Received: 6 July 2022 | Revised: 29 November 2022 | Accepted: 15 December 2022

DOI: 10.1002/eap.2845

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Disentangling the effects of different human disturbances on multifaceted biodiversity indices in freshwater fish

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Funding information
Office français pour la biodiversité

Handling Editor: Marissa L. Baskett

Abstract

Evaluating the effects of anthropogenic pressures on several biodiversity metrics can inform the management and monitoring of biodiversity loss. However, the type of disturbances can lead to different responses in different metrics. In this study, we aimed at disentangling the effects of different types of anthropogenic disturbances on freshwater fish communities. We calculated diversity indices for 1109 stream fish communities across France by computing richness and evenness components for ecological, morphological, and phylogenetic diversity, and used null models to estimate standardized effect sizes. We used generalized linear mixed models to assess the relative effects of environmental and anthropogenic drivers in driving those diversity indices. Our results demonstrated that all diversity indices exhibited significant responses to both climatic conditions and anthropogenic disturbances. While we observed a decrease of ecological and phylogenetic richness with the intensity of disturbance, a weak increase in morphological richness and evenness was apparent. Overall, our results demonstrated the importance of disentangling various types of disturbances when assessing human-induced ecological impacts and highlighted that different facets of diversity are not impacted identically by anthropogenic disturbances in stream fish communities. This calls for further work seeking to integrate biodiversity responses to human disturbances into a multifaceted framework, and could have beneficial implications when planning conservation action in freshwater ecosystems.

KEYWORDS
anthropogenic pressures, functional diversity, habitat filtering, morphology, phylogenetic diversity

INTRODUCTION

Assemblages are structured according to species sorting processes (i.e., assemblage rules) constraining the co-occurrences of species in local assemblages. While species richness has been largely used as a good metric of diversity, many studies showed the importance of adopting an integrative approach including several facets in the calculation of diversity metrics, such as phylogenetic and functional diversity so as to better understand the effects of disturbances on biodiversity (Côte et al., 2019; Gaston & Spicer, 2004; Kuczynski et al., 2018). Indeed, each facet of diversity can bring information about different processes. For instance, if species richness can be a good indicator of quantification of diversity, functional diversity can explain ecosystem functioning since it represents the diversity of ecological and morphological traits whereas phylogenetic diversity represents the evolutionary history of assemblages (Devictor et al., 2010). In this context, understanding the function and sensitivity of different facets of diversity can inform management decisions and identify hotspots for spatial prioritization and protection.

Biodiversity can be strongly affected by environmental stressors but also by anthropogenic pressures, such as land use (D'agata et al., 2014; Frishkoff et al., 2014; Odanaka & Rehan, 2019; Sol et al., 2014, 2017) which can generate a shift in functional structure of assemblages since species presenting poorly-adapted traits to new environmental conditions will be lost, for the benefit of better-adapted species (Mouillot et al., 2013). One of the consequences of anthropogenic pressures on assemblages in most of ecosystems is habitat filtering, which selects species with similar functional traits and strategies in response to environmental factors. This can lead to the loss of rare species, which are more vulnerable, with particular combinations of traits which are not shared by dominant species, and can impact ecosystem functioning (Teichert et al., 2017).

In lotic ecosystems, organisms are exposed to multiple pressures (Malmqvist & Rundle, 2002; Winemiller et al., 2010) which can lead to a strong loss of diversity (Albert et al., 2021). In streams, anthropogenic disturbances can shape communities by locally altering ecological continuity and water flow, which can lead to a change in hydro-morphological characteristics of the river (Delgado et al., 2010; Siriwardena et al., 2006; Swank et al., 2001). Moreover, the use of aquatic habitat by human activities can also strongly affect the abundance and the occurrence of species and consequently modify the structure of communities (Friberg, 2014). Finally, human-mediated introductions are known to be involved in biodiversity changes (Su et al., 2021), especially by the loss of functionally unique species (Matsuzaki et al., 2013, 2016) and the increase of functional redundancy within communities (Kuczynski & Grenouillet, 2018). Nevertheless, in rivers, it can be difficult to provide precise measures of disturbances impacts at a fine scale.

In the context of European Water Framework Directive (WFD), a number of indicators of aquatic biodiversity state have been developed, especially for fish, so as to assess ecological status of stream ecosystems since fish communities respond to numerous anthropogenic disturbances such as fragmentation, hydro-morphological alteration, or water quality degradation (Ormerod, 2003). These metrics are based on abundance, species composition and age structure of fish. One of them, the Index of Biotic Integrity (IBI, Karr, 1981; Pont et al., 2021) has been considered as a good measure of alteration of fish assemblages. But, as biodiversity is multifaceted and complex, it cannot be summarized as only one indicator and a lot of studies highlighted the importance of integrative approaches in biodiversity conservation (Brunialti, 2014; Geist, 2011; Kraus & Krumm, 2013). New indicators of functional or phylogenetic diversity (Villeger et al., 2008) have been developed, but how they respond to anthropogenic pressures remains poorly understood.

