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Ecological Modelling 146 (2001) 167–180

ECOLOGICAL  
MODELLING

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# Spatial analysis of stream invertebrates distribution in the Adour-Garonne drainage basin (France), using Kohonen self organizing maps

R. Céréghino \*, J.L. Giraudel, A. Compin

*Centre d'Ecologie des Systèmes Aquatiques Continentaux, Université Paul Sabatier, UMR C5576, 118 route de Narbonne, 31062 Toulouse Cedex 4, France*

## Abstract

We analysed the regional distribution of 283 lotic macroinvertebrate species from four insect orders (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera = EPTC) in the Adour-Garonne drainage basin (South–Western France, surface = 116 000 km<sup>2</sup>). The aim of this work was to provide a stream classification based on characteristic species assemblages. The faunistic data corresponded to the occurrence (presence or absence) of 283 species at 252 sampling sites. These data were computed with the Kohonen self organised map algorithm (SOM) (Kohonen, *Self-Organizing Maps*, volume 30 of Springer Series in Information Sciences. Springer, Berlin, Heidelberg. (Second Extended Edition 1997)). This neural network algorithm has already been successfully used in ecology (Giraudel et al., *Artificial neural networks, applications to ecology and evolution*. Springer-Verlag, (in press); Chon et al., *Ecol. Model.*, 90, 1996, 69–78) for communities patternizing. SOM enable visualisation of the complex species assemblage in a two-dimensional space, preserving the topology of the input data. Then, using the U-matrix method, it was possible to classify the data without prior knowledge. Four major EPTC regions were characterised within the drainage basin (Massif Central mountains, Pyrénées mountains, Piedmont and plains, Toulouse city agglomeration), along with their theoretical species assemblage. The number of species characterising each region ranged from 45 to 159, underlining the spatial (i.e. longitudinal and geographical) differences in EPTC assemblages. The main interest of our results is that the stability of these theoretical assemblages may be used to define representative and/or reference sites for biological surveillance, as any change in species composition within a given EPTC region can be considered as a biological indicator of environmental changes. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Self-organizing maps; Neural networks; Aquatic insects; Spatial distribution; Classification; Ephemeroptera; Plecoptera; Trichoptera; Coleoptera; Benthic fauna

## 1. Introduction

During the last decades, there have been many attempts to produce stream classifications based on aquatic communities features (e.g. Huet, 1949; Illies and Botosaneanu, 1963; Gibon and Statzner,

\* Corresponding author. Tel.: +33-561-558687; fax: +33-561-556096.

*E-mail address:* cereghin@cict.fr (R. Céréghino).

1985; Omernik, 1987; Whittier et al., 1988; Tate and Heiny, 1995). We use classification in stream management to characterize how ecosystems differ in terms of species assemblage. By knowing what the assemblage should be like, we can determine the degree to which human activity have altered it (Hawkins et al., 2000). Thus, an interest of such classifications is that the stability of species assemblages may be used to define representative and/or reference sites for biological surveillance (Hughes et al., 1986), as any structural change in populations features can indicate environmental changes in streams from a given region or a longitudinal section. The specific composition of invertebrate populations depends on the diversity and stability of stream habitats (Cummins, 1979; Ward and Stanford, 1979) which provide the possibilities of development (Malmqvist and Otto, 1987). Therefore, invertebrates are widely used as indicators of short- and long-term environmental changes in running waters (Hellowell, 1978). As an alternative, the River Continuum Concept (Vannote et al., 1980) implied a classification based on stream size or location within a stream system, but several authors have emphasized the importance of geographic differences in biotic and abiotic characteristics of streams (Culp and Davies, 1982). However, such a proposal can be evaluated in a given area by providing a geographical model, i.e. a map (Whittier et al., 1988).

Because of the very high diversity of aquatic invertebrates — 70% of the overall animal species recorded in European continental waters (Ilies, 1978) — and the difficulty to obtain specific identifications, stream classifications were often restricted to a single valley or a range of mountains (Décamps, 1968; Vinçon and Thomas, 1987; Vinçon and Clergue, 1988; Giudicelli et al., 2000), and were usually based on a single taxonomic group (e.g. one insect order). The aim of our study was to analyse the spatial distribution of 283 lotic macroinvertebrate species from four insect orders (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera = EPTC) in a 116 000 km<sup>2</sup> drainage basin (Adour-Garonne, South–Western France), in order to derive a

stream classification based on the similarity of their species assemblages. To this end, we used of a large volume of site-specific data, which were subjected to the Kohonen self organised map algorithm (SOM) (Kohonen, 1995). SOM is a neural network algorithm, which has already been successfully used in ecology (Chon et al., 1996; Giraudel et al., in press) for communities patternizing. It allows to visualise species assemblages in a two-dimensional space, and to classify the data without prior knowledge.

## 2. Study area, material and methods

The Adour-Garonne stream system (South–Western France) has a 116 000 km<sup>2</sup> drainage basin. From our laboratory database, we selected 252 sampling sites ranging from 10 to 2500 m a.s.l., i.e. representing high mountain to plain or coastal areas. Samples were taken from 1988 to 1998. Each site was sampled at two periods during a same year, i.e. in summer and winter. All samples were taken from the various substratum types using a standard Surber sampler (sampling area 0.1 m<sup>2</sup>, mesh size 0.3 mm). Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera (EPTC) are aquatic insects which are commonly identified at the species level in freshwater studies. The EPTC for our study were identified by professional taxonomists from our laboratory. We verified that EPTC species richness was significantly correlated to the overall macroinvertebrate richness in the Adour-Garonne stream system (Fig. 1). Considering the presence (1) or absence (0) of each species at each site, the database allowed the construction of a [283 species × 252 sites] matrix.

