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A multi-faceted framework of diversity for prioritizing the conservation of fish assemblages

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A B S T R A C T

Floodplain waterbodies and their biodiversity are increasingly threatened by human activities. Given the limited resources available to protect them, methods to identify the most valuable areas for biodiversity conservation are urgently needed. In this study, we used freshwater fish assemblages in floodplain waterbodies to propose an innovative method for selecting priority areas based on four aspects of their diversity: taxonomic (i.e. according to species classification), functional (i.e. relationship between species and ecosystem processes), natural heritage (i.e. species threat level), and socio-economic (i.e. species interest to anglers and fishermen) diversity. To quantitatively evaluate those aspects, we selected nine indices derived either from metrics computed at the species level and then combined for each assemblage (species rarity, origin, biodiversity conservation concern, functional uniqueness, functional originality, fishing interest), or from metrics directly computed at the assemblage level (species richness, assemblage rarity, diversity of biological traits). Each of these indices belongs to one of the four aspects of diversity. A synthetic index defined as the sum of the standardized aspects of diversity was used to assess the multi-faceted diversity of fish assemblages. We also investigated whether the two main environmental gradients at the catchment (distance from the sea) and at the floodplain (lateral connectivity of the waterbodies) scales influenced the diversity of fish assemblages, and consequently their potential conservation value. Finally, we propose that the floodplain waterbodies that should be conserved as a priority are those located in the downstream part of the catchment and which have a substantial lateral connectivity with the main channel.

1. Introduction

In view of the numerous and growing threats affecting aquatic biodiversity, conservation measures are urgently needed to preserve the most threatened and crucial freshwater ecosystems (Geist, 2011; Strayer and Dudgeon, 2010; Vörösmarty et al., 2010). Resources (e.g. money, time, people) are often limited, and as it is not possible to preserve all river stretches, it is essential to identify priority areas for biodiversity conservation (Bergerot et al., 2008; Myers et al., 2000; Thorp et al., 2008).

Several approaches and procedures have been proposed for identifying priority areas for conservation (e.g. Darwall and Vié, 2005; Margules and Pressey, 2000). Some of these have focused on only one or two aspects of the biological diversity, usually on species richness and/or endemism (Arzamendia and Giraudo, 2011; Myers et al., 2000; Tisseuil et al., 2013; Trebilco et al., 2011) but sometimes also on the threatened status of species (Bragazza, 2009) or species rarity (Solymos and Feher, 2005), while others have combined several criteria to assess the conservation value of assemblages of species (Abellan et al., 2005; Bergerot et al., 2008; Rainho and Palmeirim, in press; Stewart, 2011). Although methods based on just a few aspects of diversity are easier to apply because of the small amount of information required on each species, Mouchet et al. (2010) have pointed out that considering the taxonomic diversity alone is not sufficient to evaluate the diversity of communities because, for instance, species do not all have equal effects on ecosystem functioning. Furthermore, Ceballos and Ehrlich (2006) and Orme et al. (2005) have shown that the priority areas identified for biodiversity conservation differ depending on whether the method used was based on species richness, endemism or threatened status of species.

Against this background, we propose here a method for prioritizing areas based on four aspects of diversity: taxonomic, natural

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heritage, functional and socio-economic diversity. This method is based on the assumption that an area has a high conservation priority if it simultaneously presents numerous threatened (Darwall and Vié, 2005; Fattorini, 2006), rare (Abellan et al., 2005), native (Bergerot et al., 2008), functionally original and unique (Walker, 1992) species, as well as species having a strong socio-economic interest (Regan et al., 2007). In addition to these species characteristics, high conservation priority is hypothesized for areas where species assemblages are functionally rich (Walker, 1992) and original in their taxonomic composition in comparison with the other areas assessed (Kanno et al., 2012).

The taxonomic, natural heritage and functional aspects of diversity have been well described, and a variety of indices have been taken into account when identifying the priority areas for conservation (e.g. Abellan et al., 2005; Bergerot et al., 2008; Mouillot et al., 2013; Ricotta, 2005). However, as far as we are aware, the evaluation of the socio-economic diversity of assemblages has been overlooked in previous prioritization methods despite the acknowledged importance of biodiversity for human activities and well-being (Millennium Ecosystem Assessment, 2005). We have also considered several indices within each aspect of diversity and assessed their non-redundancy (Gallardo et al., 2011) and complementarity (Villéger et al., 2008), which must be considered when combining several indices or metrics (Lyashevska and Farnsworth, 2012).

We applied this innovative method to a series of floodplain waterbodies in a large catchment in southwest France, the Garonne. Floodplain waterbodies have been recognized as essential for the functioning of freshwater ecosystems (Amoros and Bornette, 2002; Petts and Amoros, 1996). These wetlands have been shown to provide suitable conditions for primary production by higher plants (Keruzoré et al., 2013) and for higher levels of aquatic diversity of organisms (Ward, 1998) such as macroinvertebrates (Gallardo et al., 2008), zooplankton (Kattel, 2012) and fish (Bolland et al., 2012; Lasne et al., 2007a). However, these important ecosystems and their biodiversity are increasingly threatened by human activities, such as agricultural practice, changes in the flow regime, and climate change (Kattel, 2012; Tockner and Stanford, 2002). In this study, the floodplain waterbodies were prioritized on the basis of the conservation value of their fish assemblages. Fish constitute one of the most severely threatened taxonomic groups (Darwall and Vié, 2005) due to their high sensitivity to the various changes affecting aquatic habitats (Oberdorff et al., 2002). Furthermore, fish fauna is commonly taken into account when assessing the quality of aquatic ecosystems (Gozlan, 2012; Kanno et al., 2012; Strecker et al., 2011). In addition, floodplain waterbodies are important ecosystems in the development cycle of several fish species where they may perform spawning, nursery and feeding functions (Copp, 1989; Gozlan et al., 1998; Nunn et al., 2007).

