



Characterizing the long-term taxonomic and functional variability of a stream fish assemblage

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With 4 figures and 3 tables

Abstract: While much research has been devoted to characterizing congruency in the spatial distribution of taxonomic and functional structure, the temporal aspect of this relationship is poorly known. We examined taxonomic and trophic function based variability of a stream fish assemblage using a 12-year data set of spring and summer surveys. We found the occurrence of the most abundant species was persistent, while their relative abundance was variable. Rare, satellite species formed less than 3 % of the assemblage and contributed little to variations in relative abundance. Assemblage level trophic function proved to be relatively stable across years, but showed clear seasonality. The pattern of long-term taxonomic composition indicated that seasonal differences in trophic function were primarily due to a switch to alternate food resources by some species between seasons and not due to periodic immigration/emigration of fish with different functions. Overall, our study showed significant directional changes in taxonomic variability in time, but relative stability in trophic function, and suggested that local processes (i.e. population dynamics of resident species and seasonality of food resources) influenced assemblage dynamics, while the relative role of regional scale processes (periodic immigration/emigration) was low. The study also suggests considering more direct measures for evaluating the assemblage level function of fish than using rigid guild-based categorizations.

Key words: temporal variability, stability, trophic function, feeding guilds, community organization.

Introduction

Assessing congruency between taxonomic and functional structure has become an important avenue of research, highlighting the need for a more intensive application of trait-based approaches in understanding the structure and function of ecosystems (McGill et al. 2006, Webb et al. 2010). Trait-based approaches, which characterize organisms based on their biological attributes (e.g. feeding, life-history traits), have been advocated, because they can be more directly linked to ecosystem functions (e.g. decomposition, food web organization) in a taxon independent manner. Therefore, they are more easily comparable across

ecosystems, and may also provide stronger linkages between community and ecosystem ecology (McGill et al. 2006, Webb et al. 2010).

While much research has been devoted to the determination of temporal variability based on taxonomic structure, less is known about the functional variability of assemblages (but see e.g. Grossman et al. 1982, Berg & Bengtsson 2007). We define functional variability as the temporal variability in the importance of predefined functional roles, which may determine community or ecosystem level processes. The relationship between long-term taxonomic and functional variability is especially poorly known. In fact, four extreme cases (i.e. scenarios) are possible

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in the rough scale categorization of the temporal congruency between taxonomic and functional variability. The outcome depends on the relative importance local (e.g. niche based) and regional scale (e.g. colonization dynamics) processes play in community dynamics and the variability in the function of assemblage constituting species. In the first case both taxonomic and functional structures are (relatively) stable in time. This case is possible when species composition and abundance relationships remain stable and functional roles of assemblage constituent species remain the same over time. This model suggests the importance of local scale community dynamics, with no or little role for colonization processes. In the second case taxonomic structure is stable whereas functional structure shows temporal variations. This is possible when the colonization rate of new species is low, but the functional role of species change over time due to changes in temporally variable environmental conditions or the quantity of resources they use (e.g. food resources). In the third case both taxonomic and functional structure may show temporal variability. In this model both local scale community variability and/or larger scale colonization processes have significance. Here, functional variability may reflect temporal changes in taxonomic structure and/or changes in species functions in time. Finally in the fourth case taxonomic structure may show variability, while overall functional roles remain stable over time. This is possible when species' extinction-colonization dynamics do not yield functional changes in the community (i.e. immigrating species have the same role as species which go "extinct" or emigrate from the community).

Streams are exceptionally dynamic ecosystems, where hydrologic variability (e.g. floods and droughts) have a substantial role in shaping the organization and dynamics of communities (Poff et al. 1997). Although there is a general consensus between most stream fish ecologists that the temporal variability of stream fish assemblages is mainly governed by the variability of the flow regime (Grossman et al. 1998, Magalhães et al. 2007, Grossman & Sabo 2010, Taylor 2010), recent landscape based views of stream ecosystems additionally suggest that colonization processes can have an overarching role over instream habitat variability in influencing temporal variability (Roberts & Hitt 2010). Nevertheless, characterization of long term (> 10 years) temporal variability within individual stream systems are still relatively rare and these are constrained largely to the quantification of taxonomic variability (e.g. Grossman et al. 1990, Eby et al. 2003).

In this study, we examined temporal variability in the taxonomic and functional structure of a stream fish assemblage in a near natural stream system (Kemence stream, NE Hungary). For determining functional structure, we used the trophic role of fishes because this function may provide one of the most important and most direct links to ecosystem processes (Petchey & Gaston 2006). Our questions were as follows. 1) What are the main trophic functions of fishes in the Kemence stream and how does food composition change between species, size groups and seasons? 2) How does the taxonomic and functional structure of the assemblage change over time during a twelve year period? 3) In the light of these results, what is the role of local vs regional scale processes in shaping taxonomic and functional variability of the assemblage in this system?

