

# Modelling the effect of directional spatial ecological processes at different scales

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**Abstract** During the last 20 years, ecologists discovered the importance of including spatial relationships in models of species distributions. Among the latest developments in modelling how species are spatially structured are eigenfunction-based spatial filtering methods such as Moran's eigenvector maps (MEM) and principal coordinates of neighbour matrices (PCNM). Although these methods are very powerful and flexible, they are only suited to study distributions resulting from non-directional spatial processes. The asymmetric eigenvector map (AEM) framework, a new eigenfunction-based spatial filtering method, fills this theoretical gap. AEM was specifically designed to model spatial structures hypothesized to be produced by directional spatial processes. Water currents, prevailing

wind on mountainsides, river networks, and glaciations at historical time scales are some of the situations where AEM can be used. This paper presents three applications of the method illustrating different combinations of: sampling schemes (regular and irregular), data types (univariate and multivariate), and spatial scales (metres, kilometres, and hundreds of kilometres). The applications include the distribution of a crustacean (*Atya*) in a river, bacterial production in a lake, and the distribution of the copepodite stages of a crustacean on the Atlantic oceanic shelf. In each application, a comparison is made between AEM, MEM, and PCNM. No environmental components were included in the comparisons. AEM was a strong predictor in all cases, explaining 59.8% for *Atya* distribution, 51.4% of the bacterial production variation, and 38.4% for the copepodite distributions. AEM outperformed MEM and PCNM in these applications, offering a powerful and more appropriate tool for spatial modelling of species distributions under directional forcing and leading to a better understanding of the processes at work in these systems.

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## Introduction

The importance of spatial structures for the interpretation of ecological data is now widely recognized (Legendre and Fortin 1989; Legendre 1993; Peterson and Parker 1998; Legendre and Legendre 1998; Fortin and Dale 2005). Indeed, environmental forcings of many kinds, which have spatial components, affect the spatial distributions of species in

ecosystems. This idea has long been understood by ecologists; it forms the classical environmental control model which is based on ecological niche theory (Hutchinson 1957). In this paper, we focus on directional physical processes hypothesized to influence species distributions, either directly by transporting organisms or indirectly by transporting particles, nutrients, and other elements on which the organisms depend.

For example, dominant winds or currents generate directional gradients by advecting motile organisms and affecting the physical conditions of sessile organisms. Other directional patterns are found in river networks where water is flowing downstream, carrying chemicals, particles and planktonic organisms, whereas nektonic organisms may be migrating against the prevailing current.

Some recently developed methods of analysis incorporate the spatial relationships into models of the response data. In particular, methods developed by geostatisticians consider both the spatial structures and the physical gradients (Cressie et al. 2006; ver Hoef et al. 2006; Peterson et al. 2007; Peterson and ver Hoef 2010; ver Hoef and Peterson 2010). These methods seem suitable and well adapted to analyse whole networks of streams or rivers; however, geostatistical approaches may not produce strong predictive models when only small sections of streams are sampled, which is often the case in ecological studies.

The development of the principal coordinates of neighbour matrices (PCNM; Borcard and Legendre 2002; Borcard et al. 2004) and its generalization, the Moran's eigenvector maps (MEM; Dray et al. 2006) framework, provided powerful tools to study the spatial structures of individual species and communities at multiple scales and in greater detail. These methods could be applied to directional spatial processes found in streams and rivers or along ocean currents, but their failure to consider the directional nature of these processes is a shortcoming. In these methods, the influence of broad-scale gradients must be removed (the data must be detrended) prior to analysis, thereby excluding that portion of the spatial structure (the gradient information) from the analysis. To solve this problem, Blanchet et al. (2008b) proposed the asymmetric eigenvector maps (AEM) method, an eigen-based spatial filtering method (Griffith and Peres-Neto 2006) which differs from the MEM framework.

When performing a spatial analysis using eigenfunctions, the sampled site coordinates or the connexions among the sites are decomposed into a number of spatial variables (eigenvector maps, or eigenfunctions). A detailed explanation of how eigenvector maps are constructed is presented by Dray et al. (2006) for the MEM framework and by Blanchet et al. (2008b) for the AEM framework. After their construction, the resulting spatial variables are used in linear models [multiple regression for univariate, canonical redundancy analysis (RDA) for multivariate

response data] like any other explanatory variable to model a response variable or data table. These two frameworks generate a large number of explanatory variables, often one variable less than the number of sites. It is thus important to choose the best variable(s) to model the response with an appropriate variable selection procedure such as the one proposed by Blanchet et al. (2008a).

The strength of spatial eigenfunctions is that they can be used to analyse either univariate or multivariate response data. They are also orthonormal, each spatial variable being perpendicular to the others. This is a convenient property because it ensures that there is no collinearity among the spatial eigenfunctions.

The weakness of spatial eigenfunction analysis is the difficulty of interpreting each variable independently. Various strategies have been tried to overcome that problem; the most commonly used are presented in Borcard et al. (2004).

In the present paper, our objective is to illustrate the application of AEM analysis to real ecological data using three illustrative datasets which come from different types of ecosystems (stream, fluvial lake, and ocean) and represent different spatial scales (metres, kilometres, and hundreds of kilometres), contrasting sampling designs (regular and irregular two-dimensional surfaces), and univariate or multivariate data. The three datasets have in common that directional water currents influence the response data, which generates a spatial asymmetry in the response. To show the efficiency of AEM analysis, the results will be compared to analyses carried out using the MEM and PCNM frameworks. The stream illustration assesses the spatial distribution of the crustacean *Atya innocous* in a reach of Capesterre River, Guadeloupe. The fluvial lake example is a study of bacterial production in Lake St. Pierre, Québec, Canada. The ocean example models the distribution of the copepodite stages of the crustacean *Calanus finmarchicus* along the eastern shores of Newfoundland and Labrador. These examples offer the opportunity to give extra practical details about the application of the AEM method.

The goal of this paper is to compare spatial modelling methods in different ecological situations and measure the importance of directional spatial processes in each system. The correct identification of directional processes will refine our understanding of the ecological processes at work in the ecosystems. Environmental variables were not included in the analyses in order to place the emphasis on the spatial components, either directional or isometric.

## Basic theory of the AEM method

A detailed account of the construction of AEM is found in Blanchet et al. (2008b). The steps are summarized in Table A1 and Fig. A1 (Electronic Appendix A). AEM variables are spatial eigenvectors, in the same way as MEMs. Their

construction involves a connexion diagram among sampling sites, the connexions being directional in AEM, which is not the case in MEM or PCNM. As in MEM, the links can receive weights representing the ease of communication of matter or information among the sites; the links in AEM can be based, for example, on geographic distances, flow models, or current speed. AEMs can be used in models in the same way as researchers use variables from the MEM or PCNM frameworks.

When constructing AEMs, there are very often  $n - 1$  variables created,  $n$  being the number of sites. This situation makes it impossible to test the significance of a regression model that uses all AEM variables because of the lack of degrees of freedom. A part of the AEMs model positive spatial correlation while the remaining AEMs model negative spatial correlation. In some studies, it is clear that only the AEMs modelling positive spatial correlation are of interest and should be used. For studies where the exclusive use of AEMs modelling positive spatial correlation is not clear, Blanchet et al. (2008a) described a procedure which will be used in the ecological illustrations herein, where MEMs and AEMs are used and compared. The approach consists in separating the set of spatial variables in two portions, one modelling positive spatial correlation and the other negative spatial correlation. The two groups of MEM or AEM variables are then considered as potential explanatory variables in the analysis. The two groups are tested separately for significance and the results of the two tests are combined.

Associated with each AEM eigenfunction is an eigenvalue. In contrast to the MEM framework, all AEM eigenvalues are positive, owing to their method of construction (Blanchet et al. 2008b). AEM eigenvalues are not direct measures of spatial correlation, as is the case for MEM eigenvalues which are perfectly correlated to Moran's  $I$ . The response variables need not be detrended when using AEM, contrary to PCNM and MEM eigenfunctions: the trend is an important component of directional spatial patterns, so it must be kept in the data to allow it to be brought out by the AEM analysis. In contrast, a significant spatial trend can influence the selection of PCNM and MEM variables by forcing the selection of particular eigenfunctions (in the case of regular grids, the eigenfunctions with odd ranks model gradients). With AEM, the direction of the flow, which is often correlated with the trend, is known a priori and is considered in the construction of the directional spatial variables.

## Illustrations using real ecological data

### Method of analysis

Although the three illustrative datasets described in the next sections are very different from one another, we are

going to apply the same analytical procedure when comparing the results of the different spatial modelling methods. This offers the dual advantage of showing how each method behaves in an asymmetric directional context and of rendering the three illustrations comparable.

In the three ecological illustrations, the set of eigenfunctions was used to model the response variable(s) as follows. First, a global test using all spatial variables of the considered kind was computed. Because the MEM and AEM frameworks generate too many spatial variables, the set of eigenfunctions was divided in two on the basis of their spatial correlation (positive and negative), as described in the previous section. A detailed explanation of how to split the AEM eigenfunctions in two groups is presented in the paragraph explaining the construction of AEM (three paragraphs down). In all examples, there was no prior information about the expected sign of the spatial correlation; both sets were thus tested and a Šidák correction (Šidák 1967) was applied to assess the global significance of the two sets of variables. The  $P$  values after correction will be written  $P_{\text{corr}}$  to differentiate them from  $P$ , a  $P$  value calculated prior to correction. If the model was significant at the 5% level, a forward selection procedure was applied, using two stopping criteria as proposed by Blanchet et al. (2008a), to obtain a parsimonious model. Forward selection kept choosing variables until either a given significance level (5% was used in our analyses) was reached or the adjusted coefficient of multiple determination ( $R_a^2$ ; see Eq. 1) of the reduced model reached the value for the full model containing all variables.

A single set of PCNM variables was constructed for each ecological example. The truncation distance was the smallest distance that kept all the sites linked together, except for the Capesterre River example where we used  $\sqrt{2}$  as the truncation distance (the length of the diagonal in a regular, square, unit grid).

For each illustration, the connexion diagram used to construct spatial variables through the MEM framework reflected the knowledge we had of the study area; it is thus considered optimal and will not be subject to change. The different sets of spatial variables constructed diverged only by the weights given to the links. For all examples, one set was constructed with equal weights for all links. For the first and second illustrations, weights were functions of the distance. Weights were computed by applying two functions from Dray et al. (2006) to the lengths of the links:  $f_1(d_{ij}) = 1 - (d_{ij}/\max(d_{ij}))^\alpha$  and  $f_2(d_{ij}) = 1/d_{ij}^\alpha$ . Exponents  $\alpha = 1$  and  $\alpha = 2$  were considered for each function.  $f_1$  is a concave-down function whereas  $f_2$  is concave-up. The function and exponent combination that produced the best explanation (highest  $R_a^2$ ) was selected (Tables B1 and C1,

Appendices B, C). In the third illustration (*C. finmarchicus* data), along-shelf geostrophic current speed was used instead of distance to weight the edges linking the sites. The mean current speed calculated between two linked sites was used to weight each edge of the connexion diagram. After calculation of the weights, some of them had negative values; these values were replaced by 0. Because a higher current speed means a stronger connexion between the sites, a different weighting function was used for this example:  $f_3(d_{ij}) = (d_{ij}/\max(d_{ij}))^\beta$ .  $\beta$  was set at 0.5 (concave-up), 1 (linear), or 2 (concave-down); the value of  $\beta$  that produced the best explanation (highest  $R_a^2$ ) was selected (Tables D1, Appendix D).

The connexion diagrams used to construct eigenfunctions in the AEM framework were the same as in MEM. The optimal combinations of function and exponent were recomputed for each AEM application (Tables B1, C1 and D1, Appendices B, C and D). To divide the spatial variables into positively and negatively correlated sets, Moran's  $I$  were calculated for each eigenfunction following Gittleman and Kot (1990). This procedure allows the use of an asymmetric distance matrix in the calculation of the Moran's  $I$  coefficients. The distance matrix used in this calculation was constructed from the weighted links of the connexion diagram; Fig. A2 (Appendix A) describes the procedure in detail. If the observed value was higher than the expected  $I$  value under the hypothesis of absence of spatial correlation, the eigenfunction was considered to model positive spatial correlation; otherwise it was considered to be negatively autocorrelated.

Comparisons among modelling methods was done through variation partitioning (Borcard et al. 1992). The fractions of variation were measured by adjusted  $R$  squares ( $R_a^2$ ). The equation to calculate  $R_a^2$  is (Ezekiel 1930; Zar 1999, Eq. 20.23):

$$R_a^2 = 1 - \frac{n-1}{n-m-1}(1-R^2). \quad (1)$$

where  $n$  is the sample size and  $m$  the number of explanatory variables.  $R^2$  is the coefficient of multiple determination, computed as the sum of squares explained by the model divided by the total sum of squares. Ohtani (2000) has shown that  $R_a^2$  is an unbiased estimator of the contribution of a set of explanatory variables  $X$  to the explanation of  $y$ . Peres-Neto et al. (2006) have shown that  $R_a^2$  also has that property in canonical analysis. Each independent fraction (called [a], [b], and [c] in this paper) was tested with 1,000 permutations; the  $P$  value is given. The significance level used was 0.05.

