Variation partitioning involving orthogonal spatial eigenfunction submodels

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15   *Abstract.*   When partitioning the variation of univariate or multivariate ecological data with

16   respect to several submodels of spatial eigenfunctions (e.g. Moran's eigenvector maps, MEM)

17   acting as explanatory data, a problem occurs: although the submodels are constructed to be

18   orthogonal to one another, the partitioning based on adjusted R^2 statistics produces non-zero

19   values in the intersections between spatial submodels. This phenomenon is described and two

20   solutions are proposed. The first solution is to apportion the intersection fractions proportionally

21   to the variation explained by each submodel. The second solution consists in creating a hierarchy

22   among the spatial submodels, in accordance with hierarchy theory. These solutions lead to new

23   partitioning equations that are described in an appendix to the paper. R functions are provided to

24   carry out partitioning with respect to environmental variables and spatial eigenfunction

25   submodels. This development is important for the correct interpretation of spatial modeling

26   results implying explanatory environmental data as well as submodels of spatial eigenfunctions

27   involving two or more spatial scales.

28   *Key words: adjusted* R^2*; asymmetric eigenvector maps (AEM); hierarchical partitioning; Moran*

29   *eigenvector maps (MEM); proportional apportioning; spatial analysis; spatial eigenfunctions;*

30   *variation partitioning.*

31

32 INTRODUCTION

33   A general method for partitioning the variation of a response data matrix with respect to

34 two or more matrices of explanatory variables in linear models was proposed by Borcard et al.

35 (1992). That method is well-known among ecologists: variation partitioning Venn diagrams,

36 derived from set theory, and drawn using different styles (overlapping bars, rectangles, circles,

37 squares, and so on), are now found in many papers in community ecology and other fields.

38   In early papers, the partitioning was carried out by adding and subtracting R^2 statistics

39 computed from models each involving a single explanatory matrix. For two matrices of

40 explanatory variables for example, the fractions of variation were computed as follows:

41 • First, compute the R^2 statistic associated with three linear models of a single explanatory matrix,

42 computed using multiple regression if there is a single response variable, or canonical

43 redundancy analysis (RDA) for a multivariate table of response variables containing, for

44 example, community composition data:

45 $R^2(\mathbf{Y} \mid \mathbf{X}_1)$ is the R^2 of $\mathbf{Y}$ analyzed with respect to explanatory matrix $\mathbf{X}_1$,   (1a)

46 $R^2(\mathbf{Y} \mid \mathbf{X}_2)$ is the R^2 of $\mathbf{Y}$ analyzed with respect to explanatory matrix $\mathbf{X}_2$,   (1b)

47 $R^2(\mathbf{Y} \mid [\mathbf{X}_1, \mathbf{X}_2])$ is the R^2 of $\mathbf{Y}$ analyzed by $\mathbf{X}_1$ and $\mathbf{X}_2$ bound together in a single matrix. (1c)

48 • Then, compute the fractions of variation:

49 $[a] = R^2(\mathbf{Y} \mid [\mathbf{X}_1, \mathbf{X}_2]) - R^2(\mathbf{Y} \mid \mathbf{X}_2)$ (2a)

50 $[b] = R^2(\mathbf{Y} \mid \mathbf{X}_1) + R^2(\mathbf{Y} \mid \mathbf{X}_2) - R^2(\mathbf{Y} \mid [\mathbf{X}_1, \mathbf{X}_2])$ (2b)

51 $[c] = R^2(\mathbf{Y} \mid [\mathbf{X}_1, \mathbf{X}_2]) - R^2(\mathbf{Y} \mid \mathbf{X}_1)$ (2c)

52 $[d] = \text{residual variation} = 1 - R^2(\mathbf{Y} \mid [\mathbf{X}_1, \mathbf{X}_2])$ (2d)

53 Notation: $(\mathbf{Y} \mid \mathbf{X})$ refers to the analysis (regression or RDA) of $\mathbf{Y}$ by $\mathbf{X}$ and $R^2(\mathbf{Y} \mid \mathbf{X})$ is the R^2 of

54 that analysis. Fraction identifiers [a] to [d] are shown in Fig. 1a. That method of calculation can

55 be extended to more than two explanatory matrices, as shown in Appendix A.

56   In 2006, Peres-Neto et al. showed that the R^2 statistic computed in RDA is a biased

57 estimator of the explained variation, producing increasingly high values as explanatory variables

58 are added to the analysis, even though these variables are not linearly related to the response data

59 under study. This phenomenon had already been shown for the R^2 statistic computed in multiple

60 regression (Ohtani, 2000). Peres-Neto et al. also showed that unbiased estimates of the fractions

61 computed in variation partitioning require that the partitioning equations be based on adjusted R^2

62 statistics (R^2_a, Ezekiel 1930) instead of simple R^2. To obtain R^2_a for an explanatory matrix

63 containing random variables, i.e. variables whose values result from measurements on some

64 types of random processes, the R^2 must be corrected using its degrees of freedom, which depend

65 in turn on the number of objects (n) and the number of variables (m) contained in the explanatory

66 matrix. The adjustment is based on the fact that R^2_a must be near 0 for explanatory variables that

67 are random (i.e. no effect) with respect to the response data $\mathbf{Y}$. As a result of the Peres-Neto et al.

68 (2006) paper, the variation partitioning equations (eqs. 2a–2d above) are now based on the

69 calculation of R^2_a statistics. In the R language, the method is implemented in function ***varpart()***

70 of the VEGAN package (Oksanen et al. 2011).

71   Spatial eigenfunction analysis is a method of growing interest for multiscale spatial

72 analysis of ecological data. Spatial eigenfunctions produced by these methods are called by the

73 general name *Moran's eigenvector maps* (MEM, Dray et al. 2006); distance-based MEM

74 (dbMEM), which were formerly called PCNM eigenfunctions (Borcard and Legendre 2002),

75 belong to that group. *Asymmetric eigenvector maps* (AEM, Blanchet et al. 2008a) are also spatial

76 eigenfunctions belonging to the same family. This family of methods was developed during the

77 past 10 years. Spatial eigenfunctions can be computed for points located at regular or irregular

78 intervals along transects or on maps. They have the properties of modeling the spatial variation at

79 all scales encompassed in the sampling design and of being orthogonal to one another. The

80 construction and practical use of spatial eigenfunctions is described in Chapter 7 of Borcard et al.

81 (2011) and in Chapter 14 of Legendre and Legendre (2012).

82   In many studies, the eigenfunctions are divided into a number of submodels corresponding

83 to different spatial scales of interest in a study. The eigenfunction submodels can be used as

84 explanatory data in linear modeling, including variation partitioning. These submodels are

85 orthogonal to one another, meaning that the scalar product of two submodels produces a null

86 matrix. Therefore, one expects to obtain linearly independent linear models from the

87 eigenfunction submodels, the submodels having no shared explained variation. It turns out,

88 however, that the presently available equations for variation partitioning, based on R^2_a, create

89 small non-null intersection values between submodels constructed from linearly independent

90 groups of spatial eigenfunctions. These small intersection values are most often negative. That

91 problem is revisited in the present paper.

92   METHOD

93   How does a non-zero shared fraction of variation (e.g. fraction [b] in Fig. 1a) originate?

94 Fraction [b] is not estimated from a linear model of the data but computed by addition and

95 subtraction of previously computed fractions, as shown in eq. 2b. When this equation is

96 computed using R^2 statistics, the value of [b] is 0 for two perfectly orthogonal explanatory

97 matrices, e.g. two matrices of spatial eigenfunctions corresponding to models at different scales;

98 values of [b] different from 0 indicate correlations between the two matrices, e.g. two matrices of

99 environmental variables. With adjusted R^2, however, addition and subtraction of R^2_a values in eq.

100 2b does not produce 0 for two matrices of orthogonal variables, but small positive or negative

101 values.

