182 183 184 185	in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see Verneaux <i>et al.</i> 2003). This dataset contains 27 fish species with abundance classes (ranging from 0 to 5) and 11 quantitative environmental variables describing the river morphology and water
181 182 183 184 185 186	in the ade4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see Verneaux <i>et al.</i> 2003). This dataset contains 27 fish species with abundance classes (ranging from 0 to 5) and 11 quantitative environmental variables describing the river morphology and water quality from 30 sites.
181 182 183 184 185 186 187	in the ade 4 package (Thioulouse <i>et al.</i> 2018). The dataset is a subset of the data originally collected by Verneaux (1973) with the distributions of fish species and environmental factors along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see Verneaux <i>et al.</i> 2003). This dataset contains 27 fish species with abundance classes (ranging from 0 to 5) and 11 quantitative environmental variables describing the river morphology and water quality from 30 sites. We show the results for the variation and hierarchical partitioning of the global R ² adj of

191	presentation convenience) were selected using a stepwise selection based on all environmental
192	predictors using the function ordistep in the vegan package (Oksanen et.al. 2019). Note that
193	the selection of predictors is not a prerequisite of rdacca. hp and, as previously noted earlier,
194	can generate biases and incomplete information in variation and hierarchical partitioning. Our
195	function rdacca.hp does not limit the number of predictors or groups. Note though, that
196	considering all combinations of all variables is important even though computationally
197	demanding. The selected predictors have a relatively strong correlation structure: a relatively high
198	negative correlation (r=-0.84, p <0.001) between oxy and bdo; a relatively weaker positive
199	correlation between <i>alt</i> and <i>oxy</i> (r=0.42, p =0.02), and a negative correlation between <i>alt</i> and <i>bdo</i>
200	(r=-0.38, p =0.04). This is an important point to make (often missed by practitioners) because the
201	correlation structure in the predictor space (simple pairwise correlations between predictors) may
202	not translate necessarily into high shared fractions among predictors (i.e., semi-partial R^2
203	calculated on the basis of the predictive space). As such, contrasting the correlation structure
204	among predictors and their correlation structure in predictive space (i.e., variation and hierarchical
205	partitioning) should serve useful in generating insights underlying the relational nature of
206	predictors and responses.
207	The script below demonstrates the use and outputs of rdacca.hp to decompose the
208	global R^2 adj in RDA. Decomposition of R^2 adj in CCA and db-RDA are similar to RDA and
209	shown in the Appendix S2. The standard output of rdacca.hp is as follows:
210	<pre>#install rdacca.hp from CRAN install reskares(hedaces hel)</pre>
211 212	<pre>install.packages('rdacca.hp') library(rdacca.hp)</pre>
213 214	<i>#sample data in ade4 package</i> reguire(ade4)

214 require(ade4)

```
data(doubs)
215
      #fish species as response variables
216
      spe <- doubs$fish</pre>
217
      #environmental factors as explanatory variables
218
219
      env <- doubs$env
220
      #remove empty site 8 without species
221
      spe <- spe[-8,]</pre>
222
      env <- env[-8,]
      #'dfs' is a variable containing locations rather than environmental
223
      #factor. We also removed it from the 'env' data frame
224
      env <- env[, -1]
225
      #the usual Hellinger-transformation of the species dataset
226
227
      spe.hel <- decostand(spe, "hellinger")</pre>
      #selecting variables via ordistep() in vegan
228
      ordistep(rda(spe.hel~.,env))
229
230
      #three selected variables: alt,oxy and bdo
      rdacca.hp(spe.hel,env[,c("alt","oxy","bdo")], method="RDA", type = "a
231
      djR2",trace = TRUE, plot.perc = FALSE)
232
233
      ## $Method Type
      ## [1] "RDA"
                     "adjR2"
234
235
      ##
236
     ## $R.squared
     ## [1] 0.5402
237
238
     ##
239
     ## $Var.part
                                    Fractions
                                                % Total
240
     ##
241
     ## Unique to alt
                                        0.1942
                                                   35.96
242
     ## Unique to oxy
                                        0.1367
                                                   25.31
     ## Unique to bdo
                                        0.0871
                                                   16.13
243
      ## Common to alt, and oxy
244
                                         0.0467
                                                     8.64
      ## Common to alt, and bdo
                                                    -3.31
245
                                        -0.0179
     ## Common to oxy, and bdo
                                         0.0131
                                                     2.43
246
     ## Common to alt, oxy, and bdo
                                                    14.84
247
                                         0.0801
     ## Total
                                         0.5402
                                                    100.00
248
249
     ##
250
     ## $Hier.part
             Independent I.perc(%)
251
      ##
252
     ## alt
                  0.2354
                             43.58
253
      ## oxy
                  0.1933
                             35.78
254
      ## bdo
                             20.64
                  0.1115
```

255 The function rdacca. hp returns a list containing three bits (if trace=FALSE) or four bits (if

256 trace=TRUE).

