BIODIVERSITY RESEARCH

Concordance among stream assemblages and spatial autocorrelation along a fragmented gradient

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ABSTRACT

Patterns of spatial autocorrelation of biota and distributional similarity (concordance) between assemblages of different organism groups have important implications in both theoretical ecology and biodiversity conservation. Here we report environmental gradients and spatial distribution patterns of taxonomic composition among stream fish, benthic macroinvertebrate, and diatom assemblages along a fragmented stream in south-western France. We quantified spatial patterns of lotic assemblage structure along this stream, and we tested for concordance in distribution patterns among the three taxonomic groups. Our results showed that both environmental characteristics and stream assemblages were spatially autocorrelated. For stream fish and diatom assemblages, these patterns reflected assemblage changes along the longitudinal stream gradient, whereas environmental variables and benthic macroinvertebrates exhibited a more patchy spatial pattern. Cross-taxa concordance was significant between stream fish and diatoms, and between stream fish and benthic macroinvertebrates. The assemblage concordance between stream fish and diatoms could be attributed to similar responses along the longitudinal gradient, whereas those between stream fish and benthic macroinvertebrates may result from biotic interactions. Based on potential dispersal capacities of taxa, our results validated the hypotheses that weakly dispersing taxa exhibit greater concordance than highly dispersing ones and that dispersal capacities affect how taxonomic groups respond to their local environment. Both diatoms and highly dispersing stream fish were affected by stream fragmentation (i.e. the number of dams between sites), while the effect of fragmentation was not significant for invertebrates that fly well in their adult stage, thus emphasizing the importance of the way of dispersal. These results suggest that addressing the effects of dispersal capacity on stream assemblage patterns is crucial to identifying mechanisms behind patterns and to better understanding the determinants of stream biodiversity.

Keywords

Dispersal, fragmentation, Mantel tests, partial Mantel tests, spatial autocorrelation, stream assemblage concordance.

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INTRODUCTION

Most natural ecological phenomena display geographical patchiness, and ecologists have long been aware of the importance of spatial relationships when studying species distribution (Borcard *et al.*, 1992; Legendre, 1993; Cooper *et al.*, 1997). In community ecology, a central idea is that spatial variation in local community structure comes either from environmental forcing or from biotic processes (e.g. Magalhães *et al.*, 2002). Thus, spatial structure potentially offers many insights into ecological patterns and processes (Tobin, 2004).

Spatial autocorrelation (i.e. the lack of independence between pairs of observations at given distances in space, Legendre, 1993) is a common phenomenon in ecology and has been widely documented. Both single-species distribution and composite measures of assemblages (i.e. species richness) show spatial autocorrelation, and various abiotic (i.e. climate, geology, disturbance, resources), biotic (i.e. dispersal, interspecific interactions), and historical factors have been advanced to explain spatially autocorrelated patterns (e.g. Dormann, 2007).

In lotic systems, most chemical, physical, and biotic characteristics exhibit longitudinal distributions from the source to mouth

(Vannote *et al.*, 1980; Statzner & Borchard, 1994). This upstream–downstream gradient results from the spatial structure of river networks, and it is probably the most well-known, worldwide, large-scale pattern in stream assemblages (e.g. stream fish: Matthews, 1998; benthic macroinvertebrates: Hildrew & Giller, 1994; diatoms: Potapova & Charles, 2002). Both gradients in environmental conditions and spatial constraints to organism displacements have strong implications in the spatial distribution of stream assemblages. Thus, the level of spatial structuring within stream assemblages will depend on both how strongly these assemblages respond to the environment (Murphy & Davy-Bowker, 2005) and on the dispersal abilities (i.e. contagious processes) of lotic organisms within the hydrographic network (Angermeier & Winston, 1999; Grenouillet *et al.*, 2004). Therefore, addressing the degree to which stream assemblages are spatially autocorrelated and the role of the physicochemical environment in determining this pattern is crucial to better understand the forces structuring stream assemblages (Murphy & Davy-Bowker, 2005).

Recently, considerable research effort has been devoted to describing spatial patterns of biodiversity (Heino, 2002), and the question of the among-taxon congruence in biodiversity patterns remains a major challenge in both theoretical and applied ecology. Assemblage concordance (*sensu* Jackson & Harvey, 1993) can be defined as the degree to which patterns in assemblage structure across a set of sites are similar among different taxonomic groups (Heino *et al.*, 2003; Paavola *et al.*, 2006). Although assemblage concordance (also called congruence) has been widely investigated (reviewed in Gaston & Williams, 1996; Gaston, 2000) at global (e.g. Lamoreux *et al.*, 2006), regional (e.g. Ricketts, 2001) and local (e.g. Su, 2004) spatial scales, it still remains poorly known for many ecosystems (Heino *et al.*, 2003). In particular, concordance among freshwater organism groups has been much less studied than that among terrestrial organisms (MacNally *et al.*, 2002; Heino *et al.*, 2005; Paavola *et al.*, 2006).

To date, numerous studies on assemblage concordance in freshwater systems have focused on lentic communities (Bilton *et al.*, 2006; Paavola *et al.*, 2006). Most of these studies have concluded that assemblage concordance is often low in freshwater systems, especially at small (e.g. within watershed) spatial scales (Allen *et al.*, 1999a; Paavola *et al.*, 2003; Tolonen *et al.*, 2005). Allen *et al.* (1999b) suggested that weakly concordant patterns could indicate that assemblages of different organism groups responded to the environment at different scales, and could result from different-sized organisms perceiving their environment in profoundly different ways.

