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Quantification of the spatial co-occurrences of ecological boundaries

Marie-Josée Fortin, Pierre Drapeau and Geoffrey M. Jacquez

Fortin, M.-J., Drapeau, P. and Jacquez, G. M. 1996. Quantification of the spatial co-occurrences of ecological boundaries. – *Oikos* 77: 51–60.

In this paper, we investigate spatial relationships between vegetation boundaries and environmental boundaries from a second-growth forest in southwestern Québec, Canada. Four statistics that quantify the amount of direct spatial overlap and the mean minimum distance between boundaries are introduced and used to compute the degree of spatial co-occurrences between boundaries. The significance of these statistics is determined using randomized and restricted permutation tests. Boundaries based on tree species density are found to significantly overlap the locations of boundaries delineated by the environmental data at the study site. Significant overlap is also found using boundaries defined by tree presence–absence data and environmental variables. Vegetation boundaries based on tree species density and on tree presence–absence data are not, however, at the same locations. This suggests that for the study site the two types of vegetation boundaries (tree density and presence–absence) reflect different responses to underlying environmental processes. Vegetation boundaries determined using species diversity and species richness, although spatially related to the presence–absence boundaries, did not overlap the environmental boundaries. Results of the two permutation tests (randomized and restricted) agree only when the spatial relationship between the two boundary types is strong. Overall, randomization is found to be a more conservative test for detecting boundary spatial relationships, rejecting the null hypothesis of no spatial relationship fewer times than the restricted permutation test.

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Different types of processes, including environmental changes and species interactions, can generate ecological boundaries (van der Maarel 1990). Moreover, the factors that created an ecotone may not necessarily maintain it (Holland 1988, Hansen and di Castri 1992). Processes producing vegetation boundaries include environmental gradients, treefall gaps, forest fires, insect epidemics, clear-cuts and other processes leading to site-specific variation in seed germination success, species survival and species interactions (Holland et al. 1991). Depending on the type and intensity of causal factors, vegetation boundaries can be either sharp or

smooth (Ferson 1988), and our ability to delineate them varies according to the variables (species or environmental data) or measurements (species density, presence–absence, biomass, diversity, etc.) we use (Fortin 1992).

As with other ecological phenomena, abiotic and biotic processes involved in ecotone dynamics are often intermingled, which complicates the determination of their relative contribution to the creation and maintenance of ecotones. One way to assess the relative contribution of abiotic processes is to first quantify the degree of spatial relationship between vegetation

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boundaries and those based on environmental variables (Wiens et al. 1985).

This paper describes a novel approach for quantifying spatial relationships between ecological boundaries, here vegetation and environmental boundaries. Our approach first delineates vegetation and environmental boundaries using edge detection methods for two-dimensional data (Fortin 1992). We then apply the four overlap statistics of Jacquez (1995) to quantify spatial relationships between vegetation and environmental boundaries (Fortin 1992). These statistics characterize different aspects of the relationship between boundaries, namely the spatial degree of direct overlap and the mean minimum distance between two boundaries. The significance of these statistics is determined using randomization and restricted permutation tests (Upton and Fingleton 1985, Fortin 1992). Vegetation and environmental data sets from a second-growth forest are used to illustrate the usefulness of these statistics.

Data

The ecological data used to illustrate the following analyses were gathered in an area of 650 by 1050 meters within a second-growth forest in southwestern Québec, Canada (Leduc et al. 1992, Fortin and Drapeau 1995). The study site was selected because it contained changes in environmental factors, especially changes in soil water availability in the center area due to kettles and at the north edge of the site due to a swamp and a road. The forest is composed mainly of three stands dominated respectively by sugar maple, red maple, and hemlock. A triangulated systematic sampling design was used to survey 200 vegetation quadrats measuring 10 by 20 m in size. The quadrats were placed at 50-m intervals along each row and the rows were 50 m apart. Trees of more than 5 cm diameter at breast height were noted and identified to the species level. The twelve most abundant species were used for this analysis (Fortin and Drapeau 1995). Vegetation boundaries were determined using species density, presence-absence, the Shannon diversity index (Legendre and Legendre 1983) and species richness. For each quadrat environmental variables, including geomorphological context, drainage, topography, thickness of the Ah or Oh soil horizons, texture of the B horizon, and the percentage of stones in the soil profile were used to delineate environmental boundaries.

