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APPLICATION

Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the `rdacca.hp` R package

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Abstract

1. Canonical analysis, a generalization of multiple regression to multiple-response variables, is widely used in ecology. Because these models often involve many parameters (one slope per response per predictor), they pose challenges to model interpretation. Among these challenges, we lack quantitative frameworks for estimating the overall importance of single predictors in multi-response regression models.
2. Here we demonstrate that commonality analysis and hierarchical partitioning, widely used for both estimating predictor importance and improving the interpretation of single-response regression models, are related and complementary frameworks that can be expanded for the analysis of multiple-response models.
3. In this application, we (a) demonstrate the mathematical links between commonality analysis, variation and hierarchical partitioning; (b) generalize these frameworks to allow the analysis of any number of predictor variables or groups of predictor variables as in the case of variation partitioning; and (c) introduce and demonstrate the implementation of these generalized frameworks in the R package `rdacca.hp`.

KEYWORDS
averaging over orderings, CCA, commonality analysis, constrained ordination, db-RDA, explained variation, RDA, relative importance

1 | INTRODUCTION

Canonical analyses (also called 'constrained ordinations') are widely used as inferential frameworks to determine and contrast the importance of multiple drivers (e.g. environmental conditions, landscape characteristics, spatial structure, dispersal) underlying the structure of ecological communities. Among canonical analyses methods, redundancy analysis (RDA; Rao, 1964), canonical correspondence analysis (CCA; ter Braak, 1986) and distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999) are the most used (Legendre & Legendre, 2012). A central challenge involving canonical analyses is the estimation of predictors' contributions given that the number of regression parameters increases dramatically with the number of response variables. For instance, as many as 4,000 regression slopes are generated if 200 response variables and 20 predictors are considered. However, this challenge can be resolved if the importance of individual predictors is estimated across all response variables, rather than reporting standardized effect sizes for each slope on each response variable.

Since canonical analyses are extensions of multiple regression models to multiple-response variables (Peres-Neto et al., 2006), we can adapt the existing machinery of multiple regression to estimate

the importance of individual predictors across all response variables (e.g. species). The approach we develop here is therefore based on generalizing commonality analysis, a single-response regression framework, to canonical analyses. Commonality analysis is often used to estimate the relative contribution of predictors to the total model's coefficient of determination (R^2) (Newton & Spurell, 1967; Nimon & Reio, 2011; see Ray-Mukherjee et al., 2014 for a rare application in ecology). Commonality analysis decomposes the total models' R^2 into unique fractions attributable to individual predictors as well as the shared fractions among predictors. By contrasting unique and common fractions of variation, we can improve model interpretability compared to using only standardized partial slopes (i.e. beta coefficients) for estimating overall variable importance (see Ray-Mukherjee et al., 2014 for example). This is because standardized partial slopes only consider the unique contributions of predictors and can provide inappropriate interpretations, particularly when strong or complex correlations among predictors and response variables (e.g. multicollinearity, suppression) are involved (see Azen & Budescu, 2003 for numerical examples).

Although commonality analysis is regularly applied to single-response regression models, the parallel framework for multiple-response models (canonical analyses) is the well-known framework of variation partitioning (Borcard et al., 1992; Peres-Neto et al., 2006; see Figure 1). Variation partitioning is employed by grouping predictors together into matrices and estimating the unique and shared semi-partial R^2s of each matrix compounded across all response variables (Peres-Neto et al., 2006). Although the algebra involved in commonality analysis and variation partitioning are equivalent,

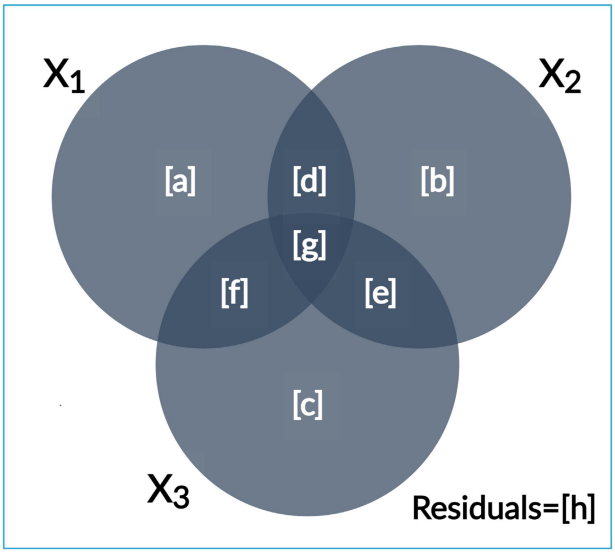

FIGURE 1 Venn diagram representing the variation partitioning of a response matrix **Y** regressed against three correlated predictors (or groups of predictors as in variation partitioning). All fractions add to 100% and the bounding rectangle represents the total variation in the response data (i.e. 100%) while each circle represents the relative portion of variation accounted by different fractions (see text for a detailed calculations and further explanation)

