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Aquatic Sciences

OVERVIEW

Functional ecology of fish: current approaches and future challenges

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Abstract Fish communities face increasing anthropogenic pressures in freshwater and marine ecosystems that modify their biodiversity and threaten the services they supply to human populations. To address these issues, studies have been increasingly focusing on functions of fish that are linked to their main ecological roles in aquatic ecosystems. Fish are indeed known to control other organisms through predation, mediate nutrient fluxes, and can act as ecosystem engineers. Here for each of the key functions played by fish, we present the functional traits that have already been used to assess them. We include traits measurable from observations on living individuals, morphological features measured on preserved organisms or traits categorized using information from the literature, and we discuss their respective advantages and limitations. We then list future research directions to foster a more complete functional approach for fish ecology that needs to incorporate functional traits describing, food provisioning and cultural services while accounting more frequently for intraspecific variability. Finally, we highlight ecological and evolutionary questions that could be addressed using meta-analyses of large trait databases, and how a trait-based framework could provide valuable insights on the mechanistic links between global changes, functional diversity of fish assemblages, and ecosystem services.

Keywords Ocean · River · Biodiversity · Functional trait · Global change · Ecosystem services · Fish

> "As the knowledge of fish, relevant and beneficial, comes from their differences, we need to study them. We say that differences among fishes come from their life and life history, their parts, their actions, their behaviour and complexion".
>
> Guillaume Rondelet, 1558, L'Histoire entière des poissons.

Introduction

In the current context of the biodiversity crisis, a key goal of ecology is to better understand the response of communities to disturbance and the implications for ecosystem functioning, to ultimately improve conservation planning. Towards this aim, a functional ecology of communities has been developing for more than two decades for many plant and animal taxa (Keddy 1992; Díaz and Cabido 2001; Lavorel and Garnier 2002; McGill et al. 2006; Violle et al. 2007; Luck et al. 2012; Winemiller et al. 2015; Moretti et al. 2017). This approach is based on the use of functional traits, defined as any biological attribute measurable on an individual that impacts organism performance and thus

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fitness (Violle et al. 2007). Choosing the relevant functional traits to describe the complementary functions of organisms that determine their roles in ecosystems is thus the cornerstone of functional ecology (Keddy 1992; McGill et al. 2006; Violle et al. 2007). Functional trait values can then be used for quantifying the functional diversity of communities (Mouillot et al. 2013), for analysing how communities are shaped by environmental (Brind'Amour et al. 2011; Mason et al. 2008a) and anthropogenic constraints (Suding et al. 2008; Villéger et al. 2010), and assessing how the functional diversity of communities modulates various ecosystem processes (Mouillot et al. 2011b; Naeem et al. 2012) and services (Díaz et al. 2007; Harrison et al. 2014).

However, while the functional ecology of plant communities has been achieving much of these challenges, the functional ecology of animal communities is still in its infancy (Fig. 1). For instance, for the last 5 years (2012–2016), there have been four times fewer publications on functional diversity of fish communities than on functional diversity of plant communities. Ray-finned fishes (Actinopterygii), hereafter called fishes, represent the most diverse class of vertebrates with 26,891 species (Nelson 2006). Fishes are not only taxonomically and phylogenetically highly diversified, they also exhibit a large diversity of biological characteristics (e.g. size, diet, mobility, behaviour; Nelson 2006). High biodiversity coupled with their abundance make fish communities central to the provision of ecosystem services by aquatic ecosystems through protein supply, control of trophic networks, regulation of nutrient cycles, and recreational activities (Holmlund and Hammer 1999). However, fish communities are under a global threat because of human disturbances including climate change, habitat degradation, biological invasions and ever increasing harvesting (Myers and Worm 2003; Olden et al. 2006; Pörtner and Knust 2007; Pinsky et al. 2011). These impacts are responsible for an increasing rate of biodiversity loss through extirpations of species and dramatic shifts in the relative abundances and body size of remaining species (Jackson et al. 2001; Graham et al. 2011; D'Agata et al. 2014). In turn, these alterations of biodiversity can disrupt ecological processes performed by fish communities and hence reduce the provision of ecosystem services (Bellwood et al. 2004, 2012; Taylor et al. 2006).

Functional ecology offers a framework to address these unprecedented challenges and should thus be applied to fish more often. The aim of this paper is thus to propose a guide to how adequately assessing functional diversity of fish communities. We first review the traits and approaches currently used to describe the fish functions that determine their contribution to key ecosystem processes and hence services. We then present the future challenges fish ecologists need to tackle to improve the current functional approaches to ultimately set better conservation planning of the services provided by fish.

A diversity of approaches to assess fish functions

Fish contribute to key ecological processes in aquatic ecosystems: controlling food-webs as consumers and prey for other organisms, contributing to nutrient cycles, and shaping biophysical habitats through ecological engineering (Holmlund and Hammer 1999) (Fig. 2). For the last

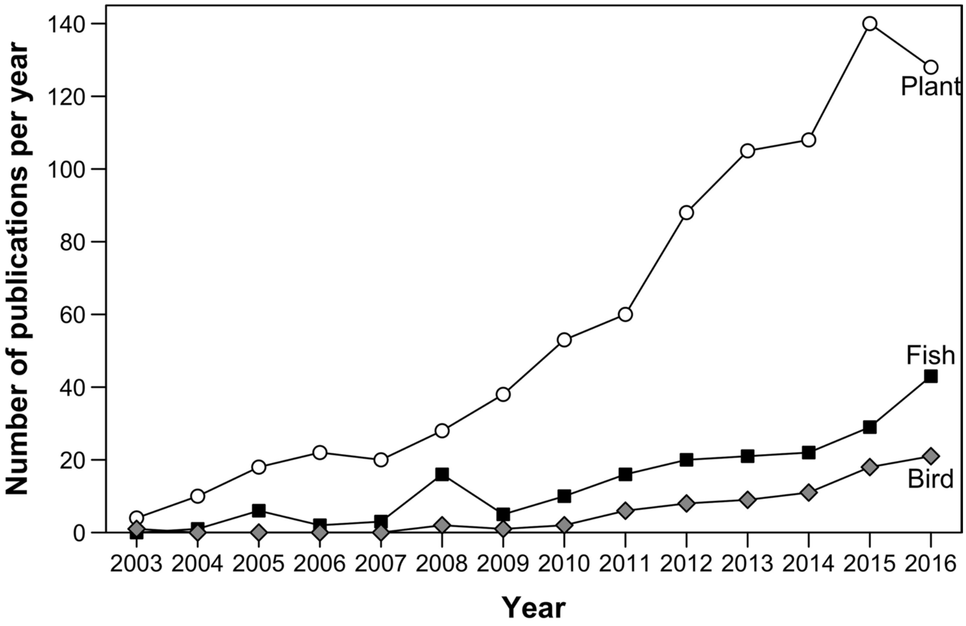

Fig. 1 Number of publications per year about functional ecology of plants, fishes and birds. Data came from searches on ISI Web of Knowledge © with following keywords for "Topic": ("plant communities" or "plant assemblages") AND ("functional traits" OR "functional diversity") (*circles*), ("fish communities" or "fish assemblages") AND ("functional traits" OR "functional diversity") (*black squares*) and ("bird communities" or "bird assemblages") AND ("functional traits" OR "functional diversity") (*grey diamonds*)