Methods

Boundary delineation

We defined boundaries to be spatially adjacent locations where the measured variable shows high rates of

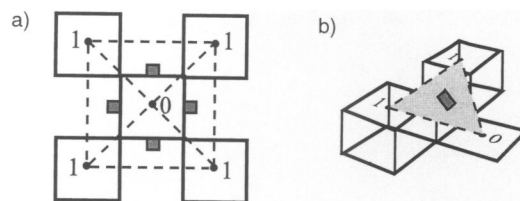


Fig. 1. Triangulation-wombling. a) Systematic triangulated spaced quadrats where the Delaunay triangulation network (dashed lines) links quadrats into triangles. The dots indicate the centroid of each quadrat. The numbers represent density values. The filled squares indicate the location of the centroid of each "triangle" formed by three adjacent quadrats. b) The three selected quadrats forming a triangle where the *z*-axis corresponds to density values. The grey surface fits the density values of the three adjacent quadrats and the slope on the surface corresponds to the magnitude of rate of change.

change (Fortin 1994). This definition includes two important aspects of boundary dynamics: the locations of high turnovers (species or variables) and the spatial proximity of their co-occurrence.

To quantify vegetational and environmental boundaries we used an edge detection algorithm that computes the first partial derivatives from irregularly spaced data (for mathematical details see Fortin 1994). This edge detection algorithm, called triangulation-wombling, computes the rate of change for each set of three adjacent locations that forms a triangle (Fig. 1). The Delaunay tessellation algorithm can be used to find the list of nearby locations that form triangles (Upton and Fingleton 1985). The magnitude of the rate of change is computed for the center point of each set of three nearest samples that form a triangle. The slope of the plane that fits the values of the variables corresponds to the magnitude of rate of change among the three nearest values. When the three nearest values are similar, the plane is approximately horizontal and the slope, which measures the magnitude of rate of change, is close to zero. When the values are dissimilar the slope differs from zero. The slope is steeper when the triangulated values differ greatly from one another, corresponding to a high rate of change within the triangle. When more than one variable is considered, the overall mean of change is the mean of the magnitude of change from each variable. Following Fortin's (1994) criterion, locations whose average rates of change are among the top 10% are considered as part of a boundary (call these locations boundary elements or BE's).

Using the mean rate of change at each location implies that each species, or variable in the case of the environmental data, has the same importance or weight, in the delineation of boundaries. Different weights can be used when there are ecological reasons to think that one species or variable is more important than another when defining boundaries.

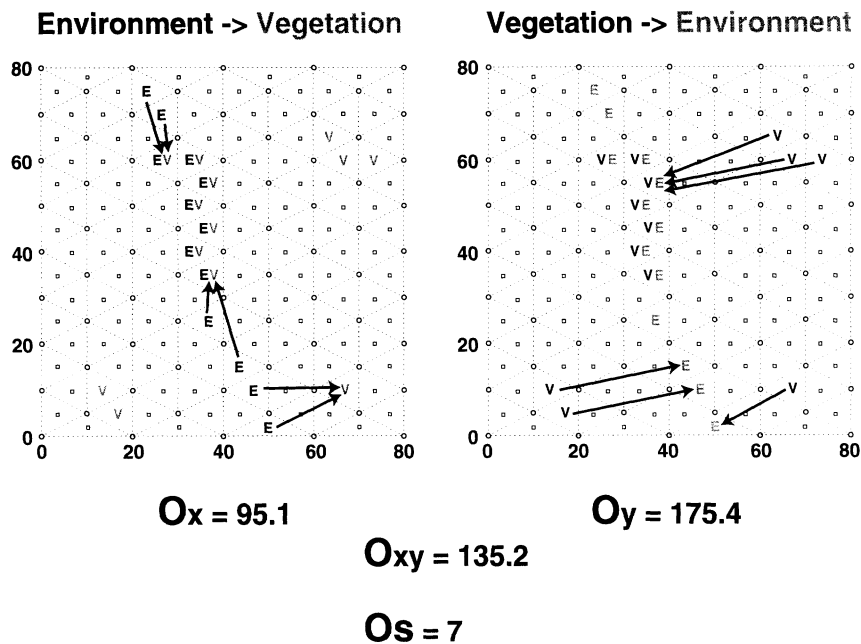


Fig. 2. Overlap statistics. The left panel shows vegetation boundaries and the right panel environmental boundaries. The O_x (95.1) is smaller than O_y (175.4) which indicates that some vegetation boundaries are not that spatially related to the environmental boundaries (O_{xy} is 135.2). The number of direct overlap, O_s , between the two types of boundaries is 7.