packages conducting commonality analysis are often constrained to single-response variables, for example, R package `yhat` (Nimon et al., 2013); while packages conducting variation partitioning (i.e. multi-response), such as the widely used R package `vegan` (Oksanen et al., 2006), are constrained to a maximum of four predictor matrices. As such, variation partitioning has not yet been generalized to multiple predictor matrices (but see Økland, 2003) and commonality analysis has not been generalized to multi-response models. Among other functionalities, our package `rdacca.hp` implements these generalizations.

Variation partitioning and commonality analysis estimate unique and shared contributions among predictors, increasing our ability to understand the complex relationships between predictor and response variables. However, estimating predictor importance based solely on unique contributions can lead to the same issues of interpreting standardized partial coefficients without considering their shared contribution across predictors. Estimating the relative importance of predictors in multiple regression (e.g. multicollinearity being an extreme case) is an old and very active area of research (see the reviews in Bi, 2012; Grömping, 2015; Nathans et al., 2012). Among them, the approach of 'averaging over orderings' across all possible subset models proposed independently by Lindeman et al. (1980; known as the LMG metric), Cox (1985) and Kruskal (1987) has been considered a critical development (Bi, 2012). These methods are based on all model subsets to allocate shared R^2 to predictors (i.e. relative importance) based on the LMG metric, which are equivalent to methods described independently including hierarchical partitioning (Chevan & Sutherland, 1991) and dominance analysis (Budescu, 1993). To clarify the inherent similarities in the calculations described above, we offer a simplified presentation of 'averaging over orderings'. Our computational presentation also describes a clear link between commonality analysis, variation and hierarchical partitioning. As introduced by the very popular paper by Chevan and Sutherland (1991), we use the term 'hierarchical partitioning' (HP) to refer to these equivalent methods. HP produces all possible combinations of predictors to determine the order in which a predictor dominates over the others (hence the name dominance analysis used by Budescu, 1993) across all subset models, and it has been widely used and recommended to estimate the relative importance of predictors in multiple regression (Grömping, 2015; Mac Nally & Walsh, 2004; Soofi, 1992; Walsh et al., 2004). Corresponding R packages are `relaimpo` for LMG (Grömping, 2006), `hier.part` for HP (Walsh & Mac Nally, 2013) and `dominanceanalysis` (Navarrete & Soares, 2019). We show that analytical results from these packages are identical (see Appendix S1). However, unlike variation partitioning, HP is not currently available for multi-response models (i.e. canonical analysis) and is therefore implemented in our package: `rdacca.hp`.

The overall goal of this paper is to unify commonality analysis, variation and hierarchical partitioning, generalizing them to unlimited number of predictor variables (or matrices of predictors as in variation partitioning). These analyses are implemented in our package `rdacca.hp` which is presented and illustrated in the following sections.

2 | UNIFYING COMMONALITY ANALYSIS, AND VARIATION AND HIERARCHICAL PARTITIONING

While variation partitioning (VP; and commonality analysis) emphasizes unique and shared variation among predictors (or groups of predictors), hierarchical partitioning (HP) describes the relative importance of individual predictors (or groups of predictors) across all possible model subsets (including the full model). Assuming a response matrix **Y** and three correlated predictors (Figure 1), the fractions of variation [a], [b] and [c] correspond to the variation in **Y** that are uniquely explained by predictors X_1, X_2 and X_3, respectively (i.e. unique semi-partial R^2; see Peres-Neto et al., 2006 for details). Fractions [d], [e] and [f] are the shared semi-partial R^2s among all combinations of two predictors while accounting (conditioning) for the contribution of the third predictor not in that submodel. Fraction [g] is the shared semi-partial R^2 among all predictors, and [h] is the fraction corresponding to the variation not explained by the model with all three predictors (i.e. residuals). Shared fractions represent the variation in the response variable explained by the correlation of the predictors involved (i.e. correlation in the predictive space). Larger shared fractions imply that more multicollinearity is present in the model. Here it is important to distinguish between the stages of predictor (or matrices of predictors) comparison and model selection. Detailed calculations involved in variation partitioning have been well described elsewhere for up to four predictors or matrices of predictors (e.g. Peres-Neto et al., 2006). Our package: `rdacca.hp` generalizes these calculations for any number of predictors (or matrices of predictors).

