Variation partitioning analyses combined with spatial predictors (Moran’s eigenvector maps, MEM) are commonly used in ecology to test the fractions of species abundance variation purely explained by environment and space. However, while these pure fractions can be tested using a classical residuals permutation procedure, no specific method has been developed to test the shared space-environment fraction (SSEF). Yet, the SSEF is expected to encompass a major driver of community assembly, that is, an induced spatial dependence effect (ISD; i.e. the reflection of a spatially structured habitat filter on a species distribution). A reliable test of this fraction is therefore crucial to properly test the presence of an ISD on ecological data. To bridge the gap, we propose to test the SSEF through spatially-constrained null models: torus-translations, and Moran spectral randomisations. We investigated the type I error rate and statistical power of our method based on two real environmental datasets and simulations of tree distributions. Ten types of tree distribution displaying contrasted aggregation properties were simulated, and their abundances were sampled in 153 regularly-distributed 20 × 20 m quadrats. The SSEF was tested for 1000 simulated tree distributions either unrelated to the environment, or filtered by environmental variables displaying contrasting spatial structures. The method proposed provided a correct type I error rate (< 0.05). The statistical power was high (> 0.9) when abundances were filtered by an environmental variable structured at broad scale. However, the spatial resolution allowed by the sampling design limited the power of the method when using a fine-scale filtering variable. This highlighted that an ISD can be properly detected providing that the spatial pattern of the filtering process is correctly captured by the sampling design of the study. An R function to apply the SSEF testing method is provided and detailed in a tutorial.

Keywords: habitat filtering, induced spatial dependence, Moran’s eigenvector maps (MEM), Moran spectral randomisations (MSR), plant community assembly, spatial correlation, spatially structured environmental variable, torus-translation test
Introduction

Understanding the processes controlling the spatial distribution of organisms in natural communities is a long-standing challenge in ecology. Conspecific individuals often display aggregated distributions because of their limited dispersal capacities (Seidler and Plotkin 2006). However, such distributions can also be caused by spatially structured habitat filters (Moran 1953, Legendre 1993, John et al. 2007, Beale et al. 2010, Vlemmixck et al. 2017). This reflection of the spatial structure of an environmental variable in the spatial structure of a species or community corresponds to an induced spatial dependence effect (Peres-Neto and Legendre 2010, Legendre and Legendre 2012), hereafter ISD, also referred to as exogeneity (Fortin and Dale 2005).

Abundance data displaying spatially structured patterns are often modelled through advanced spatial descriptors like principal coordinates of neighbour matrices (PCNM, Borcard and Legendre 2002) or their generalised form, Moran’s eigenvector maps (MEM, Dray et al. 2006), a flexible multivariate method based on the notion of spatial autocorrelation that allows the detection of coarse (i.e. gradients) and complex multiscale spatial patterns. These spatial descriptors can be integrated, together with environmental data, into a variation partitioning analysis (Borcard et al. 1992, Peres-Neto et al. 2006, Peres-Neto and Legendre 2010). The latter consists in quantifying the proportion of variation of a univariate or multivariate response dataset (e.g. abundances of a single species or a community, respectively) explained by the environment alone, by space (i.e. spatial descriptors) alone, and jointly by space and environment (fractions [a], [c] and [b], respectively; Fig. 1) (Legendre et al. 2009, Lan et al. 2011, Baldeck et al. 2013, Bauman et al. 2016, Vlemmixck et al. 2017). The pure and shared contributions of the environmental and spatial components are usually quantified through the coefficients of determinations ($R^2$) of simple and partial-linear regressions (for univariate response data) or canonical ordinations (e.g. redundancy analysis, RDA; for multivariate response data). These $R^2$ are adjusted to account for the number of explanatory variables of the model (Peres-Neto et al. 2006).

The global spatial component, the pure environmental, and the pure spatial fractions of the variation partitioning (fractions [bc], [a] and [c], respectively, in Fig. 1) have been shown to be testable with a correct type I error rate and good statistical power when using residuals permutation tests, following Anderson and Legendre (1999) (Peres-Neto and Legendre 2010). Yet, a major issue remains for the global environmental component (fraction [ab]) and the shared space-environment fraction (hereafter, SSEF; fraction [b], in Fig. 1), as neither of them can be tested by classical permutation tests (Peres-Neto and Legendre 2010, Legendre and Legendre 2012). Fraction [ab] cannot be tested by classical residuals permutation test because if the response data is spatially structured, the residuals of the model will display spatial autocorrelation, hence causing an inflation of the false discovery rate (type I error rate) (Dutilleul 1993, Peres-Neto and Legendre 2010). The SSEF – which is the focus of the present study – is therefore generally removed from [ab]. This allows [a] to be tested by the residuals permutation procedure while avoiding type I error rate inflation (Peres-Neto and Legendre 2010; see also Wagner 2003, 2004, who proposes to address this issue by means of multivariate variograms in a technique called “multiscale ordination”). Fraction [a] is thus often considered alone as the reflection of habitat filtering, since it is the only testable portion of the environmental effect. Fraction [b] (i.e. the SSEF), on the other hand, is generally partialled out and ignored or is interpreted with caution (Borcard et al. 2018), as it cannot be tested using classical permutation tests. This is because fraction [b] is computed by the subtraction of other fractions adjusted following Peres-Neto et al. (2006) (e.g. $[b] = [ab] - [a]$), and hence has zero degree of freedom (Legendre and Legendre 2012). This is a major issue in ecology, because most ecological variables and processes being spatially structured in nature (Legendre and Legendre 2012), the SSEF is likely to represent a major portion of the habitat filtering explaining the spatial distribution of species in natural communities (i.e. an ISD).