Significance test for boundaries

Depending on the type and intensity of explanatory factors, vegetation boundaries can be wide, corresponding to gradual transition zones or narrow, as occurs for zones of abrupt change. In either case, significance tests are needed to determine whether the boundaries are not due to chance and are cohesive ones (Fortin 1994).

Boundary significance can be evaluated by comparing an observed statistic describing some property of a cohesive boundary to its reference distribution (Oden et al. 1993). The reference distribution is generated by randomly permuting the observed values in a suitable manner across the sample locations at least one hundred times (Manly 1991, Fortin 1994). The number of permutations determines the minimum significance level that can be resolved by the test. For example, a reference distribution of 100 values will resolve $P \geq 0.01$, and one of 1000 values will resolve $P \geq 0.001$.

The reference distribution generated in this manner does not account for any inherent spatial structure of the data. That is, it ignores the possibility that processes underlying the spatial distribution of the data may induce spatial autocorrelation (Legendre and Fortin 1989). However, Oden et al. (1993) have shown that randomized reference distributions result in conservative significance tests for detecting significant boundaries, and that they falsely reject fewer than the null hypothesis of no significant boundaries.

The statistics used to determine boundaries (see Oden et al. 1993 or Fortin and Drapeau 1995) are defined in terms of a subgraph, where a subgraph is a set of connected boundary elements (BE's). These statistics are: 1) The number of subgraphs formed at a given threshold, 2) The maximum length (the number of edges of the longest subgraph) of the subgraphs formed at a given threshold.

Boundaries are said to exist when the number of subgraphs is significantly small. For the purpose of this research we declare boundaries statistically significant when the number of subgraphs is in the lower 5% tail of the reference distribution. Conversely, the maximum length should be large for true boundaries, and the observed maximum length is considered significant if it is in the upper 5% tail of its reference distribution.

Quantify spatial relationship between boundaries

We used the following overlap statistics (Jacquez 1995) to quantify the degree of co-occurrences between ecological boundaries. The first statistic is quite straightforward, it computes the amount of direct spatial overlap between ecological boundaries: O_s is the number of boundary elements that are at the same location (Fig. 2).

Then, the three other statistics quantify the degree of spatial lag in terms of mean minimum distance between the ecological boundaries. Each of these statistics assume different types of relationship between two boundaries. The first one assumes that the location of the X boundary (let us say the environmental boundary) affects the location of the Y boundary (let us say the vegetation boundary) and is computed as follows: The mean minimum distance from any location in the boundary elements for x (for example the environmental BE's) to the nearest location in the boundary elements for y (for example the vegetation BE's):

$$O_x = \frac{\sum_{i=1}^{N_x} \min(d_i)}{N_x}$$

where $\min(d_i)$ is the smallest euclidean distance for the i th element of the boundary x to an element of the boundary y , and N_x is the number of boundary elements for x (Fig. 2).

Conversely, the second statistic assumes that the location of the Y boundary (the vegetation boundary) affects the location of the X boundary (the environmental boundary). In the case of ecological boundaries, this is a possible type of interaction since some tree species, such as conifers, can alter surrounding soil conditions. This statistic is computed as follows: The mean minimum distance from any location in the boundary elements for y (the vegetation BE's) to the nearest location in the boundary elements for x (the environmental BE's):

$$O_y = \frac{\sum_{j=1}^{N_y} \min(d_j)}{N_y}$$

where $\min(d_j)$ is the smallest euclidean distance for the j th element of the boundary y to an element of the boundary x , and N_y is the number of boundary elements for y (Fig. 2).

Finally, the third statistic assumes that both boundaries influence one another and is the mean of the two previous statistics, and is computed as follows: The mean minimum distance between the elements of the two boundaries x (the environmental BE's) and y (the vegetation BE's) (Fig. 2):

$$O_{xy} = \frac{\sum_{i=1}^{N_x} \min(d_i) + \sum_{j=1}^{N_y} \min(d_j)}{N_x + N_y}$$

Because the overlap statistics are sensitive to different aspects of the spatial relationship between boundaries, comparing them can indicate which boundary seems to most influence the location of the other. Such information will help us to quantify the relative contribution of factors controlling the location of boundaries.