Finally, we assessed the influence of environmental characteristics on the prioritization of floodplain waterbodies. At the scale of a large catchment, the main factor that determines the composition of fish assemblages is the distance from the sea (Buisson et al., 2008; Ibarra et al., 2005; Lasne et al., 2007b). In the case of floodplain waterbodies, it has been demonstrated that the lateral connectivity between the waterbody and the main channel also influences the structure of fish assemblages (Amoros and Bornette, 2002; Bolland et al., 2012; Lasne et al., 2007a).

The objectives of this study were therefore (i) to propose a method for prioritizing areas for the conservation of floodplain fish assemblages based on various aspects of their diversity and (ii) to find out whether the distance from the sea and the lateral connectivity between the waterbody and the main channel had any effect on the prioritization proposed.

2. Materials and methods

2.1. Study area

The Garonne catchment is located in southwest France (Fig. 1). It drains a 56,536 km^2 catchment area, and the main channel flows over 580 km from its source in Spain to the Atlantic Ocean (see Gozlan et al., 1998; Ibarra et al., 2005 for more details). Its flow is influenced both by precipitation and snow melt, resulting in a flood peak in May–June and a period of low flow during the summer. Within this catchment, there is a wide diversity of floodplain waterbodies that are evenly distributed between the estuary of the Garonne River and its source. Natural floodplains are composed of various aquatic habitats ranging from lotic to lentic habitats, including floodplain waterbodies that are characterized by their level of connectivity with the main channel, their substrate (grain-size and geochemical composition), and their shape and size (Amoros and Bornette, 2002). Overall, the Garonne River and its floodplain waterbodies are very slightly impacted by human activities and the riverscape has kept most of its natural characteristics.

2.2. Data collection

In this study, we focused on the fish assemblages present in the floodplain waterbodies located along the French segment of the Garonne River. We selected 40 out of the 180 waterbodies identified along the mainstream river (Fig. 1) which were evenly distributed along the upstream–downstream gradient, had contrasting levels of lateral connectivity to the main channel, were not (or least) impacted by human activities, were submerged during the sampling period and accessible for sampling as well. We used a Point Abundance Sampling (PAS) electrofishing protocol according to Nelva et al. (1979) and Lasne et al. (2007a) to assess the composition of fish assemblages in these 40 waterbodies. This rapid and cheap method provides reproducible and quantitative samples, and hence permits spatial comparisons between sampling sites. Thirty PAS were randomly performed by wading along the entire length of each waterbody. At each PAS, the operator plunged the activated anode of a portable electrofishing apparatus as quickly as possible. According to Laffaille et al. (2005), the anode was kept turning in an area of 1 m^2 for at least 30 s to capture all species using several fine-mesh dipnets. Fish species were identified before being returned alive to the water. Presence–absence data from all the PAS conducted in a waterbody were pooled. We also collected information about the lateral connectivity between the waterbody and the main channel. The waterbodies were divided into three categories according to Gozlan et al. (1998) and Lasne et al. (2008): always connected, partially connected and not connected to the main channel during the sampling period. The distance of each waterbody from the sea was also calculated using ArcGIS 10 software (ESRI, 2011). The levels of connectivity were evenly represented along the upstream–downstream gradient suggesting that there was no marked relationship between the two variables (Kruskal–Wallis chi-squared = 0.269, p-value = 0.874).

2.3. Indices of diversity

Numerous indices have been developed to assess biodiversity (e.g. Feld et al., 2009; Pavoine and Bonsall, 2011; Ricotta, 2005; Roset et al., 2007; Vačkář et al., 2012). We selected eight indices that can be roughly assigned to three categories: taxonomic diversity, functional diversity and natural heritage diversity. The socio-economic aspect of diversity, which has been poorly explored to date, was also taken into account using an index based on the fishing interest of each fish species. These nine indices were