Thus the absence of a reliable test for fraction [b] is causing most studies to potentially ignore or wrongly interpret an important niche effect explaining species distribution data. However, although we may expect the SSEF to reflect

<table>
<thead>
<tr>
<th>Pure environmental effect $= [a]$</th>
<th>SSEF $= [b]$</th>
<th>Pure spatial effect $= [c]$</th>
<th>Residuals $= [d]$</th>
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<tr>
<td>Global environmental effect $= [ab]$</td>
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<td>Global spatial effect (MEM) $= [bc]$</td>
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<td>Total explained abundance variation $= [abc]$</td>
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<td>Total abundance variation $= [abcd]$</td>
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Figure 1. Scheme illustrating the different fractions of the variation partitioning analysis when considering two different explanatory variables (here the environment and the spatial predictors). The SSEF (fraction [b], emphasised in a grey cell) is calculated by subtracting the the pure environmental fraction to the global environmental fraction $([b] = [ab] - [a])$, while all other fractions correspond to adjusted $R^2$ values calculated using linear regressions ([ab] and [bc]) or by subtractions ([a] and [c]).
an ISD, one cannot exclude that an overlap of spatial structures in the community data and the environmental properties may occur by chance. An appropriate method to test the SSEF is therefore crucial to reliably establish the existence of a potential ISD.

In this paper, we present an original testing procedure for the SSEF. This procedure, initially suggested by Vlemmixx et al. (2017), is based on two spatially-constrained permutation methods, that is, the torus-translation (TT; Upton and Fingleton 1985, Harms et al. 2001) and the Moran spectral randomisations (MSR; Wagner and Dray 2015). These methods provide randomisation schemes that maintain the spatial structure of the environment, thus allowing generating constrained-null values of the SSEF that can then be compared to the observed SSEF while taking spatial autocorrelation into account.

Our goal, here, is to establish whether an ISD can be reliably detected by testing the SSEF, using either TT or MSR. To do so, we computed the type I error rates and statistical power of our testing procedure on a wide range of simulation scenarios that combined different spatial features of species distribution and environmental variables.

**Material and methods**

**Description of the SSEF testing procedure**

**Conditions and precautions prior to perform the variation partitioning**

The variation partitioning consists in partitioning the variation of a response variable, or matrix (y) into fractions explained solely and jointly by a set of environmental variables and a set of spatial variables. A preliminary condition to perform such analysis is for the global models of y against the complete set of environmental and spatial variables to both be significant at a predefined significance threshold (usually fixed at 0.05). The global spatial model is tested using classical residuals permutations (Anderson and Legendre 1999). The global environmental model, however, is tested by comparing the observed global adjusted R² with 999 null values obtained with a MSR-permutation procedure (Wagner and Dray 2015) in order to take spatial autocorrelation into account, hence avoiding a type I error rate inflation. Testing global models allows avoiding type I error rate inflations when performing model selections (Blanchet et al. 2008). The variation partitioning (and hence the test of the SSEF) should only be conducted if these preliminary conditions are respected. If both global models are significant, then a variable selection – preferably the forward selection with double stopping criterion (Blanchet et al. 2008; Supplementary material Appendix 1: section 1) – must be performed for the spatial variables (Bauman et al. 2018a) and can also be performed for the environmental variables (Supplementary material Appendix 1: section 2). A variation partitioning is then performed to calculate the SSEF as described in the introduction section.

**Testing the SSEF**

The procedure to test the SSEF starts by testing whether the selected set of environmental variables displays a significant spatial structure. Although this is not mandatory to perform the variation partitioning, it is a necessary condition to test the SSEF, as there can be no significant SSEF if y and the environment do not both present a spatial structure. This condition allows reducing the risk of a false positive by not performing the test if it does not make sense. The test of this condition is performed by the classical residuals permutation procedure of a global RDA of the environmental variables against the MEM variables generated from an optimised spatial weighting matrix (see Bauman et al. 2018b and Supplementary material Appendix 1: section 3 for the optimization of a spatial weighting matrix).

