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

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ABSTRACT

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*.

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