In running water systems, many studies have compared responses of different organism groups to the same underlying gradients (Paavola *et al.*, 2006), but very few of them directly addressed assemblage concordance. Such concordance among distribution patterns has been observed in running waters between macrophytes and benthic invertebrates (Ormerod *et al.*, 1987), between fish and benthic invertebrates (Kilgour & Barton, 1999), or between fish, benthic invertebrates, and macrophytes (Heino, 2001). Examining broad-scale species richness patterns in five groups of freshwater organisms (i.e. macrophytes, dragonflies,

stoneflies, aquatic beetles, and fishes), Heino (2002) showed that variation in species richness across provinces was concordant among the groups, with stoneflies being the most notable exception. However, other studies revealed low concordance between fish, benthic invertebrates, and bryophytes based on surveys of local communities (Paavola *et al.*, 2003, 2006; Heino *et al.*, 2005).

This study investigated stream assemblages in the Viaur River (south-western France) in relation to both environmental variables and spatial position along the upstream–downstream gradient. This river is characterized by a high level of habitat fragmentation, with many small dams all along the water course that could affect the spatial distribution of lotic organisms.

Here we documented patterns of spatial distribution of three taxonomic groups (stream fish, benthic macroinvertebrates, and diatoms) that are used widely as targets for stream ecological assessments. Our objectives were to (1) quantify spatial patterns of lotic assemblage structures by describing patterns of spatial autocorrelation along the upstream–downstream gradient, (2) test for concordance among the three taxonomic groups, (3) examine whether concordance was generated through similar responses of different taxa to underlying environmental gradients, (4) examine whether habitat fragmentation affected the spatial distribution patterns of stream assemblages, and finally (5) examine whether organism dispersal capacities could influence the observed distribution patterns.

METHODS

Study area

The River Viaur is located in the Adour-Garonne basin, south-western France. This hydrographic network covers approximately 1530 km² and has its source at an altitude of 1090 m and its confluence with the River Aveyron is situated 169 km downstream at an altitude of 150 m. The whole river network contains 110 streams with a total length of about 1497 km. Thirteen sampling sites were selected along the upstream–downstream gradient of the main river course (Fig. 1). Along this gradient, 22 low-head dams were reported (Fig. 1), with a height ranging from 1.5 to 2.8 m (mean = 1.96). The number of dams between sites ranged from one to five (mean = 1.58).

Data collection

At each sampling site, physical habitat and water chemistry were described, and diatoms, benthic macroinvertebrates, and stream fish were sampled. All the samples were collected during the same time period (June 2005) to avoid potential bias in the quantification of both spatial patterns and assemblage concordance due to the temporal dynamics of each taxonomic group.

To describe environmental variables, 1-L water samples were collected simultaneously with biological samples, and then analysed for pH, conductivity (Cd, mS.m⁻¹), and concentrations of chloride (Cl), silicate (SiO_2), phosphate (PO_4), dissolved nitrates (NO_3-N) and nitrites (NO_2-N), and dissolved ammonia (NH_4-N). Two thermal variables were defined from continuous water
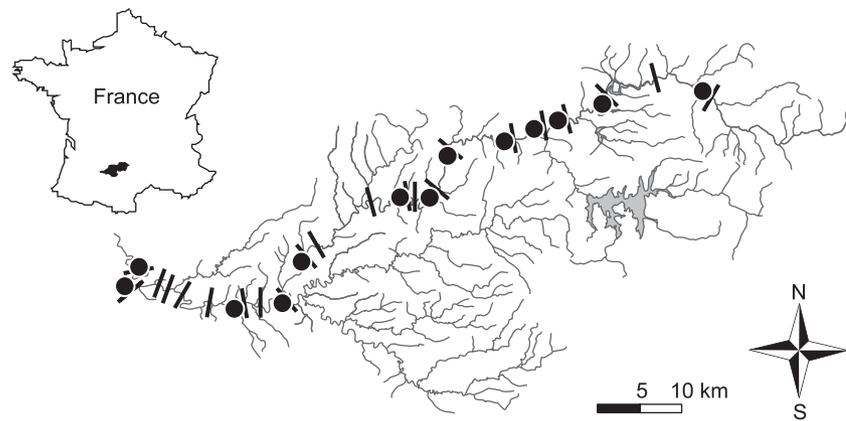
Figure 1 Location of 13 sampling sites (dots) and dams (bars) along a 169-km-long stream in south-western France.

temperature recordings: mean water temperature (Tmean, °C) and thermal coefficient of variation (TCV), both calculated over the 3-month period before sampling. Given the lability of most of the chemical variables retained in this study, our snapshot measurement may be not reflective of long-term characteristics of the sites. However, a between-year comparison demonstrated that the differences observed between sites in 2005 were roughly stable along a three years sampling (i.e. 2005, 2006, and 2007), thus suggesting that our measurement was a good surrogate of the chemical characteristics of the sites (G.L. & G.G., unpublished data).