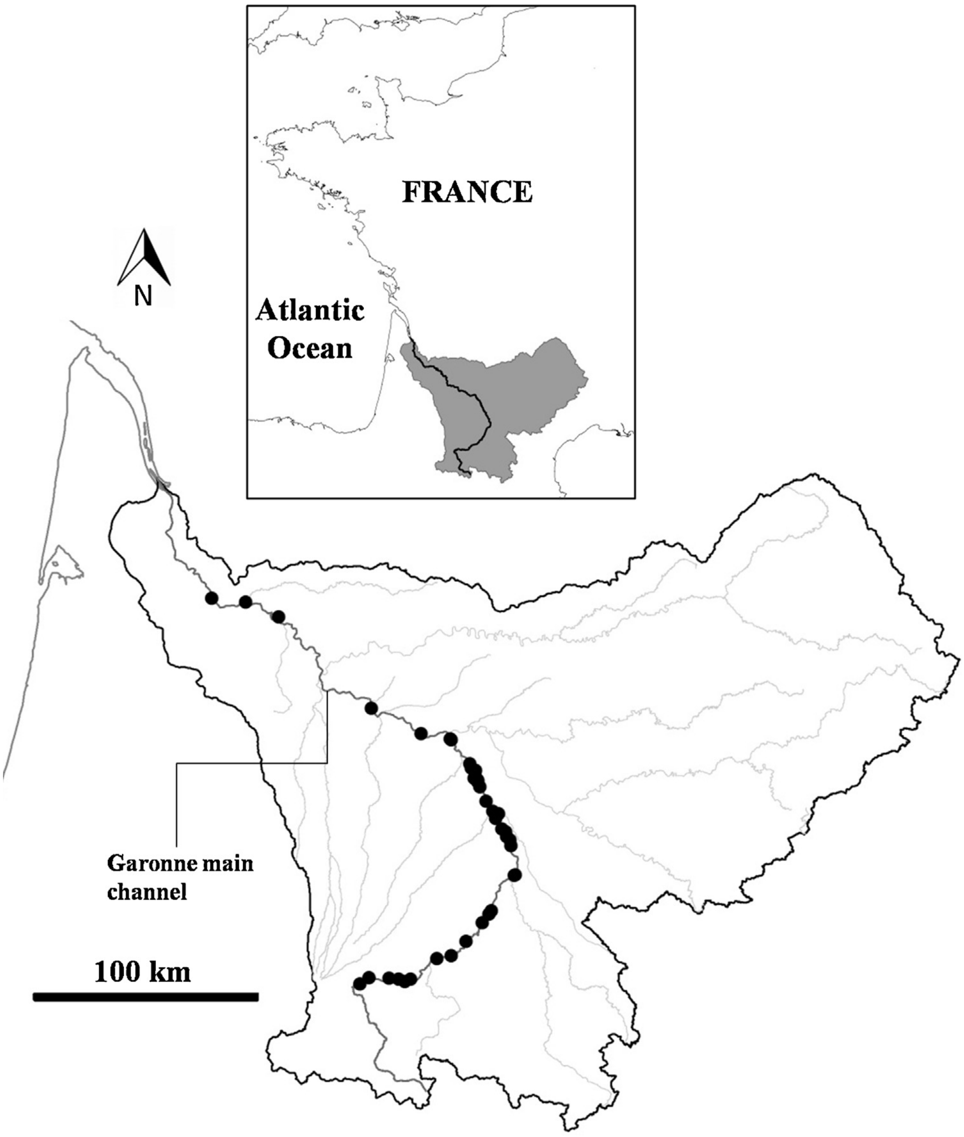

Fig. 1. Location of the Garonne catchment, showing the 40 sampling floodplain waterbodies studied (black dots).

calculated using R 2.14.2 software (R Development Core Team, 2012) and are described below.

2.3.1. Taxonomic diversity

We selected three indices evaluating different components of the taxonomic diversity of the fish assemblages.

First, we considered the Species Richness (SR) of each floodplain waterbody, i.e. the total number of species sampled in each waterbody (Eq. (1)). This index is widely used, and several studies have shown that species richness is relevant for assessing the conservation value of an assemblage of species (Heino, 2002; Isambert et al., 2011; Trebilco et al., 2011).

$$\mathrm{SR} = \sum_{i=1}^{S_{tot}} A_j \tag{1}$$

where A_i is the presence (=1) or absence (=0) of the ith species in the waterbody considered; S_{tot} is the total number of species in the dataset.

The Rarity Index (RI_α) is a measure of the rarity of the species present in the assemblage according to their occurrence frequency in the dataset (Fattorini, 2006; Kerr, 1997). Each species was assigned a weight of 1 minus the frequency of the species in the dataset. Then for each waterbody, the value of the index was computed as the mean of all the weights of the species present as indicated in Eq. (2).

$$\mathrm{RI}_\alpha = \sum_{i=1}^{S_{tot}} \frac{1}{S_{wb}} \times A_i \times \left(1 - \frac{n_i}{N}\right) \tag{2}$$

where A_i and S_{tot} are defined as above; S_{wb} is the total number of species sampled in the waterbody considered; n_i is the number of waterbodies where the ith species was sampled; N is the total number of waterbodies sampled ($N = 40$). This index was therefore higher for assemblages including fish species sampled in only a small number of waterbodies.

We also decided to consider an index representing the rarity of the fish assemblages relative to the other waterbodies sampled (RI_β) using a measure of the Bray–Curtis dissimilarity between each pair of fish assemblages (Bray and Curtis, 1957). For each waterbody, the mean dissimilarity between the waterbody considered and all the other waterbodies was computed as shown in Eq. (3).

$$\mathrm{RI}_\beta = \frac{1}{N-1} \times \sum_{\substack{j=1 \\ j \neq k}}^{N} DISS_{BC}(C_k, C_j) \tag{3}$$

where k is the waterbody considered; N is the total number of waterbodies sampled ($N = 40$); C_k and C_j represent the assemblages sampled in the waterbodies k and j, respectively; $DISS_{BC}$ represents the Bray–Curtis dissimilarity measure, and is defined in Eq. (4).

$$DISS_{BC}(C_k, C_j) = 1 - \frac{2D}{S_{wb,k} + S_{wb,j}} \tag{4}$$

where D is the number of species common to assemblages C_k and C_j; $S_{wb,k}$ and $S_{wb,j}$ are the number of species sampled in the waterbodies k and j, respectively. Thus an assemblage with a high RI_β is probably an uncommon combination of species.

2.3.2. Functional diversity

To describe the ecological and functional characteristics of fish species, we gathered information about 21 biological traits from the literature (Buisson and Grenouillet, 2009; Buisson et al., 2013; Keith et al., 2011; Logez et al., 2013), FishBase (Froese and Pauly, 2012) and from expert knowledge. These biological traits were categorical and described mean and max body length, shape and swimming factors, breeding habitat, absolute and relative fecundities, number of spawning events, egg diameter, age at female maturity, life span, larval length, type of parental care, duration of the incubation period, feeding and living habitats, trophic category, rheophily, salinity and temperature preferences, and migration behavior.

We selected three different measures of the functional diversity of fish assemblages. Following Buisson et al. (2013) and Villéger et al. (2008), we first constructed a multidimensional functional space using these 21 traits. Gower's distance was computed for each pair of species, and this functional distance matrix was then used to compute a Principal Coordinate Analysis (PCoA) (Gower, 1966; Legendre and Legendre, 1998). The first three axes of the PCoA, which accounted for 42% of the total variability, were kept. The decision to keep only three axes was due to the presence of poor communities (i.e. containing small numbers of species) within the sampled floodplain waterbodies, whereas a sufficient number of axes is required to compute the selected indices of functional diversity. The species coordinates in the three-dimensional space defined by the PCoA were then used to calculate the two following indices: functional originality (Fori) and functional uniqueness (Funi) (Buisson et al., 2013; Mouillot et al., 2013). The Fori and Funi of each species were the Euclidean distance between the position of the species in the functional space and the position of a theoretical average species of the species pool (i.e. the center of the functional space) and of its nearest neighbor in the functional space, respectively.