102 How often are these fractions negative and how small is *small*? For example, after 10000

103 repeated and independent simulations, the variation of spatially-structured response variables

104 simulated along a regular transect with 30 points, partitioned between two MEM submodels

105 (broad-scale, fine-scale), produced 9815 negative fractions [b] (identified in Figs. 1 and 2a) out of

106 10000, hence only 185 positive. The values of [b] computed from R^2_a were in the range [–0.0997,

107 0.0227]. In another experiment, a spatially-structured response variable simulated on a regular

108 grid with $8 \times 12 = 96$ points was partitioned among three MEM submodels (broad-scale, middle-

109 scale, fine-scale); the simulations produced 9959 negative fractions [d], 9651 negative fractions

110 [e], and 9880 negative fractions [f] in 10000 simulations (see Fig. 2a, a few paragraphs down, for

111 the fraction identifiers). Fractions [d] were in the range [–0.0236, 0.0012], fractions [e] were in

112 the range [–0.0169, 0.0014], and fractions [f] were in the range [–0.0235, 0.0012].

113 The problem is actually not limited to matrices of spatial eigenfunctions. R^2_a statistics are

114 not additive, so the sum of the R^2_a statistics of models computed from explanatory matrices $\mathbf{X}_1$

115 and $\mathbf{X}_2$ is never strictly equal to the R^2_a of the model computed from the union of matrices $\mathbf{X}_1$ and

116 $\mathbf{X}_2$ even when the variables in $\mathbf{X}_1$ and $\mathbf{X}_2$ are orthogonal among the groups. This problem is,

117 however, especially annoying in studies where the variation of response data is partitioned among

118 eigenfunction submodels corresponding to different spatial scales because these submodels are

119 orthogonal to one another by construction.

120 How can we remediate this problem? In other words, using adjusted R^2, how can we obtain

121 a partitioning of the variation of the response matrix by a combination of matrices of spatial

122   eigenfunctions and environmental variables, without producing fractions of shared variation

123   different from 0 between the matrices representing spatial eigenfunction submodels?

124   A first idea that comes to mind would be to refrain from using R^2_a statistics in analyses

125   involving explanatory matrices containing spatial eigenfunctions. However, the logic of the

126   correction for number of variables prior to the calculation of the fractions of variation applies to

127   spatial eigenfunctions as well: the R^2 statistic increases with the number of variables in each

128   matrix for spatial eigenfunctions, just as they do for matrices of random variables (e.g.

129   environmental), independently of their capacity to explain the variation of the response data, so

130   that the resulting R^2 statistic overestimates the amount of explained variation.

Proportional apportioning of the shared fractions

132   A first solution is to apportion the intersection fractions proportionally to the variation

133   explained by each submodel. The total variation explained by the combined submodels is entirely

134   accounted for in the partition. This solution is interesting in, and applicable to, studies where no

135   hierarchy among the spatial processes is recognized. As an example, a vegetation study where

136   broad-scale spatial structures are considered as proxies for climatic constraints, and fine-scaled

137   patterns represent edaphic conditions, would be well served by this approach since the two

138   classes of constraints are not conceptually nested. Calculation details for proportional

139   apportioning are shown in Appendix A. The results are illustrated in Figs. A1 to A3 (Appendix

140   A).

Hierarchical partitioning of the shared fractions

142   A second solution is to create a hierarchy among the orthogonal eigenfunction submodels

143   in the analysis according to the scales they represent. In the two-submodel case, for example, we

144   can state that the broad-scale (BS) submodel has priority over the fine-scale (FS) submodel. The

145   consequence of that decision on the calculations is that the BS submodel is served first in the

146   variance resource and secures for itself the small fractions found in the intersection with the FS

147   submodel. As a result, the intersection in explained variation between the two submodels, which

148   is of interest in partitioning involving two matrices of random variables or one matrix of random

149   variables and a matrix of spatial eigenfunctions (Fig. 1a), disappears in Fig. 1b where two

150   matrices of orthogonal spatial eigenfunctions (MEM) are used as explanatory variables.

151   The logic behind the second approach is the following: in most analyses of the spatial

152   variation of communities, we expect environmental control processes to be at work, and we know

153   from hierarchy theory (Simon 1962, Allen & Starr 1982, O'Neill et al. 1991) that broad-scale

154   environmental processes, like orogenic and geomorphological processes on land or currents and

155   winds in fluid environments, often generate broad-scale signatures in the response data. What is

156   more difficult is to identify the signatures of smaller-scale processes like the action of biotic

157   interactions and other forms of neutral processes. One must have a conservative attitude in

158   assessing small-scale signatures of processes in order to only focus on those that are likely to be

159   really present in data. A conservative strategy is to allow broader-scale MEM spatial models to

160   explain variation without allowing smaller-scale submodels to interfere. The hierarchy is

161   established on a priori grounds. The previously shared fractions become irrelevant, as are the

162   signs that these shared fractions would have had with specific data sets. If our ecological

163   hypothesis makes us think that we are in this kind of situation, this authorizes us to create such a

164   hierarchy among the spatial MEM submodel matrices prior to variation partitioning. The

165   advantage of this solution is that the R^2_a of the dominant MEM submodel is perfectly represented

166   in the partition result, as shown in the example. If the researcher does not have a hierarchical

167   hypothesis, he/she may use the proportional apportioning method described two paragraphs

168   above, or simply use the traditional partitioning results that have small shared, but un-

169   interpretable fractions.

170   In a study involving three explanatory matrices, one expects to find intersection fractions,

171   which are of interest, when using either three matrices of environmental variables, or two

172   matrices of environmental variables and a matrix of spatial eigenfunctions (Fig. 2a). If there are

173   three matrices of spatial eigenfunctions, one can apply the hierarchy described in the previous

174   paragraphs between eigenfunction models representing decreasing spatial scales: the broad-scale

175   (BS) submodel may be given priority over the middle-scale (MS) submodel, which in turn has

176   priority over the fine-scale (FS) submodel. The BS submodel is served first in the variance

177   resource and secures for itself the small fractions found in the intersection with the MS and FS

178   submodels. Then the MS submodel is served before the FS submodel (Fig. 2c). When there is a

179   matrix of environmental variables and two matrices of spatial eigenfunctions, a hierarchy is

180   created only between the two matrices representing spatial submodels (Fig. 2b): the

181   environmental variables have shared variation with both spatial submodels, but then the BS

182   submodel has priority over the fine-scale (FS) submodel.

183   The results are fairly simple to compute. For the two explanatory matrix case, consider the

184   fractions computed by eq. 2, now used with R^2_a instead of R^2: for the two spatial eigenfunction

185   case (Fig. 1b), add the value computed for [b] in Fig. 1a with the value of [a] and use the sum as

186   the new [a] value in the hierarchy shown in Fig. 1b. For the three explanatory matrix case, Fig. 2b

187   is obtained by adding fractions [d] and [g] of Fig. 2a to obtain the new value of [d] in Fig. 2b, and

188   adding [b] and [e] of Fig. 2a to obtain the new value for [b] in Fig. 2b. For the three spatial

189   submodel case shown in Fig. 2c, [a] is obtained by adding [a], [d], [f] and [g] from Fig. 2a; [b] is

190   obtained by adding [b] and [e] from Fig. 2a; and [c] has the same value as in Fig. 2a.

191   The same calculations can be extended to the four explanatory matrix situation. The Venn

192   diagrams are harder to draw (Fig. A4. Appendix A), but the logic is the same. Note that in all

193   cases, the residuals remain unchanged.

194   The calculation details for hierarchical partitioning involving 2, 3, and 4 explanatory

195   matrices are given in Appendix A. The results are illustrated in Figs. 1, 2 and A4 (Appendix A).

196   *Software*

197   Functions ***varpart2.MEM()***, ***varpart3.MEM()*** and ***varpart4.MEM()*** in R can be used to

198   carry out the calculations. They are provided in a Supplement. These functions offer the

199   hierarchical or the proportional methods as options. In the output tables of these functions, the

200   variation corresponding to the fractions that have disappeared is left blank although the proper

201   notation would be the empty set (Ø). These functions rely upon function ***varpart()*** of the VEGAN

202   package (Oksanen et al. 2011). Functions ***print.varpart()*** and ***plot.varpart()*** of the VEGAN

203   package can be applied to the output of these functions to print partition tables and produce Venn

204   diagrams.

205   Tests of significance of the fractions of variation explained by the eigenfunction submodels

206   can be carried out as usual with function ***anova.cca()*** of VEGAN, using all other explanatory

207   matrices in the analysis as covariables. The choice of the partitioning method for spatial

208   eigenfunction submodels does not matter because one is simply testing the significance of spatial

209   eigenfunction submodels that are orthogonal to one another. The result is only affected by the

210   presence of matrices of random (e.g. environmental) variables that are not orthogonal to the

211   eigenfunction submodels.