Material and methods

Study area

Our study area was a long term monitoring site in the Kemence stream, a third order (Strahler's classification) submontane stream located in the Börzsöny Mts, Hungary (Erős & Grossman 2005a, Erős & Schmera 2010). At this downstream section the stream has a well developed riffle-pool geomorphology with stone and gravel as the dominant substrata. The dominant trees along the stream margin are poplar (*Populus alba* (L.)) and alder (*Alnus glutinosa* (L.)). Stream width at this study site averaged ~5 m; mean water depth in representative riffle and pool habitats averaged ~10 cm and ~50 cm, respectively. Detailed data on the hydrological and morphological characteristics of representative riffle and pool patches can be found in Erős & Grossman (2005a). The study site on the Kemence stream located ~1 km above its confluence with the Ipoly River. Fish can freely swim from the species rich Ipoly River to the Kemence stream.

Sampling methodology

We used our long term monitoring data set for characterising taxonomic variability, which spanned a 12 year period from 2000 through 2011. The 150 m long study reach was sampled using a two-person backpack electrofishing team (350–450 V, Pulsed Direct Current) slowly moving upstream while fishing the whole study area (i.e. from bank to bank). Four seasonal samples (spring, early summer, late summer, autumn) were collected with multiple electrofishing passes between the period 2000 and 2002, whereas two seasonal samples (spring and late summer) were collected with single pass electrofishing from 2002 (Erős & Schmera 2010). Data from earlier samplings (i.e. from 2000 to 2002) showed that all species were captured at the reach level in this relatively small stream, even at the first pass, and relative abundance data also remained identical compared with multiple pass data (Erős 2005, Erős unpublished data). Fish were held in big buckets (100 × 50 × 60 cm) of water during fishing then identified to species level and released back to

the stream with the exception of specimens harvested for dietary analysis. So that the intensity of seasonal samplings were consistent between years we chose only the first pass data of spring and late autumn samples from the 2000–2002 period. Altogether the results of 24 seasonal samples are evaluated in this article (12 years \times 2 seasonal samples).

We collected 421 fish on six occasions (May 2000, April 2009, August 2009, August 2010, May 2011, August 2011) to characterize functional structure of the assemblage based on diet composition (i.e. trophic function). Retained fish were euthanized with an overdose of MS 222 and preserved in 5% formaldehyde solution for laboratory analysis. We collected only the minimum number of fish representing all size groups (>20 mm), which we thought would give reliable estimates of species specific diet. Sample number, however varied between species, depending on their rarity in the stream. We did not examine the diet of some extremely rare species (see Results), which altogether comprised less than 0.3% of the assemblage (relative abundance data). Further, some rare species were collected only in one season. Since the carpathian barbel is a strictly protected species, only dead specimens were collected and only in summer. In this season higher temperature conditions significantly increased the mortality of some sensitive species during electrofishing (Erős et al. pers. obs.).

In the laboratory we measured the standard length (mm) and weight (0.01 g) of each fish. Length frequency histograms were used to distinguish two main size groups (small and large) for the most abundant five species, which comprised more than 85% of the assemblage (see Table 1). Distinction between size

classes corresponded to ≤ 50 or > 50 mm for the stone loach (*Barbatula barbatula*), the gudgeon (*Gobio sp.*), the European minnow (*Phoxinus phoxinus*), and the spiralin (*Alburnoides bipunctatus*), whereas to ≤ 90 or > 90 mm for the chub (*Squalius cephalus*). With the exception of the chub, these species are small bodied and rarely exceed 10 cm. We did not distinguish size groups for the other, relatively rare species (see Fig. 1). The stomach (stone loach and burbot *Lota lota*) or the anterior one third of the gut (all other species) was examined. We calculated the frequency of occurrence (%), and the volumetric percentage (%) of the dietary items (Hyslop 1980) for each species and size groups pooled over all years, but separately for spring and summer seasons. Preliminary analyses indicated that diet data from different years showed the same pattern within seasons for the examined species (Czeglédi 2012).

We performed the diet analyses at two main resolution levels. First, we identified food composition at the lowest taxonomic level possible (usually genus and family for stream macroinvertebrates). Here we were interested to determine in detail which macroinvertebrate taxa form the diet of the species from the available resources (Czeglédi 2012, Czeglédi & Erős 2012). Second we evaluated the data at a resolution which refers to larger scale ecosystem function of fish, for example feeding of terrestrial matter vs aquatic material or plant material vs aquatic invertebrates. Here we distinguished five major diet groups as follows: 1) stream macroinvertebrates, 2) periphyton (mainly filamentous algae and diatoms), 3) terrestrial macroinvertebrates, 4) fish, 5) flying imago of aquatic insects (hereafter aquatic fallen organisms). For simplicity only the results of the latter analyses are shown in this article. Finally, we multiplied the relative abundance data (%) of each fish species with the pooled diet composition data of the corresponding species (volume %) for each sampling occasion ($n=24$) and scaled the values to 100% to estimate long term variability in assemblage level trophic function (see Fig. 2b).

Table 1. The species composition, frequency of occurrence (FrO%) and relative abundance (A%) of fishes in the Keme stream based on spring and summer surveys of 12 years (2000–2011). Species are ordered according to their overall relative abundance at the site (A%).