The data were studied using the Kohonen self organising map (SOM) algorithm. This algorithm is an artificial neural network model. It performs a non-linear projection of the data space onto a two-dimensional space. This network consists of two layers: the input layer is constituted by 283 nodes (one by species) connected to the 252 sites, the output layer is constituted by 150 neurons organized on an array with 10 rows and 15 columns laid out on a

hexagonal lattice. In the output layer, the neurons act as virtual sites and approximate the probability density function of the input data. During the learning process, an EPTC assemblage is computed for each virtual site.

The SOM algorithm is an unsupervised learning procedure which can be summarised as follows:

- The virtual sites are initialised with random samples drawn from the input data set.
- The virtual sites are updated in an iterative way: A sample unit is randomly chosen as an input unit. The Euclidean distance between this sample unit and every virtual site is computed. The virtual site closest to the input is selected and called ‘best matching unit’ (BMU). The BMU and its neighbours are moved a bit towards the input unit.

The training was broken down into two parts previously defined by Giraudel et al. (in press):

- Ordering phase (the 2000 first steps): when this first phase takes place, the sites are highly modified in a wide neighbourhood of the BMU.
- Tuning phase (75 000 steps): during this phase, only the virtual sites adjacent to the BMU are lightly modified.

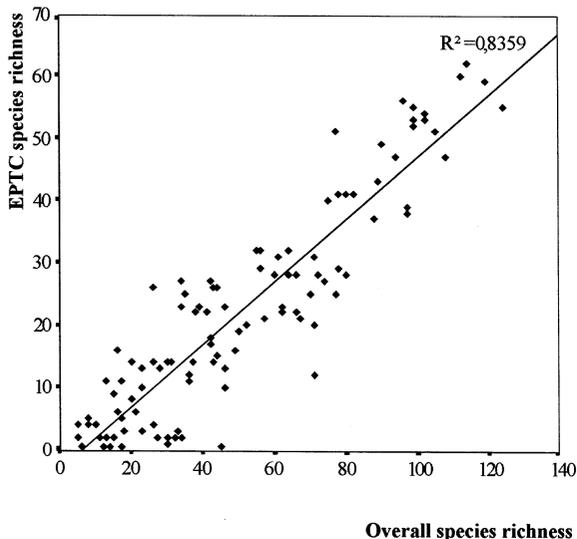


Fig. 1. Relationship between EPTC and overall species richness in the Adour-Garonne stream system.

At the end of training, the EPTC assemblage is known for each virtual site, the BMU is determined for each site, and each site is set in the corresponding hexagon of the Kohonen map. Sites which are neighbours on the grid are expected to represent neighbouring clusters of sites; consequently, sites having a large distance to each other, (according to EPTC assemblage), are expected to be distant in the feature space.

At the end of the learning process, in order to detect the cluster boundaries on the map, the unified-matrix (U-matrix) approach (Ultsch and Siemon, 1990) has been applied. The U-matrix displays the distances between the virtual sites and provides a landscape formed with light plains separated by dark ravines. The sites in the plains are similar (for EPTC assemblage) and clusters become clear. For enhancing the U-matrix method, a triangle-based cubic interpolation has been applied (Giraudel, submitted).

The SOM have been computed on a PC computer with an Intel Pentium PIII-500 using MATLAB software with a program file written by the authors.

### 3. Results

The non-linear projection of presence–absence data in a two dimensional space (Fig. 2) allowed us to classify our sites according to the similarity of their species assemblages. Four major ‘regions’ (or clusters) could be identified on the SOM (i.e. regions 1–4, see Fig. 2). Regions 1 and 2 were formed of 2 and 5 sub-regions, respectively. Then, these regions were plotted on a geographical map of the Adour-Garonne drainage basin, in order to make interpretations (Fig. 3). Region 1 encompassed sites from the Massif Central mountains (eastern part of the drainage basin) above 500 m a.s.l., with 2 sub-regions corresponding to the River Lot (1a) and the River Tarn (1b) stream systems, respectively. All sites from region 2 belonged to the Pyrenees mountains (South part of the drainage basin), and were partitioned into 5 sub-groups. Three sub-groups corresponded to catchment areas of large rivers: Rivers Lez and Garonne from 800 to 500 m a.s.l. (2a and 2e),