Moreover, most studies addressing the effects of anthropogenic pressures on biodiversity in such ecosystems focused at the scale of river basin or catchment but none at a national scale (Liu et al., 2021). However, working at such a large scale can indicate the relative importance of environmental and anthropogenic factors. One study on stream macro-invertebrates showed that natural environmental gradients could mask the effect of perturbations on biodiversity (Heino et al., 2007), contrary to what has been found in terrestrial ecosystems (Zhu et al., 2021). Other studies in stream insects showed that anthropogenic disturbances could modify the relationship between environmental factors and diversity (Agra et al., 2021).

In this study, our goal was to evaluate the effects of different anthropogenic disturbances on multifaceted diversity indices in freshwater fish communities. We hypothesized that anthropogenic disturbances could lead to a decrease of diversity, whatever the facets considered (Matuoka et al., 2020) with different contrasted effects depending on the type of anthropogenic disturbances and higher effects expected for hydro-morphological disturbances. In the comparison between anthropogenic disturbances and climatic/natural factors, we expected lower effect of anthropogenic disturbances than environmental factors (Heino et al., 2007). One of our expectations was a difference in the response to anthropogenic pressures between the different facets of diversity, in agreement with what was observed in previous studies focusing on the effect of global change (Kuczynski et al., 2018). First, we characterized spatial patterns in both richness and evenness for ecological, morphological, and phylogenetic diversity. Then, we described the relationship between the intensity of anthropogenic disturbances and the different facets of diversity so as to assess the consequences on assemblage rules. Third, we compared the relative effects of climatic variables and different types of anthropogenic disturbances on these facets of diversity.

MATERIALS AND METHODS

Fish data and study area

Fish species abundances covering the period from 2006 to 2012 were obtained from the French Biodiversity

Office (OFB) database on 1109 sampling sites all over metropolitan France. Abundances OFB database was downloaded from https://naiades.eaufrance.fr/ by searching for "accès aux données" and then "France entière" and "Hydrobiologie". Metropolitan France is constituted of six main hydrographic basins under a temperate climate. Atlantic ocean at west brings moderate winters with strong rainfall whereas Mediterranean and continental flux at south and east can bring warm summers. Concerning hydro-morphology, a strong heterogeneity in slope and altitude is observed due to relief and seas. Our database included a total of 55 freshwater fish species from which 20 were non-native. Only sites with at least five fish species were kept for analyses (Villeger et al., 2008). Fish data consisted of a standardized electro-fishing protocol conducted during low-flow periods (from May to October) for each sampling occasion. Sampling protocols were defined depending on river width and depth. Streams were sampled by wading (mostly two-pass removal), while fractional sampling strategies were undertaken in larger rivers. However, to compare inter-annual densities for a given site, only surveys performed with the same sampling protocol were selected. Sites have been sampled one or several times, depending on sites but we selected the last sampling on the period 2006–2012.

Anthropogenic disturbances and environmental conditions

Anthropogenic disturbances were extracted from the IPR+ database (Marzin et al., 2013) collected by the OFB (Office Français de la Biodiversité) (Figure 1). IPR+ database was downloaded from https://naiades.eaufrance.fr/ by searching for "accès aux données" and then "France entière" and "Hydromorphologie". We distinguished three types of disturbances linked to (1) hydro-morphology (HYDRO) (i.e., modifications and variations of flow, morphology of the river, embankment and riparian zone and presence of clogging), (2) human use of aquatic habitat (HUM) (i.e., presence of areas dedicated to fishing, presence of water sports and episodes of stocking), and (3) the percentage of non-native species (NNS). The first two variables were computed as the average value among the different descriptors coded in the IPR+ database with four levels of disturbances from null (value equal to zero) to strong (value equal to 3). Then, we computed an index of overall disturbances calculated as the mean of the two previous disturbances indices (HYDRO and HUM) and categorized into three modalities (low, intermediate, high) based on the quartiles of this mean. For environmental variables, four climatic variables were extracted from the WorldClim database (Hijmans et al., 2005): mean annual air temperature (TEMP), seasonality of air temperature (TSEAS), total annual precipitation (PREC), and seasonality of precipitation (PSEAS). Worldclim database was downloaded from https://www.worldclim.org/ by searching for "historical climate data" and then "bioclimatic variables". The upstream-downstream gradient was characterized by the first axis of a Principal Component Analysis summarizing 92% of the variation of three variables (i.e., distance to the source, stream width and surface of drainage area) describing the hydrographical network (RHT, Pella et al., 2012).