While model selection reduces the shared variation among predictors (collinearity), it reduces model interpretability by removing the ability to interpret complex relationships between predictor and response variables (see Tredennick et al., 2021 for a recent review of these issues). Comparing predictors across submodels as the first stage of model exploration can also improve the interpretation of a (final) selected model. Variation partitioning (Figure 1) is the precursor of hierarchical partitioning (HP), which is used to estimate the importance of individual predictors beyond their unique contributions (akin to standardized partial slopes) to a full model. To improve understanding of the HP algorithm proposed by Chevan and Sutherland (1991), we demonstrate that the relative importance of any individual predictor can be simply estimated as its unique contribution to the total model R^2 plus its average shared contributions with the other predictors. For example, the individual contribution of X_1 (I_{X_1}) can be calculated using its unique contribution [a] and its respective shared contributions [d], [f] and [g] (Figure 1) divided by the number of predictors involved in each of the corresponding submodels:

$$I_{X_1} = a + \frac{d}{2} + \frac{f}{2} + \frac{g}{3}. \quad (1)$$

Similarly, the individual contributions of X_2 and X_3 are calculated as follows:

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

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

and

$$I_{X_1} + I_{X_2} + I_{X_3} = R^2_{\text{Total}}. \quad (4)$$

In general, the individual contribution of any predictor i (I_{X_i}) under the HP framework can be computed as:

$$I_{X_i} = \sum_{k=1}^{p} \sum_{j=1}^{c} \frac{R^2_{SX_{i,k,j}}}{K}. \quad (5)$$

where p is the number of predictors, $R^2_{SX_{i,k,j}}$ is the semi-partial R^2 of the jth fraction shared between X_i and the other K predictors, and c is the number of combinations that X_i shared with other K predictors, with $c = \binom{K-1}{p-1}$. Note that as the number of predictors increases, the number of fractions including shared and unique R^2s increases exponentially ($2^p - 1$ fractions). To estimate the unique and shared fractions, all subset models must be fitted (Nimon & Reio, 2011) even though we commonly express the partitioning involving all predictors together, as in Figure 1, perhaps giving the wrong impression that VP is calculated only based on a single full model. HP can also be applied to matrices of predictors as in routine ecological applications of variation partitioning.

3 | PACKAGE DESCRIPTION

The `rdacca.hp` package is written in R (R Development Core Team, 2020) and can be installed from CRAN (https://cran.r-project.org/web/packages/rdacca.hp/) or as an actively updated version from Github (https://github.com/laijiangshan/rdacca.hp). The package contains two main functions: `rdacca.hp` and `permu.hp`. The former conducts both variation and hierarchical partitioning for canonical analysis without limiting the number of predictors (or matrices of predictors), whereas the latter implements significance testing for individual predictor (or a matrix of predictors) contribution using a permutation test. A S3 method, `plot.rdaccahp`, can be used to plot a bar plot of the individual contribution of predictors based on the output of `rdacca.hp()` via `ggplot2` package (Wickham, 2016). The `rdacca.hp()` depends on the `vegan` package (Oksanen et al., 2019) to calculate the raw R^2 and the adjusted R^2 of canonical analysis. The interpretation of arguments and output for `rdacca.hp()` are offered in the help documents. The arguments of `permu.hp` are nearly identical to those of `rdacca.hp`, except for the additional argument '`permutations`' which represents the number of permutations to be performed. The procedure used to estimate significance (p-values) of individual contribution in `permu.hp()` is available in Appendix S2.

4 | A WORKING EXAMPLE

We illustrate the functionalities of `rdacca.hp` using the Doubs River fish data available in the `ade4` package (Thioulouse et al., 2018). The dataset consists of the distributions of 27 fish species described by abundance classes (ranging from 0 to 5) and 11 quantitative environmental variables describing river morphology and water quality across 30 sites along the Doubs River in the Jura Mountains, near the France–Switzerland border (also see Verneaux et al., 2003). We have excluded one environmental variable (*dfs*, distance from the source) as it represents spatial positioning rather than an environmental variable per se. Note that although all predictors are continuous here, `rdacca.hp` can take categorical predictors and also matrices combining groups of environmental variables (as commonly used in variation partitioning for canonical analyses; see Appendix S3).

