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Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages

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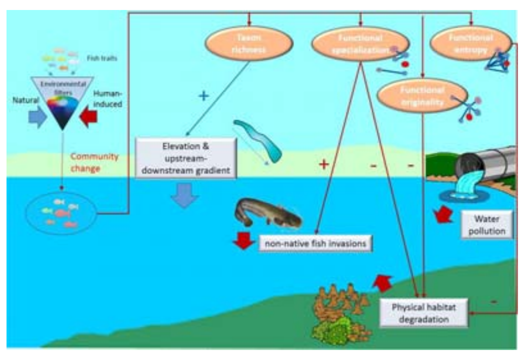
HIGHLIGHTS

- Functional trait-based ecology is poorly developed in species-poor systems.
- We show the suitability of two indices of functional diversity in riverine fish.
- Indices mostly responded to altitude, physical habitat quality and alien fish biomass.
- Taxon richness and other fish indices were poorly related to habitat alterations.
- River health misdiagnosis possible if alien fish biomass high and habitat quality good.

GRAPHICAL ABSTRACT



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ABSTRACT

Trait-based ecology has been developed for decades to infer ecosystem responses to stressors based on the functional structure of communities, yet its value in species-poor systems is largely unknown. Here, we used an extensive dataset in a Spanish region highly prone to non-native fish invasions (15 catchments, $N = 389$ sites) to assess for the first time how species-poor communities respond to large-scale environmental gradients using a taxonomic and functional trait-based approach in riverine fish. We examined total species richness and three functional trait-based indices available when many sites have ≤3 species (specialization, FSpe; originality, FOri and entropy, FEnt). We assessed the responses of these taxonomic and functional indices along gradients of altitude, water pollution, physical habitat degradation and non-native fish biomass. Whilst species richness was relatively sensitive to spatial effects, functional diversity indices were responsive across natural and anthropogenic gradients. All four diversity measures declined with altitude but this decline was modulated by physical habitat degradation (richness, FSpe and FEnt) and the non-native:total fish biomass ratio (FSpe and FOri) in ways that varied between indices. Furthermore, FSpe and FOri were significantly correlated with Total Nitrogen. Non-native fish were a major component of the taxonomic and functional structure of fish communities, raising concerns about potential misdiagnosis between invaded and environmentally-degraded river reaches. Such misdiagnosis was evident in a regional fish index widely used in official monitoring programs. We recommend the application of FSpe and FOri to extensive datasets from monitoring programs in order to generate valuable cross-system information about the impacts of non-native species and habitat degradation, even in species-poor systems.

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Scoring non-native species apart from habitat degradation in the indices used to determine ecosystem health is essential to develop better management strategies.

1. Introduction

Biodiversity loss is occurring at unprecedented rates on Earth, and freshwater ecosystems are a prime example (Strayer and Dudgeon, 2010; Tittensor et al., 2014). The EU's Water Framework directive has been highly influential in Europe to take conservation actions on major threats to freshwater ecosystems, mainly water pollution and hydromorphological alterations (EU Commission, 2003). However, effective management strategies can only be developed with a good knowledge of how multiple impacts affect aquatic biota, including biological invasions (Thomsen et al., 2014).

The loss of sensitive species is a well-known response of aquatic communities to stress (Kolkwitz and Marsoon, 1909; Friberg et al., 2011), and the basis of the myriad of taxonomic-based procedures developed, hereafter referred to as indices of biotic quality (IBQs), to assess the health status of rivers (Birk et al., 2012; Karr, 1981). Despite being widely adopted by resource managers, many criticisms have arisen from their use (Friberg et al., 2011; Jackson et al., 2016). Among the most important is that the extensive use of IBQs may have limited our ability to develop theory on how aquatic assemblages respond to stress. Ecological niche theory states that habitat acts as 'filter' selecting those species with the best set of traits for a given condition (Chase and Leibold, 2003). That is, communities geographically distant can differ in species composition but have similar trait combinations (e.g. Bonada et al., 2007).

Towards predicting the response of communities, functional ecology has been developing in recent decades (Petchey and Gaston, 2006; Statzner et al., 2001) including functional diversity (FD) measurements based on species' functional traits, i.e. attributes of organisms linked to their response to environment or their role in ecosystem processes (Maire et al., 2015; Mouillot et al., 2013; Petchey and Gaston, 2002). It is widely recognised that FD measures are a superior alternative to taxonomic-based approaches to detect the consequences of human impacts on animal assemblages (e.g. Gagic et al., 2015; Hooper et al., 2005; Villéger et al., 2010). However, their advantages over IBQs have not been specifically investigated. IBQs often use community traits in making diagnoses, but resultant scores do not explicitly account for functional diversity.

