How do biodiversity patterns of river animals emerge from the distributions of common and rare species?

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A B S T R A C T

We studied the patterns of commonness and rarity for one vertebrate (fish) and four freshwater insect taxa (*Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Coleoptera*) in southwestern France (57,000 km^2), and we analysed the relationships between the location of sites and the contribution of commonness and rarity to species richness within a large stream system. Richness patterns in fish and aquatic insects were related to the location of sites within the stream system. The number of common and rare fish species increased from up- to downstream areas as a result of downstream additions of species. The number of common insect species peaked in the intermediate section of the river continuum, whereas rarity increased with decreasing elevation. In all taxa, common species gave a closer approximation to overall patterns of species richness than did rare ones. The biodiversity patterns of river animals emerged from convergence in the distributions of common and rare species (fish), or mostly from the distribution of common species (insects). However, in fish, *Ephemeroptera* and *Plecoptera*, the rarer species became almost equally, or more strongly correlated with overall species richness when increasing information along the common-to-rare and rare-to-common sequences. These patterns suggested that rarer species show a similar or stronger affinity, on a species-for-species basis, for high richness areas than do the commoner species. These schemes have implications for biodiversity assessments, as studies using common species richness to target important areas for monitoring or conservation efforts within stream systems will not necessarily identify areas important for rare species, and *vice versa*.

Keywords:
Aquatic insects
Biodiversity
Commonness
Fish
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Rarity

1. Introduction

Understanding how biodiversity patterns emerge from the distributions of rare and common species is a key concern of conservation biology (Murray et al., 2002; Storch and Sizling, 2002; Lennon et al., 2004; Pearman and Weber, 2007). On one hand, rare species are regarded as having a high conservation priority (e.g., Prendergast et al., 1993; Myers et al., 2000), because local rarity may increase the likelihood that demographic and/or environmental stochasticity will eliminate populations. Indeed, a restricted spatial distribution (with individuals occurring with high or low densities) implies that populations will probably experience adverse conditions simultaneously (Gaston, 1998). On the other hand, our understanding of the determinants of overall patterns of species richness may gain most from consideration of why

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common species occur in some areas and are absent from others, rather than from consideration of the distributions of rare species (Vázquez and Gaston, 2004). Thus, even if rarity and commonness cannot be always explained, patterning their geographic variations and understanding their respective contribution to biodiversity patterns remains a very important part of conservation biology (Chu et al., 2003; Devictor et al., 2007).

Most of our current understanding of commonness and rarity has come from studies of terrestrial plants, birds, mammals and some insects (e.g., Thomas and Mallorie, 1985; Berg and Tjemberg, 1996; Lennon et al., 2004; Vázquez and Gaston, 2004). Studies on commonness and rarity in freshwater ecosystems have mainly been conducted from a monitoring and assessment point of view (Cao et al., 2001). Indeed, most bioassessment systems use common species to assess the ecological quality of surface waters (Nijboer, 2006), while rarity can be used in assessing the conservation value of freshwaters (Nijboer and Verdonschot, 2004). Other works addressed biodiversity aspects such as the loss of information induced by omitting rare species in ecological studies (Cao et al., 1998; Marchant, 1999; Arscott et al., 2006). However, freshwater habitats remain poorly represented in published studies on commonness and rarity, when compared to other systems (Chapman, 1999, but see Faith and Norris, 1989; Malmqvist and Rundle, 2002; Dudgeon et al., 2006). At the same time, available information suggests that freshwater biodiversity has declined as a whole faster than either terrestrial or marine biodiversity over the past 30 years (Jenkins, 2003). Whatever the studied organisms, considering rarity and commonness through numbers of species rather than in terms of species assemblages *sensu stricto* is likely to fit with a broader modelling approach, because the resulting patterns are not expected to be region-specific (i.e., any model only referring to a region-specific list of species is more prone to have local acceptance). Subsequently, modelling patterns of biodiversity such as commonness and/or rarity means that models will predict species richness by using environmental conditions (e.g., elevation, temperature) as explanatory variables (Park et al., 2003). With a large number of variables, it is possible to "overfit" the models so that they may perform well in the context of the dataset used to generate them, but fail to be robust when used elsewhere (Rushton et al., 2004). Therefore, the use of species richness and of a limited number of explanatory variables in a successful final model would be relevant to derive broadly acceptable schemes, but could also reduce the effort and cost of data collection for environmental management applications (Céréghino et al., 2005).