	FrO%	A%
<i>Phoxinus phoxinus</i> (L.)	100	25.340
<i>Barbatula barbatula</i> (L.)	100	23.801
<i>Squalius cephalus</i> (L.)	100	18.792
<i>Alburnoides bipunctatus</i> (Bloch)	100	11.165
<i>Gobio sp.</i> (L.)	100	7.708
<i>Chondrostoma nasus</i> (L.)	92	6.686
<i>Barbus carpathicus</i> (Kotlík, Tsigenopoulos, Ráb & Berrebi)	100	4.189
<i>Rhodeus amarus</i> (Bloch)	50	0.748
<i>Lota lota</i> (L.)	71	0.678
<i>Leuciscus leuciscus</i> (L.)	83	0.629
<i>Vimba vimba</i> (L.)	17	0.086
<i>Salmo trutta m. fario</i> (L.)	25	0.072
<i>Esox lucius</i> (L.)	13	0.043
<i>Alburnus alburnus</i> (L.)	4	0.032
<i>Blicca bjoerkna</i> (L.)	4	0.011
<i>Carassius gibelio</i> (Bloch)	8	0.007
<i>Rutilus rutilus</i> (L.)	4	0.005
<i>Romanogobio vladkovi</i> (Fang)	4	0.004
<i>Barbus barbus</i> (L.)	4	0.003
<i>Cobitis elongatoides</i> (Băcescu & Maier)	4	0.002
Total number of fish		23329

Statistical analyses

We examined the effects of species, season (spring and summer) and size (the latter only for the five most common species see above) on diet contents (volume %) using cluster analysis. We used the Euclidean distance and the Unweighted Pair Group Means algorithm (UPGMA) for classification (see e.g. Pusey et al. 2010). Significant groups of samples in the cluster diagrams were identified according to the randomization method of Jaksic & Medel (1990). This method employs a bootstrap randomization of the raw data (fish species samples \times variation partitions extracted from diet data) to generate a distribution of Euclidean distances reflecting the null hypothesis of no ordinate source of variation in the diet among the investigated fish-season-size group samples (Gotelli & Graves 1996). Data were iterated 10,000 times and their distributions were used to find the critical value of distance below which the probability of occurrence by chance is $< 5\%$ (Jaksic & Medel 1990; Speziár & Rezsú 2009).

We used standardized principal component analysis (i.e. correlation matrix based PCA, Legendre & Legendre 1998) to examine temporal trajectories in the relative abundance of species (%) in a multivariate space. For this purpose species with a relative abundance of less than 1% were pooled together. These rare species (13 altogether) comprised less than 3% of the overall relative abundance of the assemblage (see Table 1). Consequently, the data matrix for this analysis was based on 24