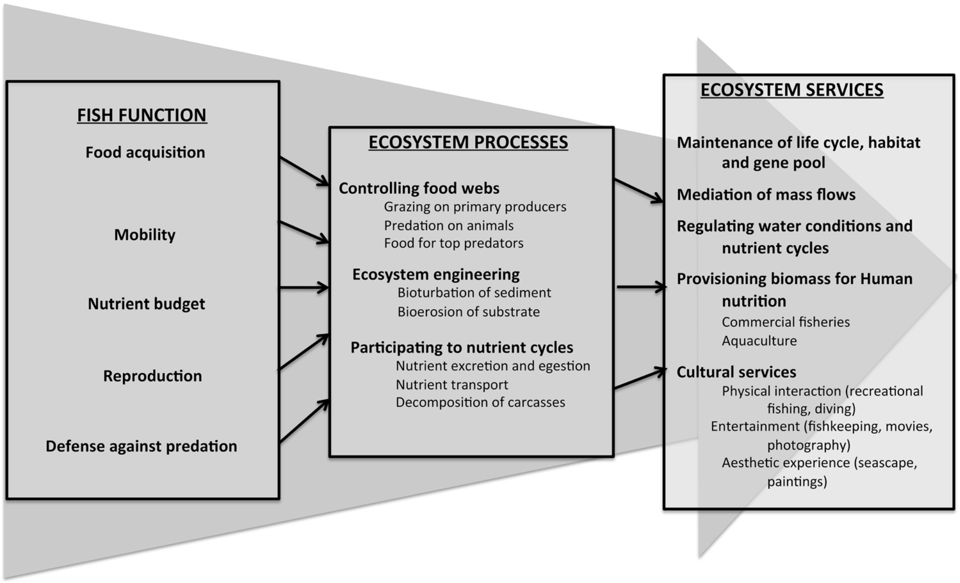

Fig. 2 Overview of how facets of fish ecology determine the services aquatic ecosystems supply. The lists of fish functions, ecosystem processes and services are not exhaustive but focused on the ones presented in the text

decades, fish functional ecology has been focusing on five biological functions related to these roles: food acquisition, locomotion, nutrient processing, reproduction, and defence against predation (Winemiller et al. 2015). In addition to the diversity of functions considered, fish functional ecology is also characterized by the diversity in how these functions are assessed. Some studies have directly quantified the roles of fishes, such as controlling biomass of algae (e.g., Fox and Bellwood 2008a) or recycling nutrients (e.g., McIntyre et al. 2008), in a given ecosystem while other assess the potential roles of fishes in ecosystems using biomechanical features (e.g., Carroll et al. 2004), morpho-anatomical measures (e.g., Winemiller 1991; Price et al. 2015) and/or categories (e.g., Mouillot et al. 2014).

In the next sections, we synthesize approaches commonly used to describe the functions performed by fishes (Table 1). Our goal is not to list all traits that have been proposed during the last three decades (especially morphology-based traits), but instead to provide an overview of the approaches that have been used to describe functions performed by fishes, including methodological guidelines, and highlight their respective advantages and limits.

Assessing how fish control abundance of other organisms through trophic interactions

Fishes are abundant in most aquatic ecosystems and they thus have the potential to control the abundance of other organisms through predation. As the structure of trophic networks is of primary importance for several ecosystem services (biomass and protein provisioning, mediating mass and energy flows to species harvested by humans), assessing how fish control other organisms through predation has been one of the cornerstones of fish ecology for the last decades. Some of these studies used a functional approach. Fishes present a large range of trophic strategies, from pure herbivores to top predators, including various levels of omnivory and detritivory (Nelson 2006). In addition to this diversity of trophic levels, fish also exhibit a large variety of strategies to acquire food, such as ambush vs. cruising predators, or different grazing strategies for herbivores (e.g., Brandl and Bellwood 2014a).

Measuring prey consumption rates

The impact of a fish species on its prey could be measured through underwater observation of food consumption rates in the field (e.g. Brandl et al. 2014) or in mesocosms that simulate field conditions (Flecker and Taylor 2004). On coral reefs, such approaches revealed functional differences between herbivorous species in term of grazed micro-habitats (Brandl et al. 2014) and previously unknown critical functional roles of some herbivorous fish (Bellwood et al. 2006a; Fox and Bellwood 2008b). When direct observations or experiments are not possible (because of low visibility, deep habitats or difficulty in acclimating species to captivity), bioenergetics models could provide an estimation of food consumption rates, but they require sampling many individuals and measuring detailed diets (based on stomach contents or stable isotope analyses), quantitative information on physiological rates (respiration, food assimilation) and may thus be hard to implement on a large number of species (Tarvainen et al. 2008).

As a practical functional trait assessing consumption rate, we propose the number (or biomass) of prey items consumed by a predator per unit of time. 'Prey items' can

Table 1 Functional traits available to describe the main functions performed by fish

Function performed by fish	Continuous trait measured on living organisms in the field or in controlled conditions	Continuous trait measured on dead organisms	Semi-quantitative or qualitative trait assessed on species using literature sources
Food acquisition	Per capita grazing or predation rate	Body size + diameter and position of eye + barbel length + size, position and shape of oral gape + shape of teeth + length and/or number of gill rakers + total length of gut	Trophic guilds based on compilation of stomach gut analyses, observations in the field and/or stable isotope analyses
	Biomechanics of prey capture (e.g. suction index)		
Mobility	Swimming speed and/or acceleration	Body size + body elongation + area and shape of transverse body section + shape and area of pectoral and caudal fins + caudal peduncle throttling	Ordered categories of mobility within/between habitat(s)
	Vertical mobility observed		Ordered categories of vertical position in the water column
Nutrient budget	Per capita excretion rates of dissolved N and dissolved P	Bioenergetics modelling based on body mass + N and P body content + N and P content in diet + daily ration + growth rate	Potential effect on nutrient cycles (recycling and translocation) through grouping species according to their size, diet and mobility
	Per capita egestion rates of feces + N-P content of feces		
	Per capita excretion rates of carbonated pellets[a]	Fish body mass (for modelling metabolic rates with water temperature)	
Reproduction	Hatching time of eggs	Mass of gonads + size of eggs/larvae + age at maturity	Type of reproductive mode
Defence against predation	Behavioural observation of flight initiation distance, boldness/shyness and social interactions	Body size and shape + color + presence of spines + toxicity of flesh	Ordered categories of common size of group + ordered categories of period of activity

Three type of traits are listed depending on the way there are measured. The level of information they provide about actual fish performance and contribution to ecosystem processes decrease from the left to the right column. See details about measurement of functional traits in the text and in Appendix S1 for morphological traits

[a] Only for marine fishes

be size-based classes of a species, a species, or a trophic group. Predation rates can be influenced by abiotic factors (e.g. temperature), by prey abundance and diversity, and by the time of observation (e.g. Tomas et al. 2005). Toward comparing the abilities of fish to control other species, measures of food consumption rates should thus be measured under standardized situations, i.e. given abiotic conditions, with a given amount and diversity of prey items and for a given period of time (e.g. Stallings 2010; Cowan et al. 2016). Measuring such a trait could thus be time consuming and could require overcoming technical limitations, but it is a crucial step towards an accurate evaluation of the biotic control imposed by fishes on organisms that are critical for ecosystem stability (e.g. macroalgae or crown-of-thorns seastar on coral reefs, Bellwood et al. 2006a; Cowan et al. 2016).

Profiling food acquisition based on morpho-anatomical traits

As assessing consumption rates is a demanding task that is not feasible for species-rich assemblages, the morphological approach has been proposed for predicting trophic impact of fish on other organisms under the assumption that morphology determines diet (e.g. Sibbing and Nagelkerke 2001; Dejen et al. 2006). The number of traits to describe food acquisition has been continuously growing since the seminal paper of Gatz (1979), but up to now, no consensus has emerged on which traits to use.

These morpho-anatomical traits describe the relative size, shape and/or position of the body parts involved in each step of the food acquisition process (e.g., detection, capture and digestion; see examples in Fig. S1 in Online Resource 1), but differ in the way these functions are measured. For instance, eye diameter is used for estimating visual acuity, but to standardize this raw measurement some studies suggested dividing diameter by either body length (Sternberg and Kennard 2014), body mass (Mason et al. 2008b) or head depth (Winemiller 1991). Here, we present a short list of morphological and anatomical traits commonly used to describe the different facets of food acquisition, from prey detection to digestion.