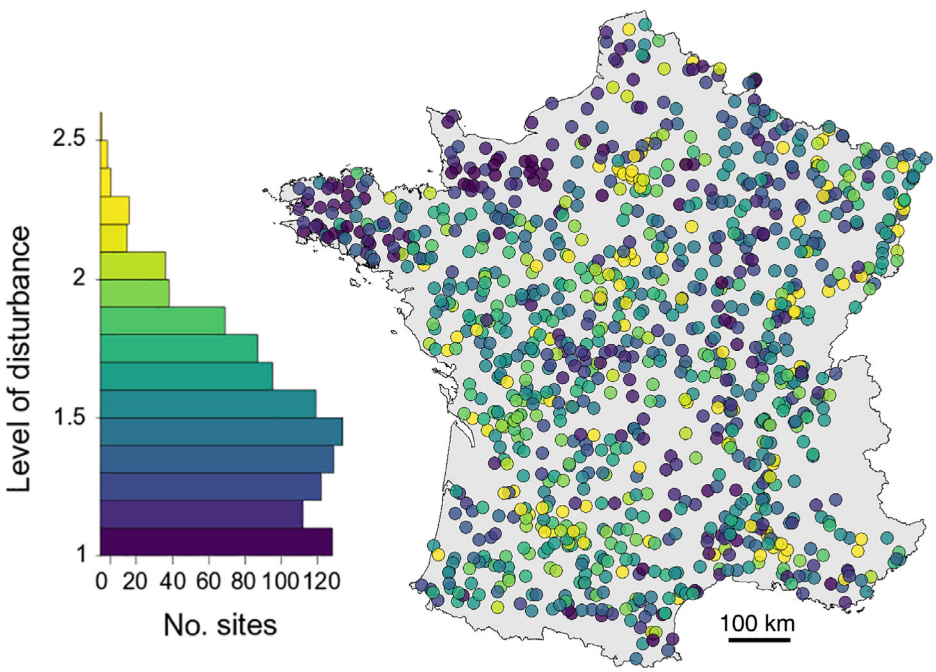

FIGURE 1 Sampling sites across France and their level of disturbance.

Trait databases

Morphological diversity of fish assemblages was described using 16 morphological measures (Toussaint et al., 2016) available on 62 species (from which 23 were considered as non-native). The database included body length, the number of barbels and 14 ratios (see Appendix S1: Figure S1) linked to prey detection (i.e., eye size and barbel length), prey capture (i.e., oral gape position and maxillary length), position in the water column (i.e., eye position and body elongation), and swimming abilities (i.e., body lateral shape, pectoral fin position, pectoral fin shape, pectoral fin size, caudal peduncle throttling, caudal fin aspect ratio, fin surface ratio, and relative fin surface).

Ecological diversity was described using 14 qualitative ecological traits available for 60 species (whose 21 were non-native) linked to life-history strategies (i.e., fecundity, spawning time, egg diameter, life span, age of first female maturity, parental care, incubation period), habitat use (i.e., rheophily, reproduction habitat, migration, salinity preference, and position in the water column), and feeding (i.e., feeding diet and feeding habitat). Those traits were downloaded from Fishbase (https://www.fishbase.se/search.php) searching the name of the species and the literature for all the species (Appendix S1: Table S1).

Indices of diversity

We used richness and evenness indices developed by Villeger et al., 2008 so as to quantify the ecological and morphological facets of diversity. We calculated two Gower distance matrices for ecological and morphological traits, separately and we performed a Principal Coordinates Analysis (PCoA) to project the species into a four-dimensional space (Maire et al., 2015). Morphological and ecological richness (MRic and ERic, respectively) corresponded to the volume occupied by co-occurring species in the morphological and ecological space, respectively (ranging from 0 to 1, 1 meaning that the maximal volume in the space is occupied). The morphological and ecological evenness (MEve and EEve, respectively) measured the aggregation of species within the morphological and ecological space, respectively (ranging from 0 to 1, 1 meaning an even distribution of species within the space). Finally, we used the phylogenetic tree from (Rabosky et al., 2018) so as to calculate indices of phylogenetic diversity on 55 species. Thus, we estimated phylogenetic richness (PRic) using Faith's PD (Faith, 1992) and phylogenetic evenness using Villéger's FEve (Villeger et al., 2008). We also included species richness in the study, as the number of species per site.

The calculations of indices were done on complete assemblages (i.e., including native and non-native species) but also on assemblages involving only native species.

Null models and standardized effect sizes

As the previous indices calculated can be influenced by specific richness, we used randomizations of species traits and phylogeny to control for this effect. We kept the same number of species and abundance per assemblage in the complete dataset but we randomized species identity. For analyses based on native assemblages, we considered only the combinations of traits as well as the species observed in the native species pool. We performed 999 randomizations so as to obtain 999 null values of the indices of diversity *per* assemblage. Then, we calculated the standardized effect size (SES) as *obs*- mean (*rand*)/sd (*rand*). *obs* was the observed index and *rand* was the 999 null values of the index. A positive SES value indicates a higher value of the index than expected randomly given the number of species, while a negative value indicates a lower value than expected (Gotelli & Graves, 1996). Hereafter, we used SES values for all indices.