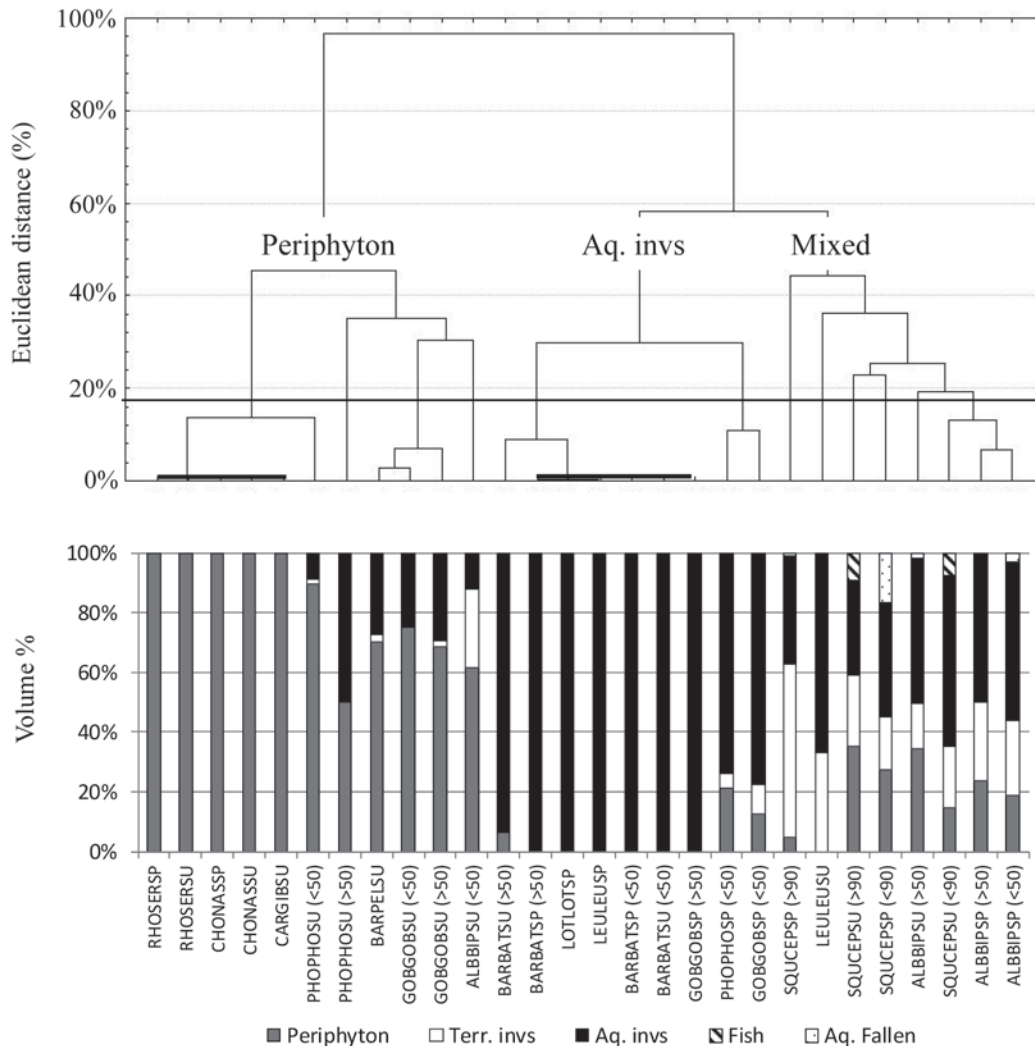


Fig. 1. Dendrogram of diet composition data of the main assemblage constituting species in the Kemece stream using the Un-weighted Pair Group Means algorithm. The bootstrap analysis indicated significantly distinct clusters at the value of 17.4, which is indicated by a continuous line in the figure. Species abbreviations are as follows. RHOSER – bitterling; CHONAS – nase; CARGIB – gibel; PHOPHO – minnow; BARPEL – Carpathian barbel; GOBGOB – gudgeon; ALBBIP – spirin; BARBAT – stoneloach; LOTLOT – burbot; LEULEU – dace; SQUCEP – chub. Abbreviations also denote season and fish size (example) as follows. SP – spring; SU – summer; < 50, less than 50 mm; > 50 more than 50 mm.

objects (12 years \times 2 seasonal samples) and 8 variables (relative abundance of 7 common species and the rare species group). Similarly, we used standardized PCA to examine temporal trajectories in the estimated changes in fish trophic function. Here, the data matrix was based on 24 objects, and the estimated volumetric data (%) of the 5 major diet groups (see above) comprised the variables. The percentage data (%) were square root transformed prior to both analyses (Legendre & Legendre 1998). Note, that this is actually the Hellinger transformation of the pure abundance data (Legendre & Gallagher 2001).

We used “time lag regression analysis” to test for pre-defined temporal patterns in the assemblage using both the taxonomic and functional data (for details, see Collins et al. 2000). In this analysis a significant positive linear relationship between the time lag (i.e. number of sampling occasions) and a multivariate distance measure of community samples indi-

cates directional change in time. If the distance between samples does not change as time lags increase, then the examined community structure is considered to be stable. Finally, a significant negative linear relationship is indicative of an unstable community with convergence (i.e. similarity) to an earlier sampling period. However, instead of using linear regression as used by Collins et al. (2000), we used Spearman rank correlation analysis to quantify the relationship between time lag and community distance, because we operated with occasions and not with exact dates in the analysis. Hereafter, we refer to the analysis as time lag analysis. We used the Euclidean distance of the square root transformed percentage data (i.e. Hellinger distance matrix) for both analyses using the same data matrices as for the two PCAs (i.e. relative abundance data and percentage volumetric diet data for the taxonomic and functional structure, respectively).