For all ecological examples, the PCNM and MEM analyses were carried out on detrended response variables if a linear trend in the direction of the hypothesized spatial process was significant at the 5% level (Borcard and

Legendre 2002). In the ocean illustration, because the response data are multivariate, the trend was removed from each response variable (copepodite stage) separately after verifying that a linear model constructed by RDA with all copepodite stages as the response and the geographic coordinates as the explanatory data was significant. AEM analysis was always conducted on non-detrended data. Because of this divergence, we carried out variation partitioning analysis using the non-detrended data as response variable(s), and added the linear trend as a supplemental explanatory variable in the variation partitioning analysis when it was significant.

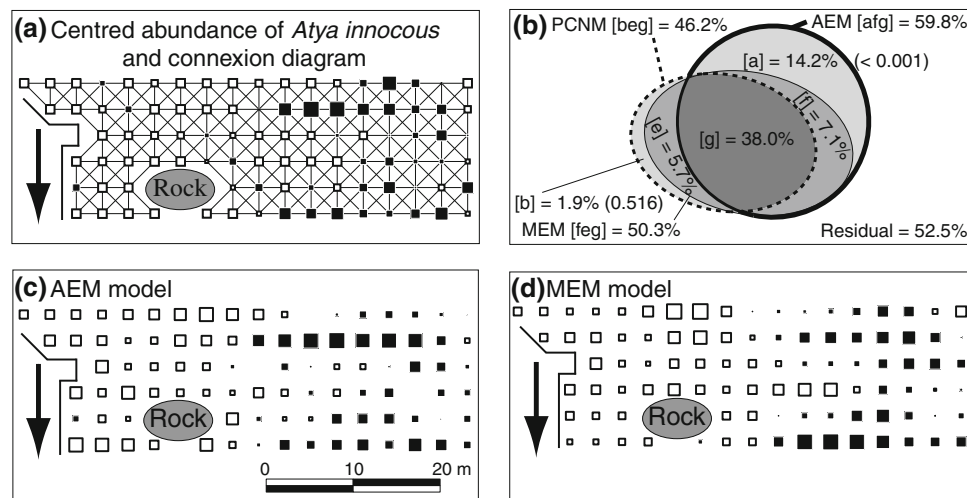
#### *River (regular grid): spatial microdistribution of a crustacean in Capesterre River (Guadeloupe)*

The microdistribution of a crustacean species, *A. innocous* (Atyidae), was studied in a mountain reach of Rivière Capesterre (16°4'3"N, 61°35'40"W) on Basse-Terre, the volcanic portion of Guadeloupe, French West Indies. Because one must work on foot in the river, the study was carried out during the dry season when current velocity was moderate. The river reach was sampled in 94 contiguous quadrats of 3 × 3 m forming a regular grid, spatially referenced on a map. Beginning downstream, electric fishing was done using a portable electrofishing device (DEKA Gerätebau, Marsberg, Germany). The low water conductivity in this type of tropical river allowed precise application of electrofishing with limited spatial influence of the anode. The initial purpose of this study was to estimate the links between the presence of *Atya* and physical microhabitat variables. Small buckets were positioned at each site to allow the crustaceans to be released after counting.

We did not find any transformation capable of normalizing the distribution of the response variable. The only significant trend ( $P < 0.001$ ) in the abundance data was perpendicular to the direction of flow. Because there was no significant trend in the direction of flow ( $P = 0.361$ ), the data were not detrended. The 53 PCNMs together explained 47.6% ( $R_a^2$ ) of the abundances of *A. innocous* ( $P < 0.001$ ). After forward selection, the six selected PCNMs explained 46.2% of the variation of the *Atya* data.

The construction of spatial variables using the MEM and AEM frameworks was based on the connexion diagram presented in Fig. 1a. The best set of variables created through the MEM framework (using function  $f_2$ ,  $\alpha = 1$ ) gave a global  $R_a^2$  of 52.7% of the *Atya* data ( $P_{\text{corr}} = 0.002$ ) and were positively autocorrelated. When the forward selection procedure was applied, six MEMs were selected (#1, 12, 13, 16, 25, and 34, presented in Fig. B2, Appendix B); they explained 50.4% of the variation ( $R_a^2$ ) of the data ( $P < 0.001$ ). The fitted values of the *Atya* model created with the six selected MEM variables are shown in Fig. 1d.





**Fig. 1** Spatial modelling of *Atya innocuus* distribution in Capesterre River, Guadeloupe. **a** Site locations and connexion diagram used to generate the AEMs and MEMs where the arrow shows the river flow direction, square bubbles represent centred data (black are positive values, white are negative, and size of squares is related to the associated value), sites are spaced by 3 m. Figure A3 (Appendix A) shows how edges linking sites perpendicular to the current were used to build AEMs. The arrow shows the river flow direction. **b** Variation

partitioning results between the selected AEMs, MEMs, PCNMs illustrated by a Venn diagram. Fraction sizes are approximations. Letters in brackets correspond to individual fractions of explained variation; values are  $R_a^2$ . Values in parentheses represent the  $P$  values of independent fractions. **c** Fitted values of the selected AEMs. **d** Fitted values of the selected MEMs. The fitted values of the selected PCNMs are not presented because they are very similar to **(d)**

The fitted values of the PCNM model (not shown) are very similar.

For variables from the AEM framework, the best model (using function  $f_2$ ,  $\alpha = 1$ ) gave a global  $R_a^2$  of 60.3% ( $P_{\text{corr}} = 0.002$ ) and was positively autocorrelated. This model offers a better depiction of *Atya* distribution than PCNMs and MEM do, with  $R_a^2 = 47.6$  and 52.7%, respectively (Table B1, Appendix B). Twelve AEM variables were selected by forward selection (#1, 2, 4, 9, 10, 11, 25, 31, 33, 35, 42, and 43 presented in Fig. B1, Appendix B). This reduced the model  $R_a^2$  to 59.8% of the variation of the *Atya* data. The fitted values of this model are shown in Fig. 1c. Variation partitioning shows that the AEM model explains the true spatial variation of *Atya* far better than the MEM and PCNM models (Fig. 1b) The variation of the undetrended data explained by the AEM model above and beyond that explained by MEMs and PCNMs is 14.2% ( $P < 0.001$ ). In comparison, the fraction explained exclusively by the MEM model, above and beyond that explained by the AEM model, is 5.3% ( $P = 0.010$ ), and the fraction explained exclusively by the PCNM model, above and beyond that explained by the AEM model, is 7.6% ( $P = 0.003$ ). Detailed results for the other weighting functions considered are presented in Table B1 (Appendix B).

The *Atyidae* prawn family is composed of widespread tropical and temperate crustaceans living mainly in running freshwaters. Most atyids have strong anatomic originalities that determine their food uptake. Those belonging to genus *Atya* are very specialized: instead of using claws like the

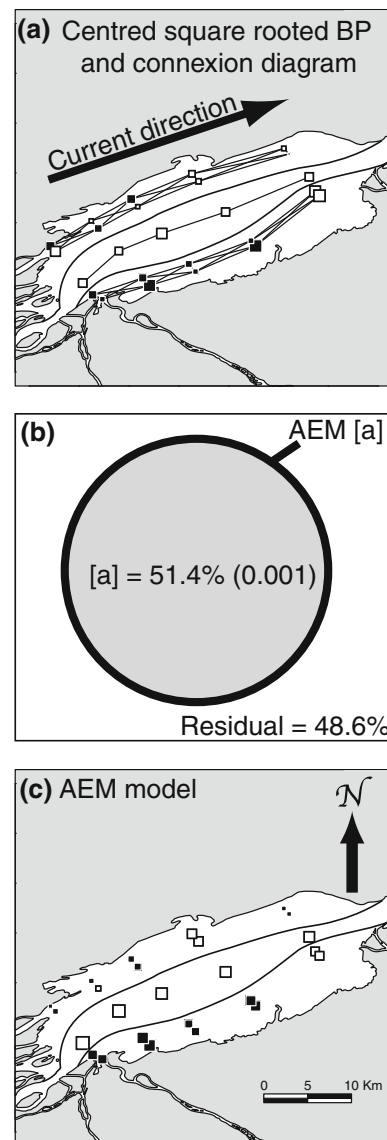
other Caribbean crustaceans, these animals have the first two pereopods ending with a big brush made of long bristles. These bristles open like umbrellas in high velocity waters, collecting suspended matter. This species is unique among the *Malacostraca* in having representatives that filter passively by means of the chelipeds (Fryer 1977). Among the three statistical methods compared in this paper, an oriented flow directional method like AEM extracts a significant part of the variation of the *Atya* spatial distribution ( $R_a^2 = 59.8\%$ ), greater than the MEM and PCNM methods do (50.4 and 46.2% respectively). Three original characteristics of *Atya* biology are particularly well described by the AEM model: (1) the *Atya* distribution is determined by water flow; the effect of the strictly directional component (water flow direction) can be evaluated as the [a] fraction in Fig. 1b; it represents here 14.2% of the variation of *Atya*; (2) the *Atya* distribution depends on the size of stream pools (Pyron et al. 1999), which, in fast flowing Caribbean rivers, are mainly located along one of the river banks, where the main flow occurs. This generates a non-even distribution of *Atya* individuals between the river banks. In a separate analysis, this lateral trend was estimated to represent 25.8% of the total variation; and (3) *Atya* is gregarious and individuals do not have distinct territories as found in other tropical crustaceans, *Palaeomonidae* for example. The result is a clumped distribution of *Atya* in the river with strong variations of abundances at very fine spatial scale. The third significant fraction of variation detected by AEM, the fraction [f + g] shared with MEM, explains 45.0% of the total variation; it

represents non-oriented spatial processes like aggregations of *Atya* individuals. Figure 1c shows the ability of the AEM model to predict null abundances in the vicinity of high densities of organisms and strong differences at very small scale. Because of its ability to combine longitudinal and lateral orientated processes, the AEM model may be considered as having greater sensitivity than the MEM model for restitution of an aggregative species distribution. These results are very consistent with *Atya* ecology and make this method very attractive for detecting the effects of directional processes on species distributions. This could be of primary importance in river ecology where strong flow directional processes can and do occur.

#### Fluvial Lake: bacterial production in Lake St. Pierre (Québec, Canada)

Lake St. Pierre (LSP) is a 300-km<sup>2</sup> widening of the St. Lawrence River (46°11'N, 72°50'W), located about mid-way between Montréal and Québec City, QC, Canada. This fluvial lake has an average depth of 3 m. Water is relatively slow flowing ( $<0.5 \text{ m s}^{-1}$ ) with the exception of the deep shipping channel which bisects the lake (12 m depth, water velocity  $>0.5 \text{ m s}^{-1}$ ). The lake has several juxtaposed and chemically distinct water masses that mix very little laterally (Frenette et al. 2006). The main water masses are: (1) North, draining the nutrient rich, brown soft waters of the Ottawa River; (2) Central, the relatively low dissolved organic carbon (DOC), clear waters of the Great Lakes that funnel through the main shipping channel; and (3) South, from three relatively turbid and nutrient-rich tributaries heavily impacted by agriculture (Vis et al. 2007). The southern mass is more heterogeneous than presented here, but for the present study, only the three main water masses are considered: North, Central, and South. Although the dominant form of organic C available to bacteria is of allochthonous origin, local carbon production by extensive macrophyte communities may be important in the shallow North and South masses.

Heterotrophic bacterial carbon production (BP) is a function of many controlling factors, nutrient availability and carbon lability being predominant. In flowing systems, nutrients can be altered by upstream processing (Newbold et al. 1982), influencing BP rates downstream (Maranger et al. 2005). In the case of a fluvial but heavily vegetated system such as Lake St. Pierre, local production of more labile substrates will influence the relative carbon quality available to the microbes not only at that site but also at sites further downstream (Wetzel 1992). Benthic exchange will also be important given the shallow nature of the system (Hopkinson et al. 1998). The original objective of this study was to look at the spatial heterogeneity of the bacterial production among the water masses. Sampling



**Fig. 2** Spatial modelling of bacterial production (BP) in Lake St. Pierre (white area of maps in **a** and **c**). **a** Site locations and connexion diagram used to generate the AEM eigenfunctions considering that current direction was used to generate AEMs. Square bubbles represent centred square-root transformed data (black are positive values, white are negative, size of squares is related to the associated value). Figure A3 (Appendix A) shows how edges linking sites within each water mass were used to build AEMs. **b** Venn diagram presenting the variation explained by the selected AEMs. Fraction sizes are approximations. The letter in brackets, [a], represents the fraction of explained variation; the value is the  $R_a^2$ . The value in parentheses is the associated  $P$  value. **c** Fitted values of the selected AEM eigenfunctions. Limits of the water masses shown in **a** and **c** are approximate

was carried out bimonthly in the summer of 2005 and covered the entire lake in a grid pattern of five longitudinal lines and five transects along the axis of flow (Fig. 2a). For this analysis, the sampling units obtained on 18 August 2005 were used. Bacterial production was measured by

radioactive leucine incorporation using the micro-tube centrifugation technique (Smith and Azam 1992). AEM eigenfunction modelling is perfectly suited for this study given the directionality of carbon processing of the bacterial community along the flow axis, the spatial heterogeneity of the system, and the sampling design. Sampling units for nutrient and DOC were obtained at the exact same time; methods for analysis are described elsewhere (Blanchet et al. in press).