The first indicator of food acquisition, and more generally of all other functions, is fish body mass because it is related to metabolism through allometric relationships (White et al. 2006). We advise using mass rather than body length, despite the latter's common use in ichthyology and even as a functional trait, because mass is more related to metabolism and trophic status than length (Akin and Winemiller 2008), and allows inter-species comparisons even when species body shapes strikingly differ (e.g., Anguilliformes vs. Scorpaeniformes).

Food acquisition starts with prey detection. This function is generally performed by visual stimuli. Maximum eye diameter relative to head size (depth at the vertical axis of eye or horizontal length from snout to opercula) has been often used as a proxy of visual acuity and/or light sensitivity (Winemiller 1991; Schmitz and Wainwright 2011; Bellwood et al. 2014). The vertical position of the eye is used to describe fish position in the water column relative to that of its prey (Winemiller 1991; Pouilly et al. 2003). For example, fishes with eyes at the top of the head are often ambush predators living on substrates (e.g., toadfishes) or fish feeding near the surface, for example on insects (e.g., four-eyes, genus *Anableps* [Anablepidae]). Prey detection can also be carried out using barbels, which are relatively common in freshwater fish (e.g., catfishes, Siluriformes, ca. 2500 species) but also occur in common marine fish such as Mullidae. Barbel length, expressed as a percentage of fish head depth, might constitute a rough measure of their tactile and gustative importance (Sibbing and Nagelkerke 2001). Anatomy of brain and especially volume of olfactory and visual lobes could discriminate strategies to detect food (e.g., visual vs. olfactory; Wagner 2001).

Once food items have been detected, the second step is prey capture. The ability to capture prey is linked to biomechanical properties of the mouth that allow ingestion of prey through biting and/or suction (Wainwright et al. 2004). Suction-feeding performance could be measured using the suction index (Carroll et al. 2004), which accounts for the epaxial muscle volume, lower jaw morphology, and buccal cavity volume (Wainwright et al. 2007). However, measuring these variables on many species is a demanding task and some morphological studies have used only shape and size of oral gape as an indicator of prey capture (Gatz 1979; Karpouzi and Stergiou 2003). Oral gape shape can be quantified as the ratio between maximal depth and maximal width of the mouth fully opened on dead individuals, which is a less demanding but also a less accurate method than observation of actively feeding individuals (Wainwright et al. 2007). Fishes with a ratio lower than unity (mouth vertically flattened) tend to feed on benthic organisms, whereas species with higher ratio (mouth laterally flattened) tend to be filtering species (Karpouzi and Stergiou 2003). Lengths of snout and of lower jaw relative to head length have also been used for describing oral gape (Bellwood et al. 2014). These traits present the advantage of being measurable on lateral pictures of animals (dead or alive) and even on fossils. Complementary to shape, maximal oral gape surface provides information about the type of prey a fish can catch. We propose the use of the unitless ratio of oral gape surface to the surface of body transversal section, assuming that both are ellipsoid. The vertical position of oral gape is also linked to the prey position before capture and prey capture mode. Fishes with an oral gape in a ventral position (e.g., Loricariidae) will tend to feed on the bottom whereas fishes with the mouth opening on the top of their head will feed near the surface (e.g., Poecilidae).

Tooth shape is involved in food processing (e.g., biting, rasping, crushing, grasping) and may vary across diets and even between modes of capture (Takahashi et al. 2007) even if it tends to be slightly variable within fish families (but see Tebbett et al. 2017). Teeth, which can be classified using functional categories based on shape such as: absent or very small (i.e. not playing a significant role in food processing), unicuspid (i.e., one raised point on the crown of teeth), multicuspid (i.e., two or more raised points on the crown of teeth), short conical, long conical or triangle serrated (Winemiller 1991). Gill rakers, when present, play a role in food acquisition, either in filtering plankton (Tanaka et al. 2006) or for gill protection. Gill rakers can be quantified by their density on gill arches and by their maximal length (Gatz 1979; Sibbing and Nagelkerke 2001), or grouped qualitatively (Winemiller 1991) based on ordinal categories (absent, short tooth-like, long and sparse, and long and comb-like). Qualitative characterization is less time consuming while providing synthetic information.

The digestive process and nutrient assimilation are complex functions involving several organs, such as the stomach, pancreas and intestine, as well as enzymes and gut microbiota. It remains challenging to find functional traits that adequately describe the digestive and assimilation processes (see Cowey and Cho 1993 for a general overview and Clements et al. 2017 for the special case of parrotfishes) while they are key to understand fish role in nutrient cycles (e.g. how much nutrients from food are egested). However, total gut length from esophagus to anus standardized to body length is a robust indicator of the ability to digest detritus and vegetal materials (Kramer and Bryant 1995; Wagner et al. 2009). Specifically, carnivorous species have short guts because animal proteins have high digestibility, while herbivores and detritivores have a longer intestine to extract nutrients from vegetal material (Cleveland and Montgomery 2003).

The morpho-anatomical traits presented above are quantified as unitless ratio between comparable body parts (e.g., eye size is compared to head size, not to body length) so that they are thus not trivially correlated with body size, which is considered as a separate trait. However, assessing how such ratios vary with fish age could reveal ontogenetic changes in functional traits (Zhao et al. 2014). From a practical point of view, in most cases they are easily measurable in a few minutes on individuals using a calliper or pictures. Morpho-anatomical traits are generally used to functionally discriminate species (e.g. Brandl and Bellwood 2013) and to quantify functional diversity of assemblages (e.g. Villéger et al. 2010; Bellwood et al. 2014) under the assumption that differences in trait values reflect difference in food acquisition strategy and hence diet. However, even if some of these functional traits are supported by biomechanical studies linking morphological features to performance for a given function (e.g., prey capture), most of these relationships have been tested only for a few fish families, such as labrids in marine ecosystems (Wainwright et al. 2002; Collar et al. 2008) and Centrarchids in freshwater ecosystems (Higham 2007a, b). Furthermore, several studies have challenged the assumption that morpho-anatomical traits can be used to infer food acquisition. First, discordance between morphological and mechanical diversity has been reported in several fish groups because species having similar morphologies can actually have different mechanics for food capture (Collar and Wainwright 2006; Konow and Bellwood 2011), and also because different morphologies can achieve the same set of functions (Wainwright et al. 2007). Second, several studies have found weak relationships between morphology and diet (Bellwood et al. 2006b; Barnett et al. 2006; Ibañez et al. 2007; Albouy et al. 2011). For instance, Albouy et al. (2011) found that morpho-anatomical traits accurately discriminate herbivorous (including omnivores) from non-herbivorous species (e.g., strictly carnivores), but are unable to predict more fine-scale aspects of fish diets (i.e., discriminate the various types of omnivores as well as diet plasticity). In other words, morpho-anatomical traits shape the space of possible prey (i.e., fundamental or potential trophic niche), which is then reduced by the prey availability (i.e., abundances in a given environment) and individual behaviour to determine the observed fish diet (i.e., realized trophic niche) (Brandl et al. 2014).

Profiling food acquisition through categories

Quantitative description of food acquisition based on morpho-anatomical traits measured on individuals is a demanding task and thus only a small proportion of the 26,891 ray-finned fish species have been functionally described using these continuous traits (but see Claverie and Wainwright 2014; Toussaint et al. 2016 for morphological traits). As an alternative, a pragmatic description of food acquisition could be based on a qualitative classification of diets based on the literature or http://www.FishBase.org (e.g. using underwater observation by experts, gut content studies, or stable isotope analyses). Diet could be coded using few categories describing trophic level (e.g. detritus, primary producers, primary consumers, secondary consumers, predators of higher trophic level), or using more detailed categories accounting for biological characteristics of prey such as size or mobility with for instance plants split into macrophytes, phytoplankton and periphyton, and invertebrates split into micro- or macro-zooplankton (e.g.

copepods vs. jellyfish), and sessile or mobile benthic invertebrates (e.g. corals and molluscs vs. echinoderms and crustaceans). This type of classification could be seen as rough, but it is still better than considering only taxonomic diversity or only guilds to assess ecological difference between assemblages (Mouillot et al. 2014).