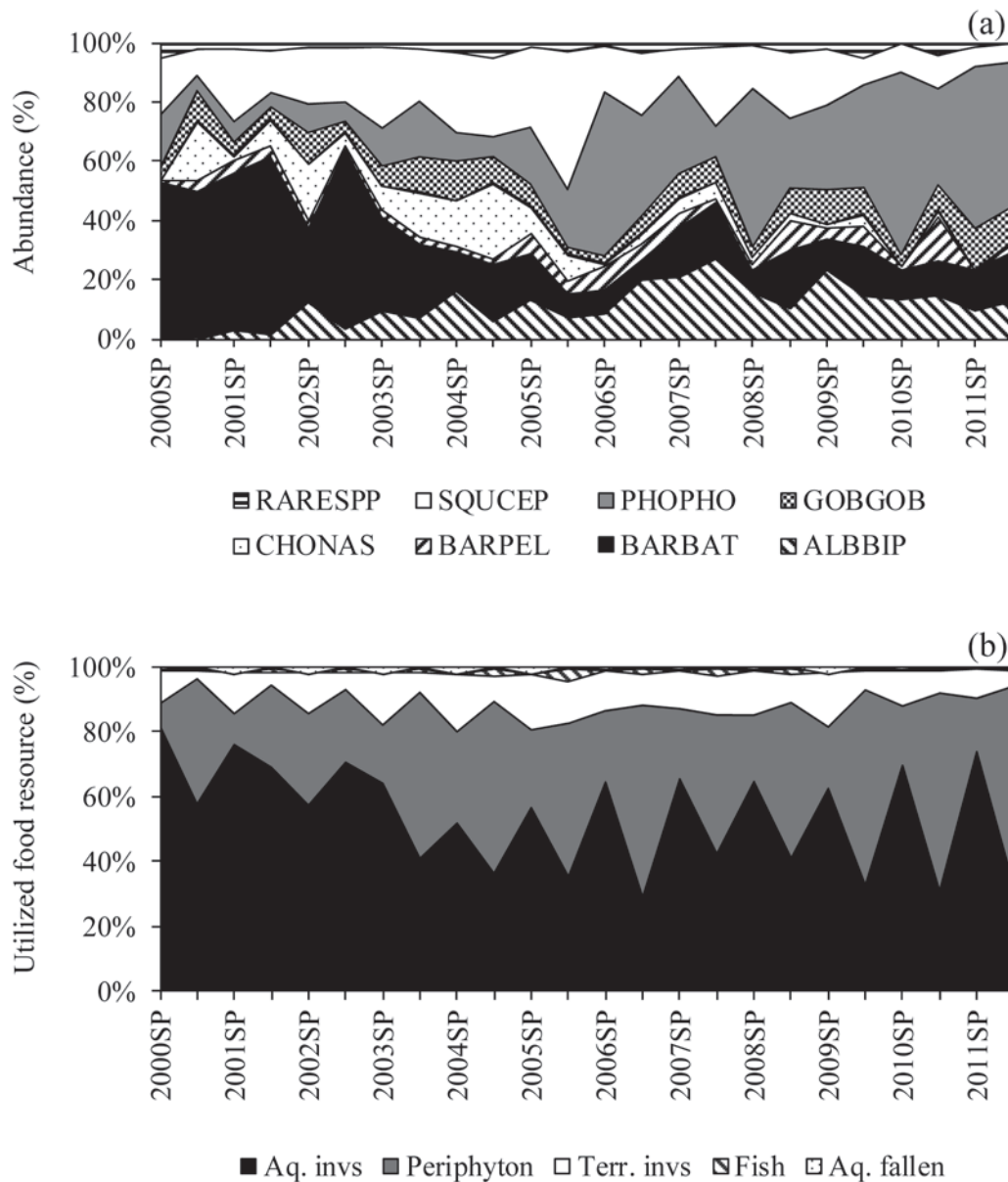


Fig. 2. Temporal changes in the relative abundance of fishes (a) and in their estimated assemblage level diet composition (b) in the Kemence stream between 2000 and 2011.

The statistical analyses were performed with the program Statistica 8.0 (StatSoft, Inc) and with the freely available software package r (R Development Core team, 2011) using the vegan package (Oksanen et al, 2010).

Results

Assemblage composition and trophic function

A total of 23,329 specimens representing 20 species was surveyed during the 12 years (Table 1). Of these the European minnow (hereafter minnow), the stone loach, the chub, the spirlin, the gudgeon, the nase and

the Carpathian barbel were abundant with other species comprising less than 3% of the assemblage.

The cluster analysis of diet data showed the main effect of season and to a lesser extent of species, however, the effect of size group was minimal (Fig. 1). The diet of some of the most common fishes (i.e. minnow, gudgeon, spirlin) contained mainly periphyton in summer (> 50%), while it contained mainly aquatic macroinvertebrates in spring, although feeding on periphyton and on terrestrial invertebrates was also relatively important in this season. The stone loach consumed benthic macroinvertebrates almost exclusively, irrespective of season. The diet of the chub was diverse in

both spring and summer and contained mainly aquatic invertebrates, periphyton and terrestrial invertebrates. Of the less common and rare species the nase (*Chondrostoma nasus*), the bitterling (*Rhodeus amarus*) and the gibel (*Carassius gibelio*) consumed only periphyton, the burbot (*Lota lota*) fed only on aquatic invertebrates, while the dace (*Leuciscus leuciscus*) consumed aquatic invertebrates in spring, but both aquatic and terrestrial invertebrates in summer.

Temporal variability in taxonomic and functional structure

Species abundance varied from season to season, although the seven most abundant species remained dominant during the 12 years (Fig. 2a). The most notable changes included the increased abundance of the minnow, a midwater omnivore, and the decline of the stone loach, a benthic invertivore. The main trophic function of the fish assemblage remained relatively constant throughout the study period (Fig. 2b). Fish in the Kemence stream consumed aquatic macroinvertebrates and periphyton predominantly, while terrestrial invertebrates, fish and fallen aquatic invertebrates formed a relatively small portion of the diet. However, the estimations indicated relatively strong seasonality in the importance of the consumption of aquatic invertebrates vs periphyton with the importance of invertebrates increasing in spring and decreasing in summer and *vice versa* for periphyton.