Assuming that common species have wider fundamental niches (wide range) than rare species (Rosenweig and Lomolino, 1997), we hypothesized that common and rare species would differ in their responses to river habitat conditions, whatever the study taxa. Subsequently, because of differences in the ecological requirements and biological traits, we predicted that rarity and commonness would make different contributions to the overall patterns of species richness depending on the considered taxa. We thus considered the distributions of both common and rare species to understand how rarity and commonness contribute to the overall biodiversity patterns in different freshwater taxa. We focused on both vertebrate (fish) and invertebrates (four insect orders, namely *Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Coleoptera*), these five groups being commonly considered at the species level in basic and applied freshwater studies, and being particularly sensitive to the impact of human activities and changes in ecosystem features (Resh and Jackson, 1993; Oberdorff et al., 2001; Compin and Céréghino, 2003). Moreover, freshwater insects are an important source of nutrition for fish, and this strong trophic link provides further justification for studying these groups together. Specifically, we sought: (i) to produce explicit models which allow to understand the relationships between the location of sites within the stream system and commonness, and (ii) to analyse the contribution of rarity and commonness to patterns of aquatic species richness. The results were used to draw a conceptual diagram summarizing patterns in species richness (rare, common and overall) within large river catchments. These schemes will have implications for biodiversity assessments, because studies using common species richness to target important areas for monitoring or conservation efforts within stream systems will not necessarily identify areas important for rare species, and *vice versa*.

2. Methods

2.1. *Study area and data collection*

The River Garonne (525 km long) has its source in the Maladetta Glacier (Spain), and reaches the Atlantic Ocean through the Gironde estuary (France; Fig. 1). The River Garonne stream system drains an area of about 57,000 km^2, with a mean annual discharge of about 545 $m^3 s^{-1}$. Compared with other French rivers (e.g., River Seine and River Rhône), the River Garonne is less disturbed by industrial pollution (Oberdorff et al., 2002). The climate of the region is influenced by oceanic processes, but this declines to the southeast where it undergoes the Mediterranean influence with dry winds and weaker rainfalls. Fish and insects were collected at unstressed sites. These sites where evenly distributed throughout the Garonne stream system (Fig. 1), and were not subjected to anthropogenic impacts such as flow regulation, chemical pollution, or urban runoff (indexed by the French Water Agency: http://www.eau-adour-garonne.fr/; see also Compin and Céréghino, 2003). The stream length selected for monitoring at each site was about ten times the stream width (from 50 m in headwaters to 500 m in plain areas).

Five hundred and fifty-four sites ranging from high mountain (2500 m a.s.l.) to plain or coastal (10 m a.s.l.) areas were sampled for fish. Fish data were collected between 1980 and 2000. All sites were sampled once by electrofishing, during low-flow periods, using two-pass removal sampling. Thirty-nine fish species were identified (detailed list in Santoul et al., 2004) among which 24 were native species. In this study, exotic fish (15 species) were not considered when selecting common species to allow comparisons with previous studies on rarity (i.e., Santoul et al., 2005). In the River Garonne, most fish where widespread, whereas few species had a local distribution. Following Santoul et al. (2005), we selected "common