The main aim of our analysis was to provide an example of how to improve our understanding and interpretation of data via multiple regression models using variation and hierarchical partitioning. Here we used RDA for multiple species analysis (but see Appendix S3 for db-RDA and CCA). The total R^2 and adjusted R^2 of RDA involving all 10 predictors were 0.714 and 0.556, respectively. The high variance inflation factor (VIF) indicates great degrees of multicollinearity among individual predictors (Table 1). The function `anova.cca()` in the `vegan` package, while setting argument `by = 'terms'`, estimates pseudo-*F* values and *p*-values based on a permutation test for each predictor (see Appendix S3). However, estimation of predictor performance in this way can be quite biased because predictors are contrasted in a nested forward manner in which predictor selection (via significance or threshold values) is conditional upon the predictors already considered in the model (i.e. order dependence; see Whittingham et al., 2006 for an in-depth discussion). As mentioned earlier, it is important to separate the phase of contrasting predictors (i.e. improve understanding and interpretation of data) from model selection ('optimize' predictive performance while reducing uncertainty related to large number of predictors). Most selection procedures use some sort of ordering of predictors while evaluating its predictor importance. Ambiguity in model selection and prediction arises because although two models for the same data may have very similar predictive performances, they may contain rather different predictors. One could assess the importance of each predictor independent of their entrance order in a model using their marginal effects (akin to a type III sum of squares, e.g. setting by='margin' in the function `anova.cca` in vegan), for example. This is the same as testing unique fractions in variation partitioning, which ignores the importance of shared variation. However, when predictors are correlated, understanding their importance based solely on their marginal effects can be much less informative or even misleading. For instance, a particular predictor could have a very small marginal effect when considered together with a group of correlated predictors. However, when combined with other less correlated predictors, it could have a strong marginal effect. Therefore, when correlation among predictors is intermediate or strong (collinearity), variation partitioning and hierarchical partitioning become important frameworks to increase model exploration and assist interpreting regression models. Here, the estimation of predictor importance in an unordered fashion is meant to complement the ordered approach, particularly when the main goal is not prediction (Nimon & Reio, 2011).

Our `rdacca.hp` package provides an exploratory model regression phase because it estimates predictor importance by estimating all possible model subsets without conditioning effects (i.e. order independence). The total number of model subsets needed for the 10 predictors in our working example is 2^{10} resulting in 1,024 models

TABLE 1 Selected outputs of `rdacca.hp` from a working example (Doubs fish data). More outputs are found in Appendix S3

Variables	VIF[a]	Unique	Average.shared[b]	Individual importance	I.perc (%)[c]	*p*-value[d]
oxy	7.62	0.053	0.074	0.127	22.8	0.008
alt	17.48	0.001	0.087	0.088	15.9	0.019
flo	6.02	0.022	0.060	0.082	14.7	0.022
nit	15.63	−0.012	0.078	0.066	11.8	0.037
slo	4.22	0.011	0.052	0.063	11.3	0.046
bdo	18.10	−0.009	0.057	0.048	8.6	0.062
har	2.99	0.021	0.017	0.038	6.9	0.097
pho	25.38	−0.006	0.034	0.028	5.0	0.146
amm	30.35	−0.014	0.039	0.025	4.4	0.141
pH	1.47	−0.009	0.001	−0.008	−1.4	0.492
Total		0.057	0.499	0.556	100	

[a]Variance inflation factor (VIF).

[b]Total average shared effects with other predictors.

[c]Individual effect divided by total adjusted R^2 found in column Individual importance.

[d]*p*-values based on permutation test based on 999 randomizations. The values can vary from one run to another.

and 1,023 (i.e. $2^{10} - 1$) fractions based on variation partitioning. Interpreting all unique and shared fractions is then quite challenging (though it often aids in understanding the complex relationships among predictors). Hierarchical partitioning (HP) reduces this challenge by combining these fractions to estimate individual predictor importance.

Although the total variation was relatively high (55.6% adjusted), most of this variation is shared among predictors (0.499 or 49.9%) and the unique contributions of predictors are generally small (Table 1), totalling 5.7% (i.e. 49.9% + 5.7% = 55.6%). The unique contributions in variation partitioning, as explained earlier, relate to the amount of variation from partial regression slopes considering all predictors in a single model. Indeed, the high variance inflation factor (VIF) of some predictors indicates a great degree of multicollinearity (Table 1). Taken together, these results indicate that predictor multicollinearity is local in the sense that they are strongly correlated (in predictor space) with only a few others. Because multicollinearity is local, hierarchical partitioning should then indicate that some individual predictors dominate over others when considering all possible subset models (i.e. in an unordered assessment of importance). As such, the individual importance of some predictors will be much greater than their unique importance.