Significance tests for spatial relationship between boundaries

Randomized and restricted permutation tests (Upton and Fingleton 1985) are used to determine whether vegetation and environmental boundaries are spatially more related than would be expected if there were no interaction between them.

Randomized permutations repeatedly sprinkle the observations at random across the sample locations. This assumes an observed value is equally likely to occur at any location, and that it is independent of the values observed at other locations. The null hypothesis under a randomized permutation implies that there are no interactions at the variable level (e.g., within each species), no interactions at the variable's set level (e.g., among the species) and no interactions between two sets of variables (e.g., between vegetation and environmental data).

However, seed dispersal processes and competition for space (Chesson 1985) are expected to result in some degree of spatial autocorrelation (Legendre and Fortin 1989) at the variable level (spatial pattern at the species level) and the variable's set level (spatial interactions among species). Therefore, a null hypothesis that takes into consideration some degree of spatial structure seems more appropriate. Call this a spatially restricted null hypothesis. The restricted null hypothesis we employ assumes that there are interactions both at the variable level (within each species) and at the variable's set level (among species). It further assumes there are no interactions between the two types of variables, since such interactions are the phenomena we explicitly wish to detect.

The reference distribution under the restricted null hypothesis is generated by using a restricted permutation test (Upton and Fingleton 1985). We accomplish this by first connecting the left and the right margins of each map as well as its top and bottom to form a two-dimensional torus (donut-like). Then one of the boundary maps is shifted over the torus, one unit of 50 m (the distance between the sampled points) at a time, while holding the second boundary map constant. The overlap statistics are then calculated using the new spatial relationships among the boundaries. The sampled area is 650 by 1050 m, and can be spanned by 13 units of 50 m in the x -axis and 21 units of 50 m in the y -axis, resulting in a total of 273 possible translations. Due to toroidal symmetry only 76 of these translations are unique, and the reference distributions are based on these 76 unique shifts. This means, for restricted permutations, the minimum P -value that can be resolved is $1/76$ or 0.0131, which is adequate for our purpose.

Significant results under both approaches (randomized and restricted) suggest that vegetation boundaries are tracking the environmental boundaries. Significant results for only one of the permutation procedures

