

# Morphology reflects differently the various facets of species traits in stream fish

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## Abstract

1. Biodiversity is a multifaceted concept for which the functional component, that influences many aspects of ecosystem functioning, remains difficult to characterise. In several taxa, many studies rely on morphological traits as proxies of species ecological attributes. However, the extent to which morphology provides a good surrogate of ecological traits has rarely been acknowledged.
2. Here, we used morphological and ecological trait databases to test whether morphological traits are linked to ecological traits and can be used to assess various biodiversity facets in 254 stream fish communities across France.
3. We firstly computed co-inertia analyses to test the association between morphological and ecological traits related to either habitat use, feeding or life-history strategies. We then computed a suite of diversity indices to investigate the relationship between morphological and ecological indices.
4. We found a strong association between morphological and ecological traits, and significant relationships between diversity indices computed on morphological and ecological traits. However, these relationships varied according to the index and type of ecological traits, with the strongest relationship observed with traits related to habitat use.
5. Although these results highlight that the use of morphological data is a promising way to understand ecological diversity, they also reveal that the choice of diversity index and the type of ecological traits targeted are particularly important and need to be taken into consideration.

## KEYWORDS

co-inertia analysis, diet, functional diversity, habitat use, life-history traits

## 1 | INTRODUCTION

Functional diversity can be seen as the diversity of ecological traits defined as characteristics influencing individuals' fitness (Violle et al., 2007). Ecological traits are traits that reflect life histories, physiological requirements and morphological adaptations of an organism (Frimpong & Angermeier, 2010). They have received increasing attention since the late 1980s (Calow, 1987; Tilman et al., 1997),

in relation to improving our understanding of the relationship between diversity and ecosystem function.

At the species level, measuring ecological traits is difficult. Thus, morphology has been used largely as a proxy of functional traits in many taxa such as birds (Ricklefs, 2012), fish (Arbour & López-Fernández, 2014; Schleuter et al., 2012), mammals (Luza et al., 2015) or plants (Flynn et al., 2009). However, ecological traits, and *a fortiori* functional diversity, encapsulate several components of the ecological niche

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such as feeding, habitat use or life-history strategies. Several ecological and morphological studies have documented relationships between morphology and one particular aspect of ecological strategy, especially for habitat use, in lizards (Higham et al., 2015; Ord & Klomp, 2014) and fish (Leal et al., 2013), and for feeding diet in fish (Berchtold et al., 2015; Ferreira Filho et al., 2014; Machado-Evangelista et al., 2015), bats (Clairmont et al., 2014) and birds (Lisney et al., 2013). Strong links between body size and reproductive life-history traits also have been established (Kingsolver & Pfennig, 2004; Stahler et al., 2013) since body size is under several selection pressures (Herrel et al., 2008; Olson & Hearty, 2010). Relationships between egg size and body size and shape of individuals have been shown in crustaceans (Fišer et al., 2013). Other studies on vertebrates also highlighted the link between body size and life-history traits such as clutch size, lifespan or size at sexual maturity (Molina-Borja & Rodríguez-Dominguez, 2004), but also with behavioural traits such as boldness (Mayer et al., 2016). Nevertheless, few studies succeeded in revealing a link between life-history traits and morphological traits other than body size. In arthropods, a strong correlation between wing morphology and diapause occurrence has been shown for several species of heteropteans (under laboratory and field conditions) since these two traits present a common genetic basis (Bégin & Roff, 2002; Harada & Numata, 1993). Some life-history traits also can be constrained by morphology, such as in lizards where the clutch size is dependent on ovarian morphology (Radder et al., 2008).

At the community level, diversity indices have been quantified on morphological traits used as proxies of ecological traits in several taxa such as birds (Flynn et al., 2009; Ricklefs, 2012) or fish (Schleuter et al., 2012; Toussaint et al., 2016). Nevertheless, the relationship between indices calculated on morphological traits and ecological traits has been poorly investigated. One study on fish showed that indices calculated on certain morphological traits were related to ecological traits (Farré et al., 2013). However, ecological traits cover different types of functions such as habitat use, feeding or life-history strategies and their relationship with several morphological traits are not straightforward. In this context, we expect that the relationship between morphological diversity indices and ecological diversity indices would vary regarding to the type of ecological traits considered. When assessing the relevance of morphology as a proxy for ecology, disentangling the role of evolutionary constraints from the functional link between morphological and ecological traits poses an additional challenge. A strong statistical link between species morphology and one aspect of ecology can result from homogeneous evolution rates of those traits (Harvey & Pagel, 1991; Webb et al., 2002), namely phylogenetic conservatism (Losos, 2008). This evolutionary inertia of traits (i.e., closely related species sharing similar ecological traits; Wiens et al., 2010), probably resulting from allopatric speciation (Pyron et al., 2015), leads to strong relationships between traits despite no shared function performed by those traits. Assessing phylogenetic constraints on traits thus is necessary to test for co-structure between morphological and ecological traits.