When we compared the amount of variation in bacterial production explained using the spatial variables generated from different modelling approaches (PCNM, MEM, and AEM), the most significant set of spatial predictors was the spatially directed AEM (Table C1, Appendix C). For AEM modelling,  $f_1$  with  $\alpha = 1$  yielded the best results. The full set of positively autocorrelated variables explained 54.0% ( $R_a^2$ ) of the variation in bacterial production. A parsimonious and highly significant model was created with 4 AEMs (# 1, 2, 4, and 10, presented in Fig. C1, Appendix C) chosen by forward selection ( $R_a^2 = 51.4\%$ ; Fig. 2c), whereas the multidirectional MEMs, built with  $f_2$  and  $\alpha = 2$ , explained a slightly smaller amount of variation ( $R_a^2 = 49.4\%$ ), but was statistically not significant ( $P_{\text{corr}} = 0.071$ ). The PCNM model was not significant for this example ( $P = 0.763$ ). Detailed results for the other weighting functions considered are presented in Table C1.

None of the measured environmental variables were able to predict BP as well as the directional spatial AEM descriptors. Bacterial production ( $\mu\text{gC L}^{-1} \text{ h}^{-1}$ ) was not related to the various nitrogen forms in the system, which were spatially highly variable (nitrate range: 0–157  $\mu\text{g L}^{-1}$ , total nitrogen range: 293–563  $\mu\text{g L}^{-1}$ ), although there was a slight negative tendency with nitrate. BP was weakly related to total phosphorus (TP) explaining only 17.8% of the variation ( $R_a^2$ ) despite the wide range in concentrations (15–56  $\mu\text{g L}^{-1}$ ). There was a slightly stronger significant relationship between BP and DOC with an  $R_a^2 = 25.4\%$ . However, AEM modelling clearly shows the importance of water flow in explaining the spatial variation of bacterial production in Lake St. Pierre.

We expected flow direction to influence the variation in bacterial production, but the fact that the selected eigenfunctions created from directional spatial connectivity alone explained 51.4% of the observed among-site variation was a surprise. The strong differences in source water among the water masses combined with the relatedness of the active bacterial communities from upstream to downstream is one possible reason why the directional spatial model explains so much of the variation among sampling sites. Compared to the other masses, the Central water flows more rapidly and likely resulted in similar substrate availability and bacterial community composition resulting in relatively homogeneous heterotrophic BP from upstream

to downstream. This relatedness in the composition of the communities has been observed elsewhere (Masin et al. 2003).

There was considerably less variation in nutrient and DOC concentrations in the Central than in the other water masses, which explains the relative homogeneity in both the measured and AEM model of BP rates (Fig. 2a, c). The overall higher rates and relative decrease in the observed and modelled rates of BP are likely to be a function of the changing abiotic conditions in space, which influenced BP. The waters entering the North and South masses are richer in nutrients; however, the widening of the river reduces the flow of these water masses, increasing algal uptake rates, which results in a greater potential source of labile carbon for bacteria and greater benthic exchange for essential nutrients such as nitrogen and phosphorus. Consequently, nutrients are depleted along the axis of flow if there are no external inputs ultimately impinging on C quality and bacterial productivity. This explains the measured and modelled patterns observed here.

Dissolved organic carbon is the main source of C used by bacteria in aquatic systems, and much of the DOC in large rivers is of allochthonous terrestrial origin coming in from the watershed (Cole and Caraco 2001). Rivers are considered to be reactors as they sequester a considerable amount of C along their flow path (Cole et al. 2007). Interestingly, despite the high macrophyte biomass and primary productivity in LSP (Vis et al. 2007), if we consider the average DOC concentrations of the water masses and their flow rates, we estimate that over 90% of the organic carbon in LSP is allochthonous. However, as the nutrients are consumed along the flow path by primary producers, labile organic carbon (OC) substrates are released and this C is thought to be rapidly sequestered by microbes whereas the recalcitrant allochthonous inputs are thought to be exported (del Giorgio and Pace 2008). Furthermore, terrestrial OC is typically low in nutrients and microbes must depend on dissolved inorganic nutrients to sustain their growth (Caraco et al. 1998). AEM may be particularly useful in predicting BP in large river reaches where no major tributaries are feeding into the section of interest, such as in this example in LSP. AEM analysis of patchier flowing systems, with great variability in localized C and nutrient inputs (Rees et al. 2005), may not work so well for rate processing estimates such as BP, but the method is still applicable to the distribution of species, as illustrated below. However, the strength of the use of AEM directional spatial variables in predicting bacterial production in LSP is that these terms fully integrate the complex interactions between the locally produced labile organic substrates, the nutrients they rely on, and their transformations along the flow path. This integration of complex processing represented in the AEM variables at

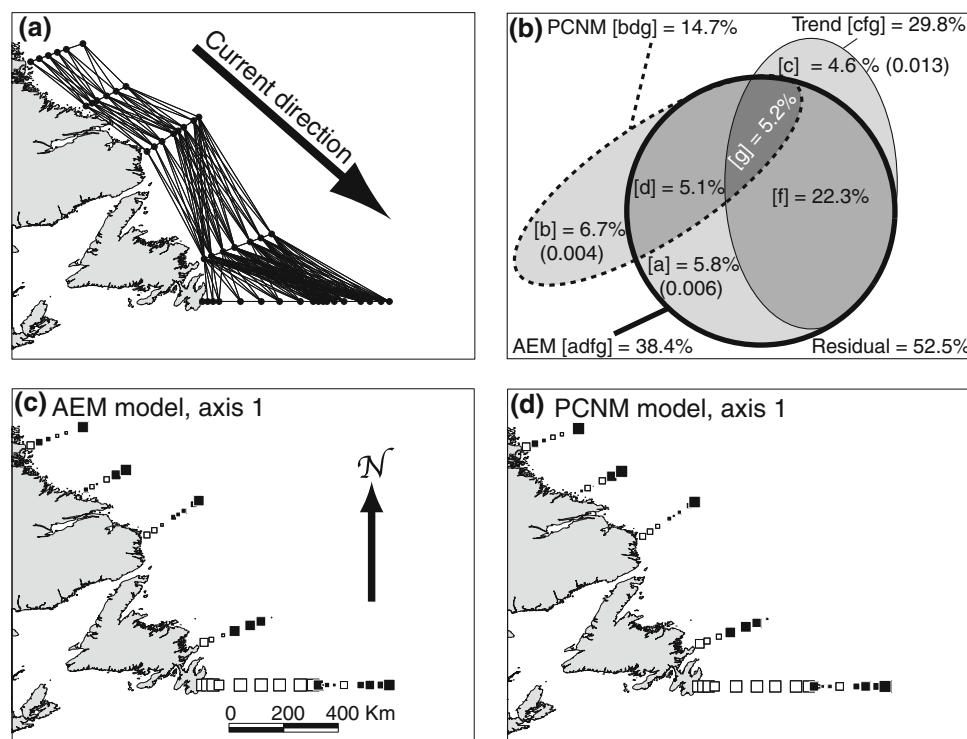
least for the spatial analysis of bacterial production in LSP proved to be more effective than classical environmental variables measured at the local sites.

#### *Calanus finmarchicus* on the Newfoundland and Labrador oceanic shelf

Zooplankton was collected on the Newfoundland and Labrador shelf as part of the Atlantic Zone Monitoring Program (Therriault et al. 1998) from 21 July to 6 August 2003. Sampling of 45 stations located along five cross-shelf sections (Fig. 3a) was completed following the protocols outlined by Mitchell et al. (2002). The placement and length of the five transects ensures sampling across the major banks of the shelf and in the inner and outer branches of the Labrador Current. At each site, a zooplankton sample was collected using vertical tow of a 0.75-m net fitted with 0.202-mm nitex mesh, from a depth 5 m above the bottom, to a maximum depth of 1,000 m, to the surface. The tow speed was  $1 \text{ m s}^{-1}$ . Samples were preserved in a 4% solution of buffered formaldehyde. The analysis

focused on the distribution of the copepod *C. finmarchicus*, a dominant species which plays a key role in the transfer of energy from phytoplankton to fish throughout much of the North Atlantic (Planque and Batten 2000). The abundance of *C. finmarchicus* was estimated from a subsample in which at least 150–200 specimens of all *Calanus* species (including two sister species, *C. glacialis* and *C. hyperboreus*) were counted and copepodites were staged. During the summer of 2003, *C. finmarchicus* represented from 30 to 100% (mean 74%) of the abundances of the three species.

In this region, the Labrador Current flows from north to south through an outer branch along the continental slope and an inner branch along the coast (Loder et al. 1998). There is some recirculation on the major banks, or topographic steering, so that turbulent eddy motion on the Newfoundland Shelf and the northern Grand Banks can be very important (Pepin and Helbig 1997). Major inflows of water carrying *C. finmarchicus* from the Labrador Sea take place through the cross-shelf channels located north and south of the three northernmost sections as well as across



**Fig. 3** Spatial modelling of *Calanus finmarchicus* distribution on oceanic shelf. **a** Site locations and connexion diagram used to generate the AEM eigenfunctions considering that current direction was used to generate AEMs. Square bubbles represent centred square-root transformed data (black are positive values, white are negative, size of squares is related to the associated value). Figure A3 (Appendix A) shows how all edges linking sites along a transect were used to build AEMs. **b** Variation partitioning results between the selected AEMs, PCNMs, and the trend are illustrated by a Venn diagram. Fraction sizes

are approximations. Letters in brackets correspond to individual fractions of explained variation; values are  $R_a^2$ . Values in parentheses represent the  $P$  values of independent fractions. **c** First and only significant ( $P < 0.001$ ) axis of a canonical RDA where the Hellinger transformed *C. finmarchicus* stages were explained by the selected AEM eigenfunctions; axis 1 accounts for 36.8% of the variation (black are positive values, white are negative, size of squares is related to the associated value). Axis 1 of the PCNM model is presented in the same way in **(d)**; this axis represents 14.8% of the variation ( $P = 0.005$ )



the central Newfoundland Shelf at a latitude of approximately 50°N.

We analysed the abundances of the six copepodite stages of *C. finmarchicus* (the distribution of each stage is shown in Fig. D1, Appendix D). The analyses were done by RDA instead of multiple regression since the response data are multivariate. RDA is the multivariate extension of multiple linear regression (Legendre and Legendre 1998, Sect. 11.1). The analyses were performed following a Hellinger transformation of the multivariate *C. finmarchicus* data. After Hellinger transformation of frequency data (e.g., community composition), multivariate linear methods of analysis such as RDA preserve the Hellinger distance among the sites, which is appropriate for the analysis of community composition data, instead of the Euclidean distance which is inappropriate (Legendre and Gallagher 2001). Results of the three modelling methods revealed substantial differences in the modelled relationships among sites. Using AEM ( $f_3$ ,  $\beta = 2$ ), the set of positively auto-correlated variables explained 51.4% ( $R_a^2$ ) of the variance. Forward selection retained AEM eigenfunctions #1 and 24 (Fig. D2, Appendix D), which yield an  $R_a^2$  of 38.4%. Detailed results for the other weighting functions considered are presented in Table D1 (Appendix D).

The full set of PCNMs variables explained 18.1% ( $R_a^2$ ) of the detrended *C. finmarchicus* data. When forward selection was carried out, 2 PCNMs were selected (#2 and 11, presented in Fig. D3, Appendix D); they explained together 14.7% ( $R_a^2$ ) of the non-detrended data. For MEM eigenfunctions applied to detrended data, no combination of  $f_3$  and  $\beta$  was significant at the 5% level after Šidák correction; the best result ( $\beta = 2$ ) was 16% of explained variation ( $R_a^2$ ) with  $P_{\text{corr}} = 0.195$ . MEMs results will not be developed further owing to this last result.

Along and cross-shelf trends in the distribution of *C. finmarchicus* contributed greatly to the overall results, but the greater strength of the AEM model is clear (Fig. 3b). The values fitted to the AEM model along the first and only significant RDA axis,  $P < 0.001$  (Fig. 3c), and the values fitted to the PCNM model along the first and only significant RDA axis,  $P < 0.001$  (Fig. 3d), illustrate the cross-shelf gradient in the distributions of the *C. finmarchicus* copepodite stages, with offshore stations generally dominated by older stages while younger copepodites were more abundant close to the coast. Model results suggest that the cross-shelf distribution is set in the northernmost reaches of the region, with limited cross-shelf exchange. The dominant features of the AEM model are the general north-to-south pattern in association among stations along with the inshore-offshore separation in the southern portion of the region (Fig. 3c, d). There is some variability in the association among stations but the indication of mixing and recirculation across the northernmost

sections and the gradual cross-shelf splitting of the inner and outer branches of the Labrador Current (and of the younger and older copepodite stages) in the middle and southern portions of the range is the only analysis that yields model results that are consistent with regional circulation on the Newfoundland Shelf. Drift simulations based on the climatological average seasonal circulation of Han et al. (2008) confirm that copepodites found on the continental shelf and Grand Banks along the southernmost transect come principally from sources located on the continental shelf in the northern part of the study area (P. Pepin and G. Han, unpublished data).