<center>EXAMPLE ON REAL DATA</center>

213   We exemplify the new procedures by applying them to the well-known Oribatid mite data

214   set that has been used in many papers dealing with variation partitioning and spatial analysis (e.g.

215   Borcard and Legendre 1992, Borcard et al. 2004, Dray et al. 2006, Borcard et al. 2011). The data

216   are available in the VEGAN and ADE4 R-language packages as well as with the Borcard et al.

217   (2011) book. The mite community composition data (70 sites and 35 species) were Hellinger-

218   transformed prior to variation partitioning (Legendre and Gallagher 2001). The three explanatory

219   matrices involved are (1) an environmental matrix containing two quantitative variables (water

220   content in percent and substrate density in g•L^{-1} of dry uncompressed matter) and two matrices

221   of dbMEM eigenfunctions that were forward-selected using the Blanchet et al. (2008b) double

222   stopping criterion. We first selected the hierarchical solution for this example because the

223   hypothesized processes correspond to the general framework exposed above: most environmental

224   constraints are of the same kind, vary at broad scale, and are expected to impose coarse patterns

225   on the community structure, while more local substrate variation and biotic interactions are

226   expected to induce fine-scale structure within the main patterns. The broad-scale MEM submodel

227   contains MEM # 1 to 4 whereas the fine-scale submodel comprises MEM # 6 to 11 and 16.

228   Fig. 3a shows the result of a classical partitioning and Fig. 3b the result of the hierarchical

229   partitioning procedure. The comparison shows how giving priority to the broad-scale MEM

230   submodel makes the interpretation easier. Note that since fractions [e] and [g] of the classical

231   partitioning were negative (a common occurrence), the final amount of variation explained by the

232   broad-scale MEM submodel, as well as the fraction common to the environmental variables and

233   the broad-scale MEM submodel, are *lower* than in Fig. 3a (the fraction identifiers [a] to [h] are

234   the same as in Fig. 2a). The total amount of explained variation remains the same, however, to

235   within rounding errors of the numbers displayed in the figure.

236   Fractions [a], [c] and [f] are unaffected by the hierarchical approach since they involve only

237   the pure contributions of the environmental and fine-scale MEM matrices and their jointly

238   explained variation. The hierarchy affects the broad-scale MEM submodel in that this submodel

239   now completely incorporates fractions [e] and [g] that, otherwise, would be common to the

240   broad- and fine-scale MEM submodels. In the hierarchical partitioning result, the R^2_a of the

241   broad-scale MEM submodel is perfectly represented in the partition result.

242   To make the numerical example complete, Fig. 3c illustrates the result of the proportional

243   apportioning method. The intersection fractions are apportioned proportionally to the variation

244   explained by each submodel, that is, fraction [b+d] of Fig. 2a for the broad-scale submodel and

245   fraction [c+f] for the fine-scale submodel. The numerical artifacts represented by fractions [e]

246   and [g] were not taken into account in calculating the relative importance of the submodels

247   because there are the quantities that must be apportioned between [b+d] and [c+f].

248   CONCLUSION

249   The development described in this paper sheds a new light on the interpretation of spatial

250   modeling results implying explanatory environmental variables as well as submodels of spatial

251   eigenfunctions involving two or more scales. Ezekiel's adjustment of the R^2 statistic yields an

252   unbiased estimate of the explained variance, but when used in the context of variation

253   partitioning it has the side effect of generating spurious non-zero joint fractions between

254   orthogonal explanatory matrices. Two solutions are proposed, and the choice between them

255   requires users to decide first if the processes underlying the spatial fractions are of a hierarchical

256   nature or not. The non-hierarchical solution translates into the proportional apportioning of the

257   joint fractions to the spatial submodels. Invoking hierarchy theory to put the two or more spatial

258   submodels in a logical order of importance allows one to ascribe each of these fractions to one

259   and only one spatial scale. This clarifies the interpretation of the spatial components of the

260   response data variation.

261   The common fractions resulting from the analysis of environmental explanatory matrices

262   are not involved in this hierarchical operation because these matrices are not *a priori* linearly

263   independent of one another or of the spatial eigenfunction submodels. For explanatory

264   environmental variables, Peres-Neto (2006) has shown that partitioning based on adjusted R^2

265   statistics (R^2_a) produces unbiased estimates of all fractions of variation: unique (e.g. [a] and [c] in

266   the two explanatory matrices case) and shared (e.g. [b]). The partitioning of univariate or

267   multivariate response data, e.g. community composition data, between environmental explanatory

268   variables and spatial submodels is of great interest since it allows ecologists to discover structures

269   in the response data that are explainable by both the environmental variables and spatial models

270   at different scales.

271   Some points in linear variation partitioning remain to be investigated. The use of

272   categorical variables in variation partitioning is still a subject of discussion. Random categorical

273   variables such as the type of soil observed at sites may be treated as a set of binary variables and

274   included as such in an environmental matrix, but fixed ANOVA factors (e.g. in a manipulative

275   field ecological experiment) are clearly of a different nature, and Ezekiel's adjustment should not

276   be applied to them. Indeed, Healy (1984) pointed out that Ezekiel's (1930) adjusted R^2 makes

277   sense and should be used when explanatory matrix **X** contains observed values of random

278 variables, but not for ANOVA factors. Therefore, the procedure developed in this Note should

279 not be applied to cases involving fixed ANOVA factors, only to orthogonal models of spatial

280 eigenfunctions. Although they are called 'spatial', eigenfunction models can also be used for

281 multiscale analysis of time series.

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326   APPENDIX A

327   Variation partitioning formulas, hierarchical and proportional methods (*Ecological Archives*

328   Exxx-xxx-A1).

329   SUPPLEMENT

330   Functions in R language to compute hierarchical and proportional variation partitioning for

331   eigenfunction submodels (*Ecological Archives* Exxx-xxx-S1).

332

FIGURE CAPTIONS

334   Fig. 1. Venn diagrams of variation partitioning results for: (a) two matrices of random variables

335    $\mathbf{X}_1$ and $\mathbf{X}_2$, e.g. environmental variables, or a matrix of random variables $\mathbf{X}$ and one of spatial

336   eigenfunctions called MEM in the figure; Identifiers of the fractions [a] to [d] are shown; (b) two

337   matrices of spatial MEM submodels between which a hierarchy was created. The fractions of

338   variation explained by MEM matrices are in gray.

339   Fig. 2. Venn diagrams of variation partitioning results for three explanatory matrices. (a)

340   Classical partitioning. (b, c) Result of hierarchical partitioning.

341   Fig. 3. Venn diagrams of the partitioning results for the Oribatid mite data: (a) classical, non-

342   hierarchical partitioning. (b) Hierarchical partitioning of the fraction shared by the two

343   submodels, taking into account the priority of the broad-scale submodel over the fine-scale

344   submodel. (c) Proportional apportioning.

(a) Two matrices of random variables X; one of them may be MEM

Variation explained by X_1

Variation explained by X_2

[a]   [b]   [c]

Residual variation = [d]

(b) Two matrices of MEM

Variation explained by MEM_1

Variation explained by MEM_2

[a]   [c]