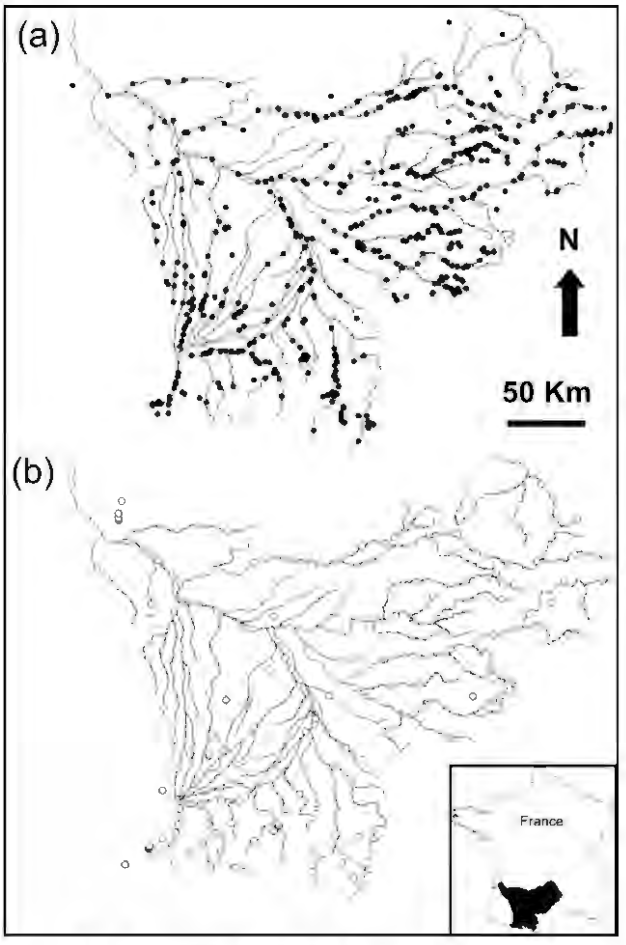

Fig. 1 – The Garonne stream system, and location of the sampling sites for (a) fish and (b) aquatic insects (*Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Coleoptera*).

species" as those species occurring in more than 5% of the sampling sites, i.e., having a wide range *sensu* Lennon et al. (2004).

One hundred and fifty-five sites ranging from 10 to 2500 m a.s.l. were sampled for aquatic insects. Samples were taken from 1988 to 1998 and each site was sampled twice (summer and winter). At each period, eight sample-units were taken from all substratum types using a standard Surber sampler (sampling area 0.1 m^2, mesh size 0.3 mm). Sample-units were distributed in proportion to the relative abundance of the various substrata (e.g., gravels, pebbles, vegetation, etc.). This scheme was intended to ensure that the substratum types sampled at the various sites reflected the within-site and the between-sites diversity of habitat conditions, i.e. the continuous gradient of physical characteristics of streams from headwaters to plains. Note that the fish and insect samples were taken at different sites, to avoid disturbing the benthos (notably during the summer sampling sessions). All samples were fully sorted in the laboratory. *Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Coleoptera* (hereafter called EPTC) were identified to species. Two hundred eighty-three EPTC species were identified (detailed list in Céréghino et al., 2001; Santoul et al., 2005), with both restricted range (i.e., local distribution) and widespread species (i.e., longitudinal or regional distribution). As for fish, we used previous inventories (Céréghino et al., 2001; Santoul et al., 2005) to select "common species" as those species occurring in more than 5% of the sampling sites.

2.2. *Data analyses*

To analyse the relationships between the location of sites within the stream system and commonness, each sampling site (for fish or insects) was characterised with four environmental variables: elevation (a.s.l., m), distance from the source (km), stream order, and reach slope (‰). The implicit use of spatial location in building regression models to explain biodiversity patterns was specifically intended to keep models simple and generally applicable. The dependent variable used (number of common species) corresponds to count data and a general linear modelling (GLM) was used because it allows a more versatile analysis of correlation than standard regression methods. For analysing common species we fitted models using a Poisson distribution and a log link function (Crawley, 1993). River was included as a random factor in the model to control pseudoreplication due to the inclusion of more than one point from each river. To correct the possible effects of under- or over-dispersion on statistical tests, deviances were scaled with the square root of the ratio deviance/degree of freedom (SAS Institute, 2000). Data were analysed with the GLIMMIX macro for SAS 8.2 (SAS Institute, 2000), fitting a mixed effects general linear model (river as a random variable and environmental variables as fixed variables). Main effects were fitted using type III tests and a stepwise backwards removal procedure was used to obtain a final model containing only significant factors.