- 257 \$Method Type: This bit shows the type of canonical analysis and whether the original or adjusted
- 258 R^2 were used in the analysis. In the example, it is RDA and adjR2.
- 259 \$R.squared: type="adjR2". In this example, the amount of variation of the fish data matrix
- explained by the three predictors (**alt**, **oxy** and **bdo**) is 54.02%.
- 261 \$Var.part: It contains output that lists with R²adj values for all fractions based on variation
- 262 partitioning (commonality analysis) if setting trace=TRUE. In this example, with three
- 263 predictors, commonality analysis decomposes R²adj into all seven fractions (i.e., 2³-1) of unique
- and common effects. Fractions can be either positive or negative (Nimon & Reio 2011, Ray-
- 265 Mukherjee *et al* 2014). In this case, the common effect between *alt* and *bod* is negative (-0.0179).
- 266 Negative common (shared) variation is possible when predictors act as suppressors of other
- 267 predictors (Pedhazur 1997; Nimon & Reio 2011; Ray-Mukherjee *et al* 2014).
- All fractions (except the residual) sum to the total R^2 adj (i.e., the value of \$R.squared).
- 269 \$Hier.part: This bit is a matrix containing the independent contribution of each predictor
- 270 in the "Independent" column, and their percentage in the "I.perc" column. In this case, the
- independent contributions of *alt*, *oxy* and *bdo* are 0.2354, 0.1933 and 0.1115, respectively; note
- again that they sum to the overall R^2 adj (0.5402). One easily know how to calculate the
- 273 independent contribution based the result of variation partitioning. For instance, the value
- (0.1933) for *oxy* is the sum of its unique effect and three average common effects (i.e., 0.1367 +
- $275 \quad 0.0467/2 + 0.0131/2 + 0.0801/3$). rdacca.hp also produces a bar graph based on the ggplot2
- 276 package (Wickham 2016) (Fig. 2). Users are encouraged to use other graph functions to generate
- 277 other types of plots based on the numerical output of rdacca.hp.

278 The following code shows how to apply rdacca.hp to conduct a variation partitioning and 279 hierarchical partitioning to two sets of matrices containing environmental variables describing 280 river morphology and water quality. Note rdacca.hp has no limit for the number of sets of 281 predictor matrices and an example with five predictor groups is provided in the Appendix S3. 282 rdacca.hp does not include the traditional representation of variation partitioning as a Venn diagram, which becomes impossible for more than four predictors. 283 284 rdacca.hp(spe.hel,list(envtopo=env[,1:3],envchem=env[,4:10]), method ="RDA", type = "adjR2", trace = TRUE, plot.perc = TRUE) 285 286 ## \$Method_Type ## [1] "RDA" "adjR2" 287 288 ## 289 ## \$R.squared 290 ## [1] 0.5558 291 ## 292 ## \$Var.part 293 Fractions % Total ## 294 ## Unique to envtopo 0.0814 14.64 295 ## Unique to envchem 0.2290 41.21 ## Common to envtopo, and envchem 44.15 296 0.2454 297 ## Total 0.5558 100.00 298 ## 299 ## \$Hier.part 300 Independent I.perc(%) ## 301 ## envtopo 0.2041 36.72 302 ## envchem 0.3517 63.28

303 Discussion

304 Multivariate regressions and canonical analysis are quintessential quantitative frameworks to

305 tackle many ecological and evolutionary problems. Variation partitioning and hierarchical

306 partitioning (HP) are frameworks that allow going beyond the usual and standard interpretation of

307 partial slopes (see Ray-Mukherjee et al. 2014 for a review). That said, our presentation of HP

308 allows realizing that both methods are interrelated, and that variation partitioning can serve as a