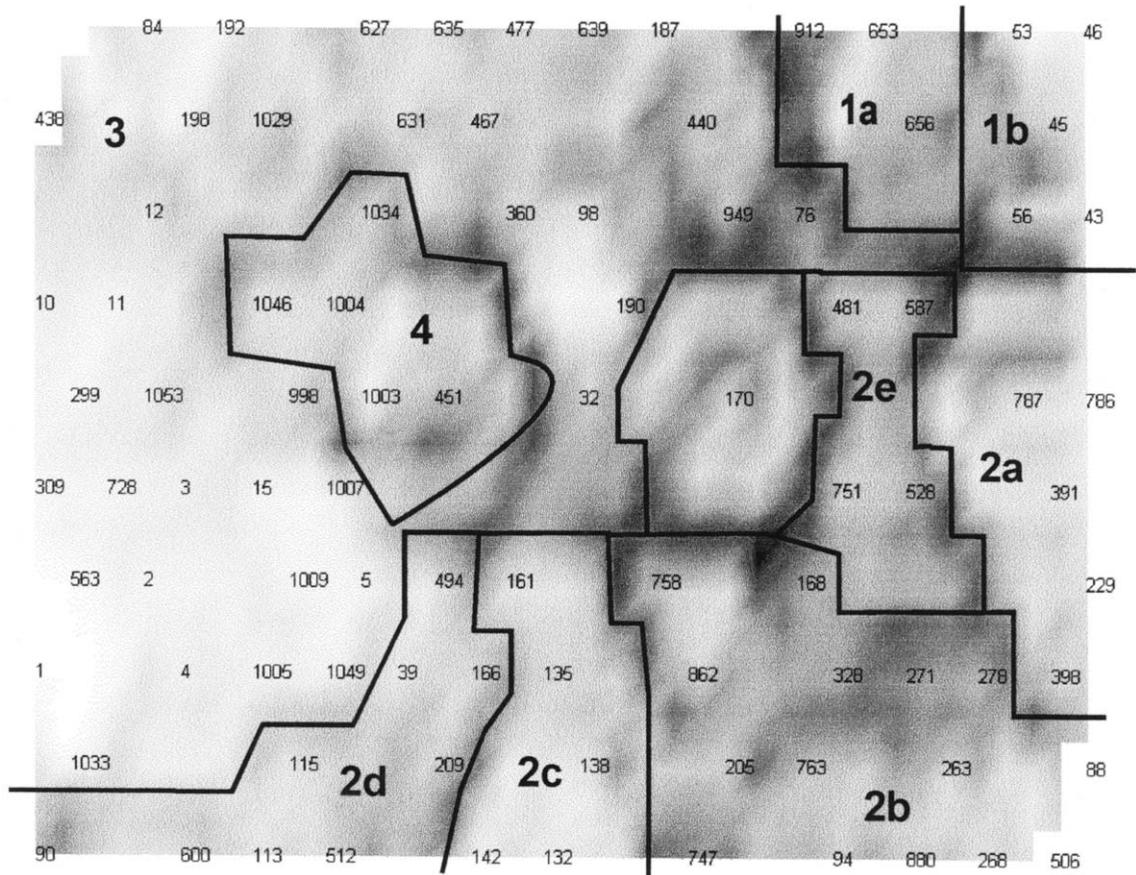


Fig. 2. Distribution of sampling sites on the Kohonen map. Numbers correspond to the code of the 252 sampling sites. In order to lighten the figure, hidden points are not represented. 1a–4 (bold) are the regions or clusters of the map (see text).

Gave d'Ossau (2b), Neste d'Aure (2c). All sites from sub-group 2d were Pyrenean springs. Sites from singular stream environments were clearly segregated by the SOM algorithm, e.g. sites 170–172 belonged to a watercress bed (see Fig. 2), and were not considered in the interpretation of the map. Region 3 clearly represented piedmont zones from the Adour-Garonne drainage basin, and included sites from both Massif Central and Pyrenees rivers. Finally, region 4 corresponded to the Toulouse city agglomeration.

The distribution of each of the 283 species (one map per species) was visualised in the Kohonen map (see example in Fig. 4). To sum-

marise EPTC assemblages characterising each region, we recorded the presence of each species in a table (Appendix A), where we also indicated the probabilities of occurrence, calculated as [number of sites where the species was recorded/total number of sites defining the region]\*100 (%). EPTC richness (Fig. 5a) ranged from 45 to 159 species according to the considered region. Richness values were the lowest in springs (2d), in the agricultural region 2e, and in the urbanised Toulouse region (4). Higher richness were observed in both piedmont and mountain regions. We also plotted the number of species occurring in 1–9 regions. Most species

occurred in only one (121 species) or two (63 species) regions. They therefore had the strongest influence upon the stream classification, and should require particular attention as indicator species. 31 and 34 species appeared respectively in 3 and 4 regions, and 4–10 species appeared in 5–8 regions. Finally, only one species — *Baetis rhodani* (Ephemeroptera) — occurred in all regions. Three main spatial distribution patterns could be identified: (1) local distribution, i.e. species occurring in a restricted geographic and/or altitudinal area (e.g. *Baetis buceratus*); (2) longitudinal zonation, i.e. species occurring in different geographic areas, but within a characteristic altitudinal range (e.g. *Brachyptera seticornis*); and (3) regional distribution, i.e. widespread species (e.g. *Baetis rho-*

*dani*). Any species association can also be pointed out, by overlapping several maps.

#### 4. Discussion

In order to classify running waters from a given area in terms of species assemblages, stream ecologists usually have an a posteriori inductive approach using a large volume of site-specific data, which are subjected to cluster and discriminant analyses, in order to derive spatial patterns (Tate and Heiny, 1995). Principal Component and Detrended Correspondance Analysis are the most common methods used to ordinate habitat variables and presence/absence data respectively (see recent applications in Giudicelli et