To further analyse the contribution of commonness and rarity to patterns of aquatic species richness in rivers, we ranked all species in each species group from the most widespread to the most restricted (common-to-rare), and from the most restricted to the most widespread (rare-to-common), and generated a sequence of patterns of species richness for increasing numbers of species (see details in Lennon et al., 2004; Vázquez and Gaston, 2004). At each stage along both series of richness patterns, we correlated the species richness pattern for the sub-assemblage with the full assemblage. This allows us to compare sub-assemblages of the n most common with the n most rare species, in terms of how well they match the full assemblage richness pattern. We also plotted, along the common-to-rare and rare-to-common sequences, the sequential richness pattern correlations against a simple measure of accumulated information in species distributions, the cumulative sum across species of the binomial variance $\sum p_i(1 - p_i)$, where p_i = proportion of study area occupied by the ith species (i.e. number of sites occupied divided per the number of sites sampled, as per Lennon et al., 2004; Vázquez and Gaston, 2004).

Finally, we summarized the results on the distributions of common species and the contribution of rarity and commonness with those from Santoul et al. (2005) on the distributions of rare species in a more readily interpretable manner, i.e., a schematic diagram, to support the discussion.

3. Results

Fish were present in all sampling sites ($n = 554$) while EPTC were recorded in 147, 137, 149 and 138 sampling sites out of 155. 75% of fish species and 55% of insect species were common, commonness being 59%, 84%, 41% and 44% within the insect groups E, P, T and C, respectively.

The fish model explained 58.1% of the total variance in numbers of common species, as estimated by the deviance of the final model (403.37) and that of the null model (961.70). Slope was negatively correlated with numbers of common species, and distance from the source was positively correlated with fish commonness ($p < 0.0001$; Table 1). Other factors under consideration (elevation, stream order) did not correlate significantly with the number of common fish species. In E, P and C, commonness increased with elevation ($p = 0.001$, $p < 0.0001$ and $p = 0.05$, respectively) but not with other factors. The corresponding models explained 77.4%, 71.6% and 61.9% of the total variance in numbers of common species, respectively. In T, commonness increased with both elevation and distance from the source ($p < 0.0001$ and $p = 0.002$, respectively). The model explained 80.0% of the total variance in numbers of common species, as estimated by the deviance of the final model (47.90) and that of the null model (239.45). In sum, the GLM showed that commonness in fish and aquatic insects can be related to the downstream location of sampling sites within a large stream system, and that biodiversity patterns of stream animals may emerge from the distributions of both common and rare species or mostly from the distribution of common species, depending upon the considered taxa.

The correlation coefficients between each of the subassemblage richness patterns and the richness pattern produced by all species increased in different ways along the

Table 1 – Models analysing the patterns of common species of the five freshwater taxa (Fish, Ephemeroptera, Plecoptera, Trichoptera and Coleoptera) distributions

Freshwater taxa	Effect	Estimate	F	df	p
Fish	Stream order		0.09	1,414	0.77
	Elevation		0.01	1,412	0.92
	Slope	−0.4544	62.57	1,415	<0.0001
	Distance source	0.3811	39.42	1,415	<0.0001
	Deviance	961.70			
	Φ	0.73			
	Variance explained	58.1%			
Ephemeroptera	Stream order		0.00	1,87	0.97
	Elevation	0.6664	11.60	1,88	0.001
	Slope		0.06	1,87	0.81
	Distance source		1.58	1,87	0.21
	Deviance	283.82			
	Φ	0.51			
	Variance explained	77.4%			
Plecoptera	Stream order		0.18	1,87	0.67
	Elevation	1.4879	25.49	1,88	<0.0001
	Slope		1.29	1,87	0.26
	Distance source		3.18	1,87	0.08
	Deviance	641.22			
	Φ	1.38			
	Variance explained	71.6%			
Trichoptera	Stream order		1.19	1,86	0.28
	Elevation	1.2994	21.55	1,87	<0.0001
	Slope		0.00	1,86	0.99
	Distance source	0.5011	9.85	1,87	0.002
	Deviance	239.45			
	Φ	0.3770			
	Variance explained	80.0%			
Coleoptera	Stream order		0.29	1,87	0.59
	Elevation	0.4262	4.03	1,88	0.05
	Slope		0.00	1,87	0.99
	Distance source		3.27	1,87	0.07
	Deviance	304.45			
	Φ	0.76			
	Variance explained	61.9%			