Assessing how fishes move within and between aquatic habitats

Mobility is a multifaceted function including space occupancy (how fish use the water column and habitats available on a horizontal scale) and swimming performance, which itself includes several components such as endurance, speed, acceleration, and manoeuvrability (Webb 1984; Blake 2004). Endurance is the ability to sustain a high swimming speed over long distance. Acceleration refers to the ability of fish to reach a very high swimming speed in a short period (few milliseconds), and contributes to either predation efficiency on mobile prey or escape from predators. Manoeuvrability reflects the ability to make precise moves, i.e. to turn quickly or to swim backward, which is important for moving in topographically complex environments, for feeding and for evading predators (Fulton et al. 2001; Higham 2007b; Bellwood et al. 2014). Mobility affects all the ecological processes mediated by fish and it has thus been studied with a functional perspective for several decades (Gatz 1979; Webb 1984; Wainwright et al. 2002; Fletcher et al. 2014).

Measuring swimming performance

Routine swimming speed could be measured in the field using underwater observations, which allows characterizing the performance of many species (e.g. coral reef fishes, Wainwright et al. 2002; Fulton 2007). Other traits describing swimming performance such as endurance at a critical swimming speed (i.e. maximum speed that can be sustained over several minutes) and acceleration rates are not easy to measure in the field and are thus generally measured on captive individuals in controlled experimental conditions (Fulton 2007; Higham 2007a). Fish position in the water column (i.e. time spent in pelagic or benthic habitats when moving or foraging) could also be recorded in the field using underwater observation or telemetry while simultaneously measuring horizontal space occupancy (e.g. Kobler et al. 2009; Brandl and Bellwood 2014a).

Profiling swimming through morphological traits

As measuring swimming performance for many species is a demanding task, functional ecologists have been using morphological traits as proxies to describe how fish use their body and fins for swimming (see examples in Appendix S1).

Swimming, as any movement in fluid, is influenced by both kinematics and hydrodynamics that are affected by the size, shape, stiffness, and type of movements of fins and of body (Blake 2004; Lauder 2015). First, body size affects a fish's ability to swim. For example, larger fishes are expected to be faster and have greater endurance than small ones, because in larger fish muscle biomass is proportionally greater relative to surface friction during swimming. On the contrary, small fishes have better manoeuvrability and can thus move in topographically complex environments such as coral reefs or aquatic plants, tree branches, or roots in rivers. Propulsion is affected by the shape of fins and the body core. Fishes can be functionally classified according to their propulsion traits into two categories (Blake 2004): (1) species relying primarily on their body and/or caudal fin (BCF) for propulsion, with a continuum for this strategy from anguiliformes (eels, morays) that rely heavily on their bodies to thunniforms (tuna, sailfish) that rely heavily on caudal fins; (2) species using mainly the median and/or paired fins (MPF), with rowing, undulating or flying movements. However, this dichotomy is not always so straightforward and some species (e.g., Sparidae in marine environments and Cichlidae in freshwaters) use the two types of swimming modes i.e. MPF for slow and precise swimming and BCF for fast or long distance swimming (Blake 2004; Fulton 2007).

Pectoral and caudal fins are the most frequently described fins in the literature, even though some species swim using undulation of their dorsal and anal fins (e.g. Balistidae). Functional traits used to describe pectoral fins are total area (i.e., area of fin spread to its maximal extension) and fin shape using aspect ratio index (squared maximal length divided by area). Aspect ratios discriminate rounded (low value) from elongated (high value) pectoral fins; rowing or undulating species tend to have relatively round fins (puffers), whereas flying ones tend to have long fins (e.g. rainbow wrasses from *Coris* genus). Aspect ratio is a good predictor of swimming speed among coral reef labrids (Wainwright et al. 2002).

Similarly, caudal fin functionality is described using total area and aspect ratio index (squared maximal depth divided by total area). Lunate caudal fins (e.g., tunas) favour high propulsion efficiency by reducing drag generated by the lateral caudal peduncle movement (Blake 2004; Bridge et al. 2016). Peduncle throttling (i.e. maximal caudal fin depth divided by the caudal peduncle minimal depth) has thus been used as a proxy for swimming performance because pelagic species tend to have a very marked peduncle throttling (i.e., the peduncle is very narrow relative to the caudal fin). In addition to shape and area of fins, stiffness should also be often measured as it influences the efficiency of the transmission of the momentum generated by muscles to the water through fins (Lauder 2015).

Swimming performance is also affected by interactions between water and the fish's body. Thus, a functional description of swimming should account for hydrodynamics. Body shape can be assessed along major body axes to distinguish between elongated and squat fishes. The elongation factor is the ratio of maximal body depth to standard length (Gatz 1979). Elongated species have high values whereas compact species have low values. The shape of transverse body section (ratio between maximal body depth relative to maximal body width) has also been used as a proxy of vertical position in the water column because most benthic fishes are vertically flattened or rounded (e.g. Pleuronectiforms, Siluriformes, Gobiidae), while most bentho-pelagic fishes have deep bodies (e.g. Percidae, Sparidae, Carangidae). However there are numerous exceptions to this pattern (e.g. wrasses, tunas).

As for the relationship between morphological traits and diet, relationships between one morphological trait, or a combination of traits, and swimming performance have been demonstrated only for a few species, mainly labrids of coral reefs (Fulton et al. 2001; Fulton 2007) and centrarchids of North-American lakes (Higham 2007a). Further studies including several families and hence morphologies are needed to generalize these findings and also to quantify the relative effect of each morphological trait on each swimming performance parameter (manoeuvrability vs. acceleration) under natural conditions. It is indeed likely that measures of potential performance under controlled conditions overestimate the realized swimming performance in the wild. For instance, MPF swimmers routinely swim on coral reefs closer to their maximal speed measured in controlled condition than BCF swimmers, because BCF swimmers have a lower manoeuvrability (Fulton 2007).

Profiling mobility through categories

Mobility could be described using categories based on expert knowledge about fish ecology already available in literature (e.g. http://www.FishBase.org), as for describing food acquisition strategy. Swimming activity could be coded using ordered categories: sedentary (fish swimming very little during a day), mobile within a habitat (fish swimming but only over short distances, e.g. within a reef or within a river pool), or mobile between habitats (Mouillot et al. 2014). These two rough classification schemes could be completed with more detailed information about the swimming abilities of species, e.g., current velocity preference for riverine fishes coded as rheophilic, limnophilic or eurytopic (Olden et al. 2006; Villéger et al. 2014), or migratory behaviour between ecosystems (e.g. anadromous, catadromous; Buisson et al. 2013). Vertical position in the water column, which affect trophic interactions (both with preys and predators) and vertical translocation of nutrient, could be coded using three ordered categories: benthic (fish staying on the bottom most of the day), bentho-pelagic (fish feeding on benthic prey and swimming in the water column most of the day) and pelagic (fish feeding in the water column) (Mouillot et al. 2014; Villéger et al. 2014).

Assessing how fishes modify their habitats

Through their foraging activities, fish can act as ecosystem engineers, i.e. they can physically alter habitats. For instance, large parrotfishes play a key role in bioerosion of coral reefs (Bellwood et al. 2003) and sediment-feeding fish can act as “biological bulldozers” (Flecker and Taylor 2004). In the same way, bioturbation induced by fish foraging or swimming increases exchanges between water and sediment which has important effects on sediment physico-chemistry and water column processes (Scheffer et al. 2003), and ultimately on organic matter remineralisation (Yahel et al. 2008). These roles could be described with a functional trait measuring the volume of substrate removed per unit area and time for each type of sediment (e.g. sandy, muddy). The turbidity induced by fish activity measured in situ or in controlled experiments could also be used as a rough estimate of the overall effect of bioturbation (Braig and Johnson 2003). An alternative to these time-demanding measurements could be to categorize the potential of a species to remove substrate according to a rough classification of species based on their diet and size for bioerosion, and based on size and position in the water column for bioturbation (Mouillot et al. 2014).