Principal component analysis of relative abundance data indicated a directional pattern in the fish assemblages over time (Fig. 3a). The first axis (PC1 35.7%) was determined mainly by the changes in the two most abundant species (Table 2). The stone loach and the minnow were the most deterministic species of samples from the earliest (negative values) and the latest (positive values) sampling periods, respectively. The second axis (PC2 21.5%) separated sam-

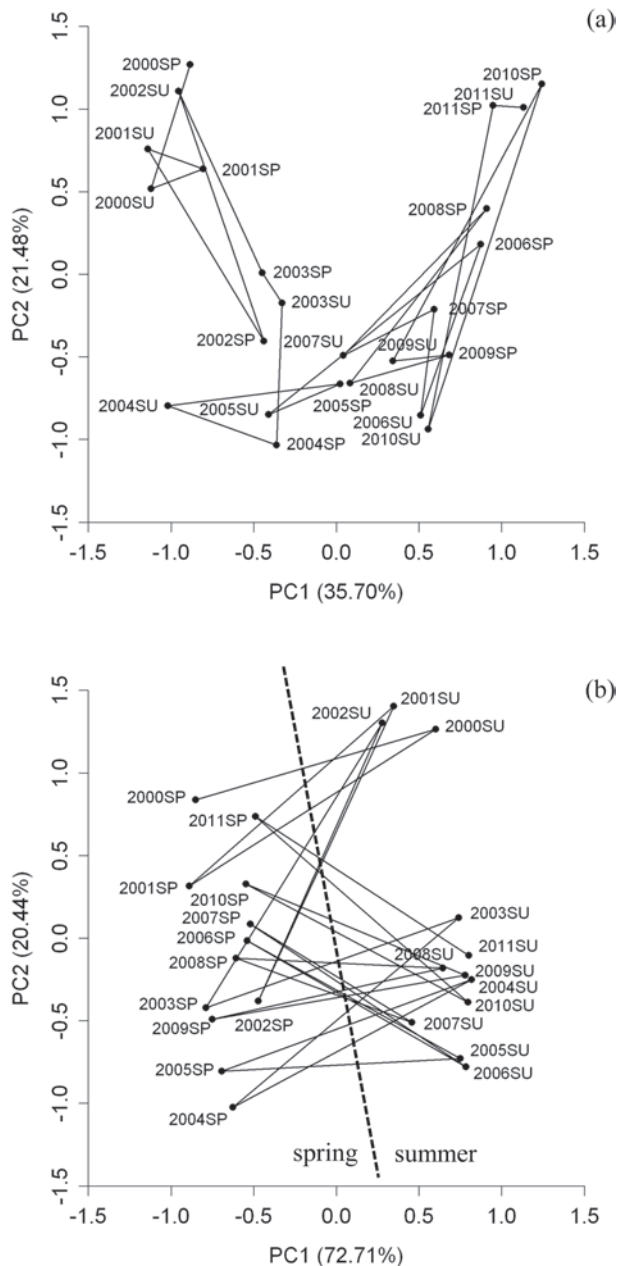


Fig. 3. PCA plots showing changes in the taxonomic (a) and functional (b) structure of the fish assemblage through time.

Table 2. Spearman correlation tests between the relative abundance data of species (taxonomic data) and the component scores of the first two PC axes (PC1 and PC2). Species abbreviations are as follows. ALBBIP, spirlin; BARBAT, stone loach; BARPEL, Carpathian barbel; CHONAS, nase; GOBGOB, gudgeon; PHOPHO, minnow; SQUCEP, chub; RARESPP, rare species.

Taxonomic data	N	Spearman r	p-level
PC1 & ALBBIP	24	0.664	<0.001
PC1 & BARBAT	24	-0.745	<0.001
PC1 & BARPEL	24	0.108	0.616
PC1 & CHONAS	24	-0.645	0.001
PC1 & GOBGOB	24	0.119	0.579
PC1 & SQUCEP	24	-0.443	0.030
PC1 & PHOPHO	24	0.937	<0.001
PC1 & RARESPP	24	-0.481	0.017
PC2 & ALBBIP	24	-0.487	0.016
PC2 & BARBAT	24	0.420	0.041
PC2 & BARPEL	24	-0.555	0.005
PC2 & CHONAS	24	-0.453	0.026
PC2 & GOBGOB	24	-0.223	0.296
PC2 & SQUCEP	24	-0.488	0.016
PC2 & PHOPHO	24	0.045	0.834
PC2 & RARESPP	24	-0.486	0.016

ples with the relative dominance of the most abundant species (positive values) from samples with species of intermediate abundance values (negative values). On the contrary, PCA of diet data (Fig. 3b) showed a relatively clear separation of samples by season along PC1 (72.7%). Here, invertebrates of various origin (i.e. aquatic, terrestrial and aquatic fallen) dominated spring samples (negative values), while the consumption of periphyton and to a smaller extent fish was characteristic of the summer samples (positive values) (Table 3). The second axis (PC2 20.4%) was not clearly interpretable. This axis rather contributed to the separation of samples by season together with PC1. Time lag analysis revealed a directional change in the relative abundance data of taxonomic structure (Fig. 4a; $r_s = 0.666$; $p < 0.001$). However, diet data did

Table 3. Spearman correlation tests between the relative abundance of diet components (functional data) and the component scores of the first two PC axes (PC1 and PC2). Diet components are abbreviated as follows. Aq. Invs.: stream macroinvertebrates; Aq. Fallen.: flying imagos of aquatic insects; Terr. Invs.: terrestrial macroinvertebrates.