Understanding the source of *C. finmarchicus* on the inner shelf has important implications for interpreting observations from a site (S27: 47°32.5'N, 52°35.2'W) sampled twice a month that is used to monitor seasonal changes in population dynamics in the region. *C. finmarchicus* from sources near the northernmost area of the species range are subject to a shorter growing season than animals from the major population centre located in the southern Labrador Sea. This can limit their ability to accumulate energy reserves, in the form of wax esters, which will have implications for the individual's ability to enter diapause in the autumn and thereby affect the environment in which they will reproduce, and thus affect their potential fitness. Late stage copepodites (stage 5) of *C. finmarchicus* on the inner shelf have been shown to have smaller energy reserves (Pepin and Head 2009) and are more likely to moult into adults in the autumn than in the following spring relative to animals located in the Labrador Sea. This affects our understanding of seasonal patterns of secondary production in different parts of the region and has important implications for how production on the continental shelf may be affected by remote forcing from other parts of the North Atlantic subpolar gyre. This may also explain why inter-annual variations in abundance of *C. finmarchicus* on the inner shelf appear to be more similar to those in the northern portions of the study region relative to those in the southern Labrador Sea (Pepin et al. 2008; Pepin, unpublished data).

## Discussion

The AEM framework shares the following property with the MEM framework: Moran's  $I$  values can be associated with the eigenfunctions representing the spatial relationships among sites. The main difference lies in the directional nature of the process represented by its eigenfunctions. The AEM framework constructs variables modelling directional (asymmetric) information whereas the MEM framework creates variables with evenly-weighted omnidirectional (symmetric) information. As shown in the examples

presented in this paper, the use of AEMs does not require the detrending of the response variables. There are two main reasons for this. Conceptually, AEMs are used when we can hypothesize that the process generating the response data is spatially directional and we want to estimate its influence on the response. Practically, the first AEM eigenfunction computed along a narrow river map, for example, is comparable to a half-sine wave, which models a broad-scale trend, whereas the first MEM eigenfunction is a full sine wave as shown in Borcard and Legendre (2002, Fig. 2). In Appendix E, we present an example where the sine waves of AEMs and MEMs are compared. This does not mean that the AEM framework should be used instead of the MEM framework when the general trend is significant. As seen in the bacterial production and *Atya* examples that did not contain significant trends, the choice of the framework to be used should be based on the hypothesis one wants to test about the physical processes at work in the system under study; AEM modelling is only used when a directional spatial process is hypothesized. Because PCNMs are a particular case of MEMs (Dray et al. 2006), they do not need to be discussed separately with regard to this point.

Calculation of different fractions, in variation partitioning, after modelling spatial distributions by non-directional (PCNM or MEM) and directional eigenfunctions (AEM), provided quantitative information about the directional and non-directional spatial processes taking place in the systems under study. The fractions of variation represented only by AEM (fraction [a] in all examples) can be interpreted as the directional influence of the spatial process on the data under study. The other fractions represent the non-directional spatial components.

We have shown with the help of the three ecological illustrations that the AEM framework can be used at any scale and that insights can be obtained at different scales within a particular system. The results in Figs. 1c, 2c, and 3c illustrate how different scales, at which the ecological processes studied occur within each system, are brought out by the analysis. In the *Atya* illustration (Fig. 1c), the selected AEM eigenfunctions differentiate the left and right sides of the river, with a wave length of roughly 25 m.

For the bacterial production illustration (Fig. 2c), the wave lengths within the three water masses are completely different. In the North portion of the lake, the spatial structure of the bacterial production has a wave length of roughly 7.5 km, whereas the South section is structured at wave lengths of over 20 km. The central water mass is even more broadly structured. In this water mass, it is likely that the spatial distribution of bacterial production is broader than the extent of the sampling area since AEM analysis cannot extract any spatial structure.

In the ocean example (Fig. 3c), the half-wave length within the transects broadens from North to South. In the

northernmost transect, *C. finmarchicus* has a spatial half-wave length of about 75 km in the east–west direction. The middle transect uncovers a broader half-wave length of roughly 125 km in from east to west. The southernmost transect presents an even broader half-wave length of over 400 km.

The different wave lengths at which each system is structured can be the result of multiple factors (environmental, biological, anthropogenic, etc.) influencing directly or indirectly, independently or in combination, the organisms under study.

The examples presented in this paper have shown that the use of an appropriate method to model spatial relationships, such as the AEM framework for directional processes, may produce large  $R_a^2$ , providing a more complete understanding of the systems under study than less specific modelling methods. AEM eigenfunctions do not always explain all the variation that PCNMs and MEMs account for, but what is not explained by the set of asymmetric spatial variables is often small and not significant when the directional forcing process is strong. Even when the fraction related to the trend but not to the AEMs ([c] in Fig. 3b) is considered to belong to the symmetric methods, the amount of variation explained does not come close to what is explained by the AEM model independently. This is another point that favours the use of AEM modelling where there is a known asymmetric spatial structure possibly caused by a strong directional process.

The asymmetric eigenvector maps framework is a broad extension of the eigen-based spatial filtering method proposed by Griffith and Peres-Neto (2006), reinforcing this family of methods. It allows users to incorporate into the spatial model the knowledge they have about the spatial process they hypothesize to be influencing the response data. The choice of weights to be applied to the edges of the connexion diagram is as important in the AEM framework as it is in the MEM framework, a point stressed by Dray et al. (2006). However, the presence of the AEM framework in the eigen-based spatial filtering family of methods forces us to make a more general decision prior to that of weighting the edges: to choose the spatial context in which the studied data belong, directional or non-directional. This is an easy decision to take in the presence of strong spatial directional processes generating asymmetry, as found in the three examples in this paper. The same can be said when the response data is assumed to be symmetric. But what to do in situations where the system under study is known to be neither fully non-directional nor perfectly directional? A rudimentary answer has been given in this paper when constructing AEM for each example. Because there are edges perpendicular to the direction of the directional process, these had to be added in both directions; Fig. A3 (Appendix A) shows in detail how this

procedure was implemented. The use of both AEM and MEM variables, as was done in this paper, can help in better understanding situations that are not fully directional or non-directional.

The technical developments presented in Fig. A3 explain how co-occurring physical forcings can be dealt with. This approach helps deal with situations where physical forcing comes from different directions. For example, estuarine systems are known to be influenced by currents of different origins (e.g., ebb and flow currents). Using the approach presented in Fig. A3 with weights on the links that represent current velocity also makes AEM an asset for more complex systems than the examples presented in this paper.

Because this paper's aim was to compare different spatial modelling methods, symmetric and asymmetric, no environmental components were considered. The potential of combining AEMs and environmental variables in contexts where there is a known spatial asymmetry in the response data is interesting. To include non-spatial information in variation partitioning will produce a more complete and informative model and will result in a better understanding of the system under study.

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# APPENDIX A

## Modelling the effect of directional spatial ecological processes at different scales

**F. Guillaume Blanchet • Pierre Legendre • Roxane Maranger • Dominique Monti • Pierre Pepin**

A TABLE (TABLE A1) AND THREE FIGURES (FIG. A1, A2, A3) DESCRIBING THE STEPS FOR THE CREATION OF ASYMMETRIC EIGENVECTOR MAPS (AEM)

Table A1, Steps used to create AEM eigenfunctions. See also Fig. A1.

- 
1. Link the sites (geographical coordinates) through a connexion diagram (Fig. A1 a and b). The connexion diagram can be derived from graph theory (Delaunay triangulation, Gabriel graph, relative neighbourhood graph, etc.) or from prior knowledge of the system under study.
  2. Set the direction of the spatial process by adding site 0 (origin) to the diagram (Fig. A1 b). It is important to note that more than one site 0 can be added to a set of samples. The bacterial production illustration is an example where a site 0 can be used for each water masse. However, when more than one site 0 are used at one time it should be reminded that only one direction is to be considered.
  3. Construct a sites-by-edges matrix based on the connexion diagram devised in step 1 and the direction of the spatial process defined in step 2 (Fig. A1 c). Identify all edges forming the various paths connecting a site to the origin. A site may be influenced directly or indirectly by an edge. As an example, site 8 in Fig. A1 b, is influenced directly by edges 10, 12, and 14 and indirectly by edges 2, 3, and 4. The data row for site 8 will thus have the value 1 for edges 2, 3, 4, 10, 12, and 14, and 0 elsewhere.

4. Give weights to the edges by multiplying the column of values representing each edge by a weight value (Fig. A1 c). In the absence of information, all edges receive the same weight of 1. It is sometimes difficult to give weights to the edges directly connected to site 0, the hypothetical site inducing the direction. The weights given to those edges can be the mean of all the weights used on the other edges, as was done in the article.
  5. Perform a singular value decomposition (SVD) or a principal component analysis (PCA) of the weighted site-by-edge matrix. If SVD is used, the site-by-edges matrix needs to be centred by column before SVD (Fig. A1 c to d). Alternatively, from the weighted site-by-edges matrix, compute a matrix of Euclidean distances followed by principal coordinate analysis (PCoA) of that distance matrix (Fig. A1 e). The left matrix of singular vectors (SVD), principal components (PCA), and principal coordinates (PCoA), which are the new spatial variables, are all equal to within a column standardization (Fig. A1 d).
  6. Since the number of eigenfunctions generated by this procedure is often equal to  $n - 1$ ,  $n$  being the number of sites, reduce the number of spatial variables by an appropriate selection procedure such as the one described by Blanchet et al. (2008b).
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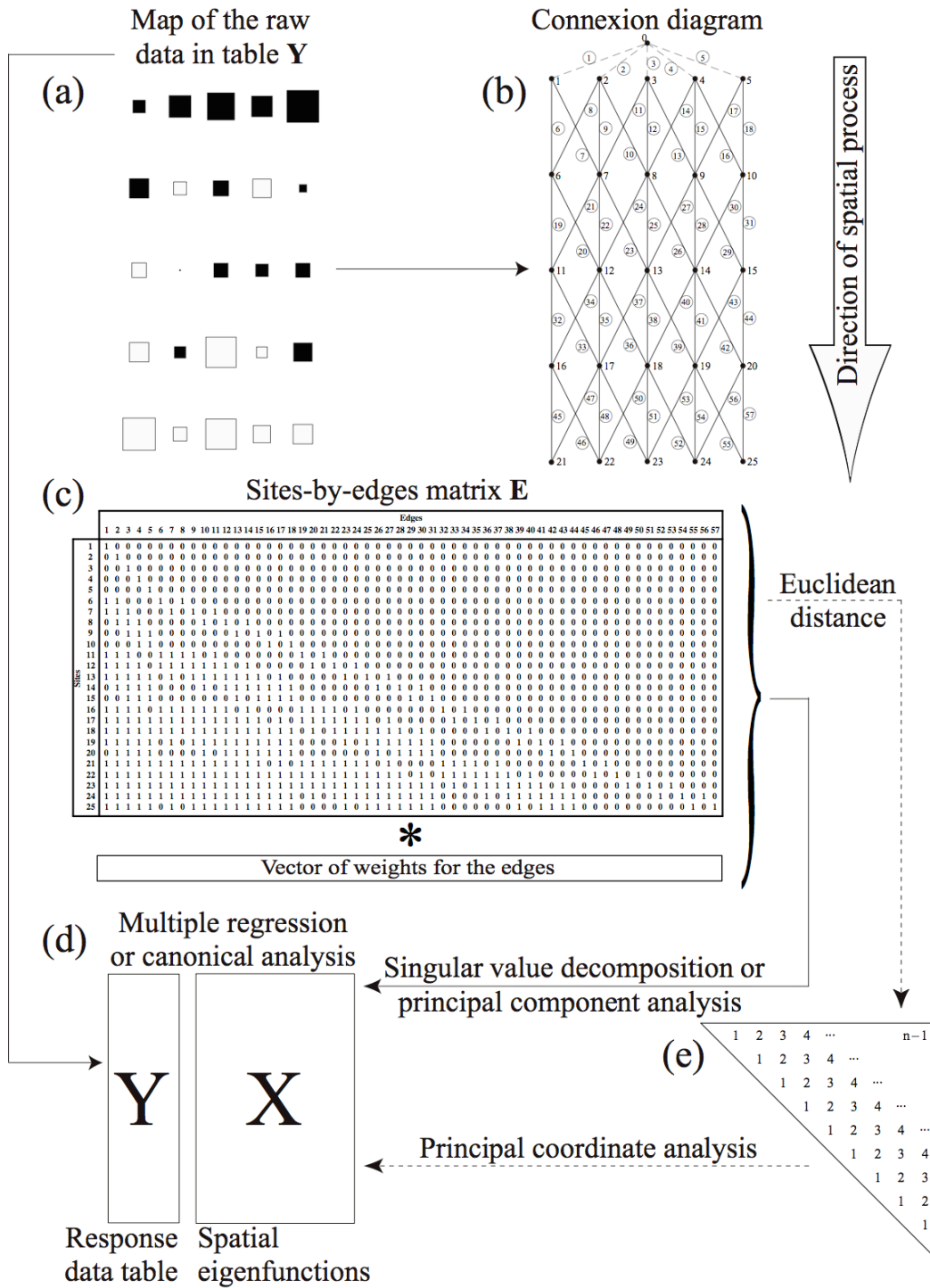


FIG. A1. Schematic representation of AEM analysis using a fictive example. (a) Data values are represented by bubbles (empty = negative, full = positive values). (b) Sites are linked by a connexion diagram (b), which in turn will be used to construct the sites-by-edges matrix **E** (c). Weights can be attributed to the edges (column) of this matrix, representing the easiness of effect transmission between nodes (vector underneath the sites-by-edges matrix). (d) Descriptors (AEM variables, matrix **X**) are obtained by calculating the left-hand matrix of eigenvectors of SVD, or the matrix of principal components (site scores) of PCA. AEM variables (matrix **X**) can also be obtained through the calculation of an Euclidean distance matrix followed by the computation of eigenvectors via principal coordinate analysis (PCoA). Redrawn from Blanchet et al. (2008).