Residual variation = [d]
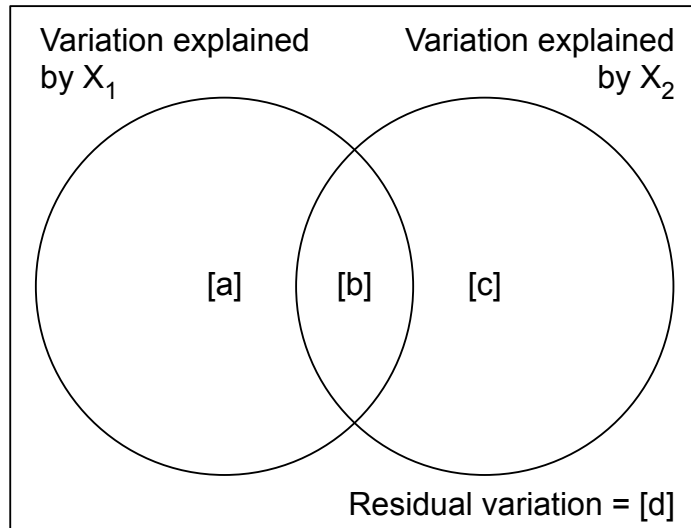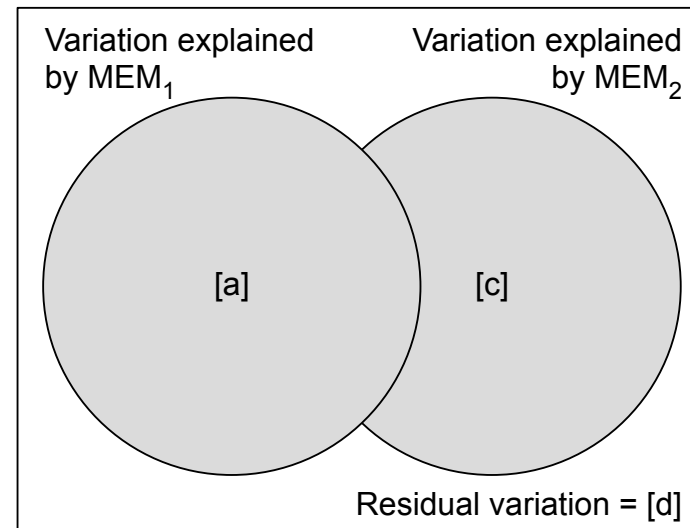
(a) Three matrices of random variables X; one of them may be MEM
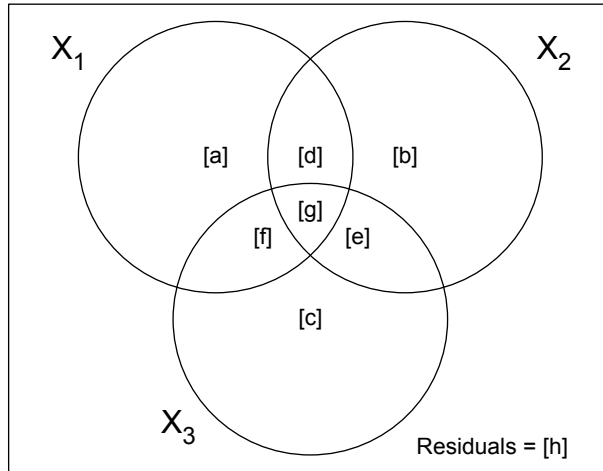
X₁ X₂

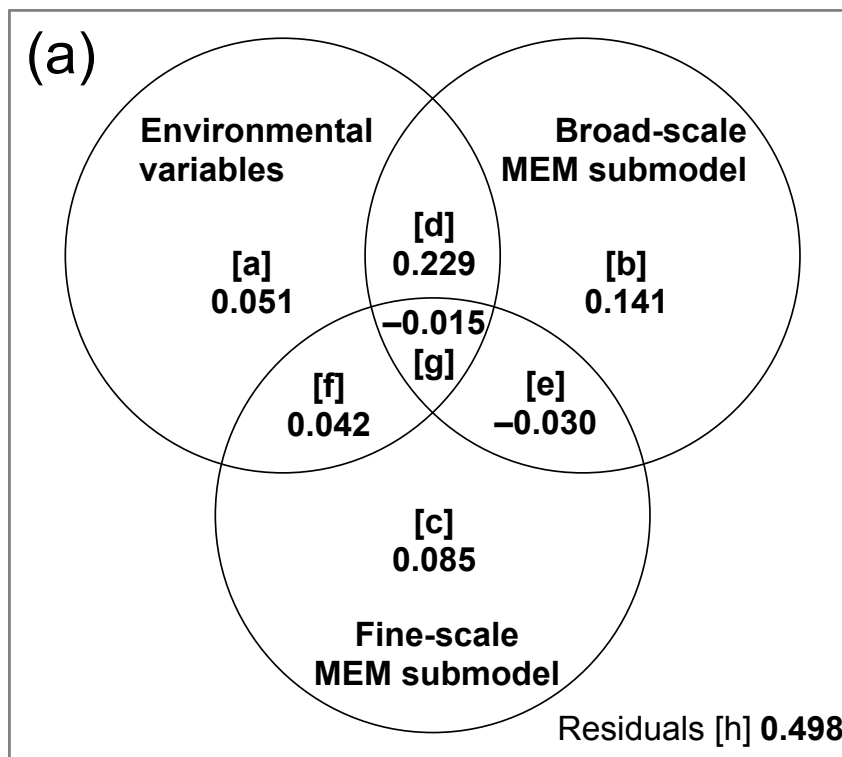[a] [d] [b]

[g]

[f] [e]

[c]

X₃

Residuals = [h]

(b) One matrix of random variables X, two matrices of MEM

X MEM₁

[a] [d] [b]

[f]

[c]

MEM₂

Residuals = [h]

(c) Three matrices of MEM

MEM₁ MEM₂

[a] [b]

[c]

MEM₃

Residuals = [h]

(a)

Environmental variables

Broad-scale MEM submodel

[a] 0.051

[d] 0.229

[b] 0.141

−0.015 [g]

[f] 0.042

[e] −0.030

[c] 0.085

Fine-scale MEM submodel

Residuals [h] **0.498**

(b)

Environmental variables

Broad-scale MEM submodel

[a] 0.051

[d] 0.215

[b] 0.111

[f] 0.042

[c] 0.085

Fine-scale MEM submodel

Residuals [h] **0.498**

(c)