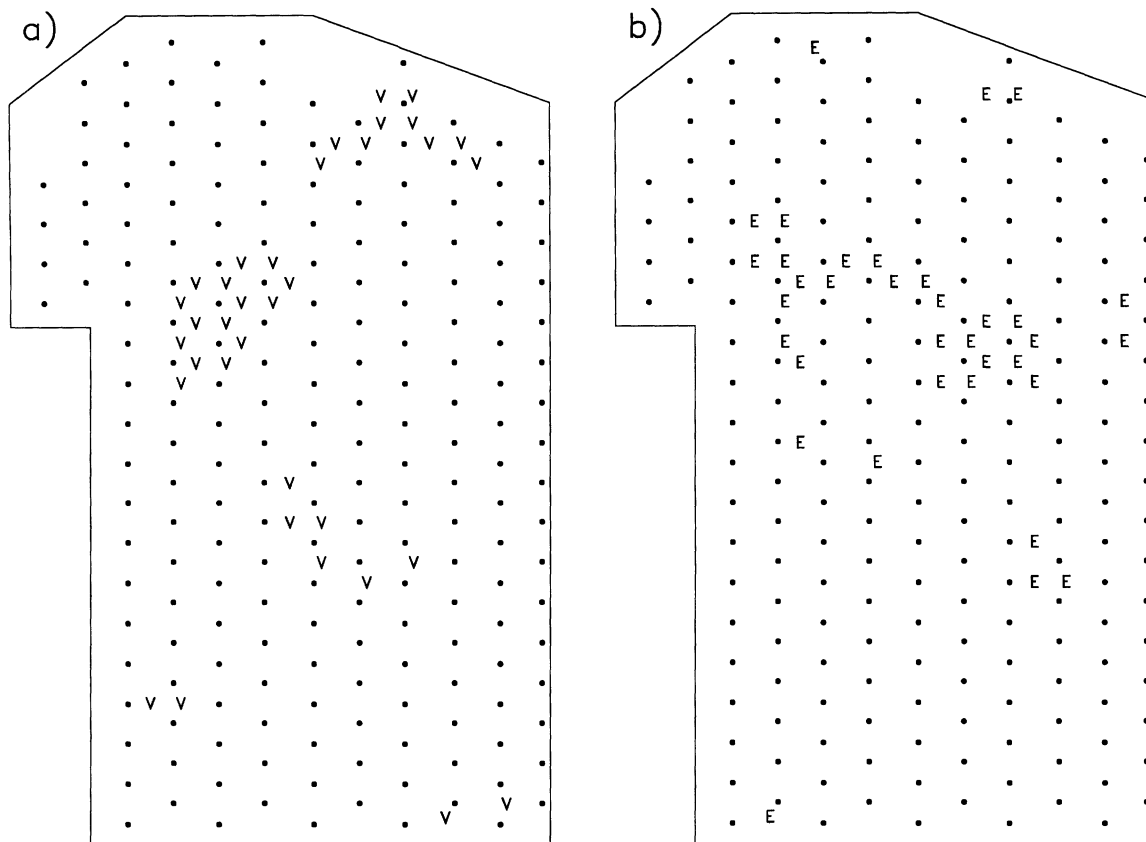


Fig. 3. The triangulation-wombed BE's (highest 10%) of a) the species density (as indicated by the letter V) and of b) the environmental variables (as indicated by the letter E). 200 systematic triangulated spaced quadrats as shown by the dots.

make interpretation more problematic, and whether the results are considered meaningful will depend on the assumptions to which the worker adheres.

Results and discussion

Boundary delineation

Delineated boundaries were obtained using the triangulation-wombling algorithm (Fortin 1994) and a Delaunay triangulation network, yielding 553 links among nearby samples. The number of boundary elements retained with the triangulation-wombling algorithm is 35 (10% of 351 triangles). Fig. 3 shows the boundary elements computed for species density and the environmental variables using the triangulation-wombling algorithm. Overall, the locations of vegetation BE's agree with the locations of change in species dominance i.e., *Acer saccharum*, *Tsuga canadensis*, and *Acer rubrum* (see Fortin and Drapeau 1995). Similarly, envi-

ronmental BE's reflect mainly change in drainage where the latter ranges from rapid to very rapid on a moraine ridge, to poor to very poor on kettles (Fortin 1992, Leduc et al. 1992). Table 1 shows the boundary statistics for the boundary elements (BE's). The delineated boundaries (BE's) for the species density and environmental data are statistically significant.

Table 1. Boundary statistics for the boundary elements, given a 10% threshold, of the different ecological variables.

	Number of subgraphs	Maximum length
Environment	13*	10*
Density	10*	17*
Presence-absence	19*	4
Richness	16*	7*
Diversity	14*	5

* indicates significant values at $P \leq 0.05$ as tested by the randomization test.

Table 2. Overlap statistics between the vegetational and environmental boundaries (BE's). Significance is determined using randomized (R) and restricted (T for torus) permutation tests.

<i>x</i>	<i>y</i>		O_s	O_x	O_y	O_{xy}
Environment	Density		10+	80.4	57.9	69.2
		R	*		*	
		T	*	*	*	*
Environment	P–A		10+	51.7	71.9	61.9
		R	*	*		
		T	*			
Environment	Richness		5	75.0	102.8	88.9
		R	*	*	*	*
		T	*	*	*	*
Environment	Diversity		2	143.3	102.3	122.8
		R	**			*
		T	*			*
Density	P–A		8+	47.2	70.9	59.1
		R	*	*	*	*
		T	*	*	*	*
Density	Richness		4	77.4	102.4	89.9
		R	*	*	*	*
		T	*	*	*	*
Density	Diversity		5	113.1	103.4	108.3
		R	*			
		T	*			
P–A	Richness		9+	64.5	72.7	68.6
		R	**			
		T	*	*		*
P–A	Diversity		5	86.4	75.9	81.2
		R	*			
		T	*			
Diversity	Richness		18+ + +	53.3	36.6	44.9
		R	**	**	**	**
		T	*	*	*	*

P–A indicates presence–absence data. * indicates significant values at $P \leq 0.05$, ** indicates significant values at $0.05 \leq P \leq 0.01$, + indicates significant values at $P \leq 0.05$ based on the binomial test, + + + indicates significant values at $P \leq 0.001$ based on the binomial test.