In our working example (Table 1 and Appendix S3), *oxy* (dissolved oxygen) had the highest individual importance (12.7%, or 22.8% of the total R^2). This is the result of *oxy* having the highest unique effect (5.3%) and the third highest average shared importance (7.4%). Although *alt* (altitude) had the highest single predictive power of $R^2 = 0.30$ (i.e. model with only one predictor), given its relatively high VIF value (17.48) and the highest sum of average shared effects (8.8%), its unique contribution was quite low (0.1%).

Consider a scenario in which other predictors have been used instead of the ones that were multicollinear with *alt*. In this case, *alt* would have been the most important predictor. Indeed, an unordered assessment via hierarchical partitioning (HP) ranked *alt* as the second most important predictor after *oxy*. This is also a result of the fact that multicollinearity for *alt* is relatively local with a few predictors (see above). Altitude is indeed a latent factor and, as such, is expected to correlate well with some predictors, so its unique effect in a global model with all predictors was expected to be small.

It is important to note that variable importance based on either variation partitioning (unique fractions akin to partial regression slopes) or hierarchical partitioning (variable importance over all subset models, leading to an unordered assessment of importance) can be negative (Table 1) due to multicollinearity (Peres-Neto et al., 2006). For example, *nit* (nitrate), *bdo* (biological demand for oxygen), *pho* (phosphate) and *amm* (ammonia) all have high VIF values and important shared variation with other predictors (Table 1). As a result, the contribution of these four variables to model prediction can be completely replaced by other predictors, leading to unique adjusted effects that are negative. Although *pH* has a low VIF value (1.47), its unique and individual contributions (via HP) are both negative (−0.009 and −0.001, respectively; Table 1); this is likely due to its narrow variation among sites (from 7.7 to 8.6). Shared variation in variation partitioning can be negative due to suppression among predictors (Legendre & Legendre, 2012), which can be easily detected when the non-adjusted fractions of the predictors involved are negative (Peres-Neto et al., 2006; Ray-Mukherjee et al., 2014). The individual effects of each variable (estimated via HP) are related to the sum of its unique and total average shared effects (estimated via variation partitioning). As such, negative individual effects might be due to either negative unique or negative average shared effects. Given that *pH*'s unique contribution (Table 1) was negative, but all its non-adjusted shared fractions were positive, the individual contribution of *pH* (via HP) is to be considered as truly unimportant (either as a predictor or as a suppressor). Finally, although `plot.rdaccahp` produces a bar graph with the individual contributions of each variable (Figure 2), users are encouraged to explore functions from other packages to generate alternative plots (e.g. complex Venn diagrams, pie charts) based on the numerical outputs of our package.

5 | DISCUSSION

Multivariate regression and canonical analyses have been used as essential quantitative frameworks to tackle many ecological and evolutionary problems. Variation partitioning and hierarchical partitioning are frameworks that allow users to go beyond the usual and standard interpretation of partial slopes (see Ray-Mukherjee et al., 2014 for a review). We show that both frameworks are interrelated, and that VP can serve as a precursor of HP. While VP estimates unique and common variation in a full model, HP is based on unique and averaging common fractions of variation. Although VP, HP and model selection can be seen as complementary and as different steps in data analysis, VP and HP overcome two commonly known issues with model selection procedures. First, candidate predictors are conditional on the variance explained by the models already retained by the selection procedure (Nathans et al., 2012; Thompson, 1995). As such, a predictor that is relevant in multiple submodels (indicating overall importance) may not be retained by model selection procedures. Second, model selection can be heavily influenced by sampling variation, meaning that if another sample were to be used, the selected predictors could vary significantly (Nathans et al., 2012; Thompson, 1995).