If the environmental variables are spatially structured, then the SSEF is tested either with torus-translations (TT) or with Moran spectral randomisations (MSR), that is, two spatially-constrained randomisation procedures. The first randomisation method (TT) applies for regular sampling designs only, where sampling quadrats are disposed according to a grid-like structure. Torus translations have been used in many studies which demonstrated significant environmental signals on floristic assemblages, in diverse regions and ecosystems (Harms et al. 2001, Noguchi et al. 2007, Itoh et al. 2010, Chuyong et al. 2011, Vlemmixx et al. 2014, 2015, 2017, Muledi et al. 2017). Here, the TT consists in spatially translating the values of the environmental variables in each quadrat by a random number of sampling units (one unit corresponding to the space between adjacent quadrats) along the y- and x-axes of the grid. Species abundance and environmental data are thus de-correlated, but their original spatial structure is preserved. The random translation procedure is repeated k times (e.g. 999 times), and each time, the SSEF (i.e. fraction [b]) is recomputed from the randomised environment ([b]=[ab] – [a]). The observed SSEF is then tested by comparing its value to the k null-values obtained after translations.

The second method, MSR, uses information on the spatial relations among sampled points, in a similar way as it is done with MEM, to re-create artificial variables (abundance or environmental) displaying spatial structures that are very similar to the original ones. More specifically, the method first uses a linear combination of MEM variables to capture the spatial patterns of the environmental variables. Secondly, it uses the detected spatial structures in a conditional randomisation procedure that maintains the original structure of the data, allowing testing a relation with another set of variables (here, the response variable(s)) while maintaining a correct type I error rate (details in Wagner and Dray 2015). MSR have the considerable advantage of being applicable to any type of sampling design, unlike TT that are restricted to regular designs. It has been shown to be a powerful method of randomisation preserving the spatial properties of univariate or multivariate data at all spatial scales, regardless of the sample size or type of sampling design (Wagner and Dray...
The procedure also addresses negative adjusted SSEF differently depending on the origin of the negative value. 1) These negative SSEF can arise from the $R^2$ adjustment procedure itself, and are then associated to explanatory variables that explain less of the response dataset than expected by chance for random normal deviates (Legendre and Legendre 2012, Borcard et al. 2018). In this case, the unadjusted SSEF is positive and the negative adjusted SSEF can be considered as a zero. The $p$-value is then computed as mentioned above. 2) However, a negative adjusted SSEF can also bear a real ecological meaning, in which case it cannot be considered as a zero and it should be tested too. This type of negative SSEF can arise when two explanatory variables are negatively correlated to one another and are both strongly correlated to the response variable (Legendre and Legendre 2012). This situation is differentiable from the first one because the unadjusted SSEF is also negative. In this case, our procedure computes the $p$-value as the proportion of null values of SSEF equal to or smaller than the true value for a one-tailed test in the lower tail. 3) A last source of negative SSEF may arise when suppressor variables are present (i.e. one variable that is not or nearly not correlated to the response variable, but is correlated to another explanatory variable, itself correlated to the response variable; see details in Azen and Budescu 2003, Beckstead 2012). Since the unadjusted SSEF resulting from a suppression effect is also negative, the SSEF testing procedure has no mean to differentiate it from a negative SSEF having actual ecological meaning. Nevertheless, suppression effects can easily be handled and avoided prior to performing the variation partitioning by 1) testing the significance of both explanatory components, and by 2) selecting an appropriate subset of MEM variables prior to performing the partitioning. We detailed and illustrated this in the Supplementary material Appendix S2.

It is worth mentioning that, although this study focuses on the SSEF, both TT and MSR could also be used to test the global environmental component (i.e. fraction $[ab]$ in Fig. 1; Vleminkx et al. 2017), as they both correct the risk of type I error rate inflation caused by spatial autocorrelation that hinders the use of a classical permutation scheme for this fraction.