We also considered a Trait Diversity index (TD) that measured the global diversity of ecological traits present in an assemblage and is related to the total number of different trait modalities carried by the species present in the assemblages. Following Buisson and Grenouillet (2009), we first calculated a dissimilarity matrix among fish species for each trait using the Jaccard distance (Legendre and Legendre, 1998) that contained the pairwise distance between species for a given trait. We then combined the 21 resulting dissimilarity matrices through their quadratic mean to derive a global dissimilarity matrix of biological traits (D). Finally, TD for a given assemblage was obtained by the product shown in Eq. (5).

$$\mathrm{TD} = P \times \left(\frac{1}{2}D^2\right) \times P^T \tag{5}$$

where P is the vector describing fish species presence–absence of the considered waterbody, P^T is the transposed of P and D is the global dissimilarity matrix of biological traits.

2.3.3. Natural heritage diversity

The conservation status and the biogeographical origin of the species present in an assemblage have both been highlighted as factors of considerable interest for conservation (Bergerot et al., 2008; Darwall and Vié, 2005; Fattorini et al., 2012; Stewart, 2011). We then considered that these two factors constituted the "natural heritage" aspect of diversity (Airamé et al., 2003; Spencer and Nsiah, 2013; Tengberg et al., 2012).

To take into account this overlooked aspect of diversity, we first used the Biodiversity Conservation Concern (BCC) index developed by Fattorini (2006) to evaluate the conservation status of fish assemblages. To determine the conservation status of fish species, we looked at the following conservation regulations: the European Directive "Fauna-Flora-Habitats" (directive 93/43/CEE, dated 21/5/1992), the Berne Convention (1979), and the IUCN Red List according to IUCN Standards and Petitions Subcommittee (2010). As shown in Eq. (6), we used the computation defined by Bergerot et al. (2008), which was a modified version of the first BCC index (Fattorini, 2006).

$$\mathrm{BCC} = \sum_{i=1}^{S_{tot}} \frac{\alpha_i \times A_i}{S_{wb}} \tag{6}$$

where A_i, S_{wb} and S_{tot} are defined as above; α_i is the weight assigned to the ith species on the basis of its conservation status. As recommended by Chantepie et al. (2011), we allocated a value of 0.5 to species included in appendices II or V of the European Directive "Fauna-Flora-Habitats" (and consequently a value of 1 for species included in both appendices), 0.5 for species included in appendix III of the Berne Convention, and increasing values from 0 to 0.8 depending on the IUCN status (0 for Not Evaluated, 0.2 for Least Concerned, and 0.8 for Critically Endangered). The species were classified as facing three categories of threat, corresponding to the sum of their conservation status. Their weights, α, were then calculated using the 2^n operator, where n is the category of threat to which the species belongs (Fattorini, 2006; Bergerot et al., 2008). Thus α can take a value of 1, 2 or 4 depending on the level of threat (see Table 1 for the weights α by species).

Secondly, we modified the Origin Index (OI) defined by Bergerot et al. (2008) to take into account the different types of origin of the species (i.e. invasive exotic, naturalized exotic and native) according to Keith et al. (2011). We weighted each species according to its origin, with a weight of 1, 2, and 4, respectively (obtained by a 2^n geometric series like that used for BCC). An approach similar to that used to compute BCC was then applied (Eq. (7)).

$$\mathrm{OI} = \sum_{i=1}^{S_{tot}} \frac{\beta_i \times A_i}{S_{wb}} \tag{7}$$

where A_i, S_{wb} and S_{tot} are defined as above; β_i is the weight assigned to the ith species depending on its origin (see Table 1 for the weights β by species). Both BCC and OI were higher for assemblages that included mainly threatened and/or native species.

2.3.4. Socio-economic diversity

We developed a Fishing Interest Index (FII) to reflect the different levels of interest in each species taken by anglers and commercial fishermen (Holmlund and Hammer, 1999). With the help of fisheries managers, we allocated each species to one of the four following categories: species without interest for fishing, species of interest to sportive anglers (species usually not kept), species of interest to recreational anglers (species usually kept),

Table 1
List of species, origin, conservation status, fishing interest, frequency of occurrence, and sum of species abundance (i.e. the total number of individuals caught) in the 40 waterbodies sampled. The weights computed for the calculation of the associated indices are shown in square brackets (see text for details). Species are sorted alphabetically by their scientific name.

Scientific name	Common name	Origin[a] [*OI weight*]	Conservation status[b] [*BBC weight*]	Fishing Interest[c] [*FII weight*]	Occurrence frequency[d]	Abundance
Abramis brama (L., 1758)	Common bream	N [4]	LC [*1*]	SA [2]	0.28	122
Alburnus alburnus (L., 1758)	Common bleak	N [4]	LC [*1*]	RA [4]	0.25	28
Ameiurus melas (Rafinesque, 1820)	Black bullhead	NE [2]	NE [*1*]	WFI [*1*]	0.05	4
Anguilla anguilla (L., 1758)	European eel	N [4]	CR [*2*]	CF [*8*]	0.35	37
Barbatula barbatula (L., 1758)	Stone loach	N [4]	LC [*1*]	WFI [*1*]	0.32	125
Barbus barbus (L., 1758)	Barbel	N [4]	H-V, LC [*2*]	SA [*2*]	0.40	48
Carassius gibelio (Block, 1782)	Crucian carp	IE [*1*]	LC [*1*]	SA [*2*]	0.15	10
Cyprinus carpio L., 1758	Common carp	NE [2]	LC [*1*]	RA [*4*]	0.12	11
Esox lucius L., 1758	Pike	N [4]	LC [*1*]	CF [*8*]	0.08	3
Gambusia holbrooki Girard, 1859	Mosquitofish	IE [*1*]	NE [*1*]	WFI [*1*]	0.18	243
Gobio occitaniae Kottelat & Persat, 2005	Languedoc gudgeon	N [4]	LC [*1*]	RA [*4*]	0.78	520
Gymnocephalus cernuus (L., 1758)	Ruffe	N [4]	LC [*1*]	SA [*2*]	0.05	2
Lampetra planeri (Bloch, 1784)	Brook lamprey	N [4]	B-III, H-II, LC [*4*]	WFI [*1*]	0.15	47
Lepomis gibbosus (L., 1758)	Pumpkinseed	NE [2]	NE [*1*]	WFI [*1*]	0.40	141
Leuciscus burdigalensis Valenciennes, 1844	Beaked dace	N [4]	LC [*1*]	WFI [*1*]	0.10	12
Micropterus salmoides (Lacépède, 1802)	Large-mouth bass	NE [2]	NE [*1*]	SA [*2*]	0.02	3
Perca fluviatilis L., 1758	European perch	N [4]	LC [*1*]	CF [*8*]	0.02	1
Phoxinus phoxinus (L., 1766)	Minnow	N [4]	LC [*1*]	WFI [*1*]	0.57	3546
Platichthys flesus (L., 1758)	Flounder	N [4]	LC [*1*]	RA [*4*]	0.02	2
Pseudorasbora parva (Schlegel, 1842)	Stone moroko	IE [*1*]	LC [*1*]	WFI [*1*]	0.38	251
Rhodeus amarus (Bloch, 1782)	Bitterling	N [4]	B-III, H-II, LC [*4*]	WFI [*1*]	0.25	83
Rutilus rutilus (L., 1758)	Roach	N [4]	LC [*1*]	RA [*4*]	0.35	286
Salmo trutta L., 1758	Brown trout	N [4]	LC [*1*]	CF [*8*]	0.15	97
Sander luciopercia (L., 1758)	Pike-perch	NE [2]	LC [*1*]	CF [*8*]	0.10	7
Scardinius erythrophtalmus (L., 1758)	Rudd	N [4]	LC [*1*]	RA [*4*]	0.20	26
Squalius cephalus (L., 1758)	European chub	N [4]	LC [*1*]	RA [*4*]	0.78	412
Tinca tinca (L., 1758)	Tench	N [4]	LC [*1*]	RA [*4*]	0.28	41