Are vegetation and environmental boundaries spatially related?

The four overlap statistics were computed to evaluate spatial coincidence of the vegetation and environmental boundaries. Table 2 shows that the overlap statistics between the delineated boundaries (BE's) from the environmental variables and the species density are all significant when tested by the restricted permutation test while only two are significant when tested by the randomization test.

The direct overlap statistic, O_s , is significant for the two tests and indicates that there are 10 BE's that are at the same location both for the species density and the environmental data. Overall, the species density boundaries seem to be spatially related to the location of the environmental data since the mean minimum distance, O_y , from the species density to the environmental data is smaller than the mean minimum distance, O_x , from the environmental data to the species density. The difference between the values of these two statistics indicates that some vegetation boundaries are not spatially related to the environmental boundaries and may be related to other factors.

Here, the delineated vegetation boundaries are based on changes in species density. Possibly, factors other

than changes in environmental conditions (e.g., perturbations and species interactions) may influence changes in density. On the other hand, it is also possible that other vegetation features, such as presence–absence, diversity and species richness may be more sensitive to environmental changes than species density, as described below.

Are boundaries of different vegetation features spatially related?

The comparison in the location of the BE's based on the different vegetation features (density, presence–absence data, diversity and species richness) can provide complementary information about the vegetation responses to environmental conditions. To examine this, boundaries based on the presence–absence data, species richness (i.e., the number of tree species per sample) and Shannon's diversity index (Legendre and Legendre 1983) were delineated using the triangulation-wombling algorithm. Table 1 shows that species richness boundaries are significant as based on the two boundaries statistics while the presence–absence and diversity boundaries are significant only with regards to

the number of subgraphs statistic. Thus at this 10% threshold the boundaries based on features other than species density are not as cohesive.

Notice that the locations of the BE's based on presence-absence data, diversity, and species richness differ from those based on species density (Figs 3 and 4). Hence, the locations of the BE's based on presence-absence data spatially differ in their location from those based on species density. The locations of the BE's based on diversity and species richness are also different from those based on species density and presence-absence data and are mainly located between in different parts of the study area than those based on density (Fig. 4b, c). Thus, the boundaries based on different vegetation features occupy different parts of the study area (Fig. 4), suggesting that not all vegetation features respond with the same intensity to environmental conditions.

The overlap statistics between the boundary elements of environmental and vegetation features (i.e., presence-absence, diversity, and species richness) were computed to explore spatial relationships between environment and vegetation (Table 2). We found environmental boundaries to overlap more strongly (especially the O_s statistic) with the presence-absence (10) and density (10) boundaries than to the species richness (5) and species diversity (2) boundaries. This direct measure of spatial relationship between the diversity and species richness boundaries and the environmental boundaries is significant only when using the restricted permutation test.

The minimum nearest neighbor overlap statistics find the strongest overlap between the environmental boundaries and the presence-absence ones (O_x) but are significant only with the randomization test. The presence-absence and environmental boundaries did not overlap significantly.

Based on the O_{xy} statistic, the environmental boundaries were found to coincide the most with species density and presence-absence boundaries followed by the species richness and then the species diversity. The spatial relations between the species richness and environmental boundaries for both the O_y and O_{xy} statistics are significant under both permutation tests. The O_{xy} statistic between the species diversity and the environmental boundaries is also significant with both permutation tests. Although the presence-absence and diversity boundaries were significant only with regard to the number of subgraphs statistic, some of the overlap statistics were significant under both permutation tests.

When vegetation features are compared among themselves, O_x statistics which are significant based on both permutation tests are those found between (1) diversity and species richness and (2) between species density and the presence-absence boundaries (Table 2). Hence, the strongest spatial relationship, measured as the largest direct overlap (O_s) and smallest mean minimum dis-

tances (O_x , O_y and O_{xy}) is between the diversity and species richness boundaries for which these statistics are significant under both permutation tests.