Simulations to calculate the statistical performances of the SSEF testing procedure

We carried out computer simulations of tree distributions in a forest environment to investigate the performance of our new SSEF testing procedure, and thereby infer a possible

Environmental data

We used environmental data from two 50-ha forest areas divided into 1250 quadrats of $20 \times 20$ m, one area located on Barro Colorado Island (BCI, Panama, Condit et al. 2012), and the other in Korup National Park (KNP, Cameroon, Chuyong et al. 2004). In each of these two areas, two variables showing contrasted spatial patterns were chosen: elevation in BCI and KNP displayed coarse grained spatial structures (further referred to as broad-scale patterns), while topographical slope was spatially correlated at a relatively much finer scale (fine-scale patterns). We also added four supplementary environmental variables artificially created by spatially randomising the elevation and topographical slope values of BCI and KNP, yielding a total of eight environmental variables to be used as explanatory variables of the simulated tree abundances (Supplementary material Appendix 1 Fig. A1). We then selected a subset of three variables displaying contrasted spatial structures (Fig. 2, step 1): the elevation in BCI (broad-scale spatial structure), the topographical slope in KNP (fine-scale), and the spatially randomised elevation values in BCI (no spatial structure). Each of these three variables was used to filter the simulated tree distributions (see sections below) in order to mimic a habitat filtering. Standardised values of the environmental variables are available in Supplementary material Appendix 1 Table A1. Supplementary material Appendix 1 Fig. A1 shows heat maps of the eight environmental variables in the 1250 quadrats.

Simulating homogeneous tree species distributions

Ten types of tree distribution patterns were simulated over each of the three 50-ha environmental maps. In distribution patterns 1 to 9, we used a spatially explicit model developed by Plotkin et al. (2000) to generate artificial, yet realistic, tree distributions following a Poisson cluster process (PCP). The first step of this process is to randomly distribute ‘parents’ with density $\rho$ over one of the three selected environmental maps. Each parent produces a number of offsprings that
Figure 2. Schematic description of the procedure used to evaluate the type I error rate and power of the SSEF test. Step 1: heat maps showing the spatial structure of the three environmental variables (broad-scale, fine-scale, and spatially randomised) used for filtering tree abundances. Step 2: examples of artificial tree distribution patterns (DP) obtained by using a Poisson cluster process, for three different values of $s^2$ and $\rho$ (DP 1 to 9), and 2) by completely randomising $x$ and $y$ coordinates (spatially random distribution, DP 10). The disposition of the 153 sampled quadrats is also shown on the right. Step 3: examples of simulated generalist (a) and specialist (b) tree distributions (using a simulation of DP 2) over one of the three environmental maps. The specialist population was negatively correlated to the environmental variable. (c) Heat map showing the spatial structure of the environmental variable in the 153 sampled quadrats (artificially joined here for simplicity). From this map, null environmental variables were generated (999 times) using either torus-translations (TT) or Moran spectral randomisations (MSR), in order to test the SSEF (maps d and e show two examples of environmental variables generated by TT or MSR). The variation partitioning was conducted if, and only if both the global model of the environment and space were significant. The SSEF test was performed only if the environment was significantly spatially structured. Step 4: Calculation of either the type I error rate or the statistical power (depending on the simulation scenario see Table 1) associated to the test of the SSEF, based on 1000 repetitions of step 3.
follows a Poisson distribution of mean \( m \). The position of each offspring around the parent is then derived from a radially symmetric Gaussian distribution of variance \( s^2 \) (thus here, the PCP corresponds more exactly to a ‘homogeneous Thomas process’, Potts et al. 2004). This procedure therefore produces clumps (or aggregates) of trees for which the number and width are controlled by parameters \( p \) and \( s^2 \), respectively. Distribution patterns 1 to 9 corresponded to the combinations of three \( s^2 \) and three \( p \) values, chosen to reproduce contrasted types of plant aggregates (Fig. 2, step 2). Additional details about individual sampling are provided in the Supplementary material Appendix 1: section 6. Distribution pattern 10 consisted in simulating a spatially randomised tree distribution (no spatial structure; Fig. 2, step 2) by generating a number of random \( x\)-\( y \) coordinates (using a random uniform distribution) that ensured obtaining an intermediate number of individuals (400 ± 50) compared to distribution patterns 1 to 9.

**Simulation scenarios**

A simulation scenario, hereafter SS, corresponded to one of the ten distribution patterns described in the previous section, that either remained independent from the environment (hereafter, generalist population), or that was filtered by one of the three environmental variables in Fig. 2 (specialist population). In total, there were therefore ten types of generalist populations (corresponding to the ten different types of distribution patterns) + three types of environmental filters \( \times \) ten types of specialist distributions (with the same spatial properties as the generalist ones) = 40 SS. A specialist population was created by first generating a generalist population. The probability to keep each individual then followed a Gaussian probability density function that depended on the value of the filtering environmental variable in its quadrat (see details in the Supplementary material Appendix 1: section 4).

All eight environmental variables (Supplementary material Appendix 1 Fig. A1) were used as explanatory variables when performing a variation partitioning on generalist and specialist populations. Table 1 summarises the different SS (properties of the environmental filter, statistical performance tested, and underlying ecological question). Supplementary material Appendix 1 Table A2 provides further details for each SS.