Environmental variables

Broad-scale MEM submodel

[a] 0.051

[d] 0.218

[b] 0.118

[f] 0.038

[c] 0.077

Fine-scale MEM submodel

Residuals [h] **0.498**
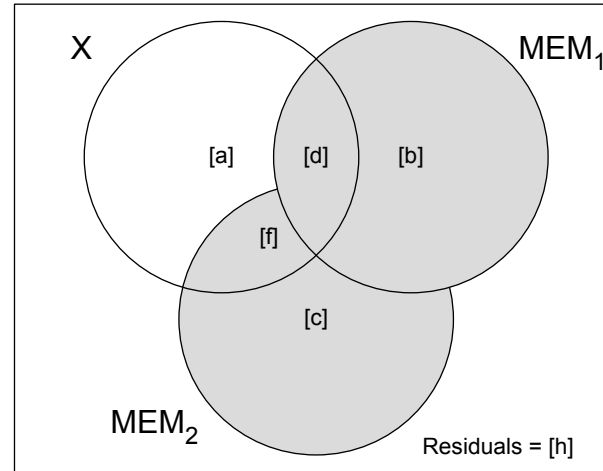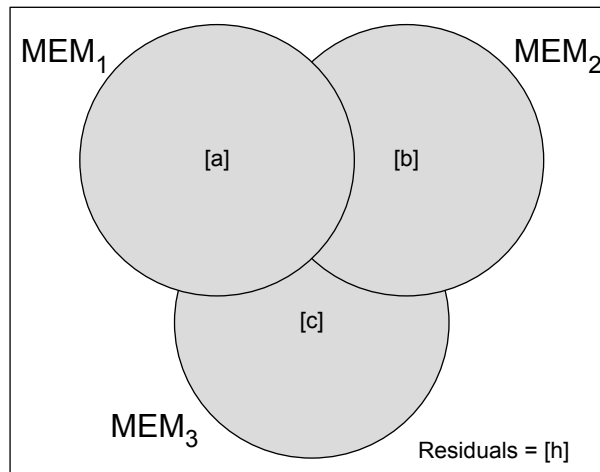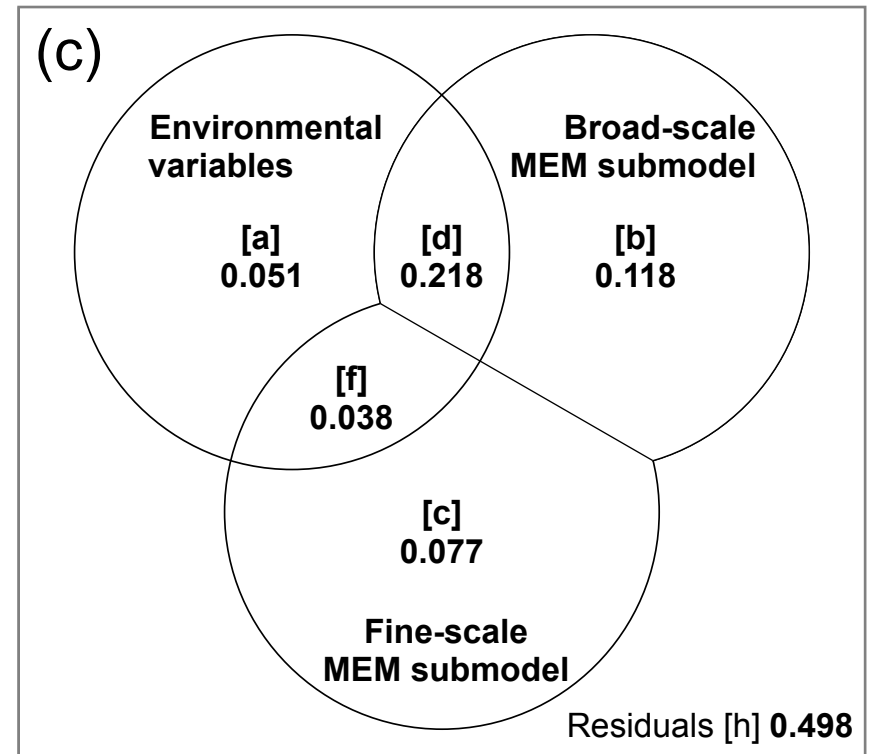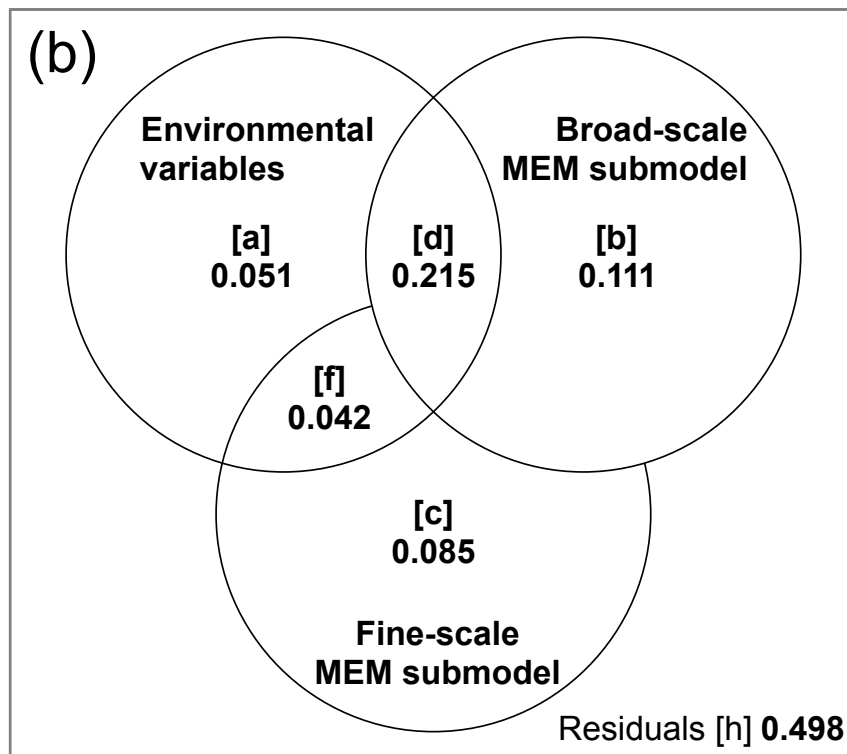
Legendre, P., D. Borcard and D. W. Roberts. 2012. Variation partitioning involving orthogonal spatial eigenfunction submodels. *Ecology* 93: xxx-xxx.

Appendix A. Variation partitioning formulas, hierarchical and proportional methods

This Appendix presents formulas for the calculation of fractions following the hierarchical and proportional variation partitioning methods for eigenfunction submodels (MEM or AEM). Classical variation partitioning (Borcard et al. 1992, Peres-Neto et al. 2006) only involves matrices of random variables. Different situations, involving different combinations of matrices of random (e.g. environmental) variables and spatial eigenfunction submodels, are described in Tables A1 to A3.
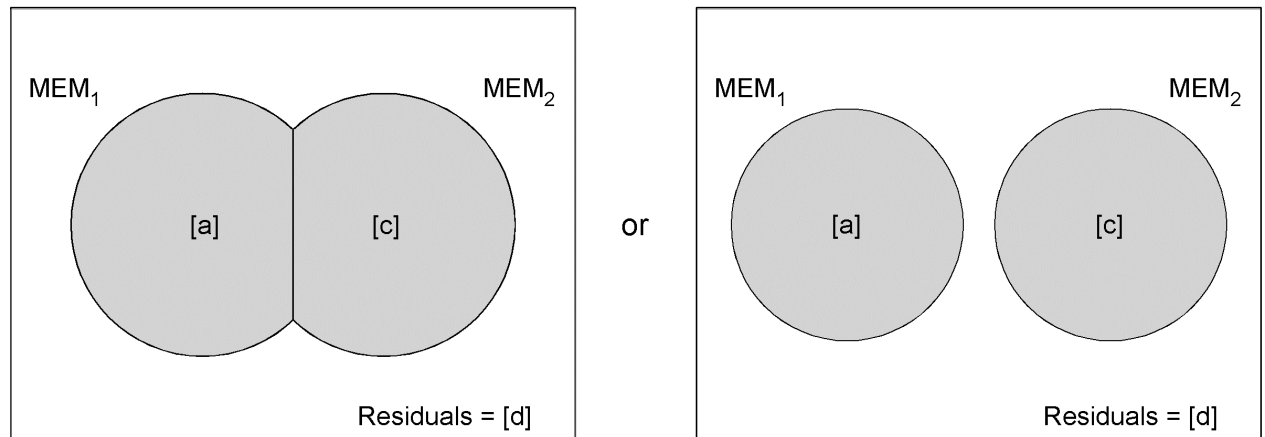
Venn diagrams illustrating the results of proportional apportioning of the shared fractions in variation partitioning are presented in Figs. A1 to A3. Figures illustrating the results of hierarchical partitioning of the shared fractions for two and three explanatory matrices are shown in the main paper, Figs. 1 and 2, and in Fig. A4 for four explanatory matrices.

Table A1. Variation partitioning for two explanatory matrices containing eigenfunction submodels. Fractions identifiers: see Figs. 1 and 2a. *Notation:* Ø is the empty set; in the present table, is denotes the absence of a value. Indications about the logic involved in the computation of some fractions follow the sign #.

Hierarchical partitioning of the shared fraction

[a] = [a] + [b]

[b] = Ø   # Transferred to [a]

[c] = [c]

[d] = [d]   # Residual fraction

Proportional apportioning of the shared fraction

[a] = [a] + ([b] × [a] / ([a] + [c]))

[b] = Ø   # Transferred to [a] and [c]

[c] = [c] + ([b] × [c] / ([a] + [c]))

[d] = [d]   # Residual fraction

Two matrices of MEM

Fig. A1. Venn diagrams illustrating the result of proportional apportioning of the shared fractions in variation partitioning involving two matrices of spatial eigenfunctions (MEM). Alternative graphical solutions are proposed. In gray, the fractions of variation explained by MEM.

Table A2. Variation partitioning in the 3-matrix case. Matrix 1 may contain random explanatory variables. (a) The last two, or (b) all three matrices, contain eigenfunction submodels. Fractions identifiers: see Fig. 3a. Notation as in Table A1.