The next strongest O_s statistic is between the presence-absence and the species richness boundaries (9) and is significant based on both permutation tests while the O_x and O_{xy} statistics are significant only with the restricted permutation tests. The overlap statistics between the species density and diversity are all significant but only with the restricted permutation test.

The direct overlap statistic, O_s

The direct overlap statistic, O_s , is simply the number of pairs of BE's for the two boundaries that have the same location. Here the rates of change that are considered as BE's are arbitrarily set as those with slope magnitude in the upper 10%. Rates of change are calculated for 351 locations, and only 35 of these are considered as BE's in each data set. Hence, the direct overlap statistic is the number of direct spatial matches found out of 35. The significance of this statistic can therefore also be computed directly by a binomial test as shown in Table 2. It is found that with the binomial test it takes at least eight (8) BE's directly overlapping for the direct overlap statistic, O_s , to be significant at $P = 0.05$. It is interesting to highlight that the significant direct overlap statistics, O_s , based on the binomial test are also significant with both permutation tests. Therefore, for this analysis, the significance of this direct overlap statistic, O_s , could be achieved by using a binomial test rather than permutation tests which involve heavy computations.

Randomization versus restricted permutation test

By comparing the results from the two permutation tests, we found (1) that when the spatial relationship between the two sets of data are strong, both permutation tests agree in finding significant relations, and (2) that randomization is a more conservative procedure, declaring significance less frequently, than restricted permutations. These results are comparable to those found by Oden et al. (1993). This seems counterintuitive at first because of expected spatial structure in the vegetation and environmental data as mentioned above. The null hypothesis under randomization does not account for spatial autocorrelation, and one might therefore expect it to declare significance more frequently because departures from the reference distribution might be caused by spatial autocorrelation as well as by true boundary overlap.

The reference distribution is constructed by reallocating the original observations across the sample locations, deriving a new map of the boundaries each time. In contrast, the restricted permutation procedure takes