Here, we investigated the link between morphological and ecological traits at the species and community levels to test whether diversity indices computed on morphological traits reflect diversity computed

on ecological traits in stream fish communities. We expected that morphological traits would constitute a good surrogate for other ecological traits, but we expected differences based on the type of ecological traits considered (habitat use, feeding and life-history traits). Firstly, at the species level, we tested phylogenetic signal to assess whether closely related species shared similar ecological and morphological traits. Secondly, we used co-inertia analyses to test the links between morphological and ecological traits according to various types of traits. Finally, at the community level, we computed diversity indices based on morphological and ecological traits and tested the relationship between these two types of indices to evaluate the extent to which morphological diversity reflected ecological diversity.

## 2 | METHODS

### 2.1 | Fish data

Fish species abundances from 2006 and 2012 were obtained from the French Biodiversity Agency (OFB). Individuals were collected by electro-fishing, using a standard protocol during low flow months (Poulet et al., 2011). At each sampling, individuals were identified to species level, counted and released. Our database contained 41 freshwater fish species representative of 13 fish families (see Table S1). Based on hydrological and morphological features, we selected 254 sites (Figure S1) which were nonimpacted by human-related activities (e.g., flow and habitat alterations, presence of obstacles, presence of areas dedicated to fishing, presence of water sport and stocking events). Each fish community was composed by at least five species and the most recent samplings were kept when multiple samplings were available for the study period.

### 2.2 | Ecological traits

In order to describe ecological strategies for the 41 freshwater fish species, we used 10 categorical traits (Table S2). These traits were grouped into three components linked to ecological strategies: habitat use (rheophily habitat [RH], salinity preference [SA], reproduction habitat [RE] and position in the water column [HA]), feeding strategy (feeding diet [FD] and feeding habitat [FH]) but also biological traits of species such as life-history traits (fecundity [FE], spawning time [ST], age of first female maturity [MA], parental care [PC]; Buisson et al., 2013; Olden et al., 2006; Villéger et al., 2013). Each fish species was described by compiling available literature, FishBase (<http://www.fishbase.org/>) and scientific reports, and the trait values reported from different sources were averaged before being coded in modalities.

### 2.3 | Morphological traits

We used 11 morphological measures including 10 computed ratios and one quantitative measure (number of barbels; Figure S2)

hypothesised as representative of species ecology. We computed ratios in relation to prey detection (number of barbels [BN] and relative eye size [ES]), prey capture (oral gape position [OG] and maxillary length [ML]), position in the water column (eye position [EP], body lateral shape [BL] and body elongation [BE]) and swimming abilities (pectoral fin position [PF], pectoral fin size [PS], caudal peduncle throttling [CP] and caudal fin aspect ratio [CF]; Toussaint et al., 2016; Figure S2).

## 2.4 | Statistical analyses

### 2.4.1 | Multi-trait analyses

We firstly computed a principal component analysis (PCA) on morphological traits (continuous data) and multiple correspondence analyses (MCAs) on ecological traits (categorical data) performed for each of the three different components of ecological strategies (i.e., feeding, habitat use and life-history traits). We quantified the degree of phylogenetic signal among species coordinates within the multivariate spaces (i.e., along the first two axes of PCA and MCAs) using the phylogeny developed by Rabosky et al. (2018) and the multivariate Kmult statistic (Adams, 2014) using the library *phylocurve*. This multivariate generalisation of Blomberg's *K* is a measure of phylogenetic signal in relation with expectations under a Brownian motion, and we tested its significance by using permutations (Adams, 2014).

We then ran co-inertia analyses (COIA; Doledec & Chessel, 1994; Dray et al., 2003) using the library *ade4*, v1.7-12 (Dray & Dufour, 2007) to analyze the co-structure between morphological and each ecological trait database (i.e., all traits together and the three ecological trait databases separately). RV coefficients were used to quantify the co-structure between the databases and were tested using permutation ( $n = 999$ ) tests (Heo & Gabriel, 1998; Robert & Escoufier, 1976). RV is correlation/co-structure coefficients between morphological and ecological databases, comprised between 0 and 1. High value (e.g.,  $>0.6$ ) indicates strong co-structure between the two databases.

### 2.4.2 | Diversity indices

We used four independent indices to quantify complementary facets of diversity in stream fish communities. The functional richness (FRic) represents the proportion of the functional space occupied by all the species in a community. The functional evenness (FEve) represents the regularity of species position and abundances (across the minimum spanning tree linking all species of the community) in the functional space and decreases when abundances and/or functional distances are less equally distributed among species. The functional divergence (FDiv) is based on the abundances weighted by the mean distance of species to the centre of gravity of the occupied volume by the community. A high value is observed

when high abundances are mainly associated with extreme trait values. Finally, the quadratic entropy of Rao (1982) represents a combination of functional richness and dispersion incorporating the abundances of species. FRic, FEve and FDiv were computed using the function *MultidimFD* from Villéger et al. (2008) and the quadratic entropy of Rao was computed using the function written by de Bello et al. (2011) which integrates the Jost's correction. Each diversity index was computed for both morphological and ecological traits.