(a) Matrix 1 contains random explanatory variables, matrices 2 and 3 contain eigenfunction submodels

---

<u>Hierarchical partitioning of the shared fractions</u> (Fig. 3b)

[a] = [a]

[b] = [b] + [e]

[c] = [c]

[d] = [d] + [g]

[e] = Ø   # Transferred to [b]

[f] = [f]

[g] = Ø   # Transferred to [d]

[h] = [h]   # Residual fraction

<u>Proportional apportioning of the shared fractions</u>

e.to.b = [e] × (([b] + [d]) / ([b] + [d] + [c] + [f]))   # Portion of [e] transferred to [b]

e.to.c = [e] × (([c] + [f]) / ([b] + [d] + [c] + [f]))   # Portion of [e] transferred to [c]

g.to.d = [g] × (([b] + [d]) / ([b] + [d] + [c] + [f]))   # Portion of [g] transferred to [d]

g.to.f = [g] × (([c] + [f]) / ([b] + [d] + [c] + [f]))   # Portion of [g] transferred to [f]

[a] = [a]

[b] = [b] + e.to.b

[c] = [c] + e.to.c

[d] = [d] + g.to.d

[e] = Ø   # Transferred to [b] and [c]

[f] = [f] + g.to.f

[g] = Ø   # Transferred to [d] and [f]

[h] = [h]   # Residual fraction

(b) Three matrices of eigenfunction submodels

Hierarchical partitioning of the shared fractions (Fig. 3c)

[a] = [a] + [d] + [f] + [g]

[b] = [b] + [e]

[c] = [c]

[d] = Ø   # Transferred to [a]

[e] = Ø   # Transferred to [b]

[f] = Ø   # Transferred to [a]

[g] = Ø   # Transferred to [a]

[h] = [h]   # Residual fraction

Proportional apportioning of the shared fractions

d.to.a= [d] × ([a] / ([a] + [b]))   # Portion of [d] transferred to [a]

d.to.b= [d] × ([b] / ([a] + [b]))   # Portion of [d] transferred to [b]

e.to.b= [e] × ([b] / ([b] + [c]))   # Portion of [e] transferred to [b]

e.to.c = [e] × ([c] / ([b] + [c]))   # Portion of [e] transferred to [c]

f.to.a = [f] × ([a] / ([a] + [c]))   # Portion of [f] transferred to [a]

f.to.c = [f] × ([c] / ([a] + [c]))   # Portion of [f] transferred to [c]

g.to.a = [g] × ([a] / ([a] + [b] + [c]))   # Portion of [g] transferred to [a]

g.to.b = [g] × ([b] / ([a] + [b] + [c]))   # Portion of [g] transferred to [b]

g.to.c = [g] × ([c] / ([a] + [b] + [c]))   # Portion of [g] transferred to [c]

[a] = [a] + d.to.a + f.to.a + g.to.a

[b] = [b] + d.to.b + e.to.b + g.to.b

[c] = [c] + e.to.c + f.to.c + g.to.c

[d] = Ø   # Transferred to [a] and [b]

[e] = Ø   # Transferred to [b] and [c]

[f] = Ø   # Transferred to [a] and [c]

[g] = Ø   # Transferred to [a], [b] and [c]

[h] = [h]   # Residual fraction

(a) One matrix of random variables X,
two matrices of MEM
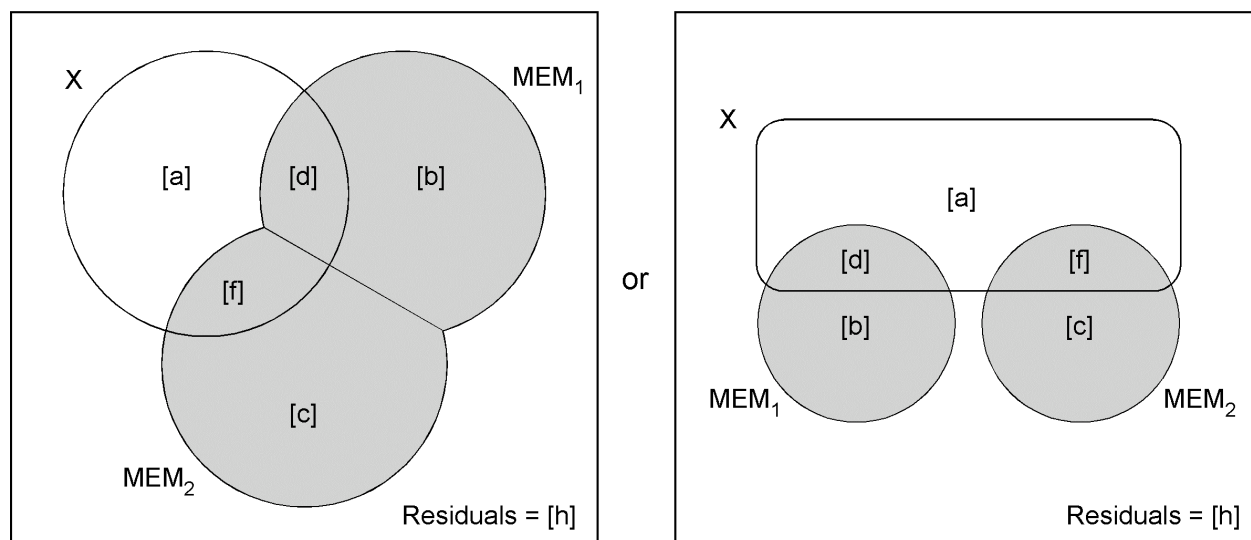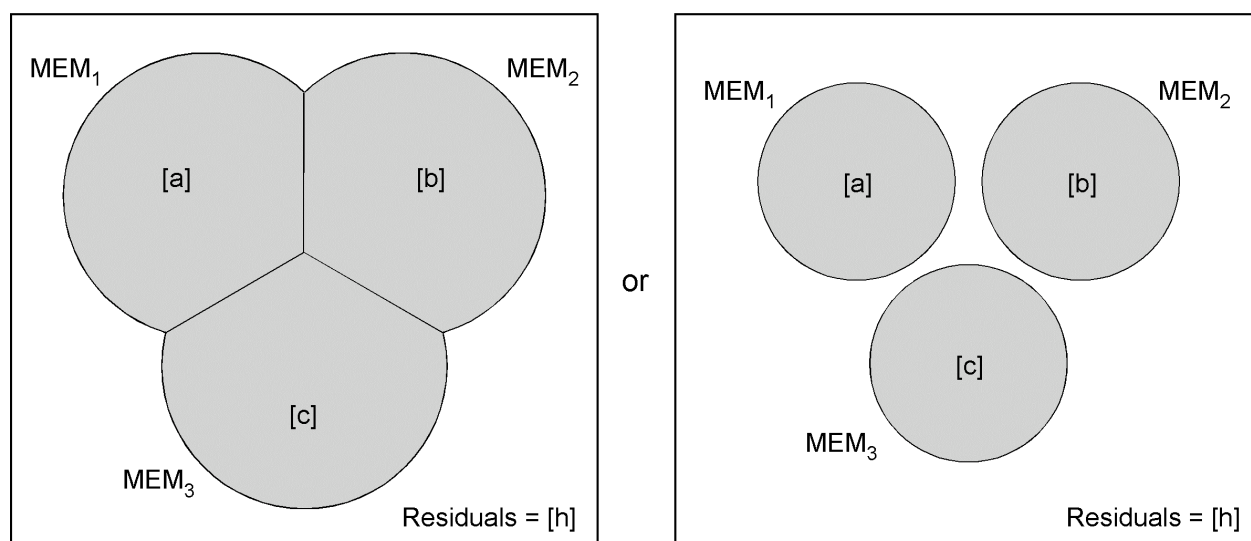

(b) Three matrices of MEM

Fig. A2. Venn diagrams illustrating the result of proportional apportioning of the shared fractions in variation partitioning involving (a) one matrix of random (e.g. environmental) variables and two matrices of spatial eigenfunctions (MEM), or (b) three matrices of spatial eigenfunctions (MEM). Alternative graphical solutions are proposed in each case. The fractions of variation explained by MEM matrices are in gray.

Table A3. Variation partitioning in the 4-matrix case, for matrices of random explanatory variables or matrices of eigenfunctions. Fractions identifiers: see Fig. A4a. Notation as in Table A1.