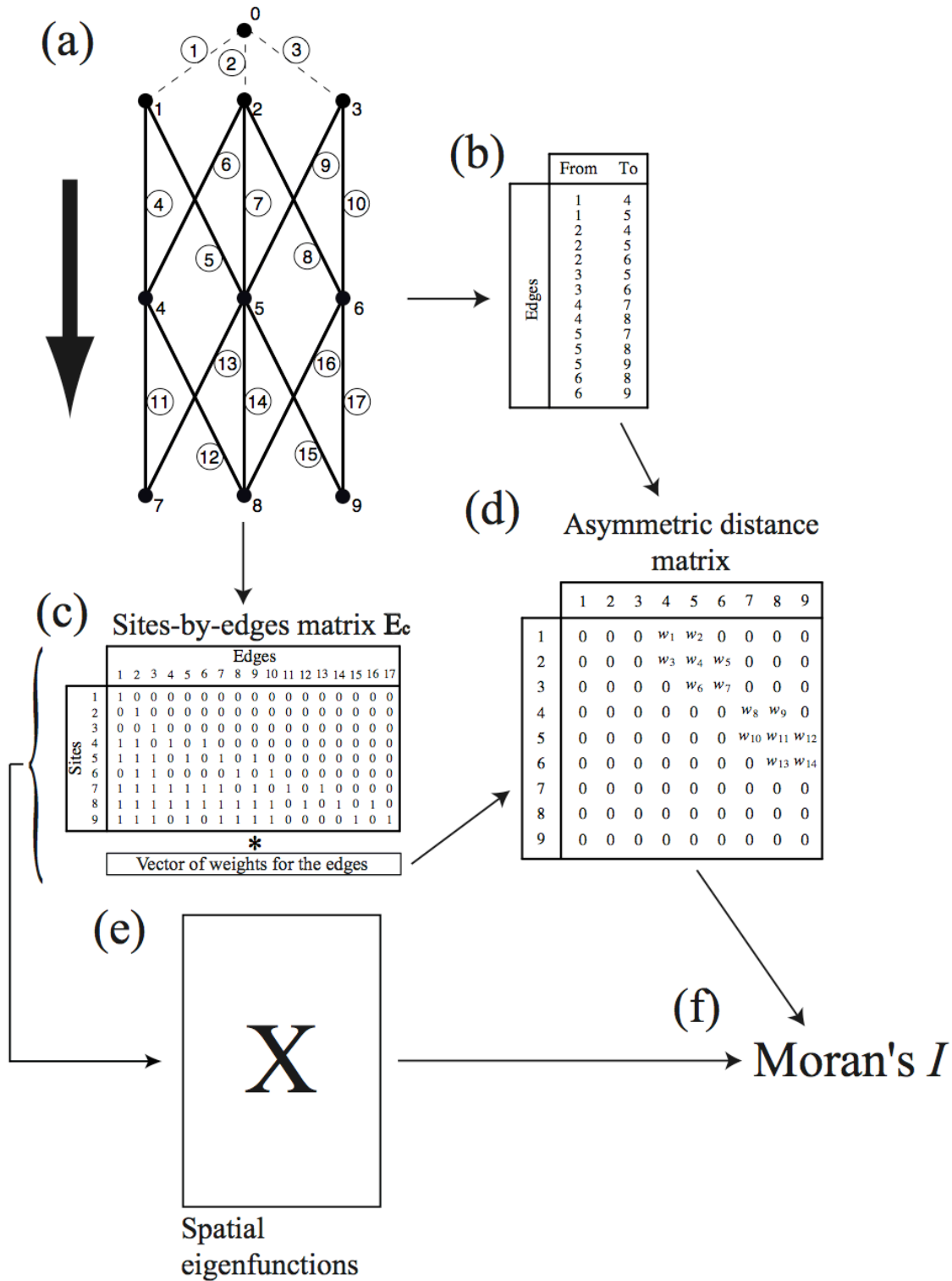


FIG. A2. Schematic representation explaining how Moran's  $I$  coefficients were calculated for AEM eigenfunctions. (a) Sites linked by a connexion diagram following the direction of the main spatial process (large arrow). Two matrices can be constructed from these linked sites: a from-to matrix defining the edges (b) and a sites-by-edges matrix (c). As described in more detail in Table A1 and Fig. A1, weights can be added to the columns (edges) of matrix  $E$  (c) and a matrix of spatial variables can be obtained (e). From the from-to matrix (b), an asymmetric distance matrix (d) can be constructed containing the edge weights. Matrix (d) is used to compute Moran's  $I$  coefficients for each spatial eigenfunction (f).

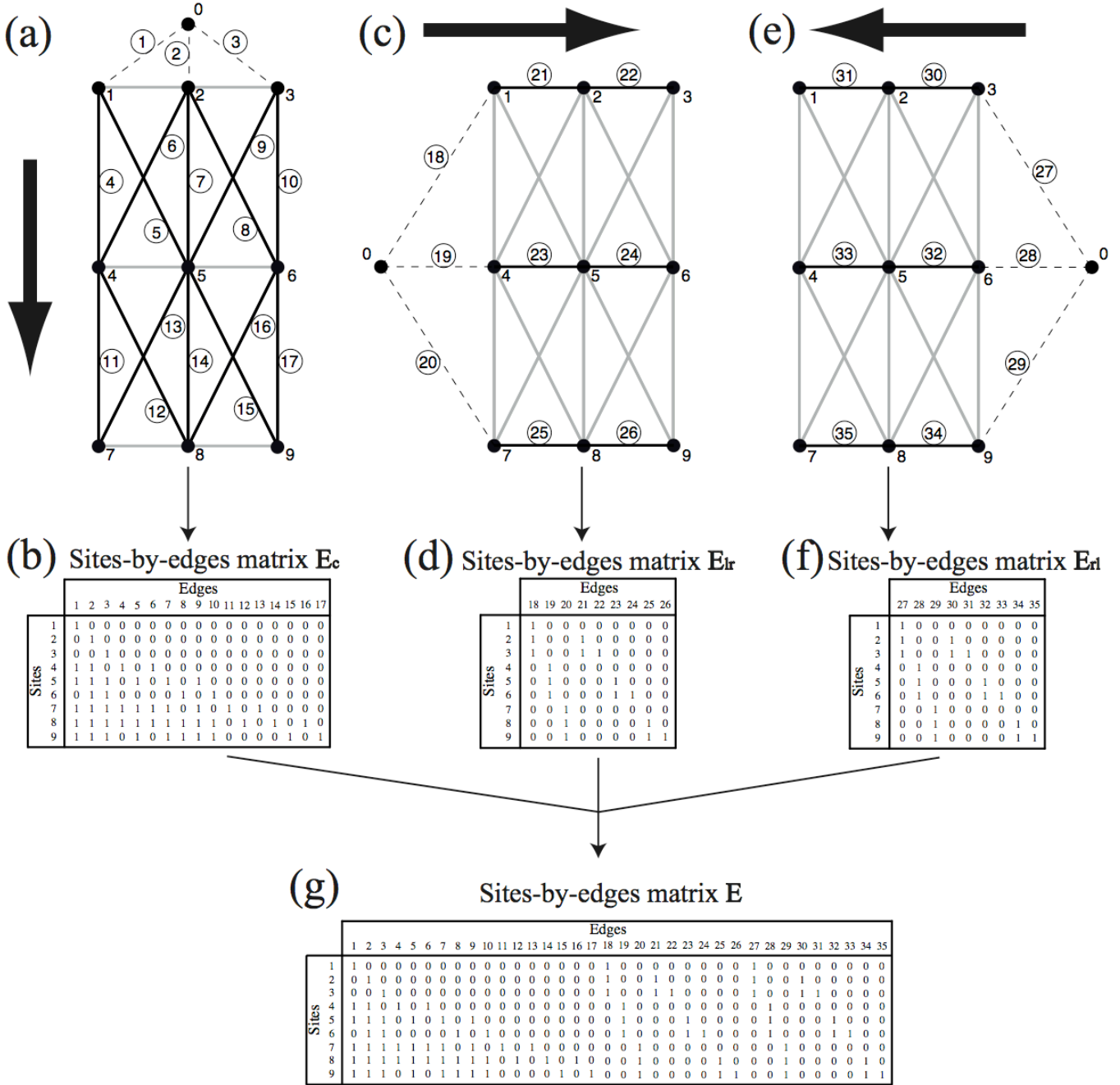


FIG. A3. Schematic representation describing how edges perpendicular to the main direction should be handled. (a) Sites linked by a connexion diagram following the direction of the main spatial process (large arrow). The resulting sites-by-edges matrix is presented in (b). The edges from left to right, perpendicular to the main direction of the spatial process, are considered in (c), and from right to left in (e). (c) will yield the sites-by-edges matrix presented in (d), and (e) the one presented in (f). The columns of matrices (b), (d), and (f) are then bound to form matrix  $E$  (g). The black edges in (a), (c), and (e) are the ones used to construct the respective sites-by-edges matrix, whereas the grey edges are not considered. No weights were added to the edges in this example to simplify the illustration.



## APPENDIX B

### Modelling the effect of directional spatial ecological processes at different scales

F. Guillaume Blanchet • Pierre Legendre • Roxane Maranger • Dominique Monti • Pierre Pepin

A TABLE (TABLE B1) AND THREE FIGURES (FIGS. B1, 23, B3) GIVING CALCULATION DETAILS FOR ECOLOGICAL APPLICATION 1: SPATIAL MICRODISTRIBUTION OF THE CRUSTACEAN *ATYA INNOCOUS* IN CAPESTERRE RIVER (GUADELOUPE)

TABLE B1.  $R^2_a$  and significance of spatial models (AEM and MEM) constructed with the different  $\alpha$ ,  $f_1$  and  $f_2$  proposed in the main text. The PCNM and MEM models were computed on detrended data, whereas the AEM models were computed on non-detrended data. The results presented for AEM and MEM refers to a subset of eigenfunctions measuring positive autocorrelation only (all variables in the subset is associated to a positive Moran's  $I$ ).

| Framework | Distance function | $\alpha$ | $R^2_a$      | $P$               | $P_{\text{corr}}$ |
|-----------|-------------------|----------|--------------|-------------------|-------------------|
| AEM       | $f_1$             | 1        | 49.1%        | < 0.001           | 0.002             |
|           |                   | 2        | 50.3%        | < 0.001           | 0.002             |
|           | $f_2$             | <b>1</b> | <b>60.3%</b> | <b>&lt; 0.001</b> | <b>0.002</b>      |
|           |                   | 2        | 54.1%        | < 0.001           | 0.002             |
|           | Binary            |          | 48.9%        | < 0.001           | 0.002             |
| MEM       | $f_1$             | 1        | 46.2%        | < 0.001           | 0.002             |
|           |                   | 2        | 46.4%        | < 0.001           | 0.002             |
|           | $f_2$             | <b>1</b> | <b>52.7%</b> | <b>&lt; 0.001</b> | <b>0.002</b>      |
|           |                   | 2        | 52.1%        | < 0.001           | 0.002             |
|           | Binary            |          | 46.4%        | < 0.001           | 0.002             |
| PCNM      |                   |          | <b>47.6%</b> | <b>&lt; 0.001</b> |                   |

\*  $P$  were calculated after 999 permutations

\*\* A Šidák correction was applied on  $P$ .

\*\*\* Bold highlights the weight used in the main text.

Note: The subset of AEMs and MEMs measuring negative autocorrelation are not presented because they yield a corrected  $P$ -value always larger than 0.99.