Statistical analyses

First, we tested for the relationship between the three levels of the index of overall disturbances previously described (low, intermediate, and high) and each facet (phylogenetic, ecological, and morphological) and component (richness and evenness) of diversity by using Kruskal-Wallis tests. Then, we checked for spatial autocorrelation using Moran's I (Fan & Myint, 2014). Since spatial autocorrelation was significant ($p < 0.001$) for all indices, we tested the relationship between climatic conditions and local disturbances and each diversity index by using linear mixed models performed with *nlme* package and integrating an autocorrelation structure (gaussian, exponential or spherical) determined by semi-variograms in all models. For each variable, we fitted a semi-variogram using gstat library so as to model semi-variance in function of distance (sill value = 1.5, range = 50,000 and nugget = 1). The shape of semi-variogram determined which autocorrelation structure was the best adjusted. Anthropogenic disturbances (i.e., HYDRO, HUM, and NSS) and climatic conditions (i.e., TEMP, TSEAS, PREC, and PSES) were considered as fixed effects whereas the upstream-downstream gradient and the elevation were considered as random effects. We did not notice evidence for multicollinearity between the explanatory variables (variance inflation factors all lower than 2). All the predictors were standardized to compare their relative strength. R software version 3.2.1 (R Core Team, 2017) was used so as to compute all the analyses. Morphological and ecological indices as well as phylogenetic evenness were computed using the function *multidimFD* available online at http://villeger.sebastien.free.fr/Rscripts.html. We used *picante* package to compute phylogenetic richness.

RESULTS

While negative values of diversity (lower than expected) were observed for ecological and phylogenetic richness, positive values of diversity (higher than expected) were observed for morphological richness (Figure 2). For ecological and phylogenetic richness, higher values of diversity were observed in the north-west of France, whereas negative or null values were observed across France. For morphological richness, stronger values were mainly observed in the center of France. Patterns of spatial autocorrelation for both components (richness and evenness) appeared less important for evenness than for richness (Figure 2).

While no difference was observed for ecological and phylogenetic evenness, significant differences in ecological and phylogenetic richness were observed among levels of disturbances ($p < 0.001$, Figure 3), with a decrease of SES values with increasing disturbance intensity. By contrast, significantly ($p < 0.001$) higher values of morphological richness and evenness were observed with higher levels of disturbance, revealing a shift from null to high SES values along the disturbance gradient (Figure 3). Positive correlations between SES of ecological richness and evenness calculated on complete and native assemblages were observed for all indices (R^2 ranging from 0.29 to 0.89, $p < 0.001$, Figure 4). While a strong correlation was observed for phylogenetic and ecological richness ($R^2 = 0.89$ and 0.75, respectively), the correlation was weak for morphological richness and evenness, as well as for phylogenetic evenness ($R^2 = 0.33$, 0.44 and 0.29, respectively). For these three indices, results showed