Stream fish were collected by a two-pass depletion method using a Deka 6000 DC electrofishing unit (Deka, Marsberg, Germany), fitted with a 20-cm ring-diameter anode. Each site was a stream reach comprising pool and riffle morphological units. Reaches were selected as the most representative of the stream section based on depth, water velocity, and visual observation of the substratum. Each sampled reach was delimited by upstream and downstream riffles to reduce fish emigration and/ or emigration during sampling, leading to a substantial variation of the surface sampled (from 290 to 780 m²) according to the morphology of the stream. All the fish collected were identified to species level, counted, and measured to the nearest millimetre (total body length). Fish collected during the two passes were stored in tanks and released to the stream at the end of the sampling session. Fish density was estimated using the method of Carle & Strub (1978) to provide an estimation of the density of each species, expressed as a number of individuals per 100 m².

Benthic macroinvertebrate assemblages were sampled using a 200-μm mesh size Surber net (Silex, Rennes, France). At each site, four subsamples (sampling area of 1/20 m²) were taken to reflect microhabitat diversity. According to previous studies (e.g. Paavola *et al.*, 2003; Heino *et al.*, 2005), four subsamples were considered sufficient to (1) cover most benthic microhabitats present at a site, and (2) characterize the assemblage when identified to the family level. All the specimens collected were counted and identified to the family level. This taxonomic resolution was preferred to genera or species because it allowed us to identify all the macroinvertebrates, whereas identifying to a more precise taxonomic resolution requires collecting flying adults and/or precise life stages. Moreover, previous studies have shown that when using abundance data, different levels of macro-

invertebrate taxonomic resolution produced largely the same description of assemblage patterns (e.g. Bowman & Bailey, 1997; Hewlett, 2000). Many studies conclude that family-level taxonomic resolution is sufficient to differentiate among sites when marked differences among sites are observed (e.g. Furse *et al.*, 1984; Waite *et al.*, 2004; Lloyd *et al.*, 2006). In our study, such marked differences occurred as sites were selected along a large environmental, upstream–downstream gradient. Moreover, numerous authors have underlined that multivariate characterizations of macroinvertebrate community composition do not seem to be sensitive to taxonomic resolution (e.g. Furse *et al.*, 1984; Marchant *et al.*, 1995; Hewlett, 2000; Bailey *et al.*, 2001), at least from family to species level. Thus, we believe that finer taxonomic resolution would not have affected our conclusions and that family-level resolution provided sufficient detail to allow distance-based comparisons among sites.

Diatom assemblages were sampled following standard procedures (CEN, 2003). Benthic diatoms were sampled from hard substrate exposed to light and free of sediments and filamentous algal growths. Diatoms were removed from five cobbles at each site by brushing and washing with distilled water into a plastic tray. The bulk sample from each site was stored in a plastic tube. Each sample was oxidized in the laboratory with oxygen peroxide to clean diatom frustules. After cleaning, the diatoms were dried onto coverslips and mounted onto glass slides in Naphrax (Northern Biological Supplies, Ipswich, UK). At least 400 frustules per sample were identified to species level and counted under a stereomicroscope at ×1000 magnification.

Dissimilarity measures

Thirteen sites resulted in $^{13}C_2 = 78$ combinations of pairs of sites. Five matrices of site-pair distances were computed, relating to (1) geographical distance, (2) environmental dissimilarities, (3) stream fish dissimilarities, (4) benthic macroinvertebrate dissimilarities, and (5) diatoms dissimilarities between each pair of site.

As opposed to simple geometric distance (i.e. geographical coordinate distance), a more ecologically relevant measure of geographical distance between sites is linear distance along the river network (Murphy & Davy-Bowker, 2005). For each pair of sites, geographical distance was thus computed using the

distance from source of each site defined from geographical information system (ArcView 9.1). For environmental variables, a dissimilarity matrix was computed using normalized Euclidean distance. For fish, macroinvertebrate, and diatom assemblages, the Bray–Curtis distance (Bray & Curtis, 1957) between all pairwise permutations of sites was used to construct dissimilarity matrices. Before analysing assemblage data, we excluded all rare taxa, i.e. those occurring in only one sample. For stream fish and benthic macroinvertebrates, raw abundance values were fourth-root transformed (see Clarke, 1993), whereas diatom raw data (i.e. percentages) were arcsine square-root transformed.

Spatial autocorrelation

Analysis of spatial autocorrelation was based on Mantel tests (Mantel, 1967; Sokal & Rohlf, 1995; Legendre & Legendre, 1998), testing for linear relationships between two sets of distance-based data. Because all pairs of sites in a given distance matrix are not independent, Monte Carlo permutations were used to test if the observed value of the Mantel test statistic (r_M) differed from those expected under the null hypothesis (i.e. no correlation between the two sets of distance values). To do this, the observations in the distance matrices were randomly permutated and the test statistic was recalculated. We evaluated the significance of each observed r_M value by comparing it with the distribution of 10,000 random permutation values obtained under the null hypothesis (Manly, 1994). If less than 5% of the permutation values were higher than the observed one, we concluded that there was spatial autocorrelation. Mantel tests were performed to test for spatial autocorrelation in both stream assemblage and habitat characteristic patterns.

Partial Mantel tests were used to examine the relationship between two dissimilarity matrices while eliminating the linear effect of a third matrix (Smouse *et al.*, 1986). We performed partial Mantel tests to assess the importance of environmental variables in influencing assemblage patterns after having removed the effects of geographical distance between sites.