Functional data	N	Spearman r	p-level
PC1 & Aq. Invs.	24	-0.763	<0.001
PC1 & Periphyton	24	0.906	<0.001
PC1 & Terr. Invs.	24	-0.657	<0.001
PC1 & Fish	24	0.795	<0.001
PC1 & Aq. Fallen	24	-0.771	<0.001
PC2 & Aq. Invs	24	0.640	0.001
PC2 & Periphyton	24	-0.347	0.097
PC2 & Terr. Invs.	24	-0.627	0.001
PC2 & Fish	24	-0.105	0.627
PC2 & Aq. Fallen	24	-0.449	0.028

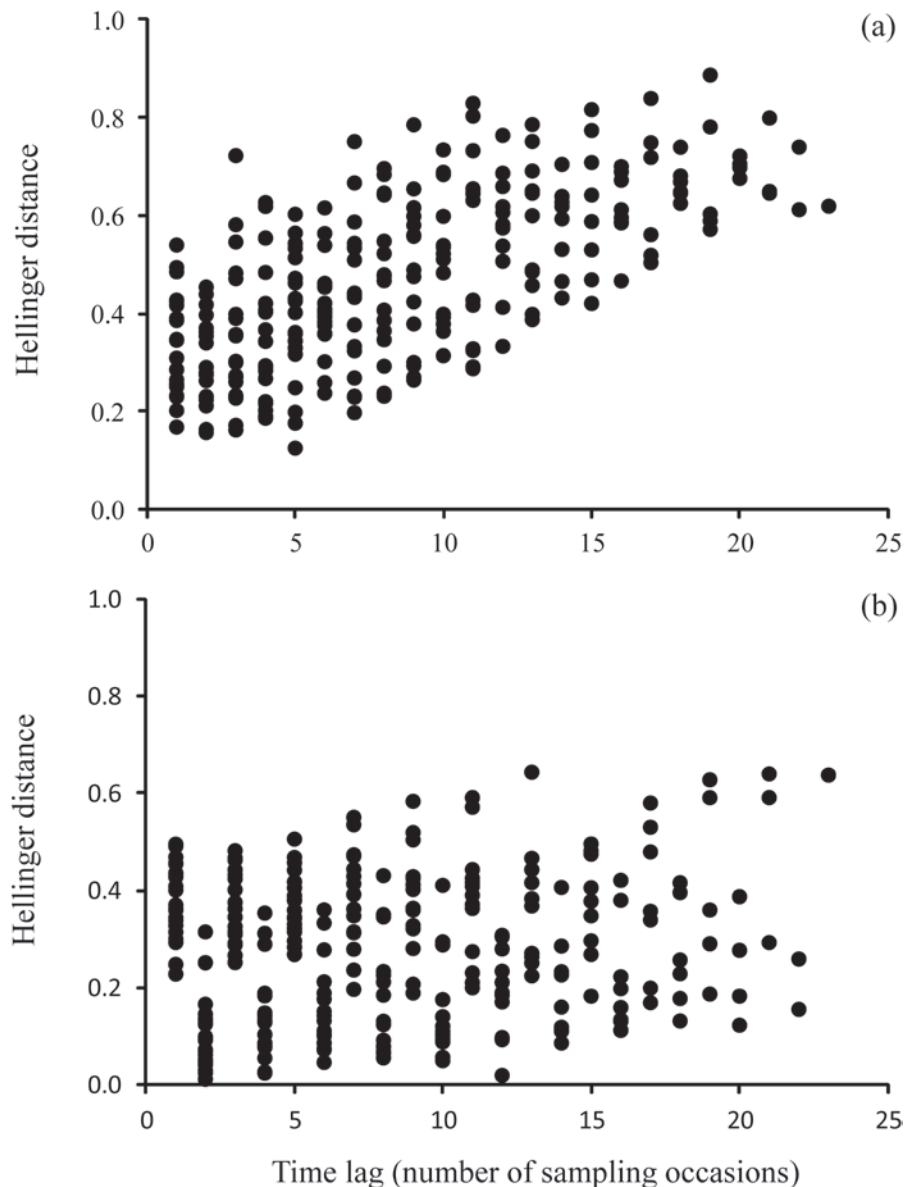


Fig. 4. Hellinger distance based similarity of taxonomic (a) and functional (b) fish assemblage data plotted against time lag (spring and summer surveys from 2000 spring to 2011 summer). See methods for further details.

not show either directional changes or convergence, thus functional structure proved to be stable based on this analysis over the 12 years period (Fig. 4b; $r_s = 0.047$; $p = 0.422$), although it showed seasonal periodicity.