Assessing how fishes mediate biogeochemical fluxes

The mineral nutrients that usually limit autotrophs in aquatic ecosystems are nitrogen (N) and/or phosphorus (P) (Elser et al. 2007). Carbon (inorganic or organic compounds) is also important for ecosystem functioning and is the main component of fish tissues and fish prey items; indeed, most fish are likely to be limited by energy (C) rather than nutrients (N or P) (Schindler and Eby 1997). Fish contribute indirectly to the regulation of nutrient cycles in aquatic ecosystems through their top-down effects on food webs, which modify the abundance of, and thus nutrient uptake by, primary producers. This indirect role is linked to their consumption of other organisms and thus could be described using the traits presented in the section above (e.g. Mouillot et al. 2014). In addition, fish also directly affect nutrient fluxes through nutrient cycling (Vanni 2002). Nutrient cycling by fish communities was historically neglected, compared to research on nutrient cycling by microbes or zooplankton, but has been studied much more over the past couple of decades, and numerous studies highlight their importance (Vanni et al. 2002, 2006; Hood et al. 2005; McIntyre et al. 2008; Layman et al. 2011; Allgeier et al. 2014). Here we present methods to assess the direct contributions of fish to nutrient cycling through their storage and release of nutrients and through their mobility.

Contribution of fish to nitrogen and phosphorus cycling through excretion and egestion

As do all animals, fish ingest, store and release nutrients. It is thus critical to quantify how fish functionally manage these elements, especially nitrogen and phosphorus, elements that are also crucial for primary production and ecosystem functioning. A nutrient budget for an individual fish can be split into three components: acquisition, storage and release (Schindler and Eby 1997; Vanni 2002). Nutrient acquisition depends on diet composition, i.e., which resources are consumed, and the nutrient content of these resources. A fraction of ingested nutrients is assimilated, the remainder being released as faeces (egestion). Assimilated nutrients are subsequently allocated to growth or reproduction, or released as metabolic wastes through gills and kidneys (excretion).

Excreted nutrients are released mainly in inorganic forms (N as ammonium and P as soluble reactive phosphorus), although organic forms (e.g., urea) may not be negligible and should be considered more often. Nutrient excretion rates of individual fish can be relatively easily assessed in the field for many species (Vanni et al. 2002; McIntyre et al. 2007; Villéger et al. 2012a; Allgeier et al. 2015a, b), although it could be difficult to do so for very large fish. Basically, individuals are kept in a small water volume for a short period (to minimize the decrease in excretion that occurs when animals are not feeding) and nutrient concentrations are measured before and after incubation to get nutrient excretion rates. Intra and interspecific variability in per capita excretion rates can range up to three orders of magnitude (Vanni et al. 2002; McIntyre et al. 2007; Villéger et al. 2012a; Allgeier et al. 2015b). These per capita excretion rates values could then be regressed against fish body mass using an allometric model, which allows investigation of both intraspecific variability due to fish size as well as interspecific differences among the allometric coefficients (Vanni et al. 2002; Torres and Vanni 2007; Pilati and Vanni 2007; Yeager et al. 2011; Villéger et al. 2012a; Allgeier et al. 2015b). For instance, for most species the allometric coefficient is lower than one, indicating that small individuals recycle proportionally more nutrients (i.e., per unit mass) than large ones (Vanni et al. 2002; Hall et al. 2007; Torres and Vanni 2007). This pattern is also true among species (Sereda and Hudson 2011; Villéger et al. 2012a; Allgeier et al. 2015b).

Egested nutrients are released in particulate form and are less bioavailable to primary producers than excreted inorganic nutrients. However, faecal nutrients are certainly remineralized by bacteria, rendering them available to primary producers. Intra and interspecific variability of egestion rate has been less studied than excretion rates and should thus be assessed more often, both in terms of quantity and quality of the organic matter released (Meyer and Schultz 1985), including location of faeces release (Krone et al. 2008).

The balance between fish growth, nutrient ingestion and nutrient release (excretion plus egestion) determines fish body nutrient content (Frost et al. 2006), which is usually described as the proportion of N and P per unit fish mass or as the N:P ratio of body tissues. Measuring body nutrient content is needed to describe the ability of fish to act as a nutrient sink by storing nutrients over long periods (from days to years) and thus to slow down nutrient cycling (Hood et al. 2005; Vanni et al. 2013). Such an effect is especially important for phosphorus (compared to nitrogen), which is sequestered in fish skeleton until fish death and is slowly released by microbial degradation of fish carcass (Vanni et al. 2013).

Measuring nutrient excretion and nutrient egestion on several captive individuals per species is a demanding task. Bioenergetics modelling allows predicting nutrient excretion rates based on a set of parameters taken from the literature or measurable on dead individuals (fish mass, growth rate, diet composition, body nutrient content and assimilation efficiency). This approach allows estimating the effect of fish on nutrient cycling at a daily scale and to compare them with other nutrient fluxes (e.g., Boulêtreau et al. 2011; Burkepile et al. 2013; Allgeier et al. 2014). Although bioenergetics modelling is cheaper and more integrative than in situ measurements (which account for immediate effects of stress and of physiological conditions of individuals on excretion rates), it incorporates the uncertainty in all model parameters and thus requires sensitivity analyses (Allgeier et al. 2014).

Beyond models built for individual species, the increasing numbers of empirical measurements of excretion rates is expected to allow for building predictive models of per capita excretion rates of any fish individuals given its mass and a few additional information such as trophic guild and/or taxonomic affiliation, as well as water temperature (e.g. Sereda and Hudson 2011).

Fishes as mediators of carbon fluxes

Beyond inorganic nitrogen and phosphorous cycles, fish communities also contribute significantly to carbon cycling.

Fish can indirectly mediate CO_2 fluxes across the air–water interface by regulating primary production through trophic cascades and nutrient excretion (Schindler et al. 1997). Besides this indirect impact, fish also contribute directly to carbon sequestration. Indeed, hypo-osmoregulation mechanisms induce bicarbonate precipitation in the gut of marine fishes (Wilson et al. 2002, 2009). This role could be measured on resting and unfed individuals kept in controlled condition (Wilson et al. 2002). However, this is a demanding task and thus only a few species have been used in such assessment. These values were however used to build a model predicting inorganic carbon mineralization rates per unit of mass based on fish body mass and water temperature by assuming that carbon mineralization is affected only by drinking rate which is linked to metabolism (e.g. Wilson et al. 2009). Further investigations are needed on a large range of species with different attributes (e.g. gut length, activity, diet) to validate this model to ultimately allow assessing this key role across marine ecosystems.

Vertical and horizontal translocation of nutrients by fish

Nutrient translocation, whereby fish physically move nutrients across habitats or ecosystem boundaries, results from the integration of three facets of the functional niche: food acquisition, locomotion and nutrient excretion. Nutrient translocation by fish communities even at a very small scale can significantly affect ecosystem functioning. For instance, fish feeding on benthic prey or detritus and excreting into the water column translocate nutrients formerly trapped in the benthos into water, where they are available for phytoplankton. This vertical nutrient translocation by these bentho-pelagic species can contribute to increased planktonic productivity (Schaus and Vanni 2000; Vanni et al. 2006).

Nutrient translocation by fish can also occur on a horizontal scale between different habitats within an ecosystem. For example, Meyer and Schultz (1985) showed that grunts (Haemulidae) feeding at night on seagrass meadows contribute significantly to the nutrient budget of the coral colonies where they rest during the day, through ammonium excretion and egestion of P-rich faeces on reefs. At a larger scale, nutrient translocation can occur among different aquatic ecosystems and even between aquatic and terrestrial ecosystems (e.g., by migratory salmon, Janetski et al. 2009).