Finally, a multivariate Mantel correlogram (Oden & Sokal, 1986; Sokal, 1986) was computed to describe the spatial structure of environmental variables and stream assemblages. The geographical distance matrix was divided into seven distance classes using Sturge's rule to set the range of pairwise distances in each class (see Legendre & Legendre, 1998 for details).

All Mantel and partial Mantel tests were conducted at $\alpha = 0.05$, with Bonferroni corrections for multiple testing.

Assemblage concordance

Mantel tests were performed to test for cross-taxon correlation between the Bray–Curtis distance matrices constructed for each taxonomic group. The strength of each pairwise relationship between matrices was measured by the Mantel statistic r_M and tested for significance using a Monte Carlo permutation procedure with 10,000 permutations. Partial Mantel correlations were used to test for possible confounding effects of geographical distance between sites on cross-taxon concordance patterns.

Stream fragmentation and dispersal capacities

To test the effect of fragmentation on stream assemblage patterns, we reported the spatial location of dams along the longitudinal gradient. Then we constructed a matrix containing the number of dams between each pair of sites. As the number of dams and the geographical distance between two sites were highly correlated ($R = 0.96$, $P < 0.0001$), the influence of number of dams on stream assemblage patterns was tested using partial Mantel tests, to eliminate the effect of geographical distance between sites.

According to the dispersal capacities of taxa, we constructed subsets of taxonomic data to test whether dispersal capacities could influence the assemblage distribution patterns. For benthic macroinvertebrates, we defined highly dispersing taxa as taxa having flying adult stage (i.e. insects). For stream fish, body size can be used as a surrogate of dispersal capacity (e.g. Peters, 1983; Hugueny, 1990). We obtained values of total length (TL) for all fish species reported in this study from the literature. We then calculated the median total length (MTL) and, according to this value, defined two species groups: weakly dispersing species (i.e. fish species for which TL was smaller than MTL) and highly dispersing species (i.e. fish species for which TL was higher than MTL). For both stream fish and benthic macroinvertebrates, separate partial Mantel tests were thus performed to test the effects of fragmentation using (1) all taxa, (2) highly dispersing taxa, and (3) weakly dispersing taxa.

All statistical analyses were performed using R (Ihaka & Gentleman, 1996) freeware and Vegan (Oksanen *et al.*, 2007) R package.

RESULTS

Stream assemblages

Among the 13 sites distributed along a 110-km-long stream gradient, fish species richness varied from four to 12, the number of macroinvertebrate families varied from 29 to 43 and diatom species richness varied from 54 to 82. In total, the number of taxa recorded for stream fish, benthic macroinvertebrate, and diatom assemblages was 15, 79, and 196, respectively. After elimination of rare taxa, we retained 12, 64, and 132 taxa for fish, macroinvertebrate, and diatom data sets, respectively.

Spatial autocorrelation

Environmental and geographical distances were significantly correlated ($r_M = 0.733$, $P < 0.001$, Table 1), indicating that local habitat conditions were spatially autocorrelated. The corresponding Mantel correlogram (Fig. 2a) indicated spatial autocorrelation among the smallest distance class. However, this positive autocorrelation contrasted with negative autocorrelation of the fourth and sixth distance classes, suggesting that environmental data did not exhibit a clear longitudinal gradient but a patchy spatial pattern.

The results of the Mantel tests comparing the assemblage and geographical distance matrices indicated spatial autocorrelation
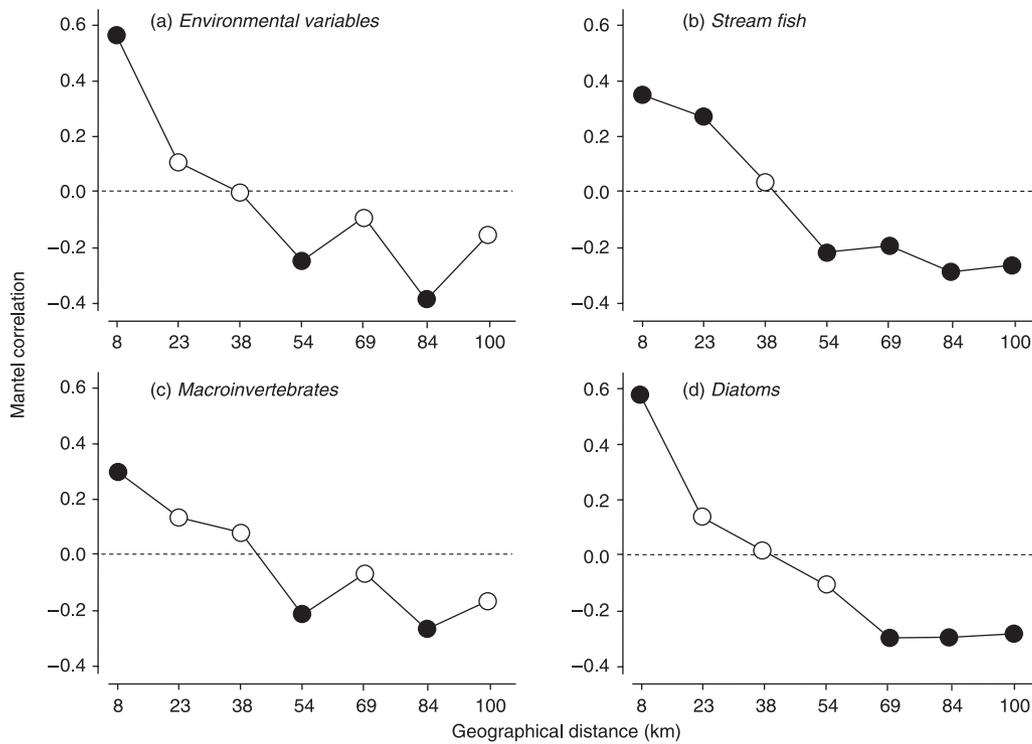
Figure 2 Mantel correlogram for spatial autocorrelation in (a) environmental variables, (b) stream fish, (c) benthic macroinvertebrate, and (d) diatom assemblages. Dark circles indicate significant correlations (assessed using a Bonferroni correction) between site dissimilarity and geographical distance (upper class limit in kilometre).