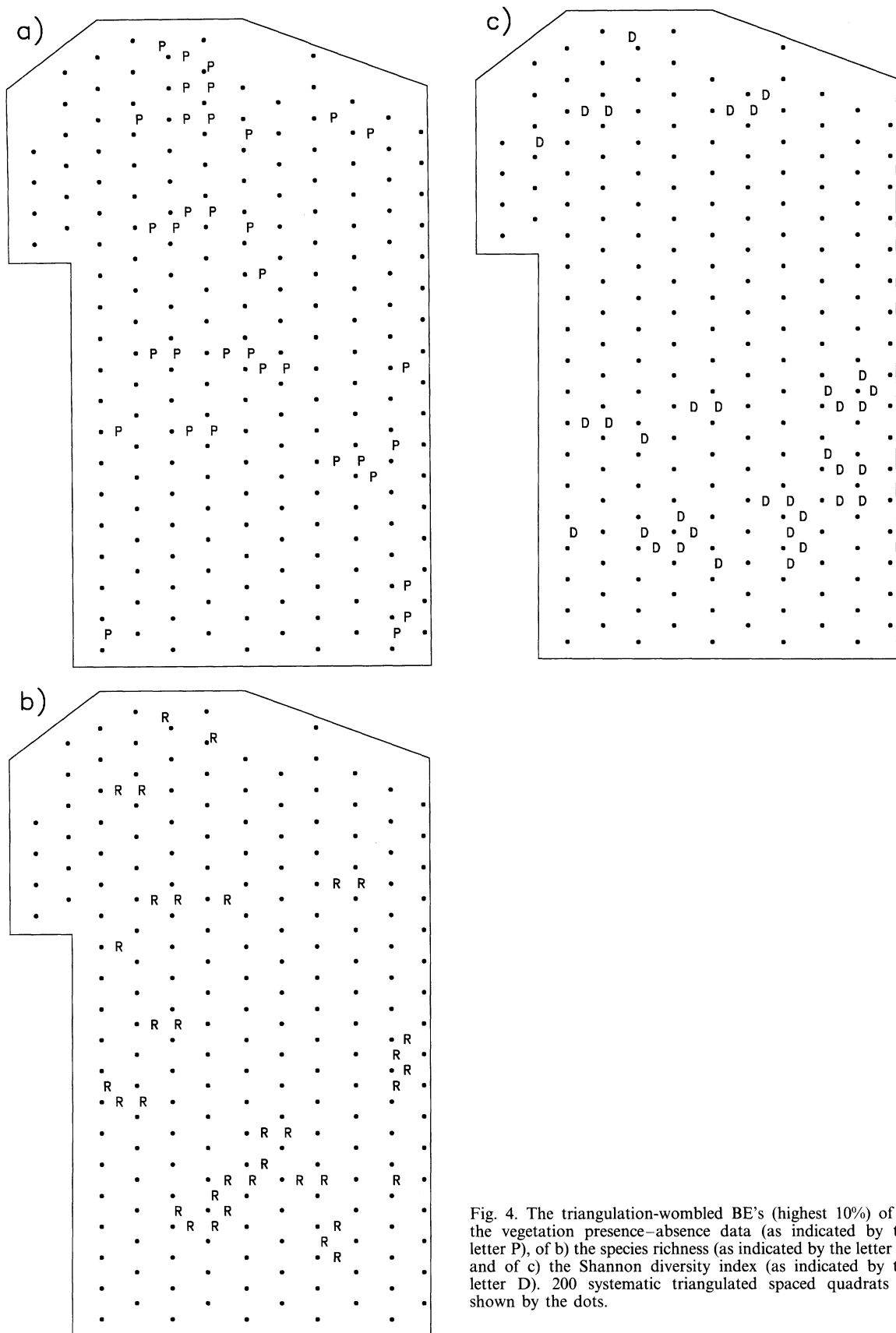


Fig. 4. The triangulation-wombed BE's (highest 10%) of a) the vegetation presence-absence data (as indicated by the letter P), of b) the species richness (as indicated by the letter R) and of c) the Shannon diversity index (as indicated by the letter D). 200 systematic triangulated spaced quadrats as shown by the dots.

the observed spatial relationships among a variable's boundaries as a fixed map, and then repeatedly reposition this map over the boundary map of the second variable. The restricted permutation procedure seems therefore more liberal, i.e., rejects the null hypothesis more times than the randomization (see Oden et al. 1993 for similar results), because it takes the spatial relationships giving rise to the boundaries as a given. All other spatial arrangements of the observations, including those which give rise to the most boundary overlap, are excluded from the reference distribution. These alternative spatial arrangements are allowed in the randomization procedure, resulting in a wider reference distribution and causing decreased *P*-values in the tail relative to the restricted permutations.

For example, the four overlap statistics between the species density and the diversity boundaries are significant only with regard to the restricted permutation test while the magnitudes of the overlap statistics are not among the strongest (the strongest being between the diversity and species richness boundaries). Based on our results we recommend that one assesses the significance of the direct overlap statistic using the binomial test (keeping in mind that the binomial procedure assumes that significant BE's are equally likely at all locations, which may or may not be appropriate for all data sets) and by using the randomization procedure for the three other overlap statistics.

Some question arises as to whether our approach to the restricted randomization is overly restrictive, thereby giving rise to an excessively narrow reference distribution and an overly liberal test (reject null hypothesis too often). An alternative restricted permutation procedure is to maintain a comparable level of spatial autocorrelation in the data when sprinkling the observed values across the localities as in Oden et al. (1993). Such a procedure has been found to be liberal as well for detecting significant boundaries. Therefore other types of permutation approaches warrant future investigation but in the meanwhile the randomization procedure offers a conservative test to assess the degree of spatial relationships between ecological boundaries.

Conclusion

To assess how different boundaries can be spatially related we used the four overlap statistics of Jacquez (1995) and we assess their significance using a binomial approach and Monte Carlo simulations (randomized and restricted). Using a real data set, we found that boundaries based on species density, presence-absence, diversity and species richness are different from one another and correspond to different spatial responses to environmental conditions. By comparing the values of the overlap statistics, we found that the environmental

boundaries were more strongly associated with the species density and presence-absence boundaries than with the diversity and species richness ones.

This research demonstrates that, using these statistics, it is possible to assess the degree of spatial relationships between two sets of boundaries. The quantification of the spatial relationship among boundaries is expected to increase our understanding of the relative importance of abiotic phenomena and biotic interactions which give rise to ecotones and edges. Furthermore, such statistics can also be used to quantify the degree of spatial co-occurrences between ecological boundaries (ecotones) and hybrid zones (Hewitt 1988), and support the study of interactions between ecological and genetic transition zones.

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