(a) Matrices 1 and 2 contain random explanatory variables, matrices 3 and 4 contain eigenfunction submodels

---

Hierarchical partitioning of the shared fractions (Fig. A4b)

[a] = [a]

[b] = [b]

[c] = [c] + [j]

[d] = [d]

[e] = [e]

[f] = [f] + [m]

[g] = [g] + [n]

[h] = [h]

[i] = [i]

[k] = [k]

[l] = [l] + [o]

[j] = Ø   # Transferred to [c]

[m] = Ø   # Transferred to [f]

[n] = Ø   # Transferred to [g]

[o] = Ø   # Transferred to [l]

[p] = [p]   # Residual fraction

Proportional apportioning of the shared fractions (Fig. A3a)

j.to.c = [j] × [c+f+g+l] / ([c+f+g+l]+[d+h+i+k])   # Portion of [j] transferred to [c]

j.to.d = [j] × [d+h+i+k]/ ([c+f+g+l]+[d+h+i+k])   # Portion of [j] transferred to [d]

m.to.f = [m] × [c+f+g+l] / ([c+f+g+l]+[d+h+i+k]) # Portion of [m] transferred to [f]

m.to.i = [m] × [d+h+i+k]/ ([c+f+g+l]+[d+h+i+k]) # Portion of [m] transferred to [i]

n.to.g = [n] × [c+f+g+l] / ([c+f+g+l]+[d+h+i+k]) # Portion of [n] transferred to [g]

n.to.h = [n] × [d+h+i+k]/ ([c+f+g+l]+[d+h+i+k]) # Portion of [n] transferred to [h]

o.to.k = [o] × [d+h+i+k]/ ([c+f+g+l]+[d+h+i+k]) # Portion of [o] transferred to [k]

o.to.l = [o] × [c+f+g+l] / ([c+f+g+l]+[d+h+i+k])   # Portion of [o] transferred to [l]

[c] = [c] + j.to.c

[d] = [d] + j.to.d

[f] = [f] + m.to.f

[g] = [g] + n.to.g

[h] = [h] + n.to.h

[i] = [i] + m.to.i

[k] = [k] + o.to.k

[l] = [l] + o.to.l

[j] = Ø   # Transferred to [c] and [d]

[m] = Ø   # Transferred to [f] and [i]

[n] = Ø   # Transferred to [g] and [h]

[o] = Ø   # Transferred to [k] and [l]

[p] = [p]   # Residual fraction

(b) Matrix 1 contains random explanatory variables, matrices 2, 3 and 4 contain eigenfunction submodels

---

Hierarchical partitioning of the shared fractions (Fig. A4c)

[a] = [a]

[b] = [b] + [f] + [i] + [m]

[c] = [c] + [j]

[d] = [d]

[e] = [e] + [k] + [l] + [o]

[g] = [g] + [n]

[h] = [h]

[f] = [i] = [j] = [k] = [l] = [m] = [n] = [o] = Ø   # Transferred to other fractions

[p] = [p]

Proportional apportioning of the shared fractions (Fig. A3b)

f.to.b = [f] × [b+e] / ([b+e]+[c+g])	# Portion of [f] transferred to [b]
f.to.c = [f] × [c+g] / ([b+e]+[c+g])	# Portion of [f] transferred to [c]
i.to.b = [i] × [b+e] / ([b+e]+[d+h])	# Portion of [i] transferred to [b]
i.to.d = [i] × [d+h] / ([b+e]+[d+h])	# Portion of [ji] transferred to [d]
j.to.c = [j] × [c+g] / ([c+g]+[d+h])	# Portion of [j] transferred to [c]
j.to.d = [j] × [d+h] / ([c+g]+[d+h])	# Portion of [j] transferred to [d]
k.to.e = [k] × [b+e] / ([b+e]+[d+h])	# Portion of [k] transferred to [e]
k.to.h = [k] × [d+h] / ([b+e]+[d+h])	# Portion of [k] transferred to [h]
l.to.e = [l] × [b+e] / ([b+e]+[c+g])	# Portion of [l] transferred to [e]
l.to.g = [l] × [c+g] / ([b+e]+[c+g])	# Portion of [l] transferred to [g]
m.to.b = [m] × [b+e] / ([b+e]+[c+g]+[d+h])	# Portion of [m] transferred to [b]
m.to.c = [m] × [c+g] / ([b+e]+[c+g]+[d+h])	# Portion of [m] transferred to [c]
m.to.d = [m] × [d+h] / ([b+e]+[c+g]+[d+h])	# Portion of [m] transferred to [d]
n.to.g = [n] × [c+g] / ([c+g]+[d+h])	# Portion of [n] transferred to [g]
n.to.h = [n] × [d+h] / ([c+g]+[d+h])	# Portion of [n] transferred to [h]
o.to.e = [o] × [b+e] / ([b+e]+[c+g]+[d+h])	# Portion of [o] transferred to [e]
o.to.g = [o] × [c+g] / ([b+e]+[c+g]+[d+h])	# Portion of [o] transferred to [g]
o.to.h = [o] × [d+h] / ([b+e]+[c+g]+[d+h])	# Portion of [o] transferred to [h]

[b] = [b] + f.to.b + m.to.b + i.to.b

[c] = [c] + j.to.c + f.to.c + m.to.c

[d] = [d] + j.to.d + i.to.d + m.to.d

[e] = [e] + k.to.e + l.to.e + o.to.e

[g] = [g] + l.to.g + n.to.g + o.to.g

[h] = [h] + k.to.h + n.to.h + o.to.h

[f] = [i] = [j] = [k] = [l] = [m] = [n] = [o] = Ø   # Transferred to other fractions

[p] = [p]   # Residual fraction

_____

(c) Four matrices of eigenfunction submodels

Hierarchical partitioning of the shared fractions (Fig. A4d)

[a] = [a] + [e] + [g] + [h] + [k] + [l] + [n] + [o]

[b] = [b] + [f] + [i] + [m]

[c] = [c] + [j]

[d] = [d]

[e] = [f] = [g] = [h] = [i] = [j] = [k] = [l] = [m] = [n] = [o] = Ø   # Transferred to other fractions

[p] = [p]]   # Residual fraction

Proportional apportioning of the shared fractions (Fig. A3c)

e.to.a = [e] × [a] / ([a]+[b])   # Portion of [e] transferred to [a]

e.to.b = [e] × [b] / ([a]+[b])   # Portion of [e] transferred to [b]

f.to.b = [f] × [b] / ([b]+[c])   # Portion of [f] transferred to [b]

f.to.c = [f] × [c] / ([b]+[c])   # Portion of [f] transferred to [c]

g.to.a = [g] × [a] / ([a]+[c])   # Portion of [g] transferred to [a]

g.to.c = [g] × [c] / ([a]+[c])   # Portion of [g] transferred to [c]

h.to.a = [h] × [a] / ([a]+[d])   # Portion of [h] transferred to [a]

h.to.d = [h] × [d] / ([a]+[d])   # Portion of [h] transferred to [d]

i.to.b = [i] × [b] / ([b]+[d])   # Portion of [i] transferred to [b]

i.to.d = [i] × [d] / ([b]+[d])   # Portion of [i] transferred to [d]

j.to.c = [j] × [c] / ([c]+[d])   # Portion of [j] transferred to [c]

j.to.d = [j] × [d] / ([c]+[d])   # Portion of [j] transferred to [d]

k.to.a = [k] × [a] / ([a]+[b]+[d])   # Portion of [k] transferred to [a]

k.to.b = [k] × [b] / ([a]+[b]+[d])   # Portion of [k] transferred to [b]

k.to.d = [k] × [d] / ([a]+[b]+[d])   # Portion of [k] transferred to [d]

l.to.a = [l] × [a] / ([a]+[b]+[c])   # Portion of [l] transferred to [a]

l.to.b = [l] × [b] / ([a]+[b]+[c])   # Portion of [l] transferred to [b]

l.to.c = [l] × [c] / ([a]+[b]+[c])   # Portion of [l] transferred to [c]

m.to.b = [m] × [b] / ([b]+[c]+[d])   # Portion of [m] transferred to [b]

m.to.c = [m] × [c] / ([b]+[c]+[d])   # Portion of [m] transferred to [c]

m.to.d = [m] × [d] / ([b]+[c]+[d])   # Portion of [m] transferred to [d]

n.to.a = [n] × [a] / ([a]+[c]+[d])   # Portion of [n] transferred to [a]

n.to.c = [n] × [c] / ([a]+[c]+[d])   # Portion of [n] transferred to [c]

n.to.d = [n] × [d] / ([a]+[c]+[d])   # Portion of [n] transferred to [d]

o.to.a = [o] × [a] / ([a]+[b]+[c]+[d])   # Portion of [o] transferred to [a]

o.to.b = [o] × [b] / ([a]+[b]+[c]+[d])   # Portion of [o] transferred to [b]

o.to.c = [o] × [c] / ([a]+[b]+[c]+[d])   # Portion of [o] transferred to [c]

o.to.d = [o] × [d] / ([a]+[b]+[c]+[d])   # Portion of [o] transferred to [d]