	Geographical	Environment	Diatoms	Macroinvertebrates	Fish
Geographical		< 0.001	< 0.001	0.006	0.004
Environment	0.733		< 0.001	0.012	0.004
Diatoms	0.811	0.502		ns	0.010
Macroinvertebrates	0.441	0.401	0.287		< 0.001
Fish	0.651	0.494	0.584	0.595	

Table 1 Mantel correlations for comparisons between geographical, environmental, and taxonomic distance matrices. Above the diagonal, *P* values (Bonferroni probabilities) (ns, not significant); below the diagonal, Mantel correlation (r_M) coefficients.

for stream fish, benthic macroinvertebrates, and diatoms (r_M = 0.651, $P = 0.004$; $r_M = 0.441$ $P = 0.006$; $r_M = 0.811$, $P < 0.001$, respectively, Table 1). For all taxonomic groups, the corresponding Mantel correlogram (Fig. 2b–d) indicated positive autocorrelation for the smallest distance class. Stream fish assemblages exhibited the highest spatial autocorrelation with significant positive autocorrelation for the first two distance classes (Fig. 2b). Both stream fish and diatoms assemblages showed negative auto-correlation among the largest classes and the overall shape of these two correlograms could thus be attributed to a biotic gradient. Benthic macroinvertebrate assemblages exhibited a different spatial pattern, without significant negative auto-correlations for the largest distance classes, revealing a patchy distribution for these assemblages. Thus, the overall shape of the Mantel correlograms revealed similar spatial patterns for both benthic macroinvertebrates and environmental variables.

After eliminating the effect of environmental distance, both diatoms and stream fish assemblages exhibited significant spatial autocorrelation ($r_M = 0.740$, $P < 0.001$, and $r_M = 0.488$, $P = 0.006$, respectively, Table 2), whereas benthic macroinvertebrates were not related to geographical distance between sites in partial Mantel tests. When the effect of geographical distance between sites was accounted for, all partial Mantel tests comparing stream assemblage and environmental distances between sites were non-significant (Table 2).

Assemblage concordance

Assemblage dissimilarity between stream fish and benthic macroinvertebrate assemblages was significantly ($P < 0.001$) correlated and showed the strongest positive correlation (Table 1). Stream fish and diatom assemblages were also significantly

Table 2 Partial Mantel tests for cross-matrix comparisons after having controlled the effects of environmental and geographical distance. Given are partial Mantel correlation (r_M) coefficients and Bonferroni probabilities (*P*) values (ns, not significant).

| | Controlled effect | | | |
| | Environmental | | Geographical | |
Cross-matrix comparison	r_M	*P*	r_M	*P*
Fish vs. geographical	0.488	0.006		
Macroinvertebrates vs. geographical	0.237	ns		
Diatoms vs. geographical	0.740	< 0.001		
Fish vs. environmental			0.032	ns
Macroinvertebrates vs. environmental			0.126	ns
Diatoms vs. environmental			−0.187	ns

Table 3 Partial Mantel tests for concordance among stream assemblages. For both macroinvertebrates and fish, separate tests were performed using highly and weakly dispersing taxa (see Methods). Given are partial Mantel correlation (r_M) coefficients and Bonferroni probabilities (*P*) values (ns, not significant) after having controlled the effects of environmental and geographical distance.

| | | Controlled effect | | | |
| | | Environmental | | Geographical | |
Cross-assemblage comparison	Data set	r_M	*P*	r_M	*P*
Fish vs. macroinvertebrates	All taxa	0.499	0.003	0.452	0.008
Diatoms vs. fish	All taxa	0.441	0.028	0.127	ns
Diatoms vs. macroinvertebrates	All taxa	0.101	ns	−0.135	ns
Fish vs. macroinvertebrates	Highly dispersing taxa	0.403	0.038	0.385	0.048
Fish vs. macroinvertebrates	Weakly dispersing taxa	0.603	< 0.001	0.567	< 0.001

correlated, while the correlation involving benthic macroinvertebrate and diatom assemblages was not statistically significant.

After eliminating the effect of environmental distance on cross-taxon concordance patterns, partial Mantel tests showed that only benthic macroinvertebrate and diatom assemblages were not significantly concordant (Table 3). When using all taxa, the highest concordance pattern was observed between stream fish and benthic macroinvertebrate assemblages ($r_M = 0.499$, $P = 0.003$). When separating taxa according to their dispersal capacities for both stream fish and benthic macroinvertebrates, the highest concordance pattern was observed between weakly dispersing taxa ($r_M = 0.603$, $P \leq 0.001$, Table 3).