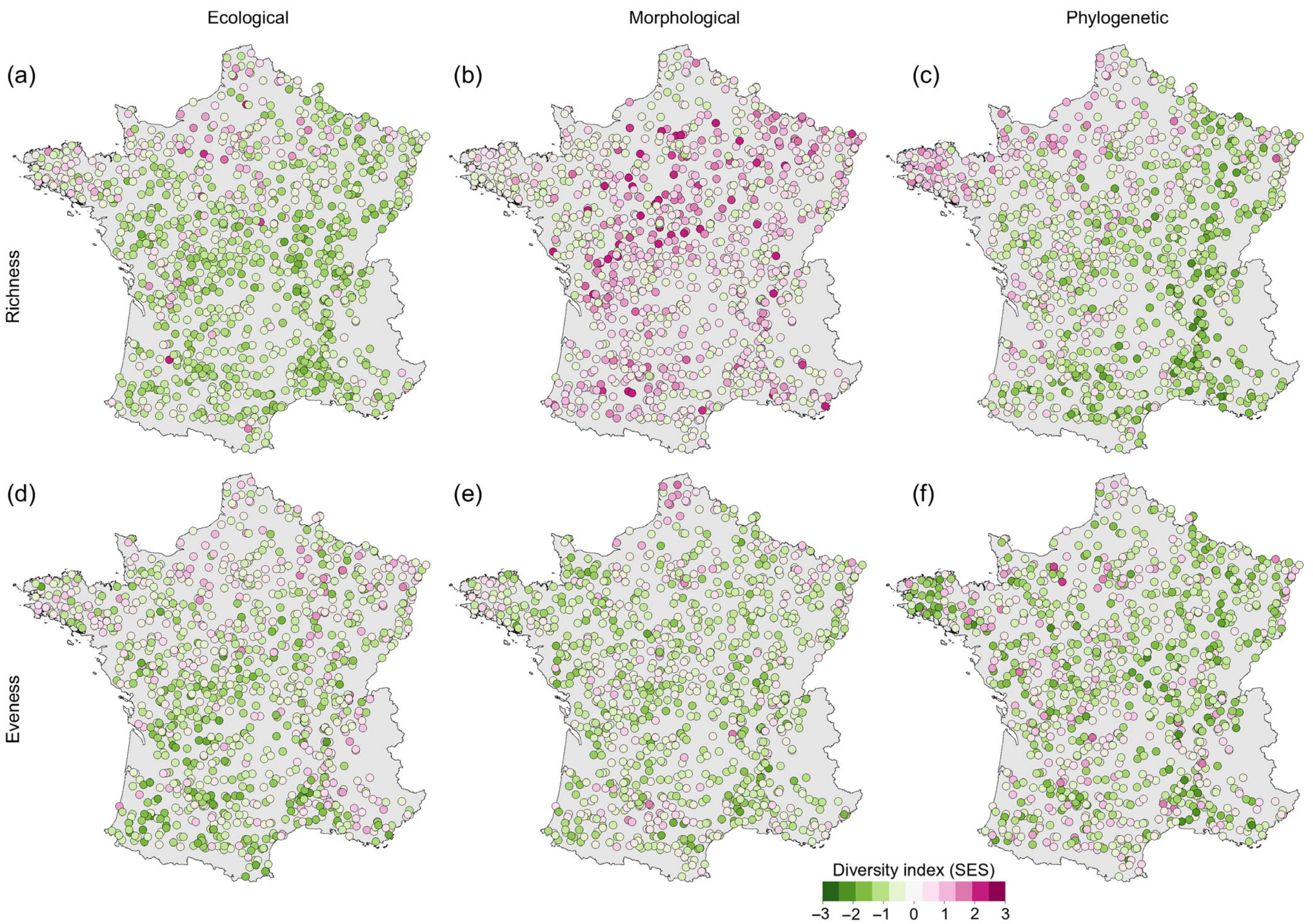

FIGURE 2 Richness and evenness for (a, d) ecological, (b, e) morphological, and (c, f) phylogenetic facets of diversity. Values of indices lower and higher than expected randomly given the number of species are indicated in green and purple, respectively.