Translocation by fish has never been considered on a per capita basis (i.e., functional trait sensu stricto) but it is determined by the combination of their diet, nutrient release rates (excretion and egestion) and vertical movements in the water column and/or horizontal movements between habitats. Translocation of nutrients can be roughly categorised (e.g., high/low potential) for each type of translocation (horizontal/vertical) based on fish mass and fish trophic guild (as a proxy of excretion and egestion rates) and their mobility within and between their habitats.

Assessing reproduction strategies

Reproduction influences fish fitness and demography and thus indirectly affects community resistance and resilience to perturbations as well as fish effects on ecosystem processes (Winemiller 2005; Winemiller et al. 2015). Life-history traits have been used in fish ecology for decades to classify species strategies [e.g. equilibrium-periodic-opportunistic model of Winemiller and Rose (1992)], to link community structure with environmental factors including competition with and predation from other organisms (Blanck et al. 2007; Mims et al. 2010), and to assess the sensitivity of populations to disturbance (Olden et al. 2006, 2008).

Many of these life-history traits are measured at the population level although they could be defined at the individual level so that they can be considered as functional traits (sensu Violle et al. 2007). For instance, it is impossible to forecast the age at first reproduction of a juvenile fish individual but it is possible to assess the probability that it will reproduce at a given age, based on the distribution of age among mature individuals present in the same population. Similarly, other life-history traits such as larval characteristics are usually assessed at the species level based on repeated observations of different populations (e.g. Olden et al. 2006; Mims et al. 2010).

We suggest focusing on reproduction investment by measuring the proportion of biomass allocated to reproductive organs or gametes for both sexes (e.g. clutch size scaled by body mass). This trait can be measured on any fish individual even if it will be null for juveniles or adults out of their reproduction period. For studies on species-rich communities, reproduction investment should be categorized based on the frequency of reproduction and relative investment in term of energy. Such a qualitative assessment could be carried out using data available in the literature and would allow distinguishing species that reproduce frequently (i.e., several times a year) with a high investment (e.g., Poeciliidae), species that reproduce frequently but with a small investment (e.g., Melanotaeniidae), species that reproduce yearly with a moderate investment (most species) and species that reproduce only once in their life with a high allocation to reproduction (e.g., Anguillidae or Pacific salmon). Larval survival and growth are related to egg size and hatching time that can be measured as continuous traits and spawning substrate that are coded using categories (Winemiller and Rose 1992; Franco et al. 2008). Larval life history could also be described using the ecoethological categories proposed by Balon (1975) and hence discriminating reproduction sites (planktonic vs. benthic) and types of parental care (e.g., no parental care, oral incubation, mouth brooding or nest guarding).

Age at first reproduction is another complementary aspect of reproduction that can discriminate species with a short immature period (e.g., Poeciliidae) from species that need several years before investing energy into reproduction (e.g., eels, sturgeons). Information on age at first reproduction is thus critical in understanding how communities respond to anthropogenic disturbances (e.g., overfishing of immature individuals) and potential invasiveness for exotic species (e.g., mosquitofish *Gambusia* spp.) (Winemiller 2005). This trait should be coded separately for females and males of protandrous or protogynous hermaphrodite species (e.g., clownfish and wrasses).

Assessing defence against predation

In most aquatic ecosystems, fishes are predated by many animals (including other fish) and thus their diversity and biomass affect the demography of aquatic top-predators (e.g., tunas, sharks, marine mammals), and more generally the structure of food webs in aquatic and even of adjacent terrestrial ecosystems through predation by terrestrial animals (e.g., birds, bears). It is therefore important to characterize fish defence strategies, because these functional traits influence species fitness, the structure of fish communities, and the functioning of aquatic ecosystems.

The probability that a fish individual will encounter a predator is affected by the overlap in their habitat use. This overlap could vary between species and individuals according to their ability to detect predators (e.g., visual or chemical cues) and their behavioural syndromes (e.g., boldness, flight initiation distance). These traits are hard to measure on many individuals in realistic conditions (but see Januchowski-Hartley et al. 2013, for a case study on coral reefs). However, it is at least feasible to categorize period of activity (nocturnal vs. diurnal) and use of habitats within an ecosystem (e.g., substrate vs. water column) at the species level (Luiz et al. 2013).

Given a potential predation risk, lowering detectability by predators is the most obvious way to avoid predation. Most fish species exhibit countershading with a dark back and a bright ventral face, which prevents them from being seen from both above and below. Other species have very specialized coloration, morphology and/or behaviour and are very well concealed (e.g., fish that mimic seagrass leaves or algae or that burrow into the substrate). Obviously, mimicry may also be linked to ambush predatory behaviour and may thus be relevant to describing food acquisition strategy. For methodological simplicity, we propose to classify species detectability roughly into three ordered categories: high (colourful), medium (countershading) and low (camouflage, crypsis or mimicry). This trait can be coded using pictures or even scientific drawings from reference textbooks.

Another way to avoid predation is to escape from capture after being detected by predators. One option is to escape by swimming, either rapidly or by turning quickly. These abilities are directly related to locomotion. The other option is to be bigger than predators. A large body section (deep and/or wide body) is hence an indirect way to avoid predation since larger fish have a smaller chance of being eaten by gape-limited predators (Price et al. 2015).

Schooling is another strategy to minimize predation risk at the individual level (Brandl and Bellwood 2014b, but see; Ford and Swearer 2013 for an example of increasing predation risk when several predators are present). Schooling could be categorized as an ordinal trait, i.e., solitary, pairing, forming small (3–20 individuals), medium (21–50 individuals) or large groups (more than 50 individuals) based on field observations (Brandl and Bellwood 2013; Luiz et al. 2013; Mouillot et al. 2014; Luiz et al. 2015).

Fish can also dissuade predators from attacking them by being inedible, because of physical or chemical protection (Price et al. 2015). Physical protection, in addition to large size, includes three main categories: bony carapaces (e.g., boxfishes, pipefishes and armoured catfishes), spines (e.g., porcupinefishes, catfishes, and scorpionfishes) and inflating bodies (puffers, porcupinefishes). Fish with chemical defences can harbour venomous spines (e.g., scorpionfishes, catfishes) or toxic organs (e.g., puffers with tetrodotoxin). We propose to classify defence against predation in five categories mixing physical and chemical defences: no physical or chemical defences, bony carapaces, non-poisonous spines, poisonous spines, and toxic organs. Classifying fish species into these categories could be done based on the information available in http://www.FishBase.org (Froese and Pauly 2017).

Challenges and future directions

The functional approach of fish communities has been increasingly used during the last decade to assess functional diversity of thousands of fish assemblages in freshwater and marine ecosystems, considered over a wide range of spatial scales, from local to global (Villéger et al. 2012b; Parravicini et al. 2014). Those studies have helped to disentangle the biogeographical and environmental drivers of functional diversity (Mims et al. 2010; Brind'Amour et al. 2011; Schleuter et al. 2012; Villéger et al. 2013; Montana et al. 2014), the links between functional diversity and ecosystem functioning (McIntyre et al. 2008; Allgeier et al. 2014) and to assess functional changes caused by disturbances (Villéger et al. 2010; Layman et al. 2011). However, beyond these significant achievements there are still gaps that need to be filled by fish functional ecologists in the near future.

Additional traits for overlooked services

Functional traits describing food acquisition, locomotion and nutrient budgets have been the most investigated during the three last decades, as they are needed to assess the key roles played by fish. However, other key facets of fish ecology deserve to be considered using a functional approach as they influence the services supplied by fish communities.