### 2.4.3 | Null models

Since functional diversity indices can be influenced by species richness, we used randomisations of species traits to control for this effect. We kept the same number of species per assemblage while randomising species identity. We performed 999 randomisations and then obtained 999 null values of the four indices of diversity *per* assemblage. Then, we measured the standardised effect size (SES;  $obs - mean(rand))/sd(rand)$ , *obs* being the observed index and *rand* the 999 null values of the index. A negative value of SES indicates lower diversity than expected given the number of species (i.e., compared to random assemblages) whereas positive value means higher diversity. While removing the effect of species richness, SES values also make comparison between sites possible since the differences observed in diversity are not the result of differences in species richness.

### 2.4.4 | Relationships between diversity indices

For each of the four diversity indices, we assessed the link between morphological and ecological indices while accounting for the effect of species richness. To do that, we fitted linear models to express each ecological index as a function of the corresponding morphological index and its interaction with species richness.

### 2.4.5 | Sensitivity analysis

In order to quantify the importance of each specific trait in the association between morphological and ecological diversity indices, we ran a sensitivity analysis by successively removing morphological traits one by one. Specifically, we firstly removed one morphological trait from the database and computed the linear regression between ecological and morphological indices, including the interaction with species richness. We then computed the difference between the  $R^2$  values obtained for the model with one trait excluded and the one including all traits, a negative value indicating that the excluded trait enhanced the correlation between ecological and morphological diversity indices.

All analyses were performed with R 4.1 (R Core Team, 2017).

### 3 | RESULTS

#### 3.1 | Multi-trait analyses

Species coordinates along the first two axes of both PCA and MCA showed strong associations with fish phylogeny, especially for salmonids and cyprinids (Figure 1), and these associations revealed significant phylogenetic signals for both morphological ( $K = 0.754$ ,  $p = 0.001$ ) and habitat-related traits ( $K = 0.472$ ,  $p = 0.004$ ). No significant phylogenetic signal was observed for feeding ( $K = 0.170$ ,  $p = 0.442$ ) or life-history traits ( $K = 0.248$ ,  $p = 0.066$ ).

Regarding morphological space, Cypriniform species were placed mainly on the negative part of PC1 and characterised by high OG, ES, CF and CP (Figure 1a). Salmoniform species were placed mainly on the positive part of PC2, with high maxillary length, whereas Percomorpharia species were more widely distributed along the first two axes. Concerning FD, both Cypriniforms and Percomorpharias were linked mainly to benthivorous feeding habitat (FH1, positive part of the first axis; Figure 1b). For habitat use, salmoniforms were characterised by rheophilic habitat and lithophilic reproductive habitat and diadromy (SA4; Figure 1c). Finally, regarding life-history traits, cypriniforms exhibited mainly negative values along axis 1 and positive ones for axis 2, and were characterised by high fecundity (FE3), no protection of eggs (PC1) and female maturity at 3–4 years (MA3; Figure 1d).

The co-structures between morphological and ecological traits were strongly significant, whatever the group of ecological traits considered (all  $p < 0.001$ , Table 1). RV coefficient was the highest for all-traits data (RV = 0.41), followed by feeding traits (RV = 0.35), and habitat and life-history traits (RV = 0.28; Table 1). The high co-structure between morphological and ecological traits was evidenced by similar positions of fish species on both morphological and ecological multivariate spaces (Figure 2a), except for a few species such as *Cobitis taenia*, *Alburnus alburnus*, *Esox lucius* or *Lepomis gibbosus*.

Axis 1 is strongly linked to ML, BE and PS for morphological traits and strongly correlated to MA, SA and FD strategy. Barbel length and BN but also OG were the most correlated morphological traits to the axis 2, whereas FH and SA were the most correlated ecological traits to axis 2. On the one hand, fish species with high values of swimming capacities such as PS and CP were positively correlated to

axis 1 (Figure 2a,d) and related to benthopelagic species (HA2) with precocious female maturity (MA1) and several spawning times (ST2), omnivorous (FD4) and limnophilic (RH2; Figure 2c). On the other hand, variables linked to prey capture such as ML and strong BE were negatively correlated to axis 1 (Figure 2a,d) and associated with freshwater-brackish-marine species (SA4), with late female maturity (MA5), carnivorous (FD5) and piscivorous (FD2; Figure 2c). Species with large body (BL) and numerous BN were positively correlated to axis 2 (Figure 2a,d) and associated with freshwater species (SA1) which are benthivorous (FH1) and invertivorous (FD1) with medium female maturity (MA2; Figure 2c). However, species with large OG and ML were negatively correlated to axis 2 (Figure 2a,d) and related to species with pelagic habitat (HA1), strong parental care (PC3) and water-column feeding (FH2; Figure 2c).