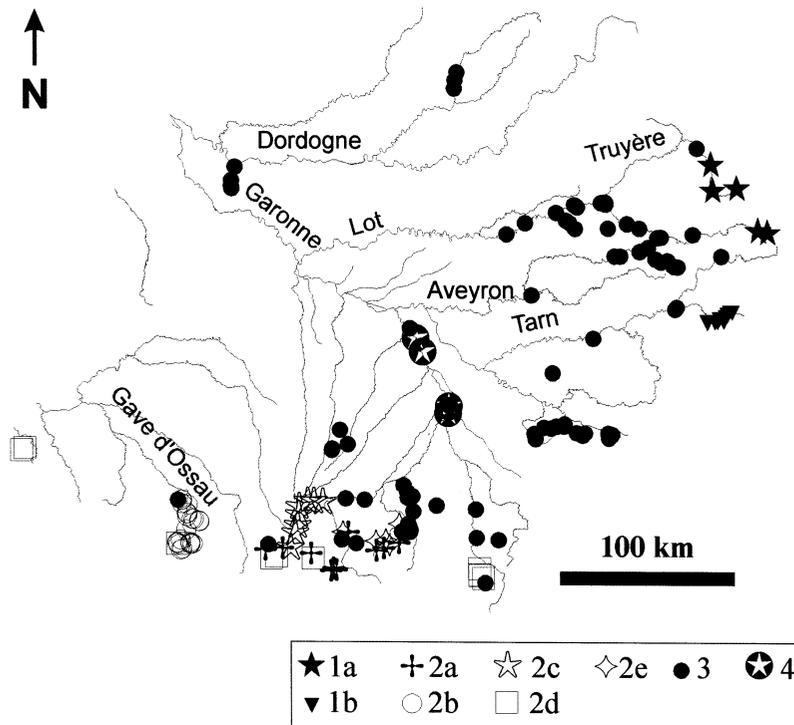


Fig. 3. Distribution of sampling sites in the Adour-Garonne stream system and correspondence with their position on the Kohonen map.

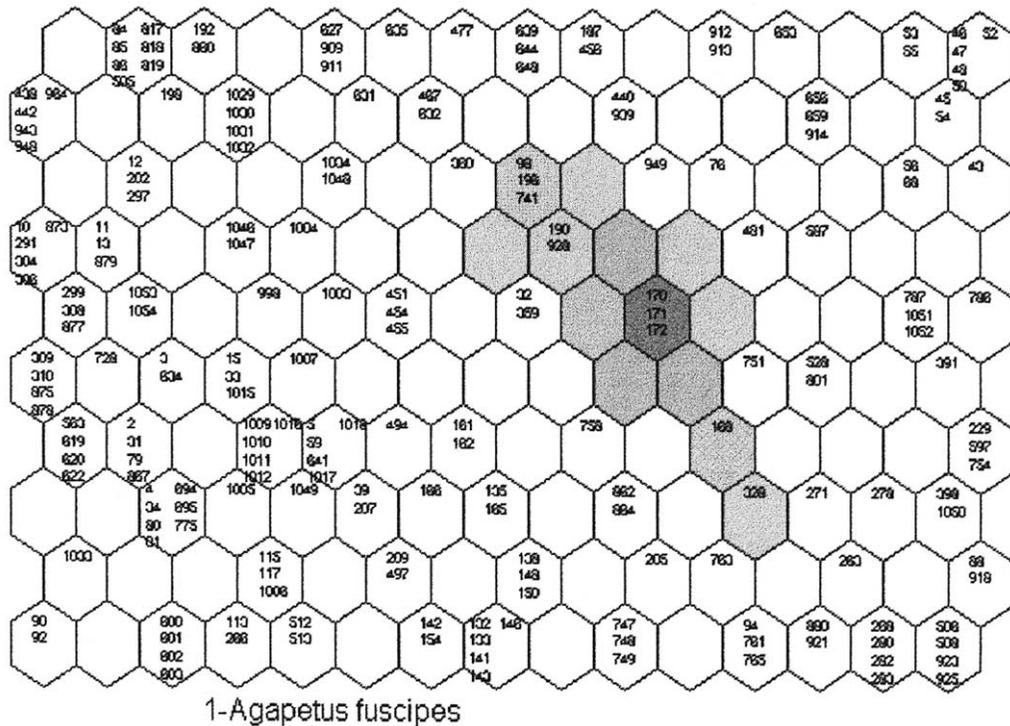


Fig. 4. Example of the representation of a species distribution on the Kohonen map (*Agapetus fuscipes*, Trichoptera). The rate of shading indicates the relative influence of the considered species upon the classification of sites.

al., 2000; Lounaci et al., 2000). However, with non-linear data such as ecological data, SOM — a non-linear projection method — should be preferred (Blayo and Demartines, 1991). Combining clustering and ordering abilities, SOM is a powerful tool to visualize high-dimensional data. For instance, SOM is convenient for detecting outliers that are displaying in a part of the map without affecting the other parts of the map. SOM allows a large choice for computation of the distance between two units; however, the use of the learning rule has to be made very prudently in order to be compatible with the chosen distance (Kohonen, 1995). In this work, Euclidean metric has been chosen, even if input data were nominal (i.e. present or absent). For this purpose, the values 0 (absence) and 1 (presence) has to be seen as a probability of presence in a given site, then the values ob-

tained in each virtual sites can take values in the interval [0; 1].

The choice of the size of the Kohonen map remains a difficult task. The obtained results for the determination of regions might be dependent of this choice. However, if a sufficiently large map is chosen, this difficulty can be tackled, and even if maps will be dependent of the stochastic aspect of the learning, the clusters obtained with the U-matrix method will be the same (Ultsch, 1999).

From the stream ecologist point of view, SOM appeared as a valuable tool which offered a clear visualisation of a relatively large volume of data, and considerably eased their analysis. Specifically, we could: (i) classify a large number of sampling sites (252) according to the similarity of their invertebrate species composition; (ii) visualise the spatial distribution of each of the 283 considered species; and (iii) eventually point