309	precursor of HP. While variation partitioning estimates unique and common variation in a single
310	full model containing all variables, HP is based on principles of all subset regression and model
311	averaging which are known to improve model inference and interpretability over traditional model
312	selection procedures (Burnham & Anderson 2002). The two main motivations for using variation
313	partitioning and HP over traditional model selection procedures are that: a) candidate predictors
314	are conditional on the variance explained by the models already retained by the selection
315	procedure (Thompson 1995; Nathans, Oswald & Nimon 2012). As such, a predictor that can be
316	quite relevant in multiple sub-models (indicating overall importance) may not be retained by
317	model selection procedures; b) model selection can be heavily influenced by sampling variation
318	(Thompson 1995; Nathans, Oswald & Nimon 2012); if another sample were to be used, the
319	selected predictors could vary. By using HP, one can analyze variable importance over all possible
320	models.
320 321	models. While most canonical analysis is used to analyze species distributional matrices, our package
321	While most canonical analysis is used to analyze species distributional matrices, our package
321 322	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems
321 322 323	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems (e.g., multiple traits). Note that we decided not to consider significance testing for independent
321 322 323 324	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems (e.g., multiple traits). Note that we decided not to consider significance testing for independent contributions in HP because predictor (or groups of predictors) relative importance is usually
321 322 323 324 325	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems (e.g., multiple traits). Note that we decided not to consider significance testing for independent contributions in HP because predictor (or groups of predictors) relative importance is usually considered as an exploratory framework for interpreting regression rather than an inferential tool.
321 322 323 324 325 326	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems (e.g., multiple traits). Note that we decided not to consider significance testing for independent contributions in HP because predictor (or groups of predictors) relative importance is usually considered as an exploratory framework for interpreting regression rather than an inferential tool. Finally, one disadvantage of the variation partitioning and HP frameworks is that the calculation
 321 322 323 324 325 326 327 	While most canonical analysis is used to analyze species distributional matrices, our package can also motivate ecologists to explore its use to different types of response matrices and problems (e.g., multiple traits). Note that we decided not to consider significance testing for independent contributions in HP because predictor (or groups of predictors) relative importance is usually considered as an exploratory framework for interpreting regression rather than an inferential tool. Finally, one disadvantage of the variation partitioning and HP frameworks is that the calculation volume increases exponentially with the increase of predictor variables. We will continue to

- 331 Currently, our rdacca.hp package has been used in peer-reviewed papers (e.g. Li et al. 2020;
- 332 Song *et al.* 2020; Sun *et al.* 2020; Wang *et al.* 2020; Xiong *et al.* 2020; Zhou *et al.* 2020).
- 333 Researchers using the rdacca.hp package in their studies, should cite this article and the
- 334 rdacca.hp package as well. Citation information can be obtained by typing:
- 335 citation("rdacca.hp").
- 336 Acknowledgements
- 337 The research was supported by the Strategic Priority Research Program of the Chinese Academy
- 338 of Sciences (XDA19050404) and the National Science and Technology Basic Resources Survey
- 339 Program of China (2019FY100204). PP-N was supported by the Canada Research Chair (CRC)
- 340 program. Otherwise there is no conflict of interest among the authors.

341 Authors' contributions

- 342 JSL conceived the idea. JSL and PP-N wrote the package and conducted the analysis. All authors
- 343 participated in writing multiples drafts.

344 References

- Bi, J. (2012) A review of statistical methods for determination of relative importance of correlated
- 346 predictors and Identification of drivers of consumer liking. *Journal of Sensory Studies*, 27, 87-
- 347 101.
- 348 Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological
- 349 variation. *Ecology*, **73**, 1045-1055.
- 350 Budescu, D.V. (1993) Dominance analysis a new approach to the problem of relative importance of
- 351 predictors in multiple-regression. *Psychological Bulletin*, **114**, 542-551.