Backwards models with Log_{10}-transformed data. Only variables with $p < 0.05$ are interpreted as statistically significant. For variables not included in the models no parameter estimate is presented and the F and p values correspond to the values when added to the final models. Deviances of the null models, dispersion values (Φ = deviance of the final model/degrees of freedom) and percentage of variance explained are given.

common-to-rare and rare-to-common sequences, whatever the taxa under consideration (Fig. 2a–e). However, for a given number of species, correlations were always greater for the former than for the latter. Thus, common species gave a closer approximation to overall patterns of species richness than did rare species. For both T and C data sets, common species

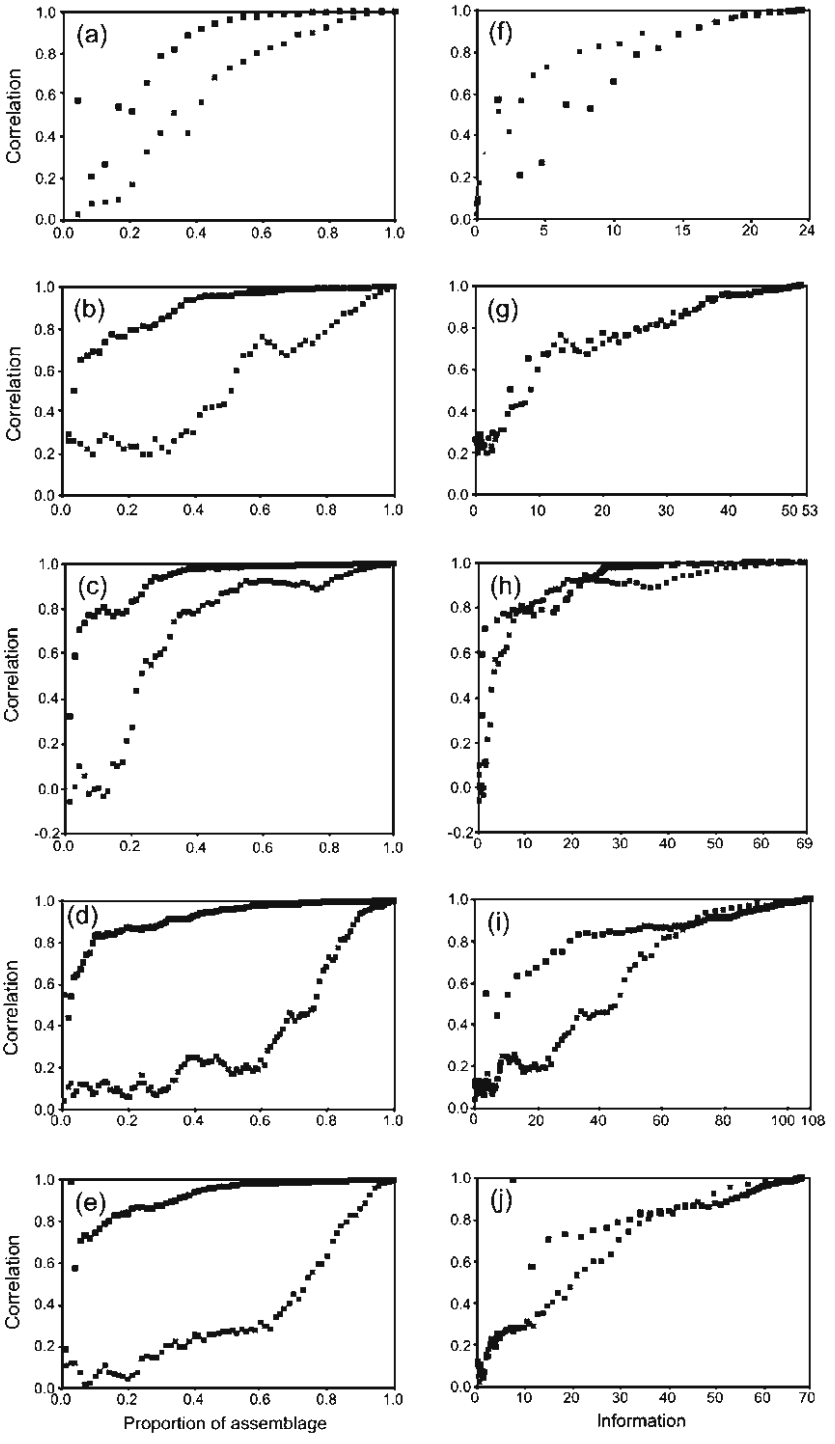

Fig. 2 – Sequential correlation between partial and full assemblage species richness patterns. Each partial assemblage was grown by adding one species at a time, correlating the richness pattern at each stage with that of the full assemblage of species. Species were added in rank order from least to most widespread (rare-to-common, black squares) and conversely (common-to-rare, grey squares). In (a)–(e) correlations are plotted against the proportion of the total number of species that are in the partial assemblage. In (f)–(j) correlations are plotted against accumulated information in species distributions, a measure of the overall numbers of records of presence or absence (see Methods for details). Plots (a) and (f) are for fish, (b) and (g) for *Ephemeroptera*, (c) and (h) for *Plecoptera*, (d) and (i) *Trichoptera*, and (e) and (j) for *Coleoptera*.

still produced a quicker rise in correlation than rare species with the increasing accumulated information, rather than numbers of species (Fig. 2i–j). For E and P, common and rare species produced a similar rise in correlation with the increasing accumulated information (Fig. 2g–h). Last, for the fish data set, the rarer species became more strongly correlated with increasing accumulated information (Fig. 2f).

4. Discussion

The biodiversity patterns of stream animals may emerge from convergence in the distributions of both common and rare species (fish), or mostly from the distribution of common species (aquatic insects), as summarized in Fig. 3. We describe biodiversity patterns through up- to downstream gradients, with common species approximating well the overall patterns of species richness. It is worth noting that the variance explained by our GLMs was about 58% in common fish and 62–80% in common insects, although we used a limited number of physical variables. The suggested schemes are thus likely to perform well in other areas. In fish, both the numbers of common (this study) and rare species (Santoul et al., 2005) increase towards downstream areas, as