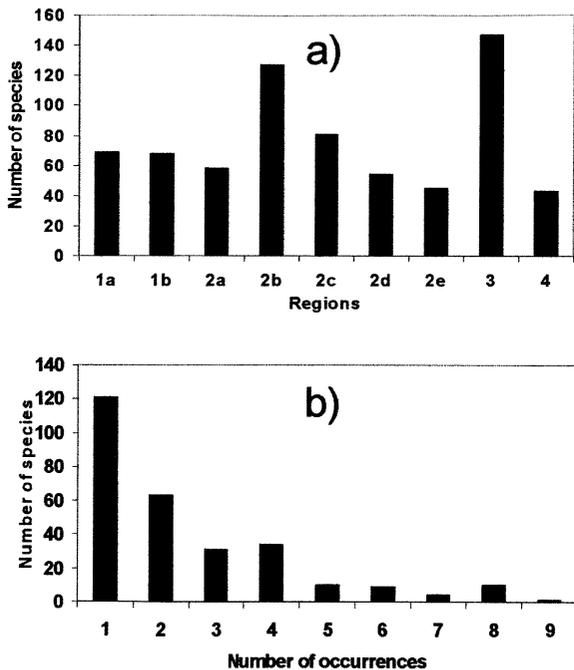


Fig. 5. Species richness patterns derived from the SOM analysis. (a) Number of species per identified region; and (b) number of species occurring in 1–9 regions.

out any negative or positive species association. Numerous site-specific data (i.e. local scale biodiversity) were compiled in order to derive spatial distribution patterns of stream macroinvertebrates at the regional scale. At the reach scale, the main environmental factors influencing the distribution of lotic species are well known (Ward, 1992), and easy to quantify in terms of habitat features, e.g. nature and heterogeneity of substrata, current velocity, water temperature, food resources (Barber and Kervern, 1973; Ward and Stanford, 1979; Newbury, 1984; Moog and Janecek, 1991). At the regional scale, a larger number of factors may influence species distribution, including historical factors such as major geological events which generated the regional diversity of habitats. However, the purpose of this study was not to identify and to

classify such factors. As a first step before further investigations, our analysis revealed several EPTC geographical zones. Such a regional classification of stream ecosystems provides a useful framework for studying and managing streams in different geographic areas (Whittier et al., 1988). The number of species characterising each region ranged from 43 to 147, underlining the expected longitudinal (e.g. high or low mountain, piedmont) and geographical (Pyrenees, Massif Central) differences (Culp and Davies, 1982). These results also support the idea that biodiversity depends on the environmental heterogeneity (Ward and Stanford, 1983), and is both reduced by environmental constancy (e.g. springs) and under severely fluctuating conditions (e.g. severe flow fluctuations due to hydro-power generation). In these conditions, SOM may help to identify disturbed sites at the regional scale. Any modification of the specific composition will create a faunal discontinuity that will be visualised in the self-organised map by the unexpected position of the considered site regarding to its geographical position. In our map, the most striking example of such a faunal discontinuity could be the segregation of the Toulouse City neighbourhoods.

Finally, this study and similar works (e.g. Frissel et al., 1986; Hughes et al., 1986; Omernik, 1987) provide an explicit scheme of the implicit knowledge that stream ecologist already have. Biotic features of streams within the same region and/or longitudinal section tend to be similar, and those characteristics tend to differ when streams belong to more distinct areas. Any tool able to provide a stream classification is therefore of obvious value to both resource managers and researchers to assess spatial and temporal variability.

### Acknowledgements

We wish to thank the French Water Agency (Agence de l'Eau Adour-Garonne) for financing this study, and an anonymous reviewer for his valuable comments on an earlier version of this paper.

**Appendix A. Distribution of EPTC species in regions 1a–4, with probability of occurrence (% , see text) of each species in each region**