- 352 Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference : a practical
- 353 *information-theoretic approach*, second edn. Springer-Verlag, New York.
- 354 Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *American Statistician*, 45, 90-96.
- 355 Cox, L.A. (1985) A new measure of attributable risk for public health applications. Management
- 356 *Science*, **31**, 800-813.
- 357 Ezekiel, M. (1930) Methods of Correlational Analysis. Wiley, New York
- 358 Grömping, U. (2006) Relative importance for linear regression in R: The package relaimpo. Journal of
- 359 Statistical Software, 17, 1-27...
- 360 Grömping, U. (2007) Relative importance in linear regression based on variance decomposition.
- 361 *American Statistician*, **61**, 139-147.
- 362 Grömping, U. (2009) Variable importance assessment in regression: Linear regression versus random
- 363 forest. *American Statistician*, **63**, 308-319.
- 364 Grömping, U. (2015) Variable importance in regression models. WIREs Computational Statistics, 7,
- 365 137-152.
- 366 Kruskal, W. (1987) Relative importance by averaging over orderings. *American Statistician*, **41**, 6-10.
- 367 Legendre, P. & Anderson, M.J. (1999) Distance-based redundancy analysis: Testing multispecies
- 368 responses in multifactorial ecological experiments. *Ecological Monographs*, **69**, 1-24.
- 369 Legendre, P. & Legendre, L. (2012) Numercial Ecology, Third edn. Elsevier.
- 370 Li, J.Y., Wang, N.L., Dodson, J., Yan, H., Zhang, X.J., Jia, P.W. & Seppa, H. (2020) Holocene negative
- 371 coupling of summer temperature and moisture availability over southeastern arid Central Asia.
- 372 *Climate Dynamics*, **55**, 1187-1208.
- 373 Lindeman, R.H., Merenda, P.F. & Gold, R.Z. (1980) Introduction to Bivariate and Multivariate

- 374 Analysis. Scott Foresman, Glenview, IL.
- 375 Mac Nally, R. & Walsh, C.J. (2004) Hierarchical partitioning public-domain software. Biodiversity and
- 376 *Conservation*, **13**, 659-660.
- 377 Nathans, L.L., Oswald, F.L. & Nimon, K. (2012) Multiple linear regression: A guidebook of variable
- 378 importance. Practical Assessment, Research & Evaluation, 17, 1-19.
- 379 Navarrete, C.B. & Soares, F.C. (2020) dominance analysis: Dominance Analysis. R package version
 380 2.0.0.
- 381 Newton, R.G. & Spurell, D.J. (1967) Examples of the use of elements for classifying regression
- analysis. *Applied Statistics*, **16**, 165-172.
- 383 Nimon, K. & Reio, T. (2011) Regression commonality analysis: a technique for quantitative theory
- 384 building. *Human Resource Development*, **10**,329–340.
- 385 Nimon, K., Oswald, F.L. & Roberts, J.K. (2013) Yhat: Interpreting regression effects. R package
- 386 version 2.0.0.
- 387 Økland, R.H. (2003) Partitioning the variation in a plot-by-species data matrix that is related to n sets

388 of explanatory variables. *Journal of Vegetation Science*, **14**, 693-700.

- 389 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara,
- 390 R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) vegan:
- 391 Community Ecology Package. R package version 2.5-4.
- 392 Oksanen, J., Kindt, R., Legendre, P. & O'Hara, R.B. (2006) vegan: Community Ecology Package. R
- 393 package version 1.8-1.
- 394 Pedhazur, E.J. (1997) Multiple Regression in Behavioral Research: Explanation and Prediction, 3rd
- 395 edn. Harcourt Brace, Orlando, FL.

- 396 Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data
- 397 matrices: Estimation and comparison of fractions. *Ecology*, **87**, 2614-2625.
- 398 R Development Core Team (2019) R: A Language and Environment for Statistical Computing. R
- 399 Foundation for Statistical Computing, Vienna, Austria.
- 400 Rao, C.R. (1964) The use and interpretation of principal component analysis in applied research.
- 401 Sankhyā A, **26**, 329-358.
- 402 Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R. & Hamer, M. (2014) Using

403 commonality analysis in multiple regressions: a tool to decompose regression effects in the

404 face of multicollinearity. *Methods in Ecology and Evolution*, **5**, 320-328.

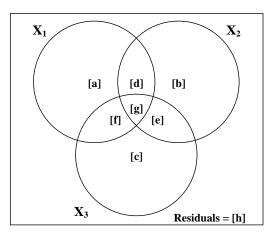
- 405 Song, S.S., Zhang, C., Gao, Y., Zhu, X.Y., Wang, R.H., Wang, M.D., Zheng, Y.L., Hou, L.J., Liu, M. &
- 406 Wu, D.M. (2020) Responses of wetland soil bacterial community and edaphic factors to two-
- 407 year experimental warming and Spartina alterniflora invasion in Chongming Island. Journal

408 *of Cleaner Production*, **250**, doi.org/10.1016/j.jclepro.2019.119502.