a result of downstream additions of species. In aquatic insects (Fig. 3b), the overall EPTC richness was reported to peak in the intermediate section of the downstream continuum of the study area (Céréghino et al., 2003). However, rarity increased with distance from the source, or declined with elevation (Santoul et al., 2005). The analyses carried out in the present work suggest that the number of common *Trichoptera* species peaks in the intermediate section of the downstream continuum, because both elevation and distance from the source (which are negatively correlated) were correlated to commonness. In *Ephemeroptera* and *Coleoptera*, commonness increased with elevation but not with other factors. Commonness also increased with increasing elevation in *Plecoptera*, although this group is rather confined to the upper mountainous sections of the stream system. Therefore, common *Trichoptera* would have the greatest influence on the patterns of commonness in EPTC, and, subsequently, on the overall EPTC richness patterns. Whilst there are a number of studies showing that there are generally a few taxa making up most of the community composition (e.g., Nijboer and Verdonschot, 2004), the number of common species in our study area may seem quite high, particularly in aquatic insects. This observation could have two explanations, which are not mutually exclusive. First, the total number of sampling sites was lower for EPTC (155) than for fish (554), which means that an insect species had to be found at eight sites to be "common", whereas for fish a species had to be found at 28 sites out of 554 to be assigned as common. Second, despite a possible bias in our perception of common EPTC species, our sampling area represents three biogeographical regions of the *Limnofauna Europea* (Illies, 1978): Pyrenees Mountains in the southern part of the stream system, Massif Central Mountains in the eastern part, and occidental plains in northwestern areas. A preliminary analysis of EPTC species distributions showed that species compositions allowed for a clear distinction of these regions in our study area (Céréghino et al., 2001). These marked biogeographical differences could thus account (at least partially) for the high number of common insect species. Random inclusion of species is directly linked to the sampling effort. The greater the sample size, the more individuals and the more rare species one should find at a given site. Nevertheless, our sampling effort was consistent (both for fish and EPTC), while the number of captured individuals followed similar trends as the species richness patterns in relation to the upstream–downstream gradient of environmental conditions. These settings thus allowed us to compare the sites to understand the relationships between the location of sites within the stream system, and commonness or rarity.