Species	Region								
	1a	1b	2a	2b	2c	2d	2e	3	4
<i>Agapetus fuscipes</i>	0,00	0,00	0,00	8,33	0,00	0,00	0,00	7,78	0,00
<i>Agapetus ochripes</i>	0,00	0,00	0,00	0,00	21,43	0,00	0,00	2,22	0,00
<i>Agraylea multipunctata</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Allogamus auricollis</i>	83,33	81,82	0,00	29,17	14,29	21,05	0,00	5,56	0,00
<i>Allogamus ligonifer</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Amphinemura standfussi</i>	16,67	81,82	0,00	0,00	0,00	0,00	0,00	5,56	0,00
<i>Amphinemura sulcicollis</i>	66,67	72,73	100,00	58,33	0,00	10,53	100,00	6,67	0,00
<i>Amphinemura triangularis</i>	33,33	0,00	0,00	50,00	0,00	0,00	40,00	1,11	0,00
<i>Anabolia nervosa</i>	16,67	0,00	0,00	0,00	0,00	0,00	0,00	17,78	0,00
<i>Anacaena globulus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Annitella pyrenaea</i>	0,00	0,00	0,00	33,33	0,00	0,00	0,00	0,00	0,00
<i>Anomalopterygella chauviniana</i>	50,00	81,82	0,00	16,67	35,71	0,00	0,00	1,11	0,00
<i>Apatania meridiana</i>	0,00	0,00	0,00	8,33	0,00	0,00	0,00	0,00	0,00
<i>Arcynopteryx compacta</i>	0,00	0,00	71,43	33,33	7,14	10,53	0,00	0,00	0,00
<i>Asiobates dilatatus</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Athripsodes albifrons</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	11,11
<i>Baetis albinatii</i>	0,00	0,00	0,00	0,00	14,29	0,00	0,00	0,00	0,00
<i>Baetis alpinus</i>	50,00	100,00	0,00	100,00	100,00	47,37	0,00	0,00	11,11
<i>Baetis buceratus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	66,67
<i>Baetis catharus</i>	0,00	0,00	0,00	50,00	0,00	0,00	0,00	0,00	0,00
<i>Baetis fuscatus</i>	0,00	0,00	0,00	29,17	42,86	0,00	0,00	4,44	88,89
<i>Baetis gemellus</i>	0,00	0,00	0,00	62,50	7,14	26,32	0,00	0,00	0,00
<i>Baetis lutheri</i>	16,67	9,09	0,00	0,00	0,00	0,00	0,00	7,78	88,89
<i>Baetis melanonyx</i>	0,00	0,00	0,00	37,50	0,00	0,00	0,00	0,00	0,00
<i>Baetis muticus</i>	0,00	0,00	0,00	70,83	28,57	15,79	0,00	3,33	0,00
<i>Baetis pavidus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Baetis rhodani</i>	100,00	81,82	0,00	83,33	100,00	31,58	0,00	26,67	22,22
<i>Baetis sinaicus</i>	0,00	0,00	0,00	8,33	0,00	0,00	0,00	0,00	0,00
<i>Beraea maura</i>	0,00	0,00	0,00	8,33	7,14	0,00	0,00	0,00	0,00
<i>Beraea pullata</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	7,78	0,00
<i>Beraeodes minutus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,56	0,00
<i>Berosus affinis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Brachycentrus submutilus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	11,11
<i>Brachyptera braueri</i>	16,67	0,00	0,00	0,00	0,00	0,00	0,00	5,56	0,00
<i>Brachyptera monilicornis</i>	33,33	100,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Brachyptera risi</i>	100,00	90,91	14,29	16,67	0,00	0,00	60,00	21,11	0,00
<i>Brachyptera seticornis</i>	100,00	72,73	42,86	29,17	0,00	26,32	60,00	8,89	0,00
<i>Brychius elevatus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Caenis beskidensis</i>	0,00	0,00	0,00	25,00	50,00	0,00	0,00	0,00	33,33
<i>Caenis horaria</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Caenis luctuosa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	6,67	0,00
<i>Caenis macrura</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,44	100,00
<i>Caenis pusilla</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	55,56
<i>Caenis rivulorum</i>	16,67	72,73	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Capnia bifrons</i>	0,00	0,00	0,00	0,00	0,00	0,00	20,00	6,67	0,00
<i>Capnia nigra</i>	16,67	0,00	0,00	4,17	28,57	0,00	0,00	0,00	0,00
<i>Capnia vidua</i>	0,00	0,00	0,00	16,67	0,00	0,00	0,00	0,00	0,00
<i>Capnioneura brachyptera</i>	0,00	0,00	28,57	16,67	0,00	21,05	0,00	0,00	0,00
<i>Capnioneura mitis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	6,67	0,00
<i>Centroptilum luteolum</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	1,11	22,22





Species	Region								
	1a	1b	2a	2b	2c	2d	2e	3	4
<i>Leuctra fusca</i>	100,00	81,82	0,00	29,17	57,14	0,00	40,00	15,56	33,33
<i>Leuctra geniculata</i>	33,33	81,82	0,00	0,00	7,14	0,00	20,00	14,44	22,22
<i>Leuctra hippopus</i>	66,67	0,00	14,29	25,00	0,00	0,00	80,00	8,89	0,00
<i>Leuctra inermis</i>	83,33	9,09	100,00	50,00	0,00	5,26	40,00	3,33	0,00
<i>Leuctra kempnyi</i>	0,00	0,00	57,14	25,00	0,00	5,26	0,00	1,11	0,00
<i>Leuctra lamellosa</i>	0,00	0,00	57,14	50,00	7,14	5,26	0,00	4,44	0,00
<i>Leuctra leptogaster</i>	16,67	0,00	28,57	20,83	7,14	21,05	60,00	2,22	0,00
<i>Leuctra major</i>	16,67	0,00	14,29	12,50	0,00	0,00	20,00	1,11	0,00
<i>Leuctra mortoni</i>	0,00	0,00	14,29	29,17	57,14	0,00	20,00	0,00	0,00
<i>Leuctra prima</i>	0,00	0,00	42,86	0,00	0,00	0,00	0,00	1,11	0,00
<i>Leuctra pseudocylindrica</i>	0,00	0,00	14,29	25,00	0,00	0,00	0,00	1,11	0,00
<i>Leuctra rauscheri</i>	0,00	0,00	57,14	29,17	0,00	0,00	0,00	0,00	0,00
<i>Limnebius nitidus</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Limnebius papposus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Limnephilus centralis</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Limnephilus rhombicus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,56	0,00
<i>Limnephilus sparsus</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Limnius intermedius</i>	0,00	0,00	0,00	0,00	7,14	0,00	0,00	7,78	0,00
<i>Limnius muelleri</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	33,33
<i>Limnius opacus</i>	66,67	0,00	42,86	8,33	7,14	0,00	60,00	20,00	0,00
<i>Limnius perrisi</i>	50,00	81,82	57,14	54,17	7,14	42,11	60,00	11,11	0,00
<i>Limnius volckmari</i>	83,33	90,91	42,86	12,50	21,43	10,53	60,00	32,22	0,00
<i>Lithax obscurus</i>	0,00	0,00	0,00	0,00	21,43	0,00	0,00	0,00	0,00
<i>Lype phaeopa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,33	0,00
<i>Lype reducta</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,33	11,11
<i>Macronychus quadrituberculatus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	22,22
<i>Melampophylax mucoreus</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Micrasema difficile</i>	0,00	63,64	0,00	8,33	0,00	26,32	0,00	1,11	0,00
<i>Micrasema gabusi</i>	0,00	0,00	0,00	37,50	0,00	15,79	0,00	0,00	0,00
<i>Micrasema longulum</i>	66,67	63,64	0,00	16,67	78,57	21,05	0,00	3,33	0,00
<i>Micrasema minimum</i>	83,33	90,91	0,00	29,17	78,57	36,84	0,00	10,00	0,00
<i>Micrasema moestum</i>	50,00	18,18	0,00	0,00	0,00	0,00	0,00	3,33	0,00
<i>Micrasema morosum</i>	66,67	81,82	0,00	4,17	0,00	10,53	0,00	3,33	0,00
<i>Micrasema servatum</i>	0,00	0,00	0,00	33,33	42,86	5,26	0,00	0,00	0,00
<i>Mystacides azurea</i>	50,00	27,27	0,00	0,00	0,00	0,00	0,00	11,11	33,33
<i>Mystacides nigra</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Nemoura avicularis</i>	33,33	72,73	0,00	0,00	0,00	0,00	0,00	3,33	0,00
<i>Nemoura cinerea</i>	50,00	27,27	28,57	16,67	0,00	0,00	20,00	14,44	0,00
<i>Nemoura erratica</i>	33,33	0,00	57,14	29,17	0,00	5,26	20,00	11,11	0,00
<i>Nemoura flexuosa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,44	0,00
<i>Nemoura fulviceps</i>	0,00	0,00	14,29	0,00	0,00	0,00	80,00	2,22	0,00
<i>Nemoura lacustris</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Nemoura linguata</i>	0,00	0,00	71,43	8,33	0,00	0,00	0,00	1,11	0,00
<i>Nemoura marginata</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,33	0,00
<i>Nemoura mortoni</i>	0,00	0,00	14,29	0,00	0,00	0,00	0,00	0,00	0,00
<i>Nemoura moseleyi</i>	0,00	0,00	28,57	12,50	0,00	5,26	0,00	0,00	0,00
<i>Nemurella picteti</i>	16,67	0,00	57,14	8,33	0,00	0,00	0,00	5,56	0,00
<i>Normandia nitens</i>	0,00	0,00	0,00	0,00	0,00	0,00	20,00	3,33	0,00
<i>Notidobia ciliaris</i>	66,67	27,27	0,00	0,00	7,14	0,00	0,00	6,67	0,00
<i>Odontocerum albicorne</i>	50,00	100,00	0,00	8,33	0,00	5,26	0,00	1,11	0,00
<i>Oecetis testacea</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,44	0,00