Besides these 40 SS (further referred to as ‘main scenarios’), three additional SS were generated. The latter adopted a different approach to simulate complementary situations, using linear combinations of MEM variables to which a random noise was added to create spatially structured species abundances and environmental variables (see details in Supplementary material Appendix 1: section 5). The first two additional SS corresponded to extreme cases in which 1) the environment and the abundance displayed totally independent spatial patterns, and 2) the environment was entirely spatially structured and totally correlated to the spatial structure of the abundance. The third additional SS corresponded to a response variable strongly correlated to an environmental variable, itself negatively correlated to three MEM variables positively correlated to the response variable. This SS therefore simulated negative SSEF corresponding to an ISD, hence allowing testing the statistical performances of our SSEF testing procedure for this type of situation.

**Sampling design**

Once all SS were constructed, the environmental and abundance data were sampled in 153 regularly-spaced quadrats among the 1250 quadrats of the 50-ha study area (12.24% of the whole area’s surface, 6.12 ha; Fig. 2, steps 2 and 3), a realistic sampling effort that fits the range of sampling sizes found in the literature (Kadavul and Parthasarathy 1999, Condit et al. 2004, Zent and Zent 2004, Biwolé et al. 2015, Muledi et al. 2017). These sampled quadrats were regularly disposed according to a 9 by 17 grid-like structure (Fig. 2, step 2), a spatial configuration that allowed performing torus-translations. Adjacent sampled quadrats were distant of 60 m both along the x- and y-axes of the grid. Supplementary details about the sampling of individuals are provided in Supplementary material Appendix 1: section 6.

**Spatial variables**

A distance-based spatial weighting matrix (db-MEM, Dray et al. 2006) was used to generate the MEM variables from the spatial coordinates of the 153 subsampled quadrats.

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Table 1. Characteristics of the 40 main simulation scenarios (SS) used in our study. The first column refers to the range of scenarios described. Column 2 indicates whether no environmental filtering is simulated (SS 1 to 10) or if there is an environmental filtering by a spatially randomised variable (SS 11 to 20) or by a variable displaying fine-scale (SS 21 to 30) or broad-scale spatial structure (SS 31 to 40) (Fig. 2, step 1). Column 3: Type of tree distribution pattern (DP; Fig. 2, step 2): aggregated (DP 1 to 9) or spatially random (DP 10). Column 4 indicates the type of statistical performance investigated: type I error rate if the SS does not model an induced spatial dependence effect (ISD), or statistical power if it does model an ISD.

<table>
<thead>
<tr>
<th>SS</th>
<th>Environmental filter</th>
<th>DP</th>
<th>Performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 to 10</td>
<td>none</td>
<td>aggregated (DP 1 to 9) random (DP 10)</td>
<td>type I error rate</td>
</tr>
<tr>
<td>11 to 20</td>
<td>spatially random</td>
<td>aggregated (DP 1 to 9) random (DP 10)</td>
<td></td>
</tr>
<tr>
<td>21 to 30</td>
<td>structured (fine-scale)</td>
<td>aggregated (DP 1 to 9) random (DP 10)</td>
<td>statistical power</td>
</tr>
<tr>
<td>31 to 40</td>
<td>structured (broad-scale)</td>
<td>aggregated (DP 1 to 9) random (DP 10)</td>
<td></td>
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</tbody>
</table>
The connectivity matrix was based on the minimum distance that kept all these quadrats connected (i.e. the largest edge of the minimum spanning tree), and the resulting links were weighted by $1 - \left( D_{ij} / 4 \right)^2$, where $D_{ij}$ is the euclidean distance between sampled units $i$ and $j$, and $t$ the threshold connection distance (details in Dray et al. 2006). The arbitrary choice of this spatial weighting matrix was motivated by the fact that db-MEM are well-suited for regular sampling designs (Bauman et al. 2018b), and because the benefit of optimising the spatial weighting matrix is small in comparison with the cost of statistical power for those sampling designs (Dray et al. 2006, Bauman et al. 2018b). We only considered the 58 MEM variables associated to positive eigenvalues and hence corresponding to positively autocorrelated patterns, as the spatially structured simulated populations (distribution patterns) all displayed positively autocorrelated patterns.

**Statistical performance of the SSEF testing procedure**

Each of the 43 SS was replicated 1000 times, and each time the SSEF testing procedure was performed on the basis of 999 TT or MSR (providing that the global environmental and spatial models were both significant). The statistical performance of the two constrained randomisation procedures (TT and MSR) to test the adjusted SSEF was assessed as the proportion of significant p-values among the 1000 replicated simulations, and either corresponded to the type I error rate or to the statistical power, depending on the SS (Table 1). A schematic overview of the different steps of our simulation procedure for the 40 main SS is presented in Fig. 2: the three environmental maps used as filters to generate specialist populations (step 1 on the figure), the ten types of simulated tree distribution patterns (step 2), the test of the SSEF (step 3) and the calculation of type I error rate and statistical power associated to this test (step 4). Note that all the simulations presented in this study are performed on univariate response variables (i.e. the abundance of one single species). The SSEF testing procedure is however equally useful in a multivariate framework (e.g. community data; see Supplementary material Appendix 4 for an illustration).