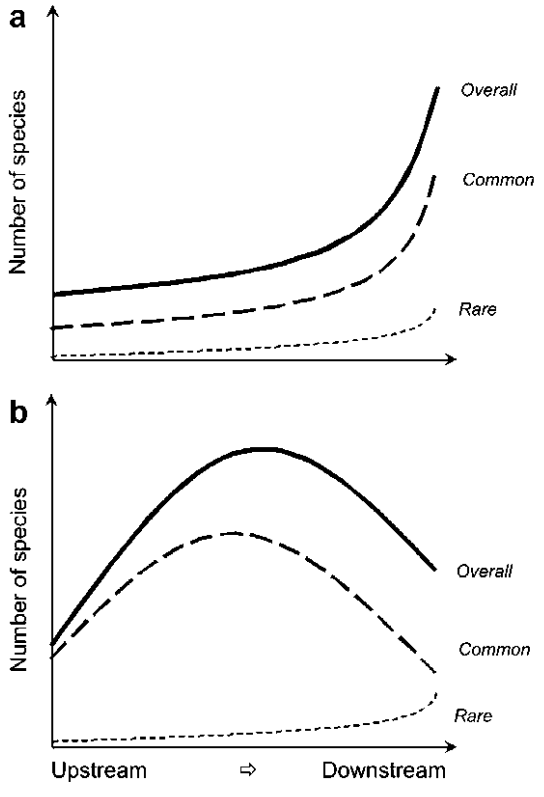

Fig. 3 – Trends in the upstream–downstream patterns of rare, common and overall species richness in (a) fish and (b) aquatic insects (*Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Coleoptera* combined) in large stream systems. The trends in numbers of rare and common species were drawn from GLMs fitted with a log link function (Santoul et al., 2005 and this study, respectively). Overall species richness patterns were interpreted from the distributions of rare and common species.

It should be noted that aquatic insects were collected with a surber sampler. Surber samplers are widely used for freshwater monitoring, but they can fail to capture the non-benthic invertebrates. However, this limitation is particularly relevant for downstream sections, i.e. where lower current velocities and deeper water allow the development of macrophytes and the presence of swimmers. For instance, *Coleoptera* are likely to occur in microhabitats such as the vegetation or the water column. In upstream sections (mountain areas, fast flowing streams on rocky substrates), almost all EPTC are benthic. Although we were really working only with the benthic fraction of these taxa diversity, surber samplers remain rele-

vant in quantitative analyses of stream organisms because they allow to standardize data collection, and thus to compare taxa diversity in space and time (Resh and Jackson, 1993).

A challenge of recent research is to assess models having the broadest capability of predicting patterns of river community organization (e.g., the European Water Framework Directive; Sachon and Wasson, 2002). The River Continuum Concept (RCC; Vannote et al., 1980) offered a "reference scheme" describing the continuous gradient of physical characteristics of streams from headwaters to mouth and the resulting functional responses under natural conditions. However, there is little chance to find a river which fits the RCC along its whole course (Compin and Céréghino, 2007), and this situation raises concerns about the possibility to identify broadly applicable patterns (e.g., as those suggested in Fig. 3), based on relevant structural attributes of aquatic communities on a large spatial scale. Specifically, rivers are increasingly affected by anthropogenic disturbance, resulting in modifications of their physical and chemical conditions, disruption of natural dispersal pathways (Kruk and Penczak, 2003), and, subsequently, in changes within animal communities. In most cases, alterations of river habitats lead to losses of taxa, and spatial discontinuities in predictable downstream gradients (Compin and Céréghino, 2003). Explicit schemes, such as distribution patterns of rare and common species within large watersheds, are therefore of obvious value to support field research and/or hypothesis testing, as well as integrated management directives.