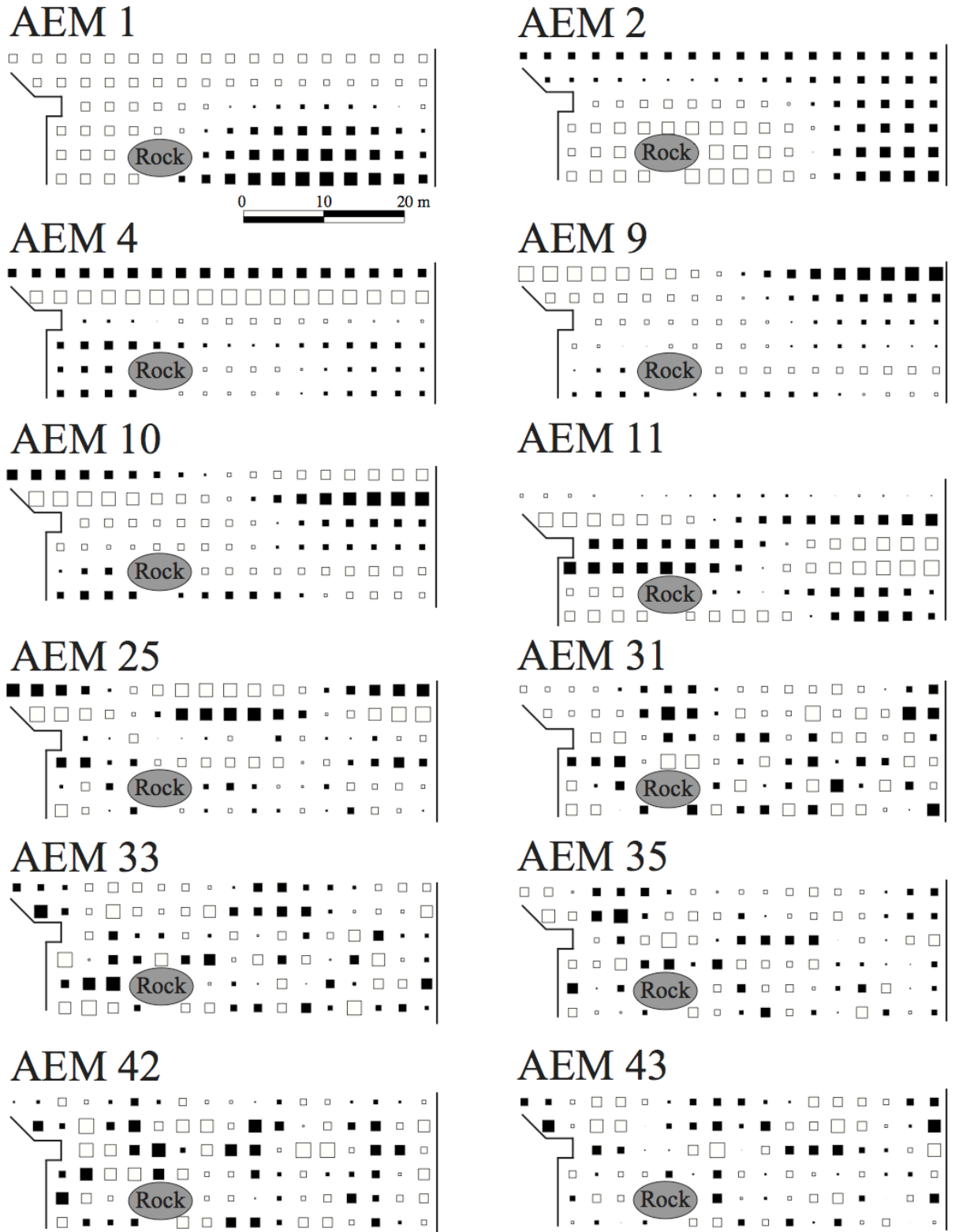


FIG. B1. AEM eigenfunctions selected to model *Atya innocous* in Capesterre river (Guadeloupe). The square bubble size is proportional to the value associated to it, whereas the color reflects the signs of the number (black = positive, white = negative).

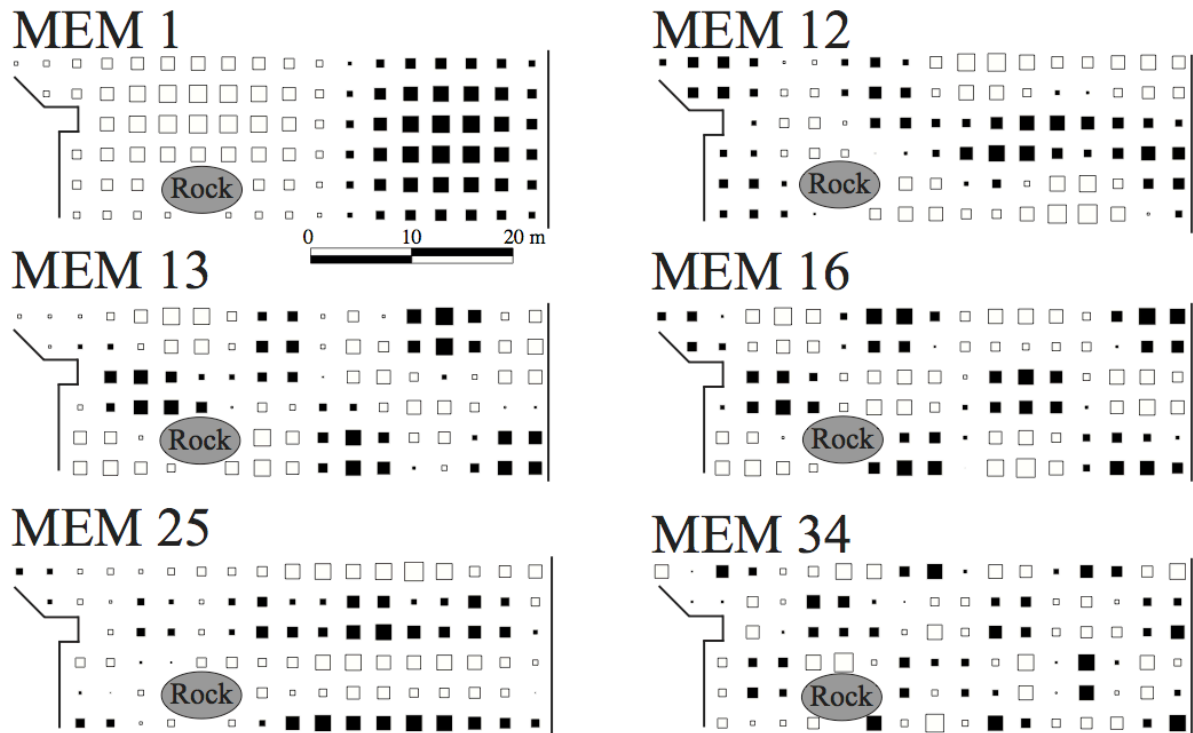


FIG. B2. MEM eigenfunctions selected to model *Atya innocous* in Capesterre river (Guadeloupe). The square bubble size is proportional to the value associated to it, whereas the color reflects the signs of the number (black = positive, white = negative).

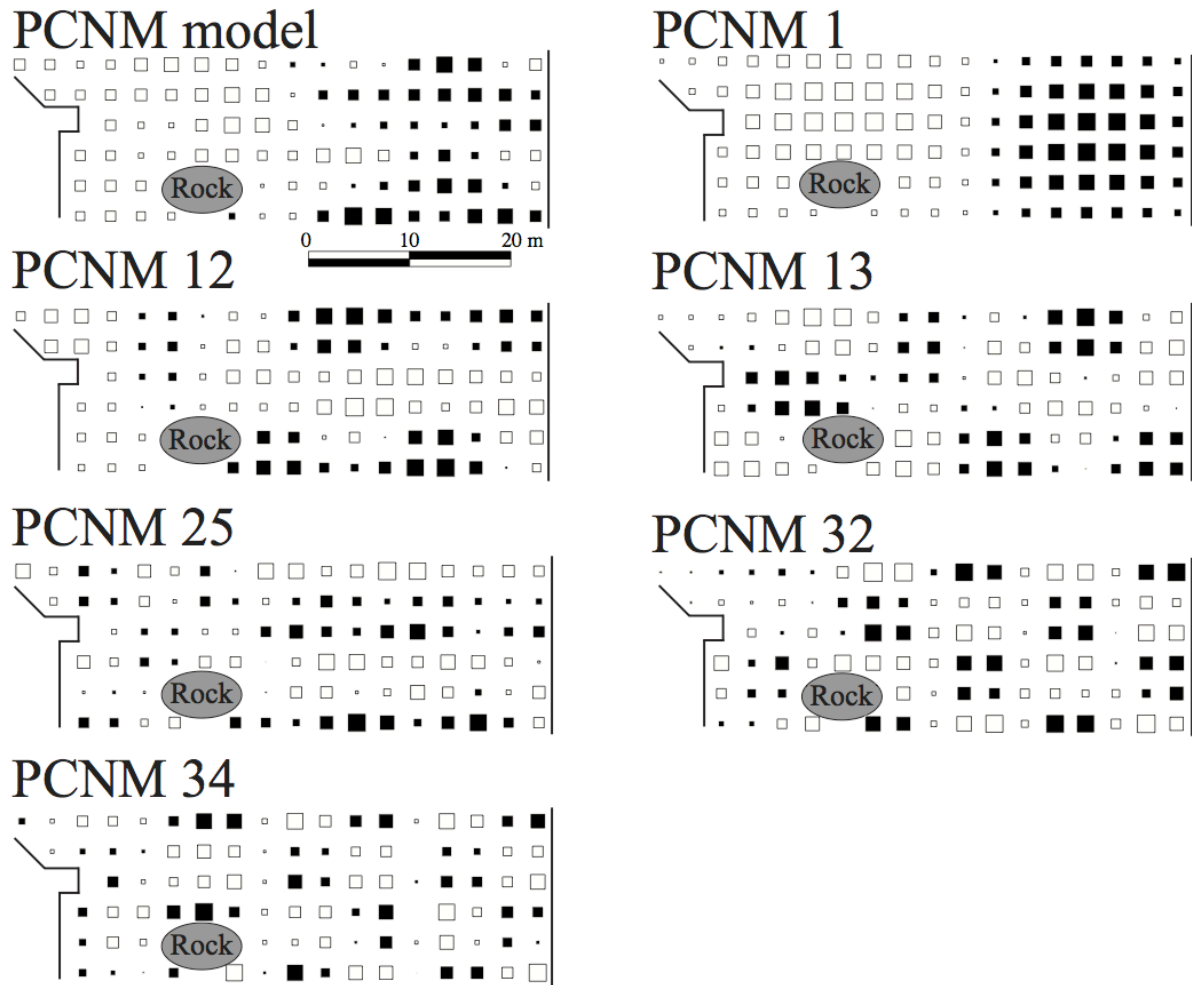


FIG. B3. PCNM model and eigenfunctions selected to model *Atya innocuous* in Capesterre river (Guadeloupe). The square bubble size is proportional to the value associated to it, whereas the color reflects the signs of the number (black = positive, white = negative).

## APPENDIX C

### Modelling the effect of directional spatial ecological processes at different scales

F. Guillaume Blanchet • Pierre Legendre • Roxane Maranger • Dominique Monti • Pierre Pepin

A TABLE (TABLE C1) AND A FIGURE (FIG. C1) GIVING CALCULATION DETAILS FOR ECOLOGICAL APPLICATION 2: BACTERIAL PRODUCTION IN LAKE SAINT-PIERRE

TABLE C1.  $R^2_a$  and significance of spatial models (AEM and MEM) constructed with the different values of  $\alpha$ ,  $f_1$  and  $f_2$  proposed in the main text. The bacterial production data was square-rooted as a normalization procedure. The PCNM and MEM models were computed on detrended data, whereas the AEM models were computed on non-detrended data. The results presented for AEM and MEM refers to a subset of eigenfunctions measuring positive autocorrelation only (all variables in the subset is associated to a positive Moran's  $I$ ).

| Framework | Distance function | $\alpha$ | $R^2_a$      | $P$          | $P_{\text{corr}}$ |
|-----------|-------------------|----------|--------------|--------------|-------------------|
| AEM       | $f_1$             | <b>1</b> | <b>54.0%</b> | <b>0.017</b> | <b>0.033</b>      |
|           |                   | 2        | 55.5%        | 0.009        | 0.019             |
|           | $f_2$             | 1        | 49.8%        | 0.035        | 0.069             |
|           |                   | 2        | 41.0%        | 0.108        | 0.205             |
|           | Binary            |          | 20.6%        | 0.198        | 0.357             |
| MEM       | $f_1$             | 1        | 26.9%        | 0.098        | 0.186             |
|           |                   | 2        | 27.1%        | 0.096        | 0.183             |
|           | $f_2$             | 1        | 48.9%        | 0.038        | 0.075             |
|           |                   | 2        | 49.4%        | 0.036        | 0.071             |
|           | Binary            |          | 27.3%        | 0.095        | 0.181             |
| PCNM      |                   |          | -25.9%       | 0.763        |                   |

\* A Šidák correction was applied to the  $P$ -values.

\*\* Bold highlights the weight used to compute the results reported in the main text.