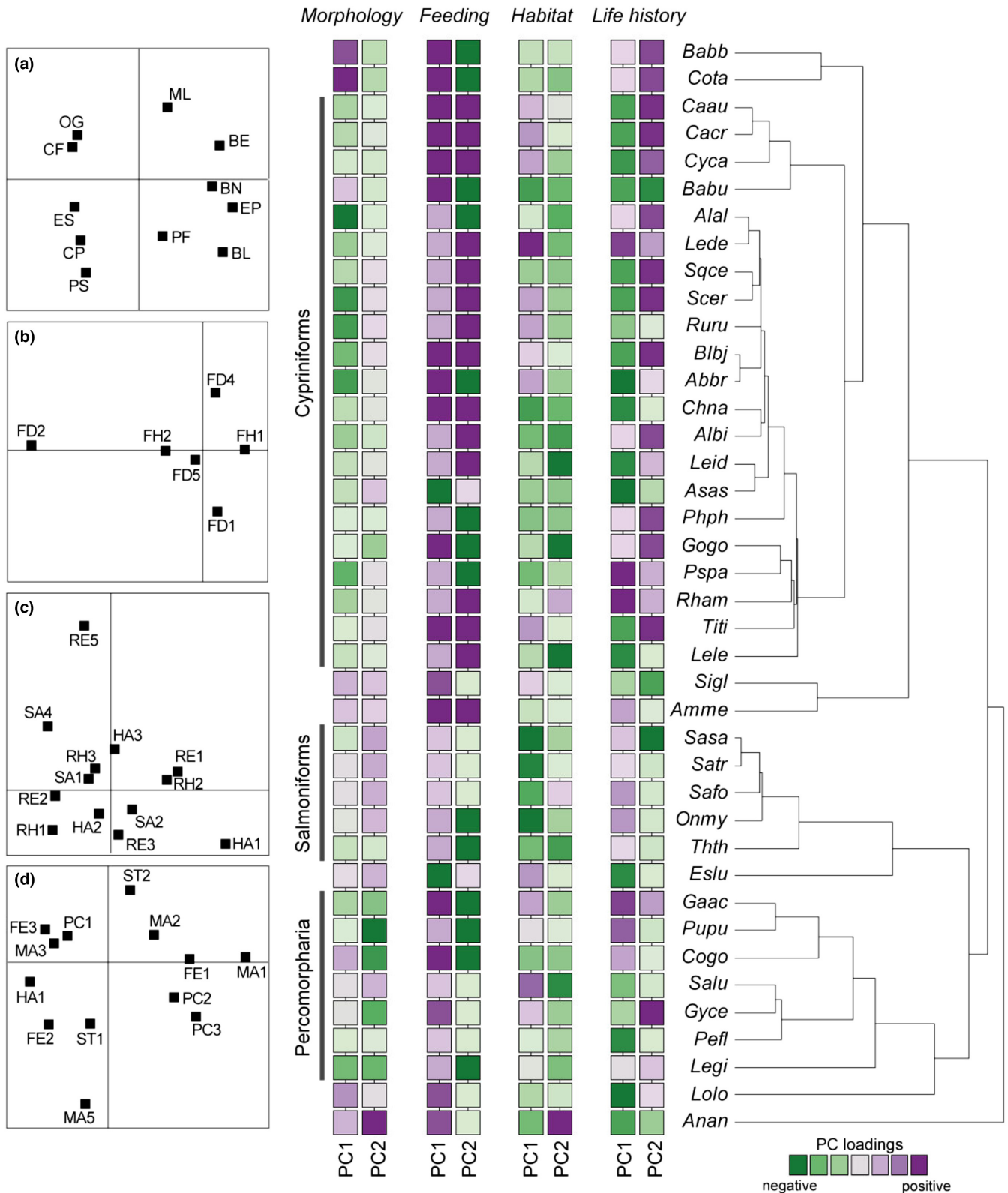
#### 3.2 | Diversity indices

Ecological FRic increased with morphological FRic (estimate = 0.188,  $p < 0.001$ ) but decreased with specific richness (estimate =  $-0.31$ ,  $p < 0.001$ ; Figure 3a). Morphological and ecological FEve were independent (estimate = 0.073,  $p = 0.10$ ) and no effect of species richness was observed (estimate = 0.016,  $p = 0.72$ ; Figure 3b). FDiv showed a positive relationship between the two facets (estimate = 0.64,  $p < 0.001$ ) whereas increasing species richness resulted in a decrease in FDiv (estimate =  $-0.193$ ,  $p = 0.0019$ ; Figure 3c). Finally, ecological Rao significantly increased with morphological Rao, independent of species richness (estimate = 0.42,  $p < 0.001$ ; Figure 3d).

#### 3.3 | Sensitivity analysis

Sensitivity analysis revealed ML and ES underpinned the correlation between morphological and ecological FRic, followed by BE and CF (Figure 4). Maxillary length exhibited the highest importance for FDiv and FEve, whereas EP and BL appeared to decrease the correlation between morphological and ecological FRic (Figure 4). Finally, none of the morphological traits appeared to strongly influence the correlations observed between morphological and ecological Rao.