Unlike traditional applications of canonical analysis to analyse species distributional matrices, our package allows for exploring the use of different types of ecological response matrices and predictors. As the relative importance of predictors (or groups of predictors) are typically used as an exploratory framework rather than an inferential tool, significance testing for individual effects in HP should only be used as reference information. As calculation speed for permutation significance testing is currently a limitation of HP framework, we will continue to optimize our package to make the necessary improvements. Although we demonstrated the application of `rdacca.hp` package using an ecological example, this package is also applicable

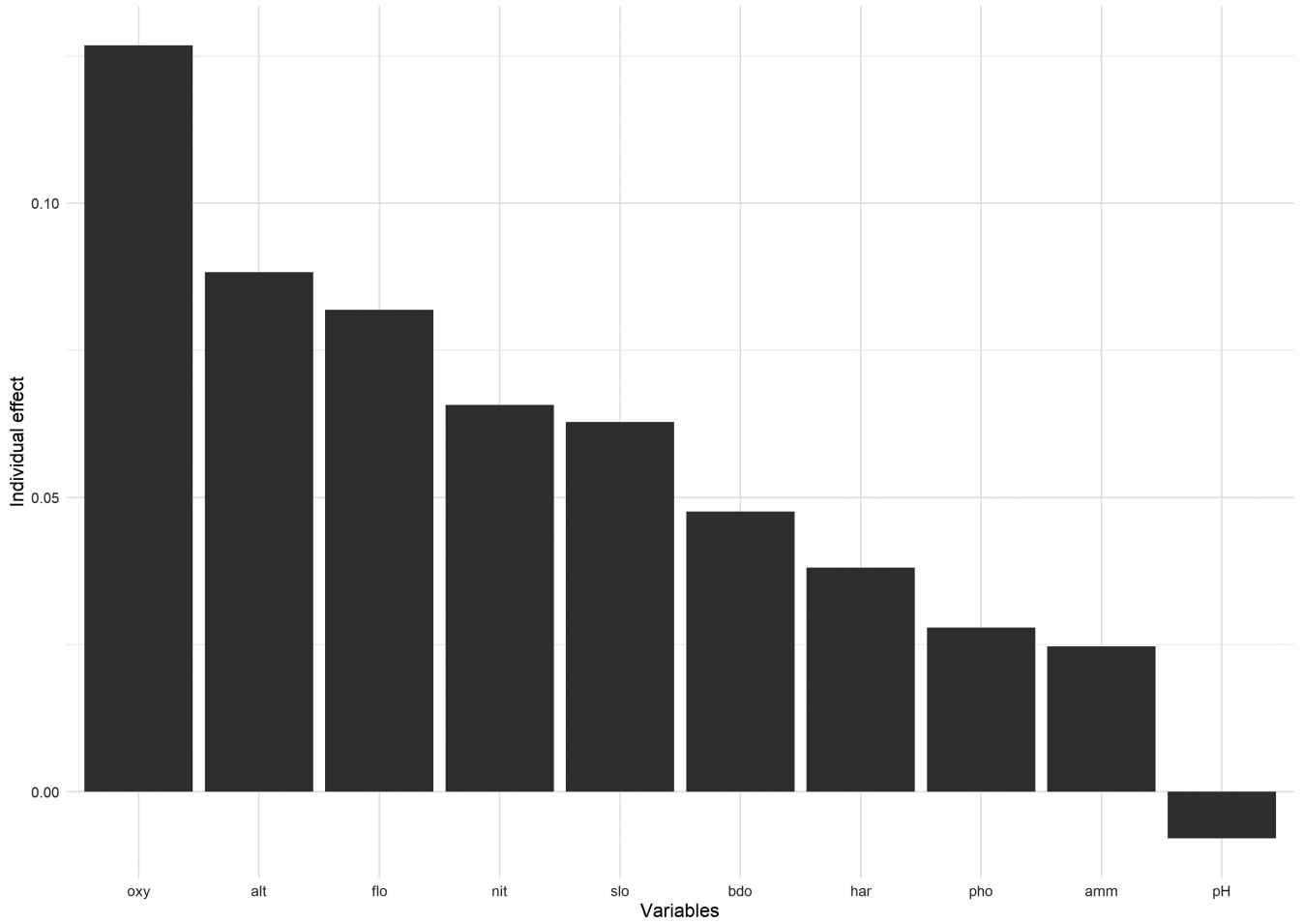

FIGURE 2 The relative importance of individual environmental variables in predicting fish abundance in the Doubs fish data by `rdacca.hp`

to other areas where canonical analysis and multiple regressions are applied.

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CONFLICT OF INTEREST

All authors declared that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.L. conceived the idea; J.L. and P.R.P.-N. wrote the package and conducted the analysis. All authors participated in the writing of multiple drafts.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All R code in this article is available at the open-access repository Zenodo https://zenodo.org/record/5796018 (Lai et al., 2021).

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