All simulations were performed in the R statistical environment (<www.r-project.org>), using packages ‘car’ (Fox and Weisberg 2011), ‘adespatial’ (Dray et al. 2018), ‘spdep’ (Bivand and Piras 2015), ‘splancs’ (Rowlingson and Diggle 2015), ‘tripack’ (Renka 2013), and ‘vegan’ (Oksanen et al. 2015). The R script used to perform these simulations is provided in Supplementary material Appendix 3. A user-friendly R function to test the SSEF of a variation partitioning – ‘envspace.test’ – was implemented in the package ‘adespatial’ and is detailed in an R tutorial (Supplementary material Appendix 4).

**Data deposition**

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4qk2k11> (Bauman et al. 2018c).

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**Results**

Overall, we found that the type I error rate associated with the test of the SSEF (SS 1 to 20, Table 1) was always below the commonly accepted threshold of 0.05 (Fig. 3a–b). Furthermore, the statistical power obtained when the abundance was filtered using the fine-scale environmental variable was considerably low compared to when it was filtered by the broad-scale environmental one (Fig. 3c–d). The frequency at which each MEM variable was selected to model the spatial patterns of the different SS are presented in Supplementary material Appendix 1 Table A3. The latter indicates that the spatial patterns resulting from the combination of the different distribution patterns and environmental variables encompassed all broad, intermediate, and fine spatial scales.

**Type I error rate**

The type I error rate associated with the test of the SSEF never exceeded 0.05 (Fig. 3a–b), and so when using either TT or MSR to generate null SSEF values. The maximum type I error rate reached 0.037 for distribution pattern 6 (numerous and medium size tree aggregates; Fig. 2, step 2) when simulating generalist tree populations (SS 1 to 10; Fig. 3a). Type I error rates were always higher for generalist populations compared to when the abundance was filtered using a spatially randomised environmental variable (SS 11 to 20; Fig. 3b). More precisely, type I error rate reached, on average, 0.023 ± 0.012 (mean and standard deviation of type I error rates obtained using TT and MSR tests) among generalist populations, while it never exceeded 0.004 in SS 11 to 20 (spatially randomised environmental filter; mean and standard deviation of 0.0017 and 0.0014, respectively).

When simulating the particular additional scenario where the filtering environment was spatially structured and where both the global environmental and spatial components (i.e. fractions [ab] and [bc], Fig. 1) were significant but had no common variation (i.e. no SSEF expected), the SSEF was close to zero and we did not observe any type I error (see additional scenario 1 in Supplementary material Appendix 1 Table A4). No excess of type I error rate (0.007) was found in the additional scenario addressing the presence of negative adjusted R² corresponding to an ISD (additional scenario 3; Supplementary material Appendix 1 Table A4).

**Statistical power**

For all distribution patterns (1 to 10; Fig. 2, step 2), the statistical power associated to the SSEF test (SS 21 to 40, Table 1) was substantially lower when using the fine-scale environmental filter (SS 21 to 30; Fig. 3c) compared to when using the broad-scale one (SS 31 to 40; Fig. 3d). More specifically, it reached, on average, 0.426 ± 0.181 (mean and standard deviation of power values obtained using TT and MSR tests) across SS 21 to 30 (fine-scale environmental filter), with a minimum and a maximum value of 0.113 in distribution pattern 1 (low numbers of small tree aggregates;
Fig. 2, step 2) and 0.688 in distribution pattern 10 (spatially randomised tree distribution), respectively. In SS 31 to 40 (broad-scale environmental filter), however, power values reached, on average, 0.855 ± 0.080, with a minimum and a maximum value of 0.671 in distribution pattern 1 and 0.950 in distribution pattern 9 (numerous and large tree aggregates), respectively. Finally, high power values (> 0.970) were observed in the particular additional scenario where the global environmental effect (fraction [ab], Fig. 1) was entirely comprised in the global spatial effect (fraction [bc]) (additional scenario 2 in Supplementary material Appendix 1 Table A4). In additional scenario 3 (modeling ISD patterns with negative adjusted SSEF), the statistical power reached 0.784.

Mean and standard deviation values (calculated over the 1000 replicated simulations) of the SSEF in each simulation scenario are detailed in Supplementary material Appendix 1 Table A5.