**FIGURE 1** Relationships between phylogenetic relatedness among species and species coordinates along the first two axes of (a) PCA for morphological traits, and MCAs for (b) feeding, (c) habitat and (d) life-history traits. Species codes: Abbr, *Abramis brama*; Alal, *Alburnus alburnus*; Albi, *Alburnoides bipunctatus*; Amme, *Ameiurus melas*; Anan, *Anguilla anguilla*; Asas, *Aspius aspius*; Babb, *Barbatula barbatula*; Babu, *Barbus barbus*; Blbj, *Blicca bjoerkna*; Ledc, *Leucaspis delineatus*; Rham, *Rhodeus amarus*; Cacr, *Carassius carassius*; Caau, *Carassius auratus*; Cagi, *Carassius gibelio*; Chna, *Chondrostoma nasus*; Cogo, *Cottus gobio*; Cota, *Cobitis taenia*; Cyca, *Cyprinus carpio*; Eslu, *Esox lucius*; Gaac, *Gasterosteus aculeatus*; Gogo, *Gobio gobio*; Gyce, *Gymnocephalus cernua*; Legi, *Lepomis gibbosus*; Leid, *Leuciscus idus*; Lele, *Leuciscus leuciscus*; Lolo, *Lota lota*; Onmy, *Oncorhynchus mykiss*; Pefl, *Perca fluviatilis*; Phph, *Phoxinus phoxinus*; Pspa, *Pseudorasbora parva*; Pupu, *Pungitius pungitius*; Ruru, *Rutilus rutilus*; Safo, *Salvelinus fontinalis*; Salu, *Sander lucioperca*; Sasa, *Salmo salar*; Satr, *Salmo trutta*; Scer, *Scardinius erythrophthalmus*; Sigl, *Silurus glanis*; Sqce, *Squalius cephalus*; Thth, *Thymallus thymallus*; Titi, *Tinca tinca*. Trait codes: BN, number of barbels; ES, relative eye size; OG, oral gape position; ML, maxillary length; EP, eye position; BL, body lateral shape; BE, body elongation; PF, pectoral fin position; PS, pectoral fin size; CP, caudal peduncle throattling; CF, caudal fin aspect ratio; RH, rheophily; SA, salinity preference, RE, reproduction habitat; HA, position in the water column; FD, feeding diet; FH, feeding habitat; FE, fecundity; ST, spawning time; MA, age of first female maturity; PC, parental care. See Table S2 and Figure S2 for details



## 4 | DISCUSSION

### 4.1 | Morphology as a proxy for ecological species traits

Our results suggest that morphology and ecological species traits are strongly linked in freshwater fish. This relationship between

different trait categories has implications for the functioning of ecosystems as morphologically distinct species might have contrasting functional roles *via* species interactions within ecological networks (Berchtold et al., 2015; Dehling et al., 2016; Oliveira et al., 2010). For instance, variability in mouth morphology across species (e.g., shape, position, size, dentition) allows different feeding modes (e.g., grazing, filtering, cutting) adapted to particular trophic resources

(Berchtold et al., 2015; Hugueny & Pouilly, 1999; Keast, 1978). Likewise, we found that morphological attributes can be used to provide information about habitat use at the species level. Although the morphology-habitat relationship has been described previously

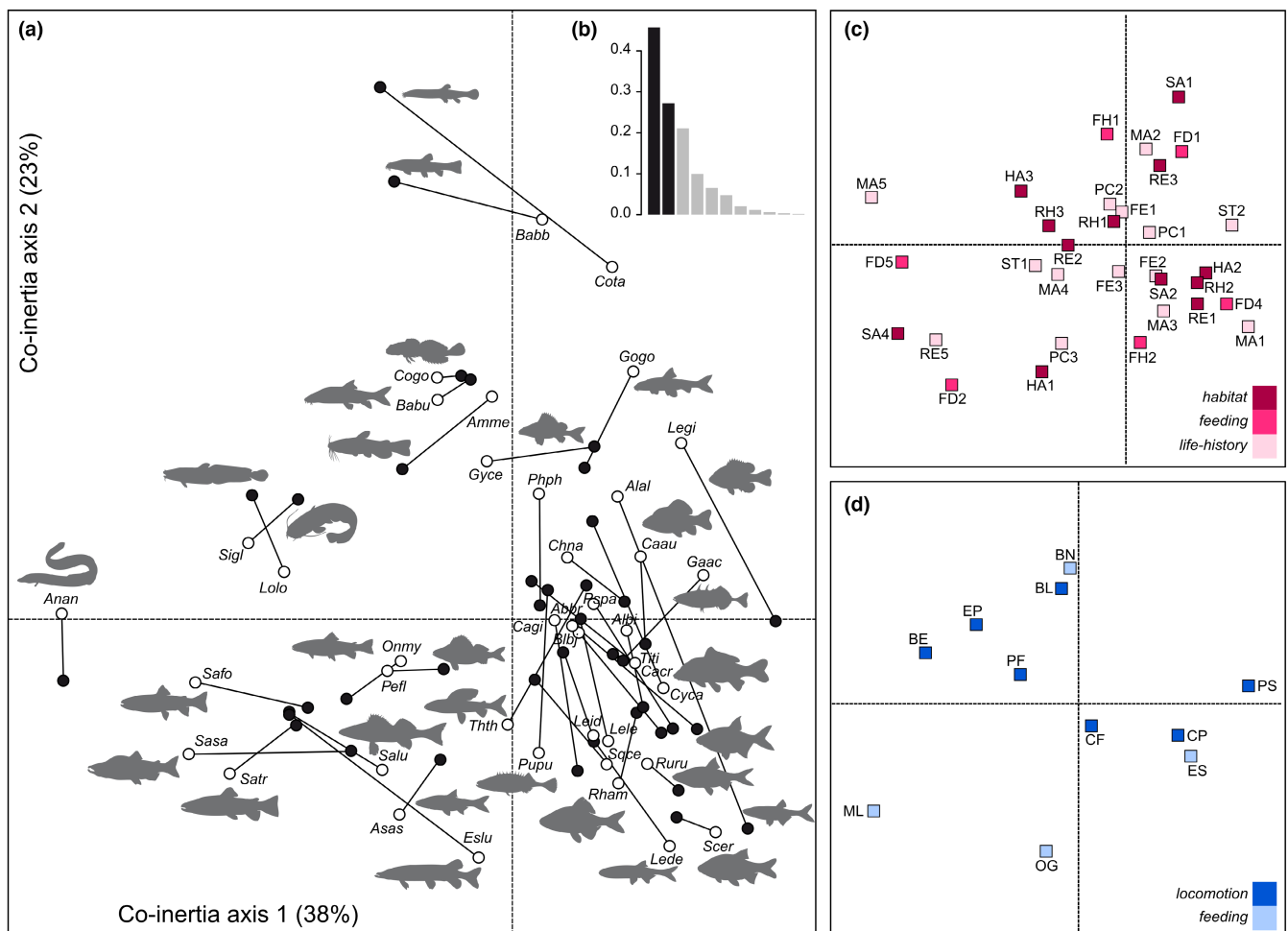
**TABLE 1** Co-inertia analyses between morphological and each ecological trait database (i.e., all traits together and the three ecological trait databases separately)