When the effect of geographical distance between sites was accounted for, only concordance between stream fish and benthic macroinvertebrates appeared significant ($r_M = 0.452$, $P = 0.008$). When separating highly and weakly dispersing taxa, the highest concordance pattern was observed between weakly dispersing ones ($r_M = 0.567$, $P < 0.001$, Table 3).

Stream fragmentation

After eliminating the effect of environmental distance, the level of stream fragmentation (i.e. the number of dams between

sites) significantly influenced distribution patterns of both stream fish and diatom assemblages ($r_M = 0.554$, $P = 0.001$ and $r_M = 0.726$, $P < 0.001$, respectively, Table 4). For stream fish, both highly and weakly dispersing species were influenced by stream fragmentation, whereas benthic macroinvertebrates were not influenced by stream fragmentation, whatever the data set considered. When the effect of geographical distance between sites was accounted for, the effect of stream fragmentation was only significant for highly dispersing fish species ($r_M = 0.672$, $P < 0.001$), whereas other partial Mantel tests were non-significant (Table 4).

DISCUSSION

Assemblage dissimilarities

Mantel correlations for comparing geographical distances and assemblage dissimilarities between sites were significant for all stream assemblages, suggesting significant assemblage changes along the longitudinal gradient.

Stream fish, benthic macroinvertebrates, and diatoms are among the most studied lotic assemblages. In stream fish ecology, longitudinal changes along the upstream–downstream gradient

Table 4 Partial Mantel tests for effects of fragmentation (i.e. number of dams between sites) on stream fish, benthic macroinvertebrate, and diatom assemblages. For both fish and macroinvertebrates, separate tests were performed using highly and weakly dispersing taxa (see Methods). Given are partial Mantel correlation (r_M) coefficients and Bonferroni probabilities (P) values (ns, not significant) after having controlled the effects of environmental and geographical distance.

| Stream assemblage | Data set | Controlled effect | | | |
| | | Environmental | | Geographical | |
		r_M	P	r_M	P
Stream fish	All species	0.554	0.001	0.302	ns
	Highly dispersing species	0.520	< 0.001	0.672	< 0.001
	Weakly dispersing species	0.384	0.038	−0.128	ns
Benthic macroinvertebrates	All taxa	0.303	ns	0.190	ns
	Highly dispersing taxa	0.277	ns	0.223	ns
	Weakly dispersing taxa	0.227	ns	0.018	ns
Diatoms	All species	0.726	< 0.001	0.106	ns

generally reflect an increase in fish species richness with increasing stream size. This typical pattern has been widely discussed (reviewed in Matthews, 1998) and different explanations have been advanced, such as habitat diversity (Gorman & Karr, 1978), differential rates of immigration and extinction (Power *et al.*, 1988), or sampling phenomenon (Angermeier & Schlosser, 1989). For benthic macroinvertebrates, it is well known that assemblage structure is influenced by both local habitat characteristics (e.g. substratum type, particle size, hydraulic constraints) and biotic factors such as predation, competition and food. Following Vannote *et al.* (1980), numerous studies have documented longitudinal patterns of macroinvertebrate functional feeding group composition along river systems. These previous works have underlined that the upstream–downstream gradient was the main factor shaping macroinvertebrate assemblages (e.g. Rossaro & Pietrangelo, 1993; Hildrew & Giller, 1994). For diatoms, many studies have indicated stronger control by local environmental conditions than by large-scale factors, emphasizing the primacy of stream water nutrient concentrations and ionic composition (e.g. conductivity) in structuring diatom assemblages (e.g. Biggs, 1990). In consequence, changes in water chemistry along the gradient of fast-flowing streams to lowland rivers can be of primary importance in controlling diatom assemblages. Indeed, previous studies have described relationships between diatom guilds (e.g. morphological growth forms) and stream size (Molloy, 1992), thus emphasizing the importance of position along the longitudinal gradient in determining patterns of diatom species distribution (e.g. Potapova & Charles, 2002).

Spatial autocorrelation patterns

Spatial autocorrelation patterns were quantified using Mantel correlograms, which provided a description of spatial structures for both local habitat conditions and stream assemblages. Following Legendre & Fortin (1989), the overall shape of the Mantel correlogram, exhibiting positive autocorrelation among the smallest distance classes and negative autocorrelation among the largest distance classes can either be attributed to a species gradient or to a structure with steps (i.e. disruptive changes along the stream course at tributary junctions, Osborne & Wiley, 1992). Such patterns were observed for stream fish and diatom assemblages, whereas environmental variables and benthic macroinvertebrate assemblages exhibited a more patchy spatial pattern.

In addition, Mantel correlograms can serve to identify correlation lengths, that is the average size of the zone of positive autocorrelation (i.e. 'zone of influence' *sensu* Legendre & Fortin, 1989). In our study, there was strong autocorrelation of both environmental variables and stream assemblages at small spatial scale (less than 20 km), and only stream fishes exhibited significant autocorrelation for the first two distance classes (around 30 km). Although few comparable estimates in autocorrelation lengths in lotic systems have been reported (Lloyd *et al.*, 2006), these results are consistent with available studies. For environmental variables, Lloyd *et al.* (2005) have described similar patterns with a zone of influence of approximately 40 km. For stream assemblages, Lloyd *et al.* (2005, 2006) noticed a spatial autocorrelation distance of about 6 km for benthic macroinvertebrate assemblages, while Wilkinson & Edds (2001) reported a zone of influence of approximately 44 km for stream fish assemblages. To our knowledge, despite extensive literature on diatom distribution patterns in streams (e.g. Pan *et al.*, 1999; Potapova & Charles, 2002), there is no similar study quantifying spatial autocorrelation length for diatom assemblages.