Discussion

The variation partitioning is the most widely used analysis to assess the relative and shared effects of environmental heterogeneity and spatial predictors on species distributions (Borcard et al. 1992, Peres-Neto et al. 2006, Peres-Neto and Legendre 2010). However, no specific procedure has been proposed to test the shared effect of space and environment (the SSEF). This is a major gap as the SSEF is expected to reflect an induced spatial dependence effect (ISD) when one is present and when the sampling design allows detecting it. The absence of a reliable test therefore jeopardises any ecological interpretation of this fraction. Hence the objective of the present study, which was to introduce a testing procedure for the SSEF. We found that the procedure presented type I error rates < 0.05, indicating a very small risk to wrongly detect ISD when there is none. Efficient statistical power values (> 0.8) were obtained when simulating large and numerous tree aggregates filtered by an environmental variable displaying a broad-scale spatial structure. The lower power values (0.113 to 0.688) observed with the fine-scale environmental filter were most likely related to a limited power of MEM at scales too close or inferior to the fine-scale spatial resolution of the sampling design, as we discussed below. The SSEF values obtained through our simulations always fitted realistic and expected values. The mean SSEF values of the generalist populations reached 0.009 (min/max: 0.000/0.022) across SS 1 to 10, which was within the range of small values expected from species unrelated to the environment. The mean SSEF values of the simulated specialist populations reached 0.129 (min/max: 0.041/0.198) and 0.289 (min/max: 0.117/0.461) when the filtering environment displayed fine-scale and broad-scale spatial structures, respectively. These correspond to the range
The interpretation of a significant SSEF. The power to detect induced spatial dependence effects depends on the scale of the environmental filter and on sampling design characteristics

It is also worth mentioning that, although it was not the primary focus of the study, tests based on both TT and MSR provided type I error rates below the significance level (0.05) as well as high statistical power values for the global environmental component (fraction [ab]; not shown).

The TT and MSR tests prevent detecting spurious induced spatial dependence effects

The risk of detecting a significant species-environment association when the environment does not influence a species distribution but when both the species and the environment are spatially structured is a well-known issue in ecology (Dutilleul 1993, Legendre et al. 2002). The latter issue arises because aggregated populations and environmental structures may overlap by chance and inflate the SSEF, which in turn may enhance the risk of detecting a spurious ISD. However, we demonstrated that the TT and MSR tests of the SSEF provided levels of type I error rate below the usual threshold of 0.05 in a wide variety of scenarios (Fig. 3a–b). These tests were thus well able to avoid the detection of a false ISD when no environmental filtering was simulated (Fig. 3a), or when the filtering environment was not spatially structured (Fig. 3b) or was structured independently from the response variable (Supplementary material Appendix 1 Table A4), and so regardless of the type of spatial patterns present in the tree distribution. Type I error rate was particularly low in the second case (Fig. 3b), but also when the abundance was spatially randomised while the environment was not structured (Fig. 3a; SS 10), which was expected since we forbid the SSEF test to be performed if the environment or the abundance was not spatially structured, to avoid unnecessary risks of false positives.

There is a situation, however, in which spurious correlations between environmental and species data are expected, that is, when a coarse gradient, or spatial trend, is present in both the environment and the species (Borcard et al. 2004). It has been advocated that spatial trends should be removed prior to using PCNM (i.e. detrending), to avoid using spatial predictors to model the trends while they could be used to model finer and more complex patterns (Borcard and Legendre 2002, Borcard et al. 2004). The statistical power and accuracy related to detrending the data or not should however be evaluated in the broader framework of MEM, given the flexibility of the method and recent advances increasing its power and accuracy (Bauman et al. 2018a, b). Regardless of whether a detrending is used or not, the presence of a trend should be tested and explicitly considered in the interpretation of a significant SSEF.
statistics. This increase of power with $s^2$ presumably arises from a higher chance of overlap between a few large tree clusters and broad-scale environmental structures, than between a more complex patchwork of abundant and relatively smaller tree clusters and environmental patterns. The same phenomenon is likely to explain the relatively higher type I error rates for generalist populations (SS 1 to 10) compared to SS 11 to 20 (where no spatial structures were present in the filtering environment). It is also likely to result from the fact that large dispersal capacities and population size increased the chance for plants to be located on more various environmental conditions than when tree distributions are highly clumped, thereby reducing the variance of the SSEF after the randomisation procedure used in the TT or MSR tests.

Spatial variable selection and variation partitioning

When constructing the spatial predictors used in the variation partitioning, the choice of the spatial weighting matrix used to generate the MEM variables did not matter much in our case, as we performed our simulations on a regular grid (Dray et al. 2006). We therefore used the same spatial weighting matrix to test a spatial signal in both the response variable and the environmental dataset. However, when the sampling design is irregular, which is often the case with real datasets, the selection of the spatial weighting matrix should be optimised separately for the response and the environmental data to ensure a maximal statistical power and accuracy of MEM for both datasets (Bauman et al. 2018b; Supplementary material Appendix 1: section 3 and illustration in Supplementary material Appendix 4).