	Eigenvalues (%)			<i>p</i>
	1st axis	2nd axis	RV	
All traits	0.38	0.23	0.415	<0.001
Habitat	0.46	0.27	0.285	<0.001
Feeding	0.42	0.39	0.346	<0.001
Life history	0.39	0.31	0.281	<0.001

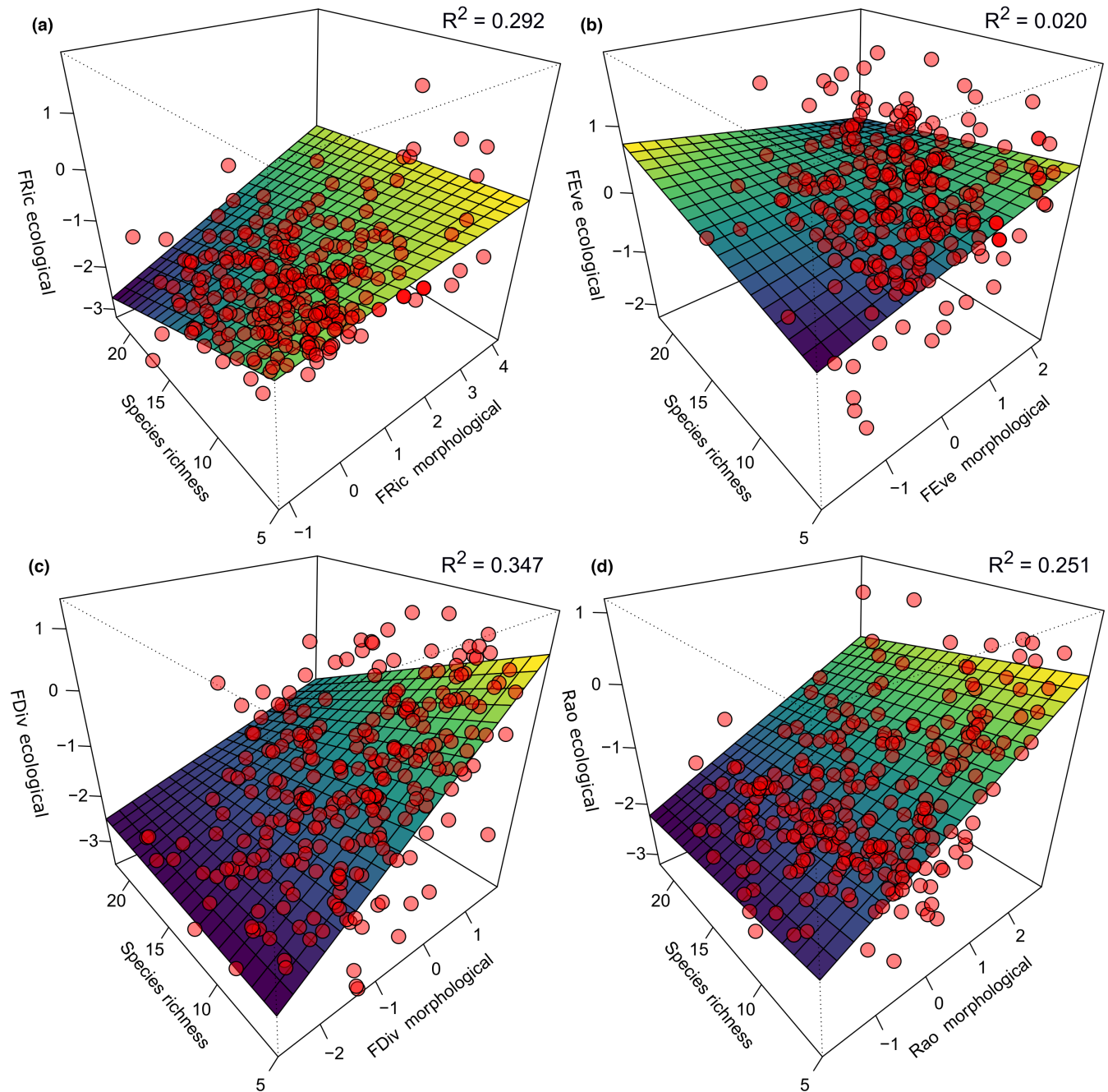
Note: For each analysis, eigen values are expressed as the percentage of variance explained by each of the first two axes. RV coefficients represent vector correlation coefficients (i.e., correlation between the two databases) with associated *p*-values from permutation tests. bold values are significant ( $p < 0.05$ ).