[a] N = native; NE = naturalized exotic; IE = invasive exotic.
[b] H-II and H-V = appendix II and appendix V of the Habitats Directive; B-III = appendix III of the Bern convention; NE, LC and CR = not evaluated, least concerned and critically endangered species according to the IUCN Red List.
[c] WFI = without fishing interest; SA = of interest to sportive anglers; RA = of interest to recreational anglers; CF = of interest to commercial fishermen.
[d] Proportion of floodplain waterbodies where the species was present; $N = 40$.

and species of interest to commercial fishermen (species of direct economic interest). The same kind of weighting and computation were applied as for BCC and OI, resulting in a species weighting of 1, 2, 4, and 8 for the four levels of increasing fishing interest, respectively (Eq. (8)).

$$\mathrm{FII} = \sum_{i=1}^{S_{tot}} \frac{\gamma i \times A_i}{S_{wb}} \tag{8}$$

where A_i, S_{wb} and S_{tot} are defined as above; γ_i is the weight assigned to the ith species on the basis of its fishing interest (see Table 1 for the weights γ by species).

2.4. Redundancy of diversity indices

To ensure that the nine indices used were not redundant within the aspects of diversity, Spearman correlation coefficients between each of the diversity indices were calculated and their significance was evaluated after a Bonferroni correction to consider the potential bias introduced by multiple tests.

Each index was then standardized using the formula shown in Eq. (9), so that each index had a value between 0 (low conservation value) and 1 (high conservation value).

$$X_{STAND} = \frac{X - X_{\min}}{X_{\max} - X_{\min}} \tag{9}$$

where X_{STAND} is the index X after standardization, and X_{min} and X_{max} are the minimum and maximum values of index X, respectively.

Giving the same range of values to each index makes it possible to limit the bias that arises when summing indices among the various aspects of diversity in order to obtain a single assessment of each aspect of diversity. For each floodplain waterbody, we thus obtained four new indices ranging in value from 0 to the number of indices in each aspect of diversity. To ensure that the aspects of diversity were not redundant, Spearman correlation coefficients were quantified between each of these four indices and their significance was evaluated after a Bonferroni correction.

The last step was to obtain a single synthetic index summarizing all the aspects of diversity considered in this study. The indices of the four aspects of diversity were standardized according to Eq. (9), and then summed to define a single value for each waterbody that represented its conservation priority (designated the "synthetic index" below).

2.5. Influence of environmental characteristics on the conservation values of the waterbodies

In order to evaluate the influence of environmental characteristics of the waterbodies on their conservation values, we tested if the distance from the sea and the lateral connectivity of the waterbodies had a significant effect on the four aspects of diversity and on the synthetic index. We chose to perform ANCOVAs using the indices of the four aspects of diversity as the response variable, the distance from the sea as the covariable, and the lateral connectivity as the factor. We checked the classical statistical assumptions of the linear model (i.e. normality, linearity and homoscedasticity) prior to the ANCOVA analyses. The interaction between the two environmental variables was first assessed, and if no significant interaction was found, the effect of each individual factor on the conservation values was tested. When a significant effect of the lateral connectivity on the conservation value was found, a multiple comparison test

Table 2
Spearman correlation coefficients between indices within each aspect of diversity. The significant coefficients after a Bonferroni correction are indicated by an asterisk.

Taxonomic			Functional			Natural heritage	
	SR	RI_α		TD	Fori		BCC
RI_α	0.42*		Fori	0.12		OI	0.12
RI_β	−0.61*	0.58*	Funi	−0.20	0.44*		

between the levels of connectivity was performed using a Tukey's post hoc test.

3. Results

3.1. Description of the fish assemblages sampled

A total of 6108 fish belonging to 27 species were sampled during the survey (Table 1). The abundance and the frequency of occurrence varied considerably between species – ranging from a single individual sampled for the European perch (*Perca fluviatilis*) to 3546 individuals for the minnow (*Phoxinus phoxinus*). The European perch was also one of the least frequently sampled species, alongside the large-mouth bass (*Micropterus salmoides*) and the flounder (*Platichthys flesus*), which were all sampled in a single waterbody, while in contrast the European chub (*Squalius cephalus*) and the Languedoc gudgeon (*Gobio occitaniae*) were sampled in 31 out of 40 waterbodies.