[a] = [a] + e.to.a + g.to.a + h.to.a + k.to.a + l.to.a + n.to.a + o.to.a

[b] = [b] + e.to.b + f.to.b + i.to.b + k.to.b + l.to.b + m.to.b + o.to.b

[c] = [c] + f.to.c + g.to.c + j.to.c + l.to.c + m.to.c + n.to.c + o.to.c

[d] = [d] + h.to.d + i.to.d + j.to.d + k.to.d + m.to.d + n.to.d + o.to.d

[e] = [f] = [g] = [h] = [i] = [j] = [k] = [l] = [m] = [n] = [o] = Ø   # Transferred to other fractions

[p] = [p]]   # Residual fraction
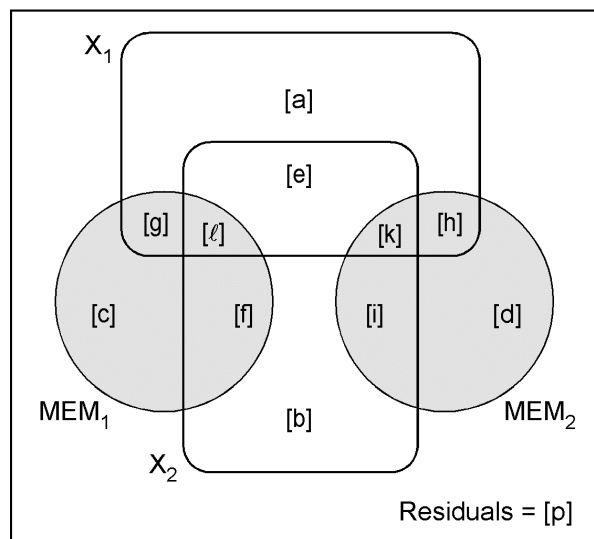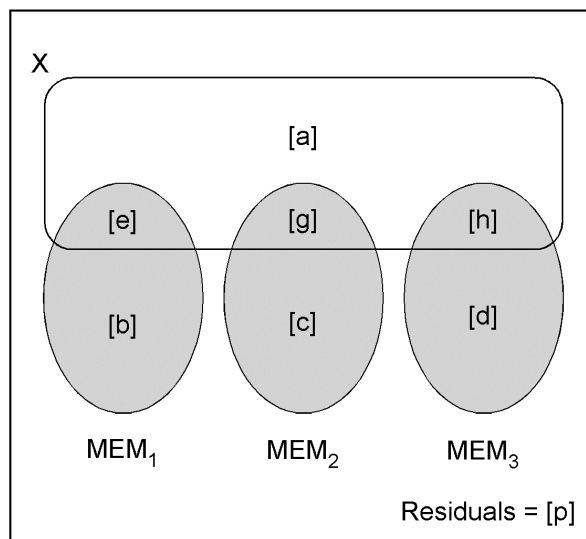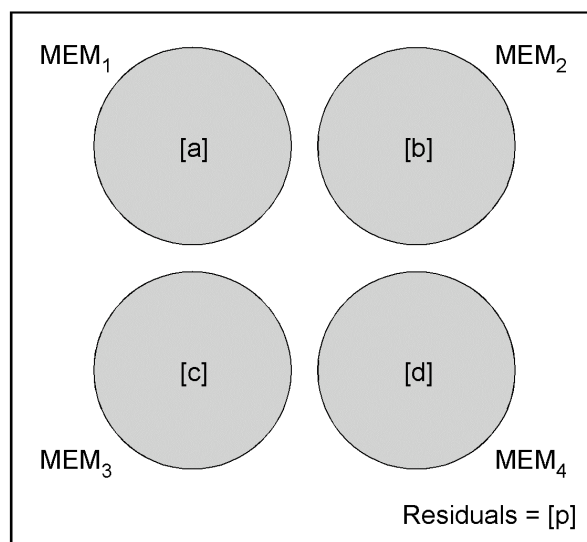

Fig. A3. Venn diagrams illustrating the result of proportional apportioning of the shared fractions in variation partitioning involving (a) two matrices of random (e.g. environmental) variables and two matrices of spatial eigenfunctions (MEM), (b) one matrix of random (e.g. environmental) variables and three matrices of spatial eigenfunctions (MEM), or (c) four matrices of spatial eigenfunctions (MEM). The fractions of variation explained by MEM matrices are in gray.
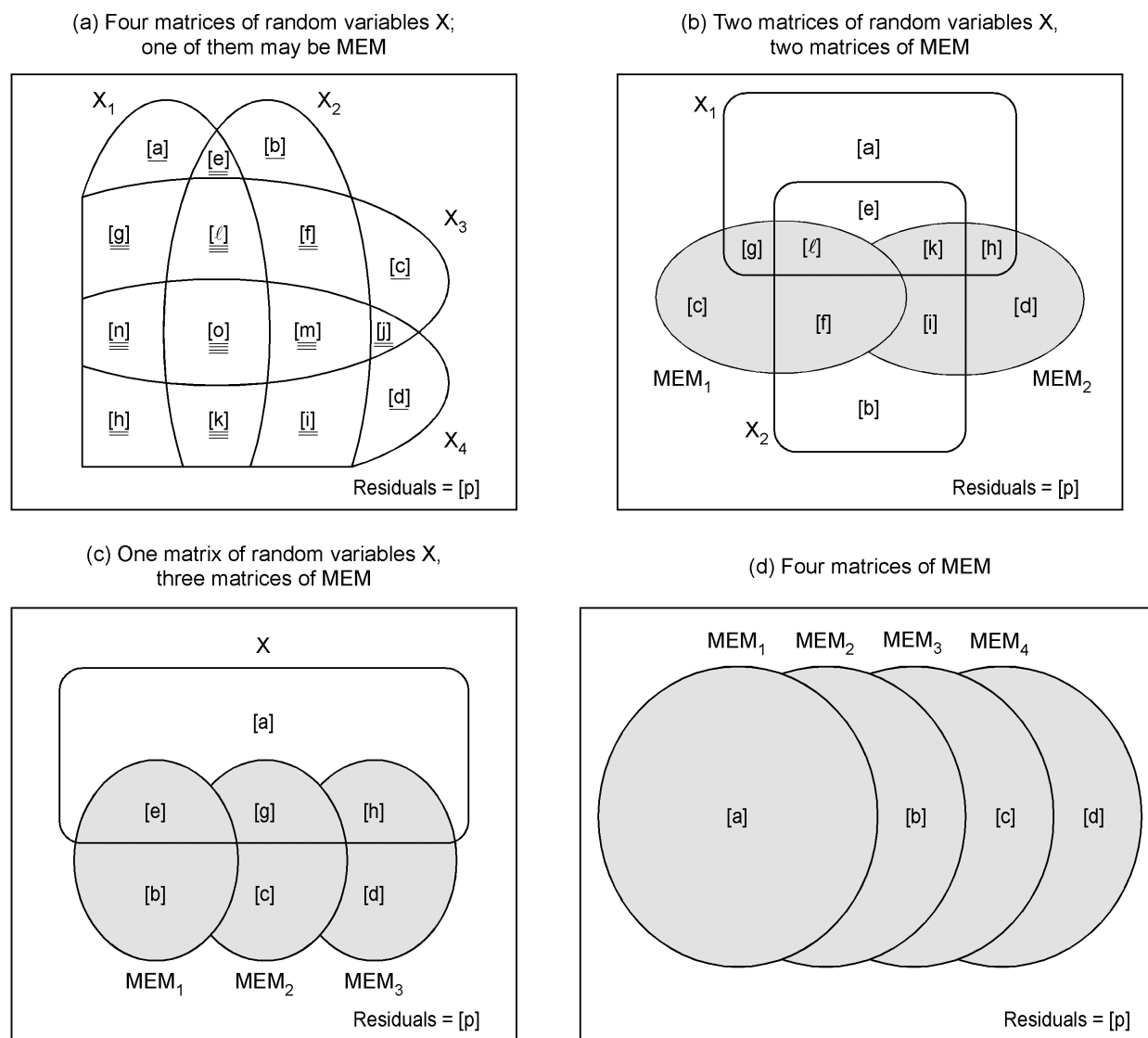
Fig. A4. Venn diagrams of variation partitioning results for four explanatory matrices. (a) Classical partitioning; the number of lines underneath the fraction identifiers corresponds to the number of explanatory matrices **X** they intersect. (b, c, d) Result of hierarchical partitioning.