as complex (Chan, 2001), it is relatively well-supported for freshwater fish (Douglas & Matthews, 1992; Leal et al., 2013; Oliveira et al., 2010; Ord & Klomp, 2014) suggesting that morphology differences might result in interspecific niche partitioning of habitat use (Cochran-Biederman & Winemiller, 2010). In the current context of extensive changes in stream structure resulting from human activities, in addition to phenological, physiological and behavioural responses, changes in morphology might be expected and thus should be monitored over time (Sheridan & Bickford, 2011). Finally, we show that morphology also can reflect life-history traits. Although this eco-morphological link has been more rarely investigated, recent studies suggest that morphology might be a good surrogate for life-history traits such as spawning period or life span (Farré et al., 2013; Watson & Balon, 1984).

Our results rely on trait categories being compared and those categories are somewhat arbitrary. The definition of trait categories ultimately is related to the question investigated. For instance, to understand community assembly, one might separate traits into  $\alpha$  (i.e., constrained by biotic interactions) and  $\beta$  traits (i.e., constrained by habitat filtering; Lopez et al., 2016), whereas a study focusing on ecosystem



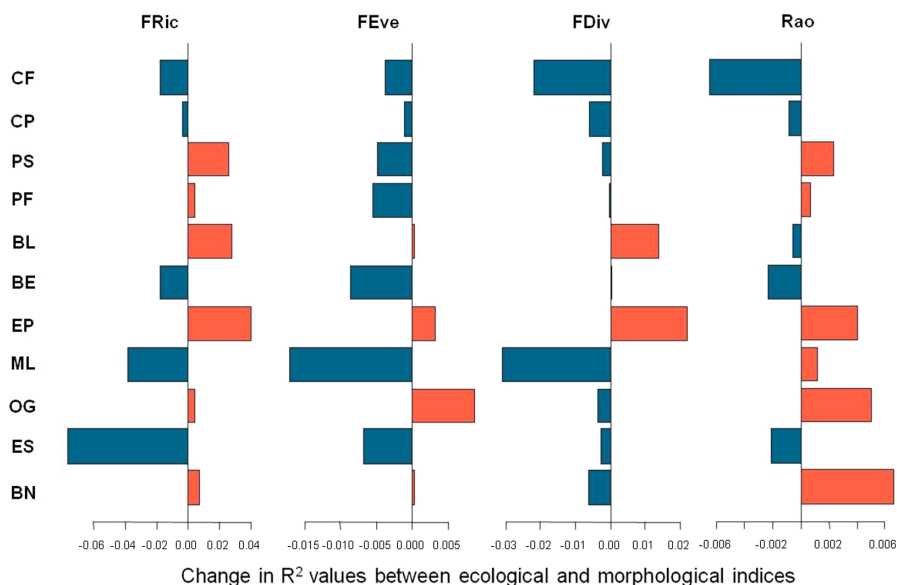
**FIGURE 2** Co-inertia analysis performed on the morphological and ecological traits. (a) Position of fish species on the F1 x F2 co-inertia plane according to their morphological (white circles) and ecological (black circles) attributes, (b) eigenvalues, (c) position of ecological traits on F1 x F2 co-inertia plane, (d) position of morphological traits on F1 x F2 co-inertia plane. Species and trait codes as in Figure 1



**FIGURE 3** Relationships between the four diversity indices computed on ecological traits and both indices computed on morphological traits and species richness.  $R^2$  are indicated for each relationship. Panels (a), (b), (c) and (d) represent FRic, FEve, FDiv and Rao indices, respectively

functioning might differentiate response traits (i.e., responding to environmental factors) versus effect traits (i.e., affecting the environment; Navas & Violle, 2009). Here, by classifying traits into morphological versus ecological, we were able to investigate whether the use of easy-to-measure traits was ecologically relevant. Nevertheless, the relationship of biological traits (such as life-history traits) and ecological traits (such as habitat of feeding habits) assumes that biology determines ecological traits. Then, ecological traits often are more readily available than biological traits. Moreover, phylogenetic constraints are a feature of biological traits and are only secondarily related to ecological traits

that are inherited from biological traits. Overall, our study supports eco-morphological relationships (barbels and oral gape linked to feeding habits and body elongation and maxillary length linked to female maturity, salinity preferences and feeding diet) for freshwater fish suggesting that morphometrics can be used as an informative surrogate for ecological species traits. Our results were consistent with those of Winemiller and Rose (1992) in North American fishes which showed a positive relationship between anadromy and slow female maturity, associated in our study with a carnivorous diet. Nevertheless, in our study, number of eggs or parental care were not correlated with other