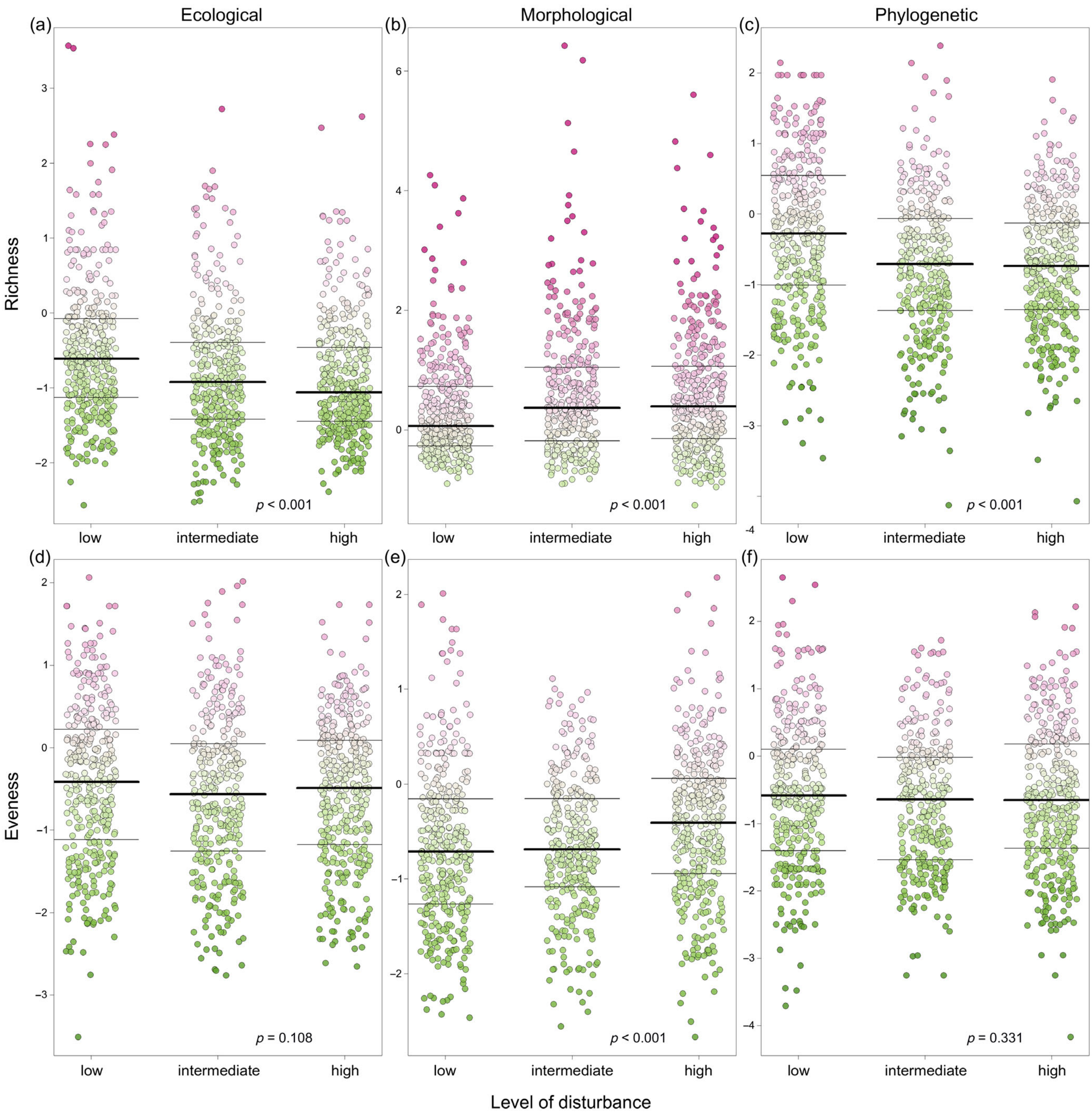

FIGURE 3 Relationships between the level of disturbance and the index values for each facet (morphological, ecological, and phylogenetic) and each component (richness, evenness) of diversity. The first row of panels represents the relationship between level of disturbances and richness, for (a) ecological, (b) morphological, and (c) phylogenetic facets. The second row presents the same relationship for evenness for (d) ecological, (e) morphological, and (f) phylogenetic facets. Horizontal thin and bold lines depict the quartiles and the median, respectively, with *p*-values of Kruskal–Wallis tests.

a relation slope lower to 1, with extreme positive and negative SES values, weaker when computed on complete assemblages.

Overall, the goodness-of-fit of models was higher for richness and SR than evenness indices (Table 1, Appendix S1: Figure S2). All indices responded significantly to climatic (i.e., both temperature and precipitation) conditions. Environmental and hydro-morphological pressures, presented similar importance, even if estimates from mean and seasonality of temperature factors were higher than those observed for anthropogenic disturbances. For native assemblages, we observed a negative effect of hydro-morphological disturbances on ecological and phylogenetic richness but a positive effect