Discussion

We found the occurrence of the most abundant species was persistent, while their relative abundance was variable. Rare, satellite species formed only a very small proportion of the assemblage on each sampling occasion. They influenced patterns in species richness (detailed data are not shown here, for this see Erős & Schmera 2010), but contributed little to variations in relative abundance. Assemblage level trophic function of fish proved to be relatively stable, although it showed clear seasonality. Temporal variability in taxonomic composition indicated that seasonal differences in fish trophic function were due to a switch to alternate food resources of the same species between seasons and not due to mass immigration of other species from outside the study area. These results thus show that local processes influenced both taxonomic and functional fish assemblage dynamics in the Kémence stream, while the relative role of regional scale (i.e. colonization) processes proved to be low and influenced only patterns in species richness.

Although both stable and temporarily highly variable assemblages have been described in the literature (Matthews 1998, Grossmann et al. 1998, Erős & Grossman 2005b), our study concurs with several studies from other biogeographic regions (e.g. Eby et al. 2003, Magalhães et al. 2007), which justified persistence in the occurrence, and resilience, but temporal variability in the abundance of the main assemblage constituting species. It is likely that temporal fluctuations in the relative abundance of the most abundant seven species were mainly driven by hydrologic changes in the Kémence stream. This is because time lag analysis indicated strong directional changes in the fish assemblage, and former studies from this system showed the legacy of a one in a hundred year flood on the successional dynamics of species diversity (Erős et al. 2003, Erős & Schmera 2010). Small water column species (like the minnow or the spirlin) are especially prone to the erosive effect of floods compared with benthic species (Schlosser 1982, Schlosser 1985). Thus it is not surprising that their relative abundance increased relatively consistently after this extreme flood event, which happened in 1999, just before our

long-term surveys started (Erős et al. 2003, Erős & Grossman 2005b). Unfortunately, however, we could not test the relative influence of high vs low flows on fish assemblage dynamics directly, due to the lack of detailed hydrologic data from the stream.

Contrary to the directional change observed in the taxonomic data set, assemblage level trophic function remained relatively stable throughout the study period as indicated by the time lag analysis (Collins et al. 2000), despite clear seasonality in food resource use. However, the basic diet data showed that increased consumption of periphyton in summer moderately influenced fish trophic function. For example, diet analyses showed that assemblage level proportion of periphyton in the diet can increase by more than 40% from spring to summer (Fig. 2) and these seasonal shifts in function were clearly mirrored in the PCA, and in the oscillating pattern of time lag analysis. The switch to periphyton can be explained by the decline of aquatic invertebrates from spring to summer in this system (Erős et al. 2005), which has also been shown in other studies (Angermeier 1982, Schlosser & Angermeier 1990).

Previous studies about the temporal variability in functional organization of stream fishes used guild based categorizations for characterizing the function of individual species (e.g. Higgins 2009, Beugly & Pyron 2010, Pyron et al. 2011). However, these categorizations (e.g. invertivore, omnivore, piscivore) are limited in predicting which diet components form the major part of the diet. They also do not really allow the sorting of a certain species to more than one trophic function, which is inevitable for a more reliable estimation of assemblage level trophic function of fish in the ecosystem. Although our approach has limitations, (because we did not have the possibility to examine diet in each sampling occasion, but used only estimations from some seasons and years), we believe that by using direct diet analysis we gave a more reliable estimation of fish trophic function at both the species and the assemblage levels. In the Kémence stream, many species were omnivores, feeding on on benthic invertebrates, periphyton and terrestrial organisms. In addition the proportion of these categories showed strong seasonal variation within and between species in the “omnivore group”. Some species were, however specific in feeding and proved to be strictly benthic invertivore (stone loach) or periphyton eater (nase) irrespective of season. These patterns in seasonality and species specific functions cannot really be characterized by using feeding guilds for functional analyses.

Our study expands former studies on the relationship between taxonomic and functional organization of fishes by using a temporal dimension. Actually, this is the first study, to our knowledge, which directly examines the relationship between the temporal variability of taxonomic and functional structure. Our findings clearly show that taxonomic variability did not significantly influence the trophic function based temporal variability of the fish assemblage in the Kemence stream. Although temporal variability in abundance yielded some changes in the importance of the two main functional roles (i.e. feeding on aquatic invertebrates vs periphyton), seasonal changes in resource use were clearly more important in shaping patterns in trophic function than changes in relative abundance through time (see Fig. 2). This work thus indicates the importance of local processes in influencing the organization of this fish assemblage, because seasonal differences and the changes in the relative abundance of the resident species influenced the variability of the assemblage more than dispersion dynamics of a variety of non resident (satellite) species from the recipient River Ipoly.

It should be emphasized that the Kemence stream is a submontane stream. As such it has a peripheral position in the stream network and filters species with relatively specific abiotic requirements, because of its low depth, stony substrate etc. Temporal variability in taxonomic and functional structure maybe larger in more lowland areas and especially in human altered landscapes (Erős et al. 2012), where assemblage dynamics of a more diverse pool of species (including high rates of colonization dynamics) may also yield diverse relationships between long-term taxonomic and functional variability. Consequently, there is a need for more intensive testing of temporal variability patterns from a variety of stream systems including other biogeographic regions to increase our understanding about the relationship between temporal variability in assemblage composition and ecosystem level function of stream fish assemblages.

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