Note: The subset of AEMs and MEMs measuring negative autocorrelation are not presented because they yield a corrected  $P$ -value always larger than 0.96.



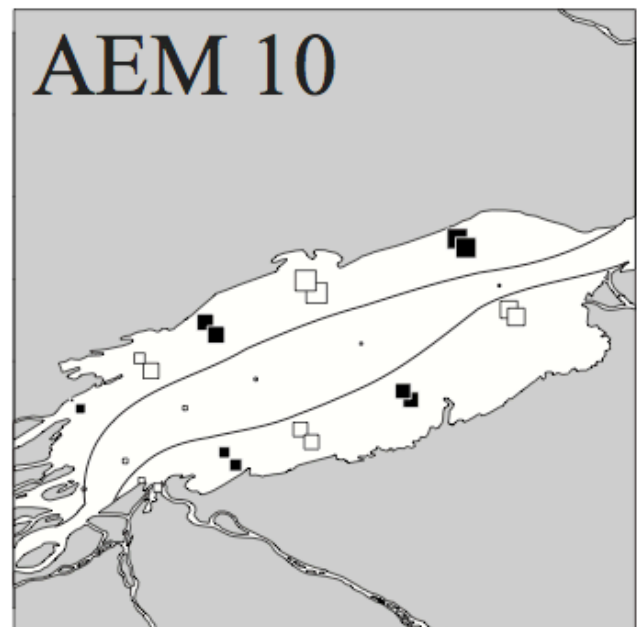
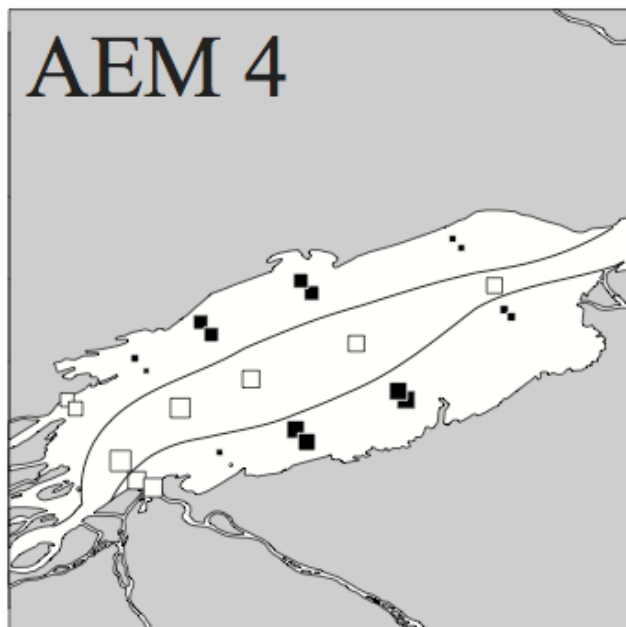
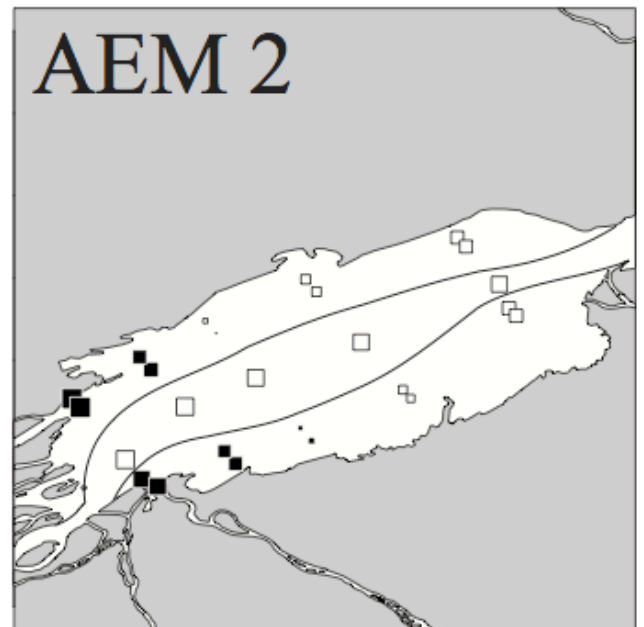
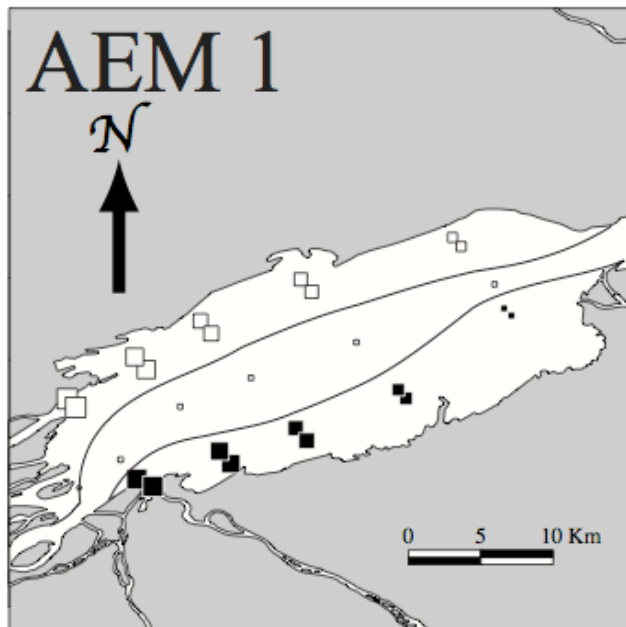


FIG. C1. AEM eigenfunctions selected to model bacterial production in Lake St-Pierre (Québec, Canada). The square bubble size is proportional to the value associated to it, whereas the color reflects the signs of the number (black = positive, white = negative).

## APPENDIX D

### Modelling the effect of directional spatial ecological processes at different scales

F. Guillaume Blanchet • Pierre Legendre • Roxane Maranger • Dominique Monti • Pierre Pepin

A TABLE (TABLE D1) AND THREE FIGURES (FIGS. D1, D2, D3) GIVING CALCULATION DETAILS FOR ECOLOGICAL APPLICATION 3: DISTRIBUTION OF THE DEVELOPMENTAL STAGES OF THE COPEPOD *CALANUS FINMARCHICUS* ON THE NEWFOUNDLAND AND LABRADOR OCEANIC SHELF

TABLE D1.  $R^2_a$  and significance of spatial models (AEM and MEM) constructed with the different  $\alpha$ ,  $f_1$  and  $f_2$  proposed in the main text. The *Calanus finmarchicus* data was Hellinger transformed. The PCNM and MEM models were computed on detrended data, whereas the AEM models were computed on non-detrended data. The results presented for AEM and MEM refer to a subset of eigenfunctions measuring positive autocorrelation only (all variables in the subset are associated to positive Moran's  $I$ ).

| Framework | Distance function | $\beta$  | $R^2_a$      | $P^*$             | $P_{\text{corr}}^{**}$ |
|-----------|-------------------|----------|--------------|-------------------|------------------------|
| AEM       | $f_3$             | 0.5      | 38.4%        | < 0.001           | 0.002                  |
|           |                   | 1        | 38.7%        | < 0.001           | 0.002                  |
|           |                   | <b>2</b> | <b>51.4%</b> | <b>&lt; 0.001</b> | <b>0.002</b>           |
|           | Binary            |          | 44.4%        | < 0.001           | 0.002                  |
| MEM       | $f_3$             | 0.5      | 14.5%        | 0.094             | 0.179                  |
|           |                   | 1        | 14.4%        | 0.118             | 0.222                  |
|           |                   | 2        | 16.0%        | 0.103             | 0.195                  |
|           | Binary            |          | 8.0%         | 0.186             | 0.337                  |
| PCNM      |                   |          | <b>18.1%</b> | <b>0.02</b>       |                        |

\*  $P$ -values were calculated after 999 permutations

\*\* A Šidák correction was applied to the  $P$ -values.

Bold highlights the weight used in the main text.

Note: The subsets of AEMs and MEMs measuring negative autocorrelation are not presented because they yield a corrected  $P$ -value always larger than 0.96.

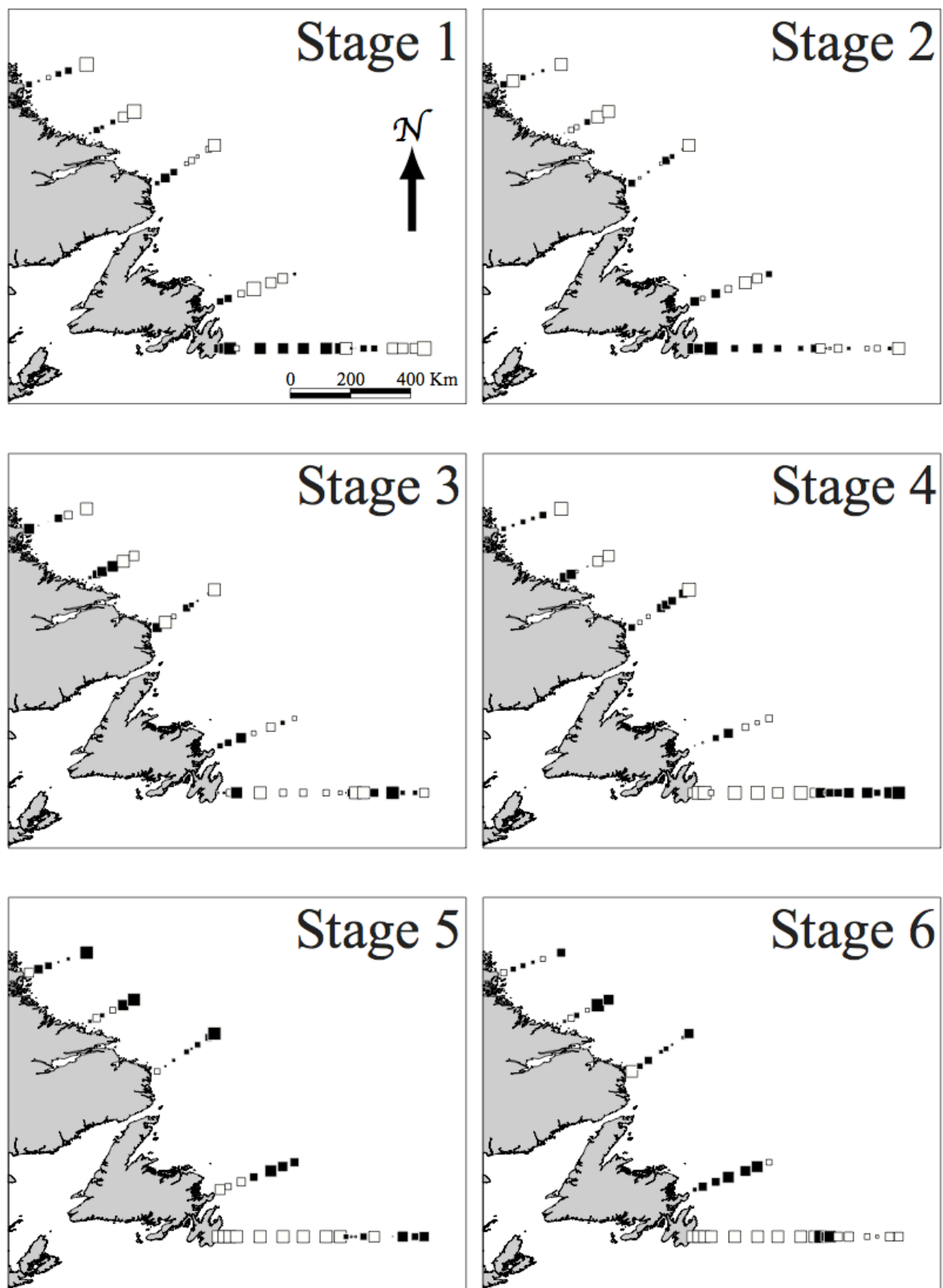


FIG. D1. Centered Hellinger-transformed abundances for each copepodite stage of *Calanus finmarchicus*. The square bubble size is proportional to the value associated to it, whereas the colour reflects the sign of the number (black = positive, white = negative).