A key issue in understanding stream assemblage distributions is knowing the extent to which they are constrained by local environmental variables vs. spatial (i.e. geographical) factors. In this study, both geographical and environmental effects have been tested to explain stream assemblage distributional patterns. While significant correlations were observed between stream assemblage and both environmental and geographical distances between sites, partial Mantel tests eliminating the effects of geographical distance revealed that correlations between stream

assemblage and environmental distances were non-significant. This is in accordance with other investigations, which have emphasized that spurious correlations between species and environmental matrices can be a result of common spatial structure among variables in those data sets, and that much of the influence attributed to environmental differences can be alternatively explained by the spatial pattern underlying the data (Wilkinson & Edds, 2001).

Once the effect of environment was removed, partial Mantel tests revealed significant spatial autocorrelation patterns for both diatom and stream fish assemblages. Two hypotheses have been advanced to explain such results: (1) assemblage composition could respond in part to attributes of local habitat that we did not characterize in our study (Fleishman & MacNally, 2006), and (2) spatial autocorrelation patterns could reflect the relative importance of biotic processes in structuring assemblages (Wilkinson & Edds, 2001). For stream fish assemblages, our results are in accordance with previous investigations, which have pointed out that the composition of neighbouring sites could influence local fish assemblage composition (e.g. Osborne & Wiley, 1992; Magalhães *et al.*, 2002; Grenouillet *et al.*, 2004). Although similar conclusions have been drawn for macro-invertebrate assemblages (Sanderson *et al.*, 2005; Mykrä *et al.*, 2007), our results did not confirm such a pattern and the overall shape of the Mantel correlograms suggested that the spatial patterns exhibited by benthic macroinvertebrates corresponded fairly closely with those exhibited for environmental variables. However, we are aware of the need for being careful when interpreting the relationships between family-level macroinvertebrate data and environmental variables. Therefore, species-level data would be useful to confirm that macroinvertebrate assemblages were mainly determined by environmental variables.

Concordance in assemblage dissimilarity

While previous studies have argued that assemblage concordance was rather low in freshwater systems, especially at small (e.g. within-basin) spatial scales (Allen *et al.*, 1999a, b; Paavola *et al.*, 2003), our results were not consistent with this assumption. Based on assemblage dissimilarity comparisons, our study revealed relatively high degree of concordance of stream fish with both benthic macroinvertebrates and diatoms. Once the effect of environment was removed, these patterns were still significant. This implies that these associations are not exclusively due to similar responses to the same environmental variables at similar spatial scales. Moreover, once the effect of geographical distance was removed, only stream fish and benthic macro-invertebrate assemblages were still significantly correlated. This emphasizes that diatom and stream fish assemblages showed similar responses along the longitudinal stream gradient, while the association between fish and macroinvertebrates could not be explained solely by similar responses to environmental gradient or position along the longitudinal gradient. Among the possible explanations for such a pattern, direct biotic interactions (i.e. top-down predator effects) have been evoked (e.g. fish vs. benthos, Kilgour & Barton, 1999; birds vs. fish, Paszkowski

& Tonn, 2000). Although trophic interactions have long been evidenced from controlled experiments (e.g. Cooper *et al.*, 1992), this sort of explanation has yet to be confirmed in large-scale field studies.

Some authors have hypothesized that strongest concordance should occur among taxa of similar size (Allen *et al.*, 1999b; Paszkowski & Tonn, 2000). Our results did not confirm this hypothesis, as no concordance was observed between diatom and benthic macroinvertebrate assemblages, whereas diatom and stream fish assemblages exhibited concordant spatial patterns. As suggested by Heino *et al.* (2005), diatoms, benthic macro-invertebrates, and stream fish may be too different in terms of ecology to exhibit concordance in diversity patterns simply determined by size. Thus, our results support the idea that concordance strength could also be influenced by trophic relations or differences in life-history traits between the pairs of assemblages under comparison (Paszkowski & Tonn, 2000).

Dispersal and stream fragmentation

Our results emphasize that dispersal capacities affect how taxonomic groups respond to their local environment. This result is consistent with other studies that showed that geographical location and stream environment were influential in accounting for community composition but less in the case of invertebrates with strongly flying adults (e.g. Townsend *et al.*, 2003; Sanderson *et al.*, 2005; Mykrä *et al.*, 2007). Although dispersal capacity has previously been found to be important in determining both spatial autocorrelation and concordance in assemblage dissimilarity (Moritz *et al.*, 2001; Pawar *et al.*, 2006), few studies have examined potential differences in concordance among groups that differ with respect to this life-history trait. Our results provide evidence favouring the hypothesis that weakly dispersing taxa exhibit greater concordance than highly dispersing ones. These findings support those of Moritz *et al.* (2001), who revealed a greater concordance between weakly dispersing invertebrates (i.e. flightless insects and snails) relative to flying insects, and recently, similar patterns have been reported in terrestrial studies (e.g. Graham *et al.*, 2006; Pawar *et al.*, 2006).