Assessing functional traits of fished and farmed fishes

Fish are a significant source of protein for most of people in the world and this service is provided by both wild fisheries and aquaculture (FAO 2010). Impacts of fishing have been studied for decades and have revealed that most fishing techniques decrease taxonomic and functional diversity of fish communities (e.g., D'Agata et al. 2014) but there is still no direct assessment of the functional diversity of the species targeted by fisheries. It would thus be relevant to assess the functional diversity of fished species (including targeted and non-targeted species) of various fisheries to quantify how this diversity is driven by the pool of species present in a ecosystem, by fishing techniques (e.g. artisanal vs. commercial, different type of nets) and by socio-economical factors (e.g. income, religion). Functional traits to consider for addressing this question should include at least size, diet, mobility and quality of flesh (e.g. lipid and protein content, proportion of muscle vs. bones).

Besides the hundreds of species targeted by fisheries, 250 fish species are now farmed in freshwater or marine ecosystems (Teletchea and Fontaine 2014). It would be of interest to compare the functional traits of farmed species to that of the non-farmed species (or populations of the same species) to quantify how the domestication process have selected some combinations of traits values (voluntary or not) and to identify the future candidate species for aquaculture (Teletchea and Fontaine 2014).

Fish functional diversity as a source of cultural services

In addition to providing provisioning and regulating services to human populations as source of protein and as regulators of biogeochemical fluxes and of biomass of other species, fish are also the basis of high-value cultural services though recreational activities, intellectual, and even spiritual interactions (Holmlund and Hammer 1999; Moberg and Folke 1999). First, some fish species are targeted by recreational fishing for food consumption, but also for entertainment only through catch and release fishing (e.g., brown trout *Salmo trutta*, common carp Cyprinus carpio in Europe) and these two types of recreational fishing generate economic activities (e.g., licence, gear, travels) (Cooke and Cowx 2004). Second, high abundance and diversity of fish certainly improve the attractiveness of clear-water ecosystems (e.g., coral reefs) for SCUBA diving and snorkelling activities. Third, wild and farmed individuals of hundreds of freshwater and marine fish species are available on the global ornamental fish market and aquarium industry has been continuously growing for the last decades (Leal et al. 2015). Fourth, fish are a source of inspiration for arts, as illustrated by the global success of the Pixar © movie "Finding Nemo" that grossed more than $900 million. Assessing which traits determine the cultural value of a fish species and/or of a fish assemblage is thus a future challenge for fish ecology. A list of candidate functional traits to explore will depend on the activity studied, with for instance size and diet for recreational fishing, and size, colour, mobility and gregarity for aesthetic-based services.

Accounting for intraspecific variability of functional traits

One of the biggest challenges in functional ecology is how to deal with the intraspecific variability of traits (Violle et al. 2012). In practice, for most traits, values are recorded for a set of individuals and these values are averaged at the species level assuming that intraspecific variability is weak compared to interspecific variability. However, many traits are known to vary among individuals from the same species (Bolnick et al. 2003), through allometric relationships with body mass (e.g., nutrient excretion rates; Vanni et al. 2002), marked ontogenetic changes between juvenile and adult life stages (e.g., shifts in diet, morphology and/or body stoichiometry; Zhao et al. 2014) and/or through phenotypic plasticity linked to the abiotic and biotic environment (e.g., body shape of pelagic vs. littoral Eurasian perch; Vrede et al. 2011). Therefore, intraspecific variability should be more frequently assessed to measure its magnitude relatively to interspecific variability (Dumay et al. 2004), to understand its biological (e.g., sexual dimorphism, ontogeny, genes) and ecological determinants (e.g., abiotic environment, trophic subsidies), and to ultimately assess its impact on ecosystem functioning (Bolnick et al. 2011).

When a species has high intraspecific variability, it could be split into several functional entities (corresponding to sex and/or age class or to populations), which would each have lower inter-individual trait variability than the species as a whole, and community scale metrics could then be computed on these functional entities. This solution could be applied to both continuous and categorical traits.

For continuous allometrically scaled traits, the intercept and slope of the relationship between individual trait value and body mass could be used as functional traits.

Building large databases of traits values

Fish ecologists have been measuring functional traits for more than three decades (Gatz 1979). However, since the set of traits often differs among studies, conducting meta-analyses remains a hard task. We hope that the list of traits we propose will inspire others to measure functional trait values on a large number of species, as has been achieved for plants (Kattge et al. 2011) and corals (Madin et al. 2016). Towards this goal it is necessary to detail experimental settings to use for measuring fish traits on living individuals (e.g., incubation time for excretion assessment, Whiles et al. 2009) or on preserved individuals (e.g., morphological traits, Bellwood et al. 2014), for instance through publication of a handbook for fish functional ecology similar to that for plants (Cornelissen et al. 2003) or for terrestrial invertebrates (Moretti et al. 2017). Several recent technological developments (e.g. 3D modelling, Porter et al. 2015; machine-learning algorithms, Voesenek et al. 2016; X-ray videos, Camp et al. 2015; high-throughput sequencing, Leray et al. 2013) will increase our ability to measure traits and performance on many individuals and/or to test links between traits and performance on large set of species.

Such large databases would be of great help in studying trait distribution on a large number of individuals and species. For instance, we know that adult fish size varies by six orders of magnitude (from ca. 1 g to ca. 1 ton) among the 26,891 ray-finned fish species (Nelson 2006), and that size distribution is strongly right-skewed with most of fish species being small (Blanchet et al. 2010). In contrast, the global distribution of most traits remains little known as they have only been published for subsets of less than 1000 species (but see Claverie and Wainwright 2014 for morphological traits and Mouillot et al. 2014 for categorical traits). Similarly, correlations between traits are known for only a small set of species while they could reveal ecological constraints (Vanni et al. 2002; Price et al. 2015). Importantly, large databases are also needed to test whether biomechanical traits are better than morphological traits to explain functions such as prey capture or swimming, or roles such as herbivory or bioerosion, across large sets of species.

More generally, large functional trait databases would benefit from, and would confer benefits upon, the growing effort to build fish phylogenies (Rabosky et al. 2013). First, coupling phylogenetic and functional information on the same species could shed light on functional convergence between species from different families (e.g. Grubich 2003), or functional divergence between phylogenetically close species (e.g. Westneat et al. 2005). Functional convergence will confirm that some trait combinations are favoured in particular environments or to perform a given function (Friedman et al. 2016), while functional divergence within a clade will prove that evolutionary radiation occurred (Winemiller 1991; Price et al. 2011). Second, coupling fish phylogenies with functional traits would allow testing for the existence of phylogenetic trait conservatism among a large number of taxa and within clades (e.g., families, orders) (Münkemüller et al. 2012). Quantifying the strength of such conservatism would be helpful in testing whether phylogenetic diversity and functional diversity bring independent information on species (Cadotte et al. 2011), which has profound implications for both the conservation (e.g., setting priorities for the different facets of biodiversity, Mouillot et al. 2011a) and functioning (different facets together explain ecosystem processes, Cadotte et al. 2011) of fish assemblages. Moreover, if a strong phylogenetic conservatism is found within a clade, it would facilitate predicting trait values for species poorly described in the literature and/or relatively inaccessible, based on values from phylogenetically close species.

Disentangling the determinants of fish functional diversity and assessing how anthropogenic disturbances modify services provided by fish

Freshwater and marine aquatic ecosystems are facing accelerated rates of changes, including fishing, non-native species introductions, and environmental changes such as climate warming, habitat loss and pollution (Halpern et al. 2008; Vörösmarty et al. 2010). These disturbances are known to change the taxonomic structure of communities (Myers and Worm 2003; Leprieur et al. 2008), and as fish often play dominant roles in these ecosystems (Fig. 3), there is an urgent need to assess the associated changes in functional diversity of fish communities to design relevant conservation measures that can protect this key facet of biodiversity.