According to Keith et al. (2011), eight species were not native to the Garonne catchment. Three of them were classified as invasive species, and five as naturalized exotic species. According to the IUCN Red List (IUCN Standards and Petitions Subcommittee, 2010), only the European eel (*Anguilla anguilla*) was critically endangered (CR), while four species were classified as not evaluated (NE), and 22 species were classified as least concerned (LC). Moreover, three species were cited in the conservation regulations used to calculate the BCC: the barbel (*Barbus barbus*), the bitterling (*Rhodeus amarus*), and the brook lamprey (*Lampetra planeri*). Recorded fish species were almost equally distributed across the four categories of fishing interest: five were of interest to commercial fishermen, eight to recreational anglers, five to sportive anglers and nine had no fishing interest.

3.2. Indices of diversity

The various indices were not distributed consistently. For example, within the natural heritage aspect of diversity, BCC has many small values (mean = 0.361), whereas OI has a lot of high values (mean = 0.833). The diversity indices were not greatly correlated within each aspect of diversity (Table 2). The greatest Spearman correlation was found between SR and RI_β ($\rho = -0.61$). This finding suggests that the different indices used were not redundant within each aspect of diversity and could be pooled to obtain a single descriptor of each aspect of diversity. Nor did we find any strong correlation between the indices of the four aspects of diversity (Spearman correlation coefficients less than 0.30; Table 3), making it possible to define the synthetic index as the sum of the standardized indices of each aspect of diversity. The synthetic index theoretically ranges from 0 to 4, but here it ranged from 1.27 to 3.30 (mean = 2.406). The fish assemblages sampled in the 25% top-ranked waterbodies according to the synthetic index (i.e. values superior to 2.67) were typical of assemblages usually found in the Garonne catchment. Most of them were typical of the downstream part of the Garonne catchment: mainly eel (*Anguilla anguilla*) with European perch (*Perca fluviatilis*), rudd (*Scardinius erythrophtalmus*) and flounder (*Platichthys flesus*). The other ones were typical of the upstream part of the Garonne catchment: mainly brown trout (*Salmo trutta*) accompanied to minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*).

Table 3
Spearman correlation coefficients between the four aspects of diversity. The significant coefficients after a Bonferroni correction are indicated by an asterisk.

	Taxonomic	Functional	Natural heritage
Functional	−0.12		
Natural heritage	−0.12	0.07	
Socio-economic	0.30*	−0.07	0.17

Table 4
Results of the ANCOVAs relating the distance from the sea (*Distance*; d.f. = 1), the lateral connectivity (*Connectivity*; d.f. = 2) and their interaction (*Distance × Connectivity*; d.f. = 2) to the conservation values (i.e. the four aspects of diversity and the synthetic index). The *F*-test statistic value and *p*-value are shown. If a significant relationship was found (*p*-value < 0.05, indicated by an asterisk), the direction of the relationship was specified by (+) or (−), depending on whether the effect of the distance from the sea was positive or negative, and by ordering the levels of lateral connectivity according to their average conservation values (Tukey's post hoc tests).

	F	*p*-value	Influence[a]
Taxonomic diversity			
Distance	11.66	0.002*	−
Connectivity	0.44	0.644	
Distance × Connectivity	1.02	0.371	
Functional diversity			
Distance	0.43	0.518	
Connectivity	3.31	0.048*	NC < PC < AC
Distance × Connectivity	0.43	0.653	
Natural heritage diversity			
Distance	1.34	0.256	
Connectivity	5.93	0.006*	NC < PC = AC
Distance × Connectivity	2.44	0.102	
Socio-economic diversity			
Distance	5.41	0.029*	−
Connectivity	2.79	0.075	
Distance × Connectivity	1.24	0.303	
Synthetic index			
Distance	7.19	0.011*	−
Connectivity	4.82	0.014*	NC < PC < AC
Distance × Connectivity	0.50	0.613	

[a] NC, not connected; PC, partially connected; AC, always connected.

3.3. Influence of environmental characteristics on the conservation values of the waterbodies

The ANCOVAs performed between the indices of the four aspects of diversity and the two environmental variables identified significant relationships (Table 4). The interaction between the distance from the sea and the lateral connectivity was not significant for any of the aspects of diversity ($p > 0.05$). We found that the distance from the sea had a significant effect on the taxonomic and socio-economic aspects of diversity: both these aspects decreased as the distance from the sea increased (Table 4). On the other hand, the lateral connectivity had a significant effect on the functional and natural heritage aspects of diversity: the waterbodies not connected to the main channel of the river had a significantly less diversity for both these aspects (Table 4). Lastly, both environmental variables had a significant effect on the synthetic index, but the interaction between them was not significant (Table 4). The value of the synthetic index fell significantly as the distance from the sea increased and the level of connectivity with the main channel decreased (Table 4 and Fig. 2).

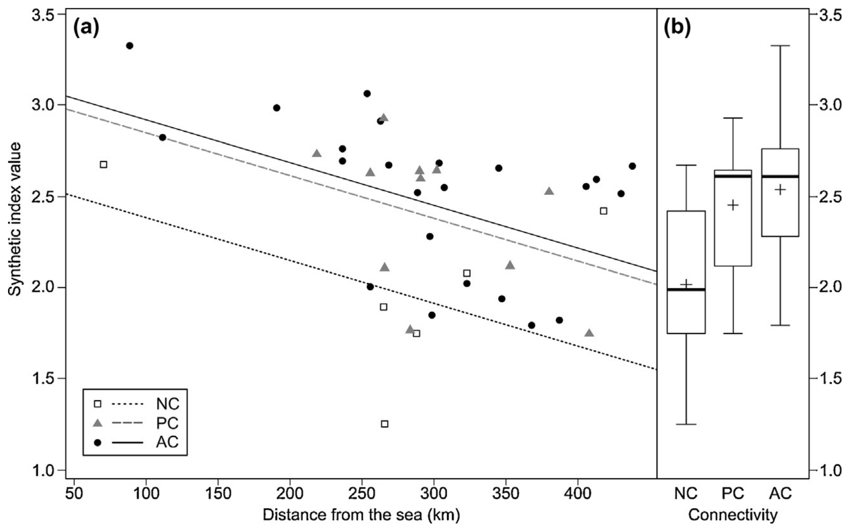

Fig. 2. Effects of the lateral connectivity with the main channel and the distance from the sea on the synthetic index. (a) Relationship between the synthetic index and the distance from the sea (in kilometers) according to the level of lateral connectivity with the main channel of each floodplain waterbody (white squares = not connected – NC; gray triangles = partially connected – PC; black dots = always connected – AC). The regression lines between the synthetic index and the distance from the sea for each level of connectivity are also shown. (b) Boxplot of the synthetic index for each level of lateral connectivity. The median is denoted by the bold horizontal line, the mean is indicated by the cross, the box delimits the interquartile range, and the whisker lines extend to the observed maxima and minima.