In a previous study, Gilbert and Bennett (2010) highlighted a problem of accuracy related to the MEM used in variation partitioning analyses. They also showed that the fractions associated to a spatial effect (i.e. [b], [c] and [bc]) were overestimated, even when the environment had no spatial structure. However, as illustrated by our results, our SSEF testing procedure displayed a correct type I error rate throughout the wide range of simulation scenarios that were used. This discrepancy is likely to arise 1) from the fact that the authors considered the value of the SSEF even though the environment was not spatially structured, and 2) from the absence of a test for the SSEF. In addition, to evaluate accuracy, the authors compared what they called the “true variation” of the different partitioning fractions (i.e. the reference values at the level of a complete grid of 129 x 129 cells, that is, 16 641 cells) to the values obtained from different sampling designs of very small samples with respect to the complete grid (i.e. either 64 or 256 cells). It seems therefore that the lack of accuracy that they attribute to MEM may have simply arisen from the sampling procedure. This may be confirmed by two recent studies in which the power and spatial $R^2$ estimation accuracy of MEM have been shown to be high in a wide variety of simulation scenarios, when considering the reference values of variation on the sampled cells instead of on a much bigger grid (Bauman et al. 2018a, b). It is also worth mentioning that using distance-based MEM has recently been shown to yield poor results in terms of power and accuracy for irregular sampling designs, compared with the more powerful and accurate graph-based MEM (Bauman et al. 2018b). The use of distance-based MEM in studies based on irregular sampling designs is therefore expected to yield inaccurate estimations of the fractions of the variation partitioning. In those cases, the highest accuracy of MEM is reached with an optimisation of the selection of the spatial weighting matrix combined with the forward selection with double stopping criterion (Bauman et al. 2018a, b). These recent studies, together with our results, strongly suggest that variation partitioning can be reliably performed provided that: 1) preliminary conditions are met (significance of both the global environmental and the global spatial models), 2) an optimal set of MEM variables is selected among multiple spatial weighting matrices (Bauman et al. 2018b, Supplementary material Appendix 4), and 3) the SSEF is only tested when the environment displays a significant spatial structure.

Conclusion

In this study, we showed that our testing procedure did not detect any ISD when there was none, that is, when the environment was not spatially structured or when no environmental filtering occurred (Supplementary material Appendix 1 Table A3). We also showed that the procedure was able to detect a significant SSEF when an ISD had been simulated, and so in many contrasting simulation scenarios (provided that the scale of the spatial patterns was not too close or inferior to the fine-scale spatial resolution of the sampling design). In the SSEF testing procedure, both TT and MSR – when used with a well-selected subset of MEM variables (Supplementary material Appendix 2) – were able to detect an ISD related to negative SSEF while avoiding confusion with suppression effects and negative value obtained by the $R^2$ adjustment. In addition, both TT and MSR can be used to test the global environmental component while controlling for spatial autocorrelation issues, hence avoiding the type I error rate inflation of classical permutation tests. It is worth mentioning that in real data studies, a significant SSEF may also be caused by spatially structured unmeasured environmental variables that are correlated to one or several of the measured structured environmental variables (Borcard and Legendre 1994, Peres-Neto and Legendre 2010). This, however, is also true for fraction [ab] and fraction [a], as an unmeasured variable could always be correlated to both the response data and the spatially structured or not spatially structured portion of variation of a measured explanatory variable. Inferring causal relations should always be done with caution, and a priori hypotheses and ecological theory or knowledge should underlie the choice of the environmental variables measured and included in the variation partitioning to allow strong interpretations of the SSEF and the other fractions of the variation partitioning analysis (McIntire and Fajardo 2009).
Acknowledgements – We are very grateful to Daniel Borcard, Pierre Legendre and Cajo ter Braak for their constructive comments and suggestions.

Funding – JV is currently funded by the labEX CEBA (Centre d’Étude de la Biodiversité Amazonienne, managed by CNRS, France) and was funded by the Belgian Fund for Training to Research in Industry and Agriculture (FRIA) when the study was designed. DB is a PhD candidate currently funded by the Fund for Scientific Research of Belgium (F.R.S.-FNRS).

Statement on authorship – DB and JV contributed equally to the study. JV, DB and OH conceived the study; DB and JV designed the methodology, analysed the data, led the writing of the manuscript, and designed the new R function; DB integrated the function to the package adespatial; OH and TD contributed to the discussion and made constructive revisions of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References


Supplementary material (available online as Appendix oik-05496 at <www.oikosjournal/appendix/oik-05496>). Appendix 1–4.