This influence of dispersal capacities was clearly apparent when testing for effect of stream fragmentation. For highly dispersing fish species, assemblage dissimilarity increased with the number of low-head dams between sites, whereas no similar pattern was observed for highly dispersing macroinvertebrates (i.e. flying insects). Despite abundant literature assessing the ecological effects of large dams (Poff & Hart, 2002), studies have typically focused on comparisons between assemblages directly below and directly above dams, whereas little research has been undertaken on the cumulative impacts of low-head dams (but see Cumming, 2004; Santucci *et al.*, 2005). Most available studies provide no evidence that multiple low-head dams led to substantial, assemblage-level fragmentation (e.g. Santucci *et al.*, 2005; Chick *et al.*, 2006). It is worth noting that these studies did not take dispersal capacities into account and we argue that considering life-history disparities between subsets of taxa could reveal hidden patterns. However, the paucity of other studies

precludes a wider comparison, and additional investigations are necessary. In particular, similar approaches focusing on streams characterized by various levels of fragmentation should be helpful to generalize our findings and to further explain potential variation in the cumulative effects of dams within and among stream systems.

Several points concerning the dispersal capacities of taxa would now require further investigations. First, we stress that only potential dispersal capacities were assessed in this study and do not necessarily reflect dispersing behaviour. As dispersal in both invertebrates and stream fish is difficult to obtain directly, a large number of studies rely on indirect estimation of dispersal. Although some authors reported a wide variability in the dispersal abilities among flying macroinvertebrates (e.g. caddisflies, Hoffsten, 2004), several studies have indicated flightless taxa to exhibit lower dispersal abilities than active fliers (reviewed in Bilton *et al.*, 2001) and larger active dispersers have been recently shown to attain greater observed distances than smaller active dispersers (Jenkins *et al.*, 2007). Second, although family-level data for macroinvertebrates have been shown to provide similar patterns as species-level data across long environmental gradients, families do not necessary function similarly to species in respect to dispersal. As a result, previous studies have stressed that because they used family-level resolution, different patterns that exist at lower taxonomic levels (genus, species) may have been obscured (e.g. Van de Meutter *et al.*, 2006). Nevertheless, these authors showed that dispersal tendencies significantly differed among families, suggesting that this taxonomic level could provide a reliable first approach for assessing the effects of dispersal on macroinvertebrate distribution patterns. Finally, it is worth noting that organism groups that were influenced by stream fragmentation (i.e. highly dispersing stream fish and diatoms) were exclusively aquatic taxa, while invertebrates with strongly flying adults did not exhibit such a pattern. This emphasizes that not only the dispersal capacities of taxa, but also the way of dispersal (i.e. water or air) was important in the determination of observed patterns. Therefore, taking into account both quantitative and behavioural information about dispersal capacities of taxa would greatly enhance further similar studies comparing dispersal capacities across taxa.

CONCLUSION

Very few investigations have assessed both spatial autocorrelation patterns and assemblage concordance among different stream assemblages, but such approaches would clearly enhance our knowledge of stream assemblage distribution. Nevertheless, quantitative studies of assemblage concordance are still in their infancy (Paszkowski & Tonn, 2000) and other similar approaches should now be conducted at different spatial scales to better separate environmental and spatial effects on assemblage concordance patterns. While this study encompassed 13 sites along one major gradient (i.e. the longitudinal river gradient), recent studies have pointed out the need to account for hydrological connectivity and the directional component of spatial autocorrelation within dendritic stream networks (reviewed in

Campbell Grant *et al.*, 2007). Therefore, it would be of first interest for further studies to assess assemblage concordance when considering the spatial structure (i.e. branching pattern) of hydrographic networks. Similarly, it would be informative to test the influence of temporal dynamics of the assemblage on concordance patterns. Different taxonomic groups with contrasted life history dynamics may exhibit variations in concordance patterns through time. These variations may provide insights into the strength of biotic interactions between assemblages.

Recently, conservation studies have increasingly focused on community dissimilarity as a better criterion than alpha diversity because it maximizes the overall representation of biodiversity in the landscape (Pawar *et al.*, 2006). Our study points out significant effects of spatial structure on stream assemblage distribution patterns, and these results have a number of implications for stream bioassessment and biodiversity conservation.

In stream ecology, diatoms, benthic macroinvertebrates, and stream fish are the most commonly surveyed groups (e.g. Hering *et al.*, 2006), but studies assessing the ecological status of stream ecosystems are typically based on a single taxonomic group (Paavola *et al.*, 2003). Although concordant assemblage dissimilarities could claim for the use of one group as a surrogate for other groups, recent studies have warned against the use of surrogate groups without caution. Indeed, the degree of assemblage concordance depends critically on the spatial extent of the study, and it appears to arise from a variety of mechanisms (Paavola *et al.*, 2003, 2006). As a result, stream assemblage gradients may not only be related to environmental variables but also to biogeographical constraints and neighbourhood dispersal processes (Mykrä *et al.*, 2007).

Overall, studying assemblage concordance is a powerful approach for detecting general patterns (Paszkowski & Tonn, 2000), and our study suggests that the importance of local environmental variables can vary with respect to the dispersal capacities of taxa. Other life-history (i.e. reproductive) characteristics are expected to affect spatial distribution patterns. Taking spatial structure into account and addressing the effects of functional characteristics on stream assemblage patterns would therefore be crucial to identifying mechanisms behind patterns and to better understanding the determinants of stream biodiversity.

ACKNOWLEDGEMENTS

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