- 409 Soofi, E.S. (1992) A generalizable formulation of conditional logit with diagnostics. Journal of the
- 410 *American Statistical Association*, **87**, 812-816.
- 411 Sun, X.J., Diekman, M., Yan, X., Zou, Y., Sang, W.G. & Axmacher, J.C. (2020) Diversity and seasonal
- 412 changes in carabid assemblages of a mature, secondary and plantation forest mosaic in the
- 413 Zhangguangcai Mountains in northeastern China. *Insect Conservation and Diversity*, **13**, 340-
- 414 350.
- 415 ter Braak, C.J.F. (1986) Canonical correspondence-analysis a new eigenvector technique for
 416 multivariate direct gradient analysis. *Ecology*, 67, 1167-1179.
- 417 Thioulouse, J., Dray, S., Dufour, A.B., Siberchicot, A., Jombart, T. & Pavoine, S. (2018) Multivariate

- 418 *Analysis of Ecological Data with ade4*. Springer.
- 419 Thompson, B. (1995) Stepwise regression and stepwise discriminant analysis need not apply here: A
- 420 guidelines editorial. *Educational and Psychological Measurement*, **55**, 525-534.
- 421 Verneaux, J. (1973) Cours d'eau de Franche-Comté (Massif du Jura). Recherches écologiques sur
- 422 *le réseau hydrographique du Doubs. Essai de biotypologie.* Thèse d'état, Besançon.
- 423 Verneaux, J., Schmitt, A., Verneaux, V. & Prouteau, C. (2003) Benthic insects and fish of the Doubs
- 424 River system: typological traits and the development of a species continuum in a theoretically
- 425 extrapolated watercourse. *Hydrobiologia*, **490**, 63-74.
- 426 Walsh, C.J. & Mac Nally, R. (2013) hier.part: Hierarchical Partitioning. R package version 1.0-4.
- 427 Walsh, C.J., Papas, P.J., Crowther, D. & Yoo, J. (2004) Stormwater drainage pipes as a threat to a
- stream-dwelling amphipod of conservation significance, Austrogammarus australis, in
 southeastern Australia. *Biodiversity and Conservation*, 13, 781-793.
- 430 Wang, Y., Yang, X.D., Ali, A., Lv, G.H., Long, Y.X., Wang, Y.Y., Ma, Y.G. & Xu, C.C. (2020)
- 431 Flowering phenology shifts in response to functional traits, growth form, and phylogeny of
- 432 woody species in a desert area. *Frontiers in Plant Science*, **11**, doi: 10.3389/fpls.2020.00536
- 433 Wickham, H. (2016) Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- 434 Xiong, Q.L., Luo, X.J., Liang, P.H., Xiao, Y., Xiao, Q., Sun, H., Pan, K.W., Wang, L.X., Li, L.J. &
- 435 Pang, X.Y. (2020) Fire from policy, human interventions, or biophysical factors? Temporal-
- 436 spatial patterns of forest fire in southwestern China. Forest Ecology and Management, 474,
- 437 doi.org/10.1016/j.foreco.2020.118381
- 438 Zhou, S.L., Sun, Y., Li, Z.X. & Huang, T.L. (2020) Characteristics and driving factors of the aerobic
- 439 denitrifying microbial community in Baiyangdian Lake, Xiong'an New Area. *Microorganisms*,

440 **8**, doi:10.3390/microorganisms8050714



442

443 Figure 1. Venn diagram representing the variation partitioning of a response matrix Y regressed

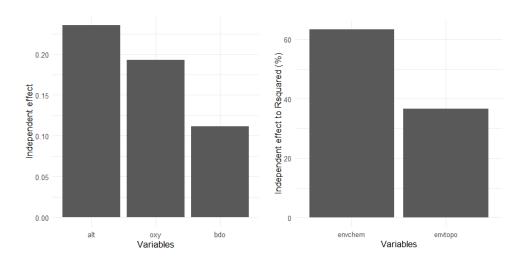
444 against three correlated predictors (or groups of predictors as in variation partitioning). All

fractions add to 100% and the bounding rectangle represents the total variation in the response

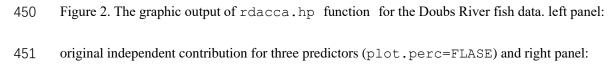
446 data (i.e., 100%) while each circle represents the relative portion of variation accounted by

447 different fractions (see text for a detailed calculations and further explanation).

448



449



452 their relative contribution for two groups to the overall adjusted R^2 (plot.perc=TRUE).