4. Discussion

4.1. Prioritization method based on non-redundant aspects of diversity

In order to identify priority areas for biodiversity conservation, one solution is to develop methods that take into account several aspects of the biological diversity of the communities occurring in those areas (Girardello et al., 2009; Margules and Pressey, 2000). In this study, we focused on various measures of assemblage diversity that have been used by Bergerot et al. (2008), Chantepie et al. (2011) and Filipe et al. (2004) to select priority areas for freshwater fish conservation. These previous studies proposed several methods of prioritization that combined several indices each describing a single component of the diversity of fish assemblages. However, Mason et al. (2005) and Villéger et al. (2008) have pointed out that within a given aspect of the diversity (e.g. functional diversity) different evaluations can be complementary and even necessary to fully understand the functioning of species assemblages. Based on these findings, we have developed an innovative method which makes it possible to select priority areas according to a combination of four aspects of the diversity of fish assemblages: taxonomic, natural heritage, functional and socio-economic aspects of diversity. Each aspect was summarized using a single index combining one, two or three diversity indices. However, when several numerical indices are combined to assess one single characteristic, it is essential to assess their redundancy (Gallardo et al., 2011). The combination of two or more indices describing similar patterns would lead to an overestimation of the factor being assessed, and would also reduce the interest of this multi-faceted approach (Lyashevska and Farnsworth, 2012). Consequently, non-redundant indices should be considered as a priority when assessing assemblage diversity (Mouchet et al., 2010). In this study, we found that none of the indices selected was strongly correlated within or between the different aspects of diversity. The greatest correlation was found between species richness and β-diversity. This may have been due to the limited regional pool of species present (27 different species in the 40 waterbodies), the limited number of species in the fish assemblages (a maximum of 12 species with an average of seven species), and also to the fact that the most dissimilar assemblages in terms of species composition are usually those with the highest species richness when using Sorensen or Bray–Curtis dissimilarity indices (Jost, 2007; Koleff et al., 2003). The absence of strong correlations between the different aspects of diversity suggests that the aspects were not redundant, and indeed may be viewed as complementary. Complementarity is essential to enhance the multi-faceted approach as it reduces the ecological redundancy of the assessment. For instance, accounting for complementarity when designing new methods for conservation prioritization may reduce our propensity to select areas characterized by the presence of a lot of different species (i.e. high species richness), but which may all perform the same function in the ecosystem (Walker, 1992) or be devoid of conservation interest.

In spite of the complementarity of the aspects of diversity included in our approach, some components of the diversity were not taken into consideration. The main aspect that is lacking is probably the phylogenetic diversity of the assemblages. It has often been combined with other aspects of diversity in order to assess the diversity of ecological communities (Cadotte et al., 2010; Moritz, 2002) or to identify priority areas for conservation (Devictor et al., 2010; Redding and Mooers, 2006; Strecker et al., 2011). Unfortunately, we were not able to include this aspect of diversity, because no DNA description was available for some of the species occurring in the Garonne catchment, especially for some recently described species such as those of the genus *Gobio* (description based on morphological features; Keith et al., 2011; Kottelat & Persat, 2005). Nevertheless, the phylogenetic aspect of diversity could be easily included in our method as a fifth aspect when these phylogenetic data become available, using non-redundant indices from amongst those reviewed in Cadotte et al. (2010) or Helmus et al. (2007), for example.

4.2. Influence of environmental characteristics on the conservation values of the waterbodies

At the scale of a large catchment, fish species richness has been reported to be higher in the downstream part (Ibarra et al., 2005; Lasne et al., 2007b). We have demonstrated that the distance from the sea had a significant, negative influence on the taxonomic diversity of the floodplain fish assemblages, which is the aspect including species richness. As in those previous studies, the most diverse assemblages according to their taxonomic diversity were indeed found in the downstream part of the Garonne catchment, and this relationship was probably a direct consequence of the longitudinal fish zonation described in Huet (1959).

We also found that the socio-economic aspect of diversity decreased as the distance from the sea increased. This relationship seemed to result from the presence of a higher proportion of species without fishing interest (e.g. the minnow *P. phoxinus* or the stone loach *B. barbatula*) in the upstream part of the catchment, whereas the proportion of species of interest to commercial fishermen (e.g. the pike *Esox lucius* or the European eel *A. anguilla*) was higher in the downstream part of the catchment. Finally, the distance from the sea also significantly influenced the synthetic index. This indicated that the floodplain waterbodies in the downstream part of the catchment were more likely to have higher conservation priority on the basis of the indices considered in this study. This finding is not consistent with Chantepie et al. (2011), who demonstrated that the floodplain waterbodies in the Loire catchment in France that are of least conservation interest are those closest to the sea. However, this previous study focused solely on a river segment of 100 km, in the downstream part of the catchment, even though the Loire River flows over a distance of 1000 km. Moreover, the authors included only four diversity indices (species richness plus three indices based on the rarity, the conservation status and the origin of the species) in their assessment. Consequently, it looks as though the relationship between the conservation value of floodplain waterbodies and their distance from the sea depends significantly on whether all or only part of the catchment is taken into consideration, and also on the aspects of diversity included in the assessment.