The functional diversity of fish assemblages could be measured using multivariate indices based on several traits (Petchey and Gaston 2006; Mouillot et al. 2013; Villéger et al. 2013). Measuring functional diversity within and between assemblages and analysing observed values using null-models or structural-equation modelling, has been helpful in disentangling the assembly rules that shape fish assemblages from local to regional scales (Peres-Neto 2004; Mason et al. 2007; Schleuter et al. 2012; Villéger et al. 2012b; Mouchet et al. 2013; Leitão et al. 2017). Disentangling the effect of environment on fish functional diversity could also be achieved without computing indices, thanks to statistical analyses using matrices of environmental conditions and species presence/absence or abundance

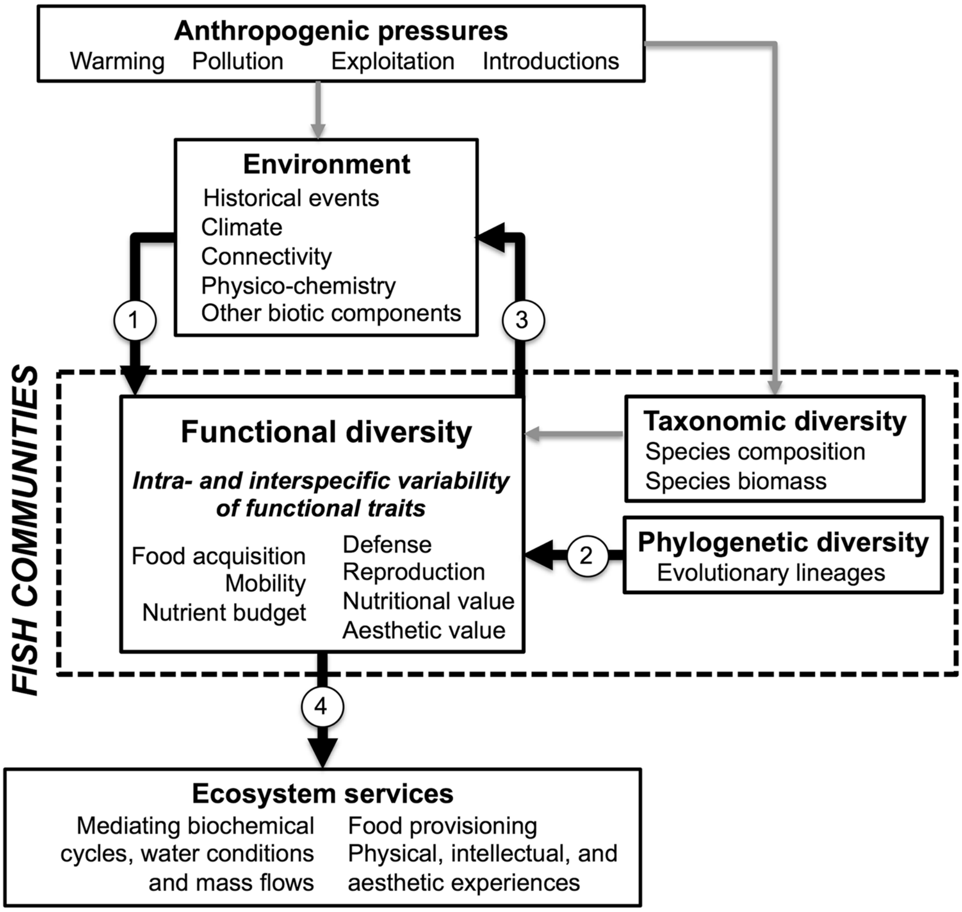

Fig. 3 The functional approach of fish to study the consequences of global change on ecosystem services. Anthropogenic disturbances (*thin grey arrows*) modify aquatic environments (e.g. physico-chemistry, habitats) and the taxonomic structure of fish assemblages (i.e. composition and abundance of species). Assessing functional diversity of fish assemblages (i.e. diversity of species trait values weighted by species abundance) helps to understand how environment (including historical legacies) determines structure of fish communities (*black arrow* 1) and hence to forecast impacts of anthropogenic disturbances. Assessing relationships between fish functional and phylogenetic diversity is needed to understand how evolution shaped current traits diversity among lineages (*black arrow* 2). Assessing functional diversity of fish is also needed to understand how they affect their environment (*black arrow* 3) and provide ecosystem services to human populations (*black arrow* 4)

in the same sites and matrix of species traits, namely RLQ (e.g. Pease et al. 2012) and fourth-corner methods (e.g. Brind'Amour et al. 2011).

These studies were based on morpho-anatomical traits describing fish strategies, as the aim was to understand how local environmental conditions and/or biotic interactions filter the functional space available given the regional pool of species, thereby favouring only a subset of functional strategies in local communities (Petchey and Gaston 2006). In contrast there is an urgent need to assess the variability between assemblages in terms of functional traits related to fish roles. Such an approach could allow linking the physical environment to ecosystem functioning through fish functional diversity. For instance, McIntyre et al. (2008) found that fish assemblages in riffle habitats have higher nutrient recycling potential than fish assemblages from run habitats because large detritivorous species tend to prefer low-current habitats.

Furthermore, even if investigations at large scale are developing (e.g., Schleuter et al. 2012; Mouillot et al. 2014), a remaining challenge of functional diversity assessments is to provide continental and global maps of fish functional traits. This has already been achieved for a few taxa thanks to a consensus on traits to use and the collective effort to measure traits on thousands of taxa (e.g., mammals, Safi et al. 2011 and woody plants, Swenson et al. 2012). Such large-scale functional biogeography aims to assess the spatial congruence between taxonomic, functional, and phylogenetic diversity, and especially to test if species hotspots are also functional hotspots or if the accumulation of species only contributes to a higher functional redundancy (Mouillot et al. 2011a; Parravicini et al. 2014). A high functional redundancy might indicate a high resistance of ecosystem functions to species loss, which is a key issue in the context of ongoing global environmental change. In the same way, testing whether taxonomic coldspots have a lower functional redundancy is also an important question, as it would imply that ecosystem functioning in such species-poor regions is highly vulnerable to species loss (Bellwood et al. 2004; Mouillot et al. 2014).

Anthropogenic disturbances directly modify species composition and biomass of fish communities through exploitation or exotic species introductions. They also indirectly affect fish communities through habitat loss, land use or climate change. For a decade, several studies have shown that disturbances alter the functional diversity of fish communities by selecting for "winner" and "loser" species (or even individuals, Franssen et al. 2013) according to their functional features (Olden et al. 2006; Villéger et al. 2010). However, there are still few studies on this topic and the next challenge will be to find the combinations of traits that explain the responses of species to each type of disturbance (Mouillot et al. 2013). More importantly, this evaluation should also include traits related to species' roles, which and are the main determinant of changes in ecosystem functioning following disturbance, and may be indirectly filtered by disturbance (McIntyre et al. 2007; Layman et al. 2011; Bellwood et al. 2012). For instance, fishing is known to reduce mean fish body size and total fish biomass but predicting its consequences on nutrient cycling requires detailed knowledge of intra and interspecific variability in nutrient excretion rates. Indeed, reducing mean individual size has a positive effect on excretion rates per unit of fish mass (because of allometric scaling of excretion rates) while the decreases in total fish biomass decrease the recycling potential of fish communities. In addition, species that are most heavily fished by artisanal fisheries could also be those that have the highest excretion rates per unit of mass (McIntyre et al. 2007; Layman et al. 2011).

Aside from investigating local changes in functional diversity, it would also be of interest to investigate how disturbances modify the similarity among fish communities. For example, studies show a trend towards increases similarity between freshwater fish faunas, i.e. functional homogenization (Clavero and Garcia-Berthou 2006; Villéger et al. 2014), due to humans transporting the same fish species outside their native range. It is thus urgent to assess the level of functional homogenization due to other disturbances (e.g. fishing, warming), considering all facets of fish functional diversity. Ultimately, a crucial question to test is how changes in functional similarity among communities would affect the resistance and resilience of ecosystems to disturbances (Bellwood et al. 2004).

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