Here, we assess how taxonomic richness and the functional structure of freshwater fish assemblages respond to fish invasions and environmental degradation in an extensive area of north-eastern Spain. This region has a long-history of anthropogenic disturbances (e.g. water pollution, physical habitat degradation, and non-native invasions; Figuerola et al., 2012; Maceda-Veiga et al., 2017a; Mas-Martí et al., 2010) and allow us to assess the relative contribution of these three factors to variation in the structure of fish assemblages in a wide range of orographic conditions (Sabater et al., 2009). If suitable for river biomonitoring programs, fish diversity measures should respond to three major threats to riverine ecosystems, namely water pollution, physical habitat degradation and non-native fish invasions and, to a minor degree, to natural factors, including altitude. However, the low fish species richness in Mediterranean rivers (often <4 species, e.g. Maceda-Veiga et al., 2017a) contrasts with the higher richness in other European rivers and may limit the performance of FD indices to detect effect of stressors (see Maire et al., 2015). Nonetheless, this region is highly prone to non-native fish invasions, with tributaries containing mostly native species and lowland mainstems mostly non-native species (up to six invasive species in Maceda-Veiga et al., 2017a).

The life-histories of native fish populations, including endemic (*Barbus haasi* Mertens 1925, *Luciobarbus graellsii* Steindachner, 1866) and widely distributed species (*Salmo trutta* Linnaeus, 1758, *Anguilla anguilla* Linnaeus, 1758), are adapted to the hydrological dynamism of Mediterranean rivers (e.g. Vinyoles et al., 2010; Doadrio, 2011). However, fish species introduced in this area, including globally distributed invaders (e.g. *Alburnus alburnus* Linnaeus, 1758, *Cyprinus carpio* Linnaeus, 1758), appear to perform better in hydrological regimes generated by damming and water abstractions than in natural rivers (Maceda-Veiga et al., 2017a).

The objectives of our study are: i) to test whether three FD indices (functional specialization, originality and entropy) identify the impacts of human activities better than does taxonomic richness in species-poor fish assemblages, and ii) to compare the diagnostic value of traditional IBQs and FD indices in detecting two major threats to rivers, namely habitat degradation and the release of non-native species, which may not necessarily co-occur (see Benejam et al., 2009). We expected that FD indices would provide better inferences of how fish invasions, water pollution and physical habitat degradation affect fish assemblages than would do species richness alone, because community-habitat relationships should be mediated via functional traits (e.g. Suding et al., 2008). If FD indices have potential to become new monitoring tools in species-poor systems, we expected them to perform better than a regional fish index and other IBQs widely used by water agencies in compliance with the EU's Water Framework Directive.

2. Materials and methods

2.1. Study area

The study area is located in north-eastern Spain and comprises 15 catchments, including the complete Ebro River and part of the Garonne basin (Fig. 1). Except the Garonne, all rivers flow east from the Cantabrian, Pyrenean or low mountains to the sea. Overall, the selected river basins drain an extensive area of up to 99,700 km^2 and the variety of human impacts over large-scale natural gradients provide an excellent study system (see also Sabater et al., 2009). Approximately 40% of all sampling sites ($N = 389$) have non-native species. The range of values for widely used indicators of pollution (e.g. conductivity and nutrients) is wide in invaded (conductivity = 79–4108 μS cm^{-1}; nitrate = 0–25 mg l^{-1}) and non-invaded sites (conductivity = 20–4108 μS cm^{-1}; nitrate = 0–30 mg l^{-1}). Similarly, the altitudinal range of sites with non-native (3–984 m.a.s.l.) and native species was wide (3–1814 m.a.s.l.) (see Maceda-Veiga et al., 2017b for further details).

Most of these rivers are small and follow a typical Mediterranean hydrological regime, with severe droughts in summer and torrential floods in autumn. In large rivers, however, streamflow peaks in spring because of snowmelt. We surveyed in low flow conditions because this is when fish populations can be most efficiently sampled using electrofishing (see below). These conditions are also likely to intensify the effects of anthropogenic stressors on aquatic organisms (Petrovic et al., 2011).

2.2. Fish surveys

We assembled fish data from 430 surveys performed in north-eastern Spain from 2002 to 2008 (e.g. Sostoa et al., 2003; Maceda-Veiga and de Sostoa, 2011). Our surveys followed an international standardized