While several studies have highlighted an increase in species richness as the lateral connectivity increases (Bolland et al., 2012; Chantepie et al., 2011; Lasne et al., 2007a; Tockner et al., 1998), the relationship between the taxonomic aspect of diversity and the lateral connectivity did not appear to be significant in the present study. This was probably due to the fact that we included two other indices (i.e. rarity of species and rarity of assemblages) in addition to species richness when we defined the taxonomic aspect of diversity. However, we did show that the lateral connectivity had a significant effect on the natural heritage aspect of diversity. Fish assemblages sampled in the most disconnected waterbodies tended to display lower natural heritage diversity than the other two levels of lateral connectivity. As previously suggested by Chantepie et al. (2011) and Lasne et al. (2007a), this effect was probably due to the presence of exotic and not threatened species (e.g. the black bullhead *Ameiurus melas*) in the typical assemblages of ponds, which were sampled in the most disconnected waterbodies. We also found that the lateral connectivity had a slight but significant influence on the functional diversity, which also tended to have lower values in the most disconnected waterbodies. As previously highlighted by Gozlan et al. (1998), a higher proportion of cyprinid species seemed to be present in the disconnected waterbodies. Given that cyprinids are dominant in the pool of species considered (14 cyprinid species out of the 27 species sampled in our study), these species can be expected to be close to the hypothetical average species in the defined functional space, and also roughly similar to each other (Buisson et al., 2013). In addition, the simultaneous presence of species with very similar functional characteristics (e.g. the common carp *Cyprinus carpio* with the Crucian carp *Carassius gibelio*) and the absence of species with a high level of functional originality (e.g. the bitterling *R. amarus*) or uniqueness (e.g. the flounder *P. flesus*) in the disconnected waterbodies strengthened the trend observed. Consequently, the combination of these two patterns may explain the lower functional diversity found in the disconnected waterbodies.

Finally, the conservation priority (i.e. the value of the synthetic index) was significantly lower in the most disconnected waterbodies than in the other two lateral connectivity levels. This finding is consistent with Chantepie et al. (2011) and Lasne et al. (2007a), who previously demonstrated that the conservation value of fish assemblages occurring in disconnected floodplain waterbodies of the Loire catchment in France was lower than in the waterbodies with higher levels of lateral connectivity.

Our findings therefore suggest that the floodplain waterbodies that should be conserved as a priority (based on the combination of the four aspects of diversity considered) are those located in the downstream part of the Garonne catchment and which are also at least partially connected to the main channel (Fig. 2). The negative effect of the loss of lateral connectivity of waterbodies on their conservation value has already been recognized for freshwater fish (Bolland et al., 2012; Chantepie et al., 2011; Lasne et al., 2007a), and for other taxa such as macrophytes (Keruzoré et al., 2013) and macroinvertebrates (Gallardo et al., 2008). Nevertheless, Tockner et al. (1998) have shown that different non-fish taxa displayed maximum species richness in floodplain waterbodies with intermediate levels of lateral connectivity. The influence of the lateral connectivity on different aspects of diversity thus deserves to be further explored.

In this study, we have limited our analysis to the effect of the upstream–downstream gradient and the lateral connectivity on the conservation prioritization. However, we have not explored its response to anthropogenic disturbances which is an assessment frequently conducted when evaluating the ecological quality or the conservation interest of an ecosystem (Oberdorff et al., 2002). In the method proposed here, we have accounted for several indices whose value can be artificially increased due to the inclusion of fish assemblages modified by human activities. For instance, the presence of non-native species in an assemblage may occasionally increase the conservation value of this assemblage (e.g. species richness, functional uniqueness) in spite of their low conservation interest. Nevertheless, accounting for the origin and the conservation status of these species makes it theoretically possible to counterbalance this methodological bias. At the scale of the Garonne catchment, this effect was however limited due to the overall low anthropogenic disturbance of the sampled waterbodies. Moreover, the number of non-native species sampled in the waterbodies was small and all these species are already present in the entire Garonne catchment (e.g. the stone moroko *Pseudorasbora parva*, see Poulet et al., 2011) reducing the risk of artificially increasing the conservation value of fish assemblages including non-native species. However, this is an issue that has to be tackled when using a conservation prioritization method that considers indices such as those proposed in this study. Although our multi-criteria approach strongly limits this issue by including indices based on the conservation status and the origin of species, disturbed environments should preferably be removed from the assessment.

4.3. Use of the prioritization method by decision-makers and conservation managers

In the present study, the prioritization of areas for conservation by decision-makers can be assessed at two different levels. On the one hand, depending on their needs and constraints, decision-makers can actually select the aspects of diversity that they want to focus on. For instance, they can avoid including aspects that may be less appropriate for their needs (Ascough et al., 2008), such as the socio-economic aspect of diversity, when they prefer to limit their assessment to a purely ecological approach. On the other hand, they can base their prioritization on the four different aspects of diversity included in our study (perhaps plus some others), and consequently use the synthetic index we have developed.

The prioritization method proposed here is a scoring procedure method (see Margules and Usher, 1981 for a review). Scoring procedures rank areas in order of value or priority on the basis of one or several criteria, and have traditionally been used to select priority areas for biodiversity conservation (Abellan et al., 2005; Rosset et al., 2013). Although scoring procedures may be less appropriate for selecting priority areas for conservation than more complex methods (e.g. Zonation software, see Moilanen et al., 2008 for further information on its possible applications to freshwater ecosystems), the scoring procedure used here was more relevant than a landscape conservation approach. This was due to the fact that we were interested in prioritizing floodplain waterbodies that were individual spatial points without any particular spatial relationship with one another (except for their location along the upstream–downstream gradient).

The prioritization method we propose here may not be restricted to floodplain fish assemblages. Once relevant information about the conservation status, biogeographical origin, ecological traits and socio-economic characteristics of the species of interest are available, our method could easily be applied to other taxonomic groups and ecosystems following the framework defined in this study. Expanding the method developed here could make it of great interest for assessing the conservation value of floodplain waterbodies with regard to freshwater taxa other than fish, as is beginning to be done for macroinvertebrates (Gallardo et al., 2008), zooplankton (Kattel, 2012), and aquatic macrophytes (Keruzoré et al., 2013). This would make it possible to assess the congruence between several aspects of diversity for different taxonomic groups, and to achieve a more general assessment of the conservation value of freshwater ecosystems.

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