**FIGURE 4** Importance of each morphological trait in driving the relationship between morphological and ecological diversity indices. For each trait, the values represent the differences in correlation ( $R^2$  values) between the ecological diversity index and the morphological diversity index computed with or without the trait considered. Positive differences (in red) indicate that the correlation was stronger without the trait, suggesting that this trait blurred the correlation, whereas negative differences (in blue) suggest that this trait enhanced the correlation. Trait codes as in [Figure 1](#)

life-history traits such as maturity. In our study, these traits (anadromy, carnivorous diet and slow maturity) were associated with two main morphological traits: maxillary length and body elongation.

A strong correlation between traits might result from common evolutionary constraints on these traits, masking biologically relevant links between them (Hugueny & Pouilly, 1999) and resulting in the violation of the assumption of statistical independency of observations (Münkemüller et al., 2012). Consistent with other recent studies (Bower & Winemiller, 2019), our results showed that some trait categories (i.e., morphological and habitat-related traits) exhibited a significant phylogenetic signal (particularly apparent among salmoniforms and cypriniform species). However, although feeding-related traits and life-history traits were not phylogenetic conserved, those traits also showed clear associations with morphological traits, thus revealing that the link between morphological and ecological traits did not result only from shared evolutionary history (i.e., phylogenetic constraints), but also could reflect the effects of environmental filters acting on trait patterns of stream fish assemblages resulting in niche conservatism (Bower & Winnemiller, 2019; Lamouroux et al., 2002).

## 4.2 | Morphological diversity as a proxy of ecological diversity

Although diversity indices are known to be potentially influenced by species richness (Mason et al., 2008), our null model approach allowed us to compare the different metrics after removing the species richness effect (Gotelli & Ulrich, 2012). As found previously, our results showed significant relationships, although with some exceptions, between morphological and ecological diversity indices (Farré et al., 2013). This suggests that congruence between morphological and ecological diversity is driven not only by species richness, but also by a biologically relevant link between the shape of individuals and their ecological strategies, according to the index and type of ecological traits. Few studies were interested in the link

between morphological and ecological indices, since morphological traits are currently assumed to be convenient proxies of ecological traits in several taxa (Flynn et al., 2009; Ricklefs, 2012; Schleuter et al., 2012). However, here we show that this relationship is not always supported. No relationship was observed between morphological and ecological evenness, suggesting that morphology does not constitute a good proxy of ecological traits for this index and that species might be evenly distributed within the morphological volume while randomly distributed within the ecological trait volume. Moreover, our results showed redundancy for ecological diversity but not for morphological diversity. This result suggests that functions based on ecological traits are more limited (i.e., less numerous) and thus, ecological niche saturation can be reached more quickly than for morphological diversity (Olivares et al., 2018).

Our sensitivity analysis revealed contrasting effects of morphological traits on the correlation observed between morphological and ecological diversity indices. In particular, two traits related to food acquisition (i.e., ML and ES, Villetiger et al., 2008) consistently enhanced the correlation, suggesting that morphometrics is strongly related to the trophic niche at the community level (Ingram & Shurin, 2009). Moreover, although body size is currently known to be one of the most important morphological traits linked to life-history strategies (Fišer et al., 2013; Kingsolver & Pfennig, 2004; Stahler et al., 2013), our results suggest that other morphological traits such as BE, ML or the presence and size of barbels can be considered as good proxies of some ecological traits such as female maturity, salinity preferences or feeding habits and diet.

## 5 | CONCLUSION

Overall, morphological traits seem to be relevant proxies of ecological traits for freshwater fish species. Although documenting ecological traits is resource-intensive, morphological traits are much easier to quantify since they can be measured for each species of



interest in an automated and consistent way allowing comparison of measurements over time. Based on a selection of non-impacted fish communities, our study pinpoints that morphometrics can be used to describe communities and thus define hotspots of ecological diversity potentially related to ecosystem functioning. We highlighted the importance of some morphological factors such as eye size, maxillary length and caudal fin aspect ratio in the relationship between ecological and morphological diversity. Morphological diversity is expected to respond faster to the loss of a species than ecological diversity for which redundancy is higher. This suggests that the two facets of diversity could be differently impacted by environmental disturbances, especially anthropogenic ones. However, the relationship between morphological and ecological diversity remains unknown in disturbed environments, which calls for further studies investigating this question.

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#### AUTHOR CONTRIBUTION

J.C., L.K. and G.G. conceived the research and prepared the manuscript; J.C. and L.K. computed analyses. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

#### DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

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