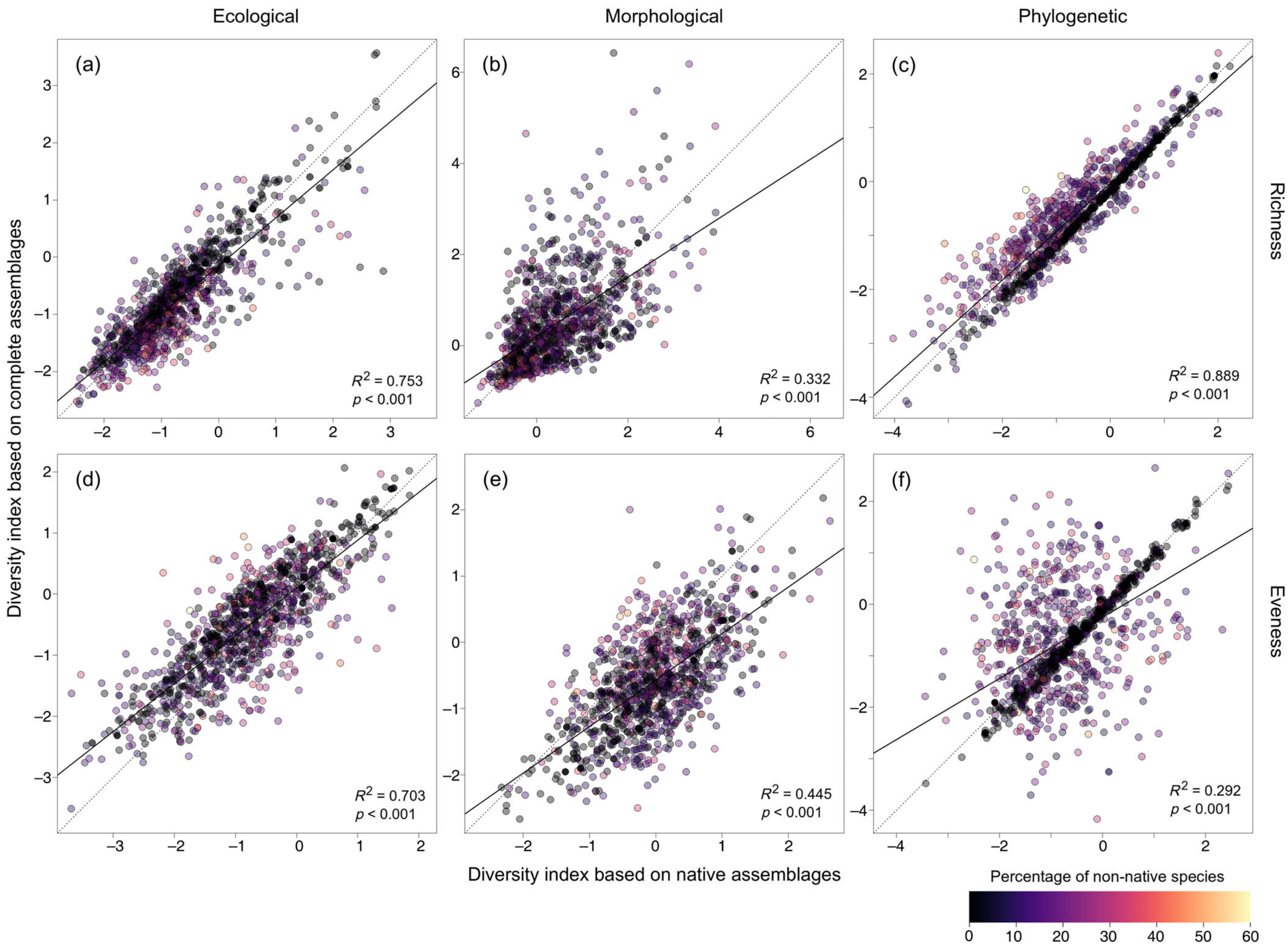

FIGURE 4 Relationships between diversity indices calculated on native assemblages only and complete assemblages for each component and facet of diversity. The first row of panels represents the relationship between level of disturbances and richness, for (a) ecological, (b) morphological, and (c) phylogenetic facets. The second row presents the same relationship for evenness for (d) ecological, (e) morphological, and (f) phylogenetic facets. The black line represents the linear relationship between the two indices, the dotted line represents $y = x$.

on morphological evenness. The presence of non native species (complete assemblages) exhibited similar results and revealed a positive effect on morphological richness. The models showed a significant negative effect of the aquatic habitat use on ecological richness only. This negative effect was stronger on complete assemblages, especially for morphological richness and evenness (Table 1, Appendix S1: Figure S2). Concerning the effect of climatic variables on native assemblages only, we observed a negative effect of temperature seasonality for almost all richness and evenness indices, except ecological evenness, but a positive effect of temperature mean on morphological and phylogenetic richness and a negative effect of temperature mean on ecological and phylogenetic evenness. Rainfall mean and, especially, rainfall seasonality, negatively influenced almost all indices (Table 1, Appendix S1: Figure S2). Similar results were observed on complete assemblages, with the loss of some effects for few indices.

DISCUSSION

Our results showed significant responses of all considered indices to anthropogenic disturbances and climatic drivers. We observed a decrease of ecological and phylogenetic richness with the intensity of disturbances whereas a weak increase was observed in morphological richness. Our study also highlighted contrasted effects of anthropogenic variables on diversity indices, with a strong importance of hydro-morphological and habitat use variables.

Spatial patterns in diversity indices

Our results showed spatial patterns in multifaceted diversity indices. Overall, low diversity values were mainly observed across France for all indices except for

TABLE 1 Results of linear mixed models of the effects of climatic variables and anthropogenic disturbances on standardized effect sizes (SES) of diversity indices (Eric, MRic, and PRic: ecological, morphological, and phylogenetic richness, respectively; EEve, MEve, and PEve: ecological, morphological, and phylogenetic evenness, respectively), computed on native assemblages only (Native) and entire assemblages (Complete).

Diversity indices	HYDRO	HUM	TEMP	TSEAS	PREC	PSEAS	R^2
Native							
ERic	**−0.017 (0.03)**	**−0.016 (0.03)**	−0.005 (0.49)	**−0.105 (<0.001)**	**−0.023 (0.002)**	**−0.023 (0.007)**	0.16
MRic	−0.015 (0.20)	−0.0006 (0.95)	**0.031 (0.0096)**	**−0.046 (0.0001)**	**−0.024 (0.028)**	**−0.048 (0.0001)**	0.57
PRic	**−0.17 (<0.001)**	−0.035 (0.28)	**0.137 (0.0002)**	**−0.211 (<0.001)**	**−0.473 (<0.001)**	−0.008 (0.80)	0.29
EEve	0.016 (0.62)	0.021 (0.48)	**−0.283 (<0.001)**	0.004 (0.89)	**−0.062 (0.04)**	0.062 (0.07)	0.07
MEve	**0.13 (<0.001)**	−0.030 (0.17)	−0.022 (0.35)	**−0.27 (<0.001)**	**−0.04 (0.042)**	**−0.079 (0.0017)**	0.12
PEve	**−0.18 (<0.001)**	−0.05 (0.07)	**−0.21 (<0.001)**	**−0.49 (<0.001)**	−0.035 (0.22)	−0.002 (0.96)	0.01
Complete							
ERic	**−0.02 (0.009)**	**−0.031 (0.0001)**	**−0.028 (0.0008)**	**−0.086 (<0.001)**	**−0.024 (0.0012)**	**−0.015 (0.066)**	0.13
MRic	**0.034 (0.003)**	**−0.043 (0.0001)**	**0.043 (0.0003)**	0.012 (0.29)	−0.011 (0.27)	**−0.064 (<0.001)**	0.55
PRic	**−0.104 (0.0005)**	−0.033 (0.23)	**−0.150 (<0.001)**	**−0.490 (<0.001)**	−0.049 (0.077)	−0.018 (0.57)	0.25
EEve	0.014 (0.62)	−0.003 (0.93)	**−0.272 (<0.0001)**	0.00005 (0.99)	**−0.063 (0.027)**	**0.089 (0.005)**	0.08
MEve	**0.162 (<0.001)**	**−0.080 (0.0002)**	−0.025 (0.33)	**−0.121 (<0.001)**	**−0.054 (0.025)**	−0.008 (0.74)	0.05
PEve	−0.024 (0.47)	−0.016 (0.63)	**0.088 (0.02)**	**−0.097 (0.005)**	−0.046 (0.15)	**−0.085 (0.020)**	0.01