Species	Region								
	1a	1b	2a	2b	2c	2d	2e	3	4
<i>Oligoneuriella rhenana</i>	0,00	0,00	0,00	0,00	21,43	0,00	0,00	4,44	66,67
<i>Oligoplectrum maculatum</i>	16,67	72,73	0,00	0,00	92,86	0,00	0,00	6,67	11,11
<i>Orectochilus villosus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	33,33
<i>Oreodytes rivalis</i>	0,00	0,00	0,00	41,67	92,86	0,00	0,00	0,00	0,00
<i>Oulimnius troglodytes</i>	33,33	81,82	0,00	0,00	0,00	0,00	0,00	20,00	55,56
<i>Oulimnius tuberculatus</i>	66,67	27,27	0,00	0,00	0,00	0,00	0,00	30,00	0,00
<i>Oxyethira falcata</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Pachyleuctra benllochi</i>	0,00	0,00	85,71	25,00	7,14	10,53	20,00	0,00	0,00
<i>Paraleptophlebia submarginata</i>	16,67	72,73	0,00	8,33	0,00	0,00	0,00	4,44	0,00
<i>Pelodytes caesus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Pelodytes rotundatus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	11,11
<i>Perla bipunctata</i>	0,00	100,00	0,00	0,00	0,00	0,00	0,00	6,67	0,00
<i>Perla burmeisteriana</i>	16,67	0,00	0,00	0,00	0,00	0,00	0,00	5,56	0,00
<i>Perla grandis</i>	0,00	0,00	100,00	54,17	0,00	0,00	40,00	0,00	0,00
<i>Perla marginata</i>	66,67	81,82	42,86	25,00	7,14	10,53	100,00	14,44	0,00
<i>Perlodes intricata</i>	0,00	0,00	85,71	12,50	0,00	0,00	20,00	0,00	0,00
<i>Perlodes jurassica</i>	33,33	27,27	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Perlodes microcephala</i>	83,33	9,09	14,29	45,83	7,14	26,32	60,00	5,56	0,00
<i>Philopotamus montanus</i>	33,33	81,82	0,00	25,00	0,00	0,00	0,00	2,22	0,00
<i>Philopotamus variegatus</i>	33,33	90,91	0,00	20,83	0,00	10,53	0,00	0,00	0,00
<i>Phothydraena testacea</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Platambus maculatus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Plectrocnemia brevis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Plectrocnemia conspersa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	6,67	0,00
<i>Plectrocnemia laetabilis</i>	0,00	0,00	0,00	0,00	0,00	1,11	1,11	0,00	0,00
<i>Plectrocnemia scruposa</i>	0,00	0,00	0,00	12,50	0,00	0,00	0,00	0,00	0,00
<i>Polycentropus flavomaculatus</i>	83,33	81,82	0,00	0,00	0,00	0,00	0,00	24,44	44,44
<i>Polycentropus kingi</i>	0,00	0,00	0,00	0,00	7,14	0,00	0,00	0,00	0,00
<i>Potamanthus luteus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	10,00	100,00
<i>Potamonectes griseostriatus</i>	0,00	0,00	0,00	8,33	0,00	0,00	0,00	0,00	0,00
<i>Potamophilus acuminatus</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Potamophylax latipennis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,44	0,00
<i>Procloeon bifidum</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,44	0,00
<i>Protonemura angelieri</i>	0,00	0,00	0,00	12,50	0,00	21,05	0,00	0,00	0,00
<i>Protonemura beatensis</i>	50,00	100,00	71,43	70,83	71,43	21,05	100,00	3,33	0,00
<i>Protonemura bipartita</i>	0,00	0,00	0,00	0,00	0,00	0,00	20,00	0,00	0,00
<i>Protonemura intricata</i>	50,00	100,00	71,43	37,50	7,14	0,00	100,00	12,22	0,00
<i>Protonemura meyeri</i>	100,00	0,00	0,00	16,67	0,00	0,00	60,00	10,00	0,00
<i>Protonemura praecox</i>	66,67	90,91	71,43	45,83	0,00	10,53	40,00	0,00	0,00
<i>Protonemura pyrenaica</i>	0,00	0,00	85,71	70,83	0,00	26,32	100,00	10,00	0,00
<i>Protonemura risi</i>	0,00	0,00	85,71	20,83	0,00	5,26	40,00	17,78	0,00
<i>Protonemura tuberculata</i>	0,00	0,00	14,29	12,50	0,00	15,79	0,00	0,00	0,00
<i>Protonemura vandeli</i>	0,00	0,00	71,43	41,67	0,00	15,79	20,00	0,00	0,00
<i>Protonemura vercingetorix</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Psychomyia pusilla</i>	83,33	18,18	0,00	8,33	78,57	0,00	0,00	28,89	88,89
<i>Ptilocolopus granulatus</i>	0,00	0,00	0,00	29,17	0,00	15,79	0,00	7,78	0,00
<i>Rhithrogena diaphana</i>	33,33	81,82	0,00	0,00	0,00	0,00	0,00	2,22	11,11
<i>Rhithrogena germanica</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Rhithrogena hercynia</i>	66,67	72,73	0,00	62,50	78,57	21,05	0,00	5,56	0,00
<i>Rhithrogena kimminsi</i>	0,00	0,00	0,00	12,50	0,00	31,58	0,00	0,00	0,00
<i>Rhithrogena loyolaea</i>	0,00	0,00	0,00	12,50	0,00	21,05	0,00	0,00	0,00