The greater contribution of common species to patterns of species richness in all taxonomic groups calls for mechanistic explanations, to better understand why common species concentrate in some areas and occur in low numbers in others. Indeed, if significant correlations were generated between fish or insect species richness (rare, common), and distance from the source and/or elevation, the latter does not reflect direct causal relationships. The literature supports the idea that temperature plays an important role in explaining the relationship between elevation or distance from the source (i.e., the downstream gradient) and fish assemblages (e.g., Bardonnet and Gaudin, 1991). Temperature governs the species population dynamics through growth and fecundity (Lobon-Cervia et al., 1996), by acting as a physicochemical habitat filter (Poff, 1997) with respect to species traits such as metabolism, energetic demands and reproduction. Other underlying factors related to the downstream gradient may explain site to site differences in fish species richness. Downstream addition of fish species (rare, common, overall) may result from increased living space in larger stream sections, increased habitat diversity (e.g., access to floodplain habitats and backwaters), and greater habitat stability such as reduced flow variability (Schlosser, 1987; Rahel and Hubert, 1991). Conversely, headwater streams with uniform habitat of low volume and shallow pools favour small fishes (Schlosser, 1987). From lithophilous to phytophilous reproduction guilds (Balon, 1975), fish require specific substrates for egg deposition, the quality and heterogeneity of which is strongly dependent on the downstream location of sites (Penczak and Mann, 1990; Reyjol et al., 2003). Furthermore, Oberdorff et al. (2002) reported a decrease in invertivorous species richness and abundance and an increase in omnivorous species richness and abundance from upstream to downstream areas. Several abiotic factors may influence benthic diversity (e.g., flow regime, water temperature and chemistry, substrate nature and composition, and food resources), and the relative importance of these factors is always difficult to assess because they interact in nature. However, the diversity of aquatic insect communities strongly depends on the diversity and stability of stream habitats (Cummins, 1979; Vinson and Hawkins, 1998; Heino et al., 2003), which provide the ecological niches for the development of species (Malmqvist and Otto, 1987). Specifically, stream flow determines the spatiotemporal variability of physical microhabitats (Moog and Janecek, 1991; Robinson et al., 1992), thus influencing the benthic community structure through the prominent role of substrate size and composition, current velocities, and bed scour. Therefore, the higher flow variability observed in intermediate (mountainous – piedmont) sections of the river continuum certainly has a positive influence on habitat heterogeneity, to the benefit of most insect species (i.e., those common species, which create most of the spatial structure in richness patterns of aquatic insects).

Many species in biological communities are rare, and this is true of aquatic animal communities (Marchant et al., 1999). Common species made a greater contribution to species richness in all data sets, and this is often true of biological communities (Pearman and Weber, 2007). However, in some taxa, the rarer species became almost equally (*Ephemeroptera*, *Plecoptera*), or more strongly correlated (fish) with species richness when increasing information along the common-to-rare and rare-to-common sequences. These patterns suggest that these rarer insect or fish species show a similar or stronger affinity, on a species-for-species basis, for high richness areas than do the commoner species. Such an assumption also fits with the observation that areas which carry more rare species (e.g., large and high-ordered streams in our study) may also concentrate an important fraction of the regional biodiversity (Santoul et al., 2005). Finally, throughout the world, governmental action plans aim at delineating natural zones of ecological, faunistic and floristic interest (e.g., the Natura 2000 network in Europe). The first objective of such plans is to identify areas which concentrate conservation values, i.e., hot-spots of species richness, areas containing rare species or endangered habitats. Among the questions usually asked to the scientific experts, two are of particular interest: (i) which environmental variables may explain variations in numbers of species? and (ii) within a given regional system, which areas contain rare species? To address these concerns, distribution patterns of species richness, and rarity and commonness must in general be derived from environmental conditions. From our analyses, it appeared that: (i) simple variables such as distance from the source and elevation were able to predict variations in the numbers of species (both rare and common) for fish and insects, respectively, and (ii) there was a marked concentration of rare fish and insect species in large and high-ordered streams. Finally, if common species approximated well the overall patterns in species richness, fish and aquatic insects showed different responses to the downstream gradients in physical variables, almost certainly because of differences in ecological requirements. Although

our study illustrates the importance of including both vertebrate and invertebrate taxa in analysing animal biodiversity patterns, it remains one of a very few attempts to do so.

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