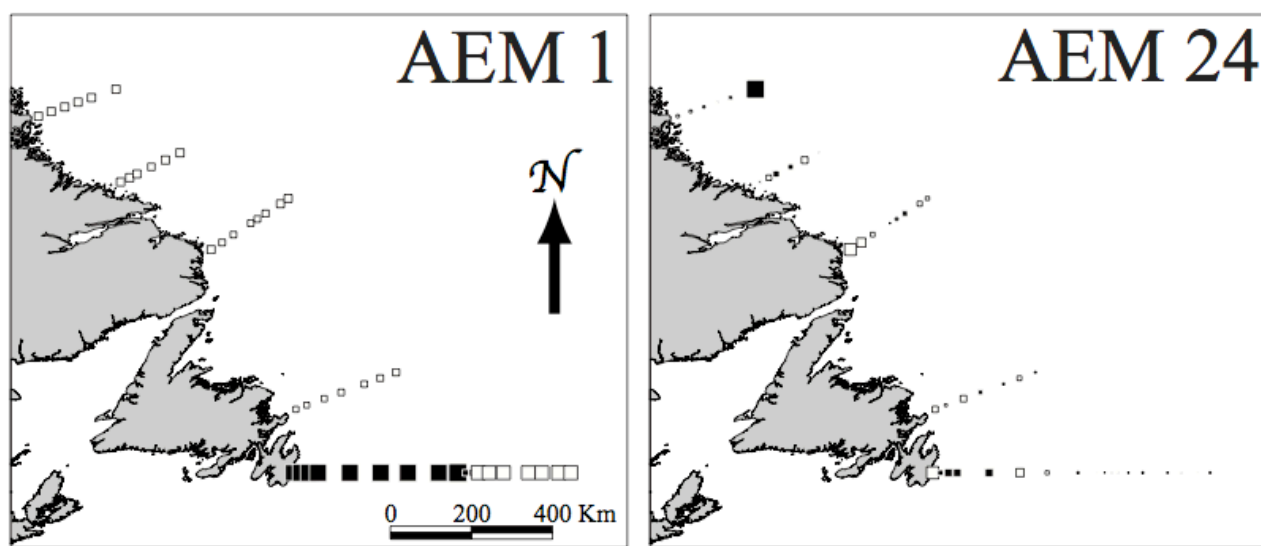


FIG. D2. AEM eigenfunctions selected to model *Calanus finmarchicus* on the Newfoundland and Labrador continental shelf. The square bubble size is proportional to the value associated to it, whereas the colour reflects the sign of the number (black = positive, white = negative).

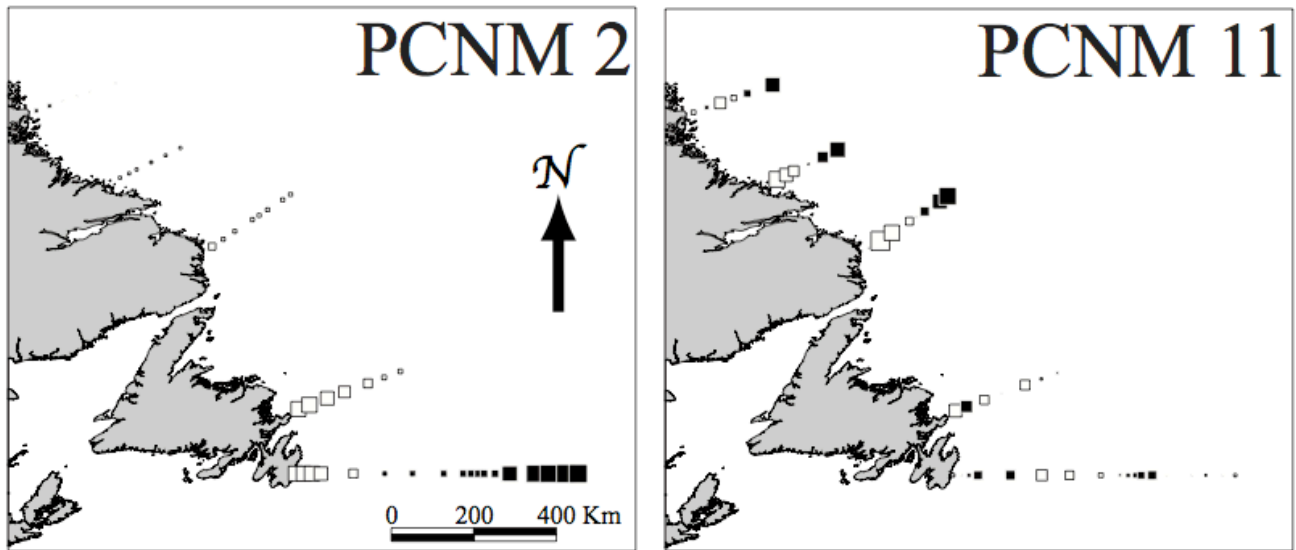


FIG. D3. PCNM eigenfunctions selected to model *Calanus finmarchicus* on the Newfoundland and Labrador continental shelf. The square bubble size is proportional to the value associated to it, whereas the colour reflects the sign of the number (black = positive, white = negative).

## APPENDIX E

### Modelling the effect of directional spatial ecological processes at different scales

F. Guillaume Blanchet • Pierre Legendre • Roxane Maranger • Dominique Monti • Pierre Pepin

TWO FIGURES (FIGS. E1, E2) DESCRIBING THE SINE WAVE STRUCTURE OF SPATIAL EIGENFUNCTIONS AND COMPARING CHOSEN AEM AND MEM EIGENFUNCTIONS ALONG A TRANSECT

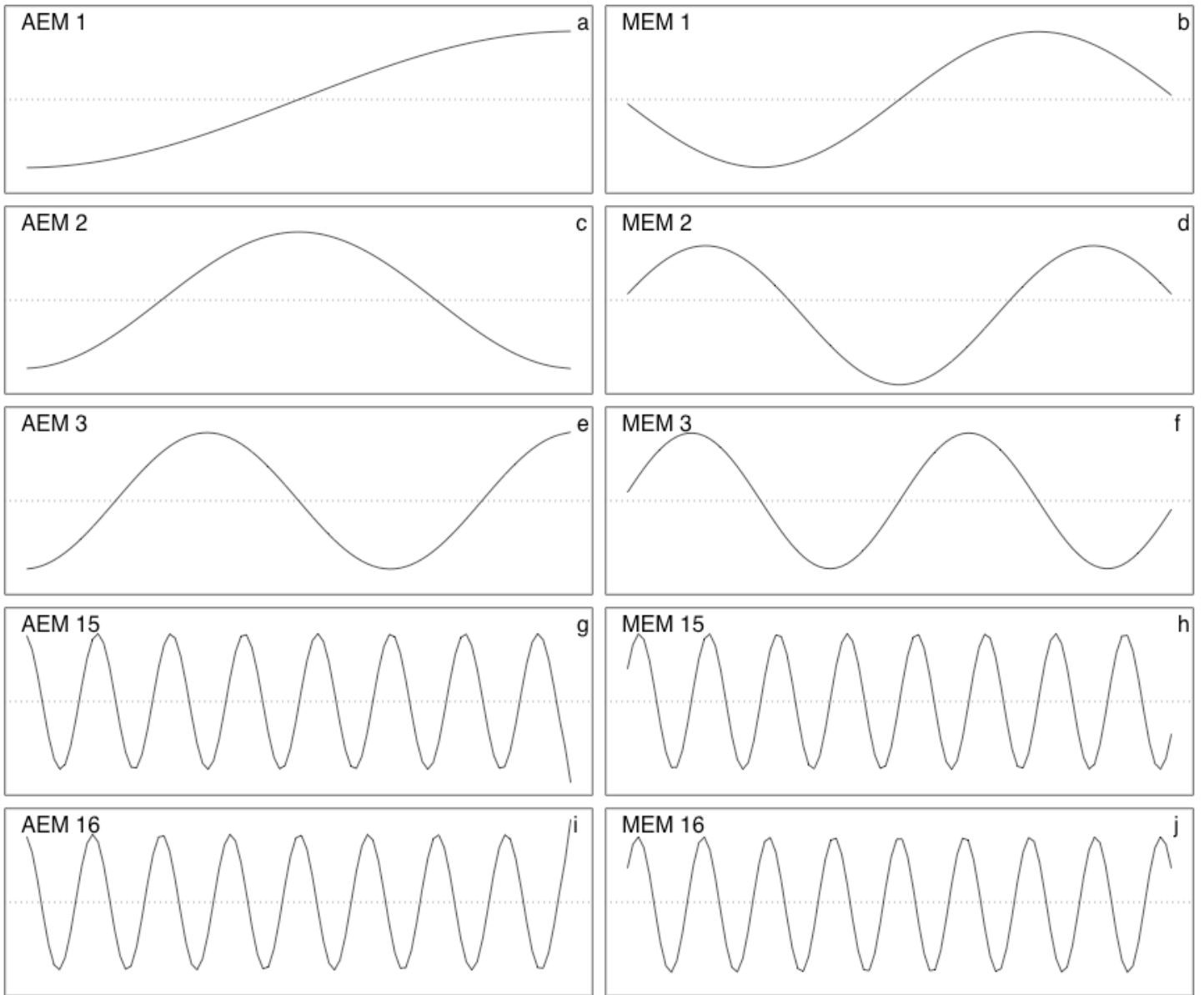


FIG. E1. Comparison of eigenfunctions calculated within the AEM (a, c, e, g, i) and the MEM (b, d, f, h, j) frameworks for a transect with 100 regularly-spaced sites. For conciseness, only AEM and MEM eigenfunctions #1, 2, 3, 15, and 16 are compared. AEMs have larger waves lengths than MEMs. Also, AEM eigenfunctions do not start or end near zero (dotted line).



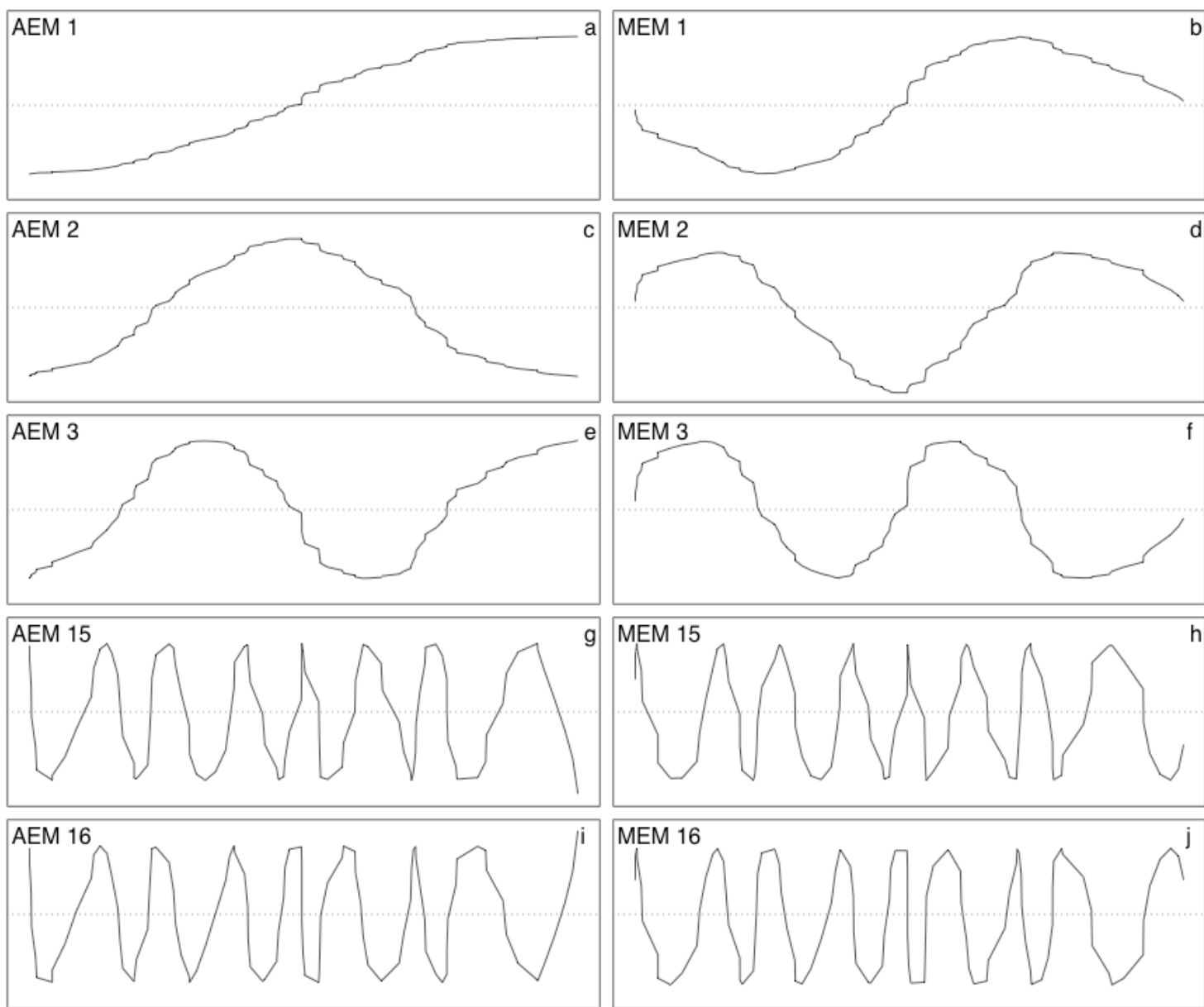


FIG. E2. Comparison of eigenfunctions calculated within the AEM (a, c, e, g, i) and the MEM (b, d, f, h, j) frameworks for an irregular transect with 100 irregularly-spaced sites. The irregular transect was generated by sampling from a uniform  $[0, 100]$  distribution 100 times and sorting the data in increasing order. For conciseness, only AEM and MEM eigenfunctions #1, 2, 3, 15, and 16 are compared. All eigenfunctions were drawn along the same transect. In addition to what was explained in Fig. E1, this figure shows the robustness of the two approaches to conserve their structure even when computed for an irregular set of points.