Species	Region								
	1a	1b	2a	2b	2c	2d	2e	3	4
<i>Rhithrogena semicolorata</i>	100,00	63,64	0,00	91,67	92,86	21,05	0,00	26,67	0,00
<i>Rhyacophila angelieri</i>	0,00	0,00	0,00	0,00	0,00	10,53	0,00	0,00	0,00
<i>Rhyacophila denticulata</i>	0,00	0,00	0,00	25,00	0,00	0,00	0,00	7,78	0,00
<i>Rhyacophila dorsalis</i>	0,00	0,00	0,00	0,00	28,57	0,00	0,00	8,89	44,44
<i>Rhyacophila eatoni</i>	0,00	0,00	0,00	33,33	0,00	0,00	0,00	0,00	0,00
<i>Rhyacophila evoluta</i>	0,00	0,00	0,00	8,33	14,29	47,37	0,00	0,00	0,00
<i>Rhyacophila fasciata</i>	16,67	81,82	0,00	0,00	14,29	0,00	0,00	4,44	0,00
<i>Rhyacophila intermedia</i>	0,00	0,00	0,00	50,00	0,00	26,32	0,00	0,00	0,00
<i>Rhyacophila laevis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,22	0,00
<i>Rhyacophila martynovi</i>	0,00	0,00	0,00	33,33	0,00	15,79	0,00	0,00	0,00
<i>Rhyacophila meridionalis</i>	16,67	90,91	0,00	45,83	100,00	5,26	0,00	2,22	0,00
<i>Rhyacophila mocsaryi</i>	16,67	90,91	0,00	8,33	0,00	10,53	0,00	0,00	0,00
<i>Rhyacophila nubila</i>	16,67	9,09	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Rhyacophila obliterated</i>	33,33	0,00	0,00	0,00	7,14	0,00	0,00	0,00	0,00
<i>Rhyacophila occidentalis</i>	0,00	0,00	0,00	20,83	21,43	0,00	0,00	0,00	0,00
<i>Rhyacophila philopotamoides</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	2,22	0,00
<i>Rhyacophila rupta</i>	0,00	0,00	0,00	0,00	7,14	10,53	0,00	1,11	0,00
<i>Rhyacophila tristis</i>	0,00	0,00	0,00	70,83	0,00	42,11	0,00	1,11	0,00
<i>Scarodytes halensis</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Sericostoma personatum</i>	83,33	90,91	0,00	0,00	0,00	5,26	0,00	7,78	0,00
<i>Silo nigricornis</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	1,11	0,00
<i>Silo piceus</i>	33,33	27,27	0,00	0,00	0,00	0,00	0,00	1,11	0,00
<i>Stenelmis canaliculata</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,56	55,56
<i>Synagapetus insons</i>	0,00	0,00	0,00	12,50	0,00	0,00	0,00	0,00	0,00
<i>Taeniopteryx schoenemundi</i>	16,67	27,27	0,00	0,00	7,14	0,00	40,00	7,78	11,11
<i>Tinodes assimilis</i>	0,00	0,00	0,00	4,17	0,00	0,00	0,00	0,00	0,00
<i>Tinodes dives</i>	0,00	0,00	0,00	8,33	0,00	0,00	0,00	0,00	0,00
<i>Tinodes waeneri</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,33	0,00
<i>Wormaldia triangulifera</i>	0,00	0,00	0,00	12,50	0,00	0,00	0,00	6,67	0,00
<b>Number of species</b>	<b>69</b>	<b>68</b>	<b>59</b>	<b>130</b>	<b>82</b>	<b>54</b>	<b>45</b>	<b>159</b>	<b>59</b>

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