Note: The indices were log-transformed when the distribution was not Gaussian. Given values are slope regression coefficients and *p*-values are indicated in brackets (in bold when significant at $p < 0.05$).

Abbreviations: HUM, human use; HYDRO, hydrological and morphological disturbances; NNS, percentage of non native species; PREC, total annual precipitation; PSEAS, seasonality of precipitation; SR, Species richness; TEMP, mean annual temperature; TSEAS, seasonality of temperature.

morphological richness. Kuczynski and Grenouillet (2018) found similar results on the same area, with mostly negative SES values for ecological and phylogenetic indices across France. In our study, nevertheless, higher values were observed in the North of France and Brittany for phylogenetic and ecological richness but also evenness. Another study, on phylogenetic diversity (Blanchet et al., 2014), found similar results with stronger values in Northern France. On the contrary, for morphological diversity, our results showed lower values for these two areas, especially for richness suggesting that morphology, usually used as a good proxy of ecological strategies, can reflect different patterns from those found using ecological traits.

Effect of anthropogenic disturbances on diversity and assemblages

Our results indicate a decrease of phylogenetic and ecological diversity with the increase of local disturbances. Previous studies showed contrasted results concerning this question but an increase of diversity in several taxa was observed (Galand et al., 2016; Geedicke et al., 2016; Murray et al., 2017), suggesting that disturbances could promote the cohabitation of different species and support the intermediate disturbance hypothesis (Moi et al., 2020). Regarding functional diversity, our study showed antagonistic results with a significant decrease of ecological diversity with increasing disturbances and, on the contrary, a weak increase of morphological diversity with disturbances, confirming contrasted responses between ecological and morphological diversity previously observed at the European scale (Kuczynski et al., 2018). These results suggest that habitat filtering for ecological and phylogenetic diversity significantly increased with the level of disturbances whereas limiting similarity increased with the level of disturbances for morphological traits (Abgrall et al., 2017; Escobedo et al., 2017). Indeed, human disturbances could act as selective filters which can shape the structure of communities (Mykrä et al., 2016; Ribeiro et al., 2016; Teichert et al., 2017).

Importance of the type of anthropogenic disturbances and environmental factors on facets and components of diversity

Our results highlighted the relative effect of both climatic variations and anthropogenic disturbances (habitat use and hydro-morphological disturbances) as strong drivers of communities. Environmental factors played an important role in the response of indices, with a strong negative effect of temperature and rainfall seasonality on several indices. It has already been showed that seasonality strongly impacts diversity of communities in tropical terrestrial ecosystems (Correa et al., 2021; Dzekashu et al., 2022; Oita et al., 2021) but few studies highlighted such a result in lotic ecosystems, especially temperate (Epele et al., 2022; Li et al., 2019). Most studies in lotic ecosystems (Faulks et al., 2011) but also in other ecosystems highlighted the predominance of environmental factors such as altitude or temperature seasonality (Howard et al., 2019). Seasonality of climatic variables seems to lead to habitat filtering and select for species with similar ecological traits but also closely-related species from an evolutionary perspective, in agreement with the stress-dominance hypothesis (SDH) (Kuczynski & Grenouillet, 2018). Environmental stochasticity thus tended to decrease diversity by eliminating species which are not well adapted to their environment and not able to face strong environmental fluctuations (Kuczynski & Grenouillet, 2018). Nevertheless, our result is in agreement with what has been previously found in neotropical fish where variance partitioning analysis revealed relative similar importance of environmental and anthropogenic gradients, much lower than dispersal variables (Borges et al., 2020). Other studies showed that natural environmental gradients could mask the effect of perturbations on biodiversity (Heino et al., 2007) and modify the relationship between environmental factors and diversity (Agra et al., 2021).

Although climatic variables (e.g., mean and seasonality of temperature) appeared to be the main drivers shaping the diversity and structure of fish communities, local disturbances could also strongly rearrange these assemblages, as it has been shown on several taxa (Steibl & Laforsch, 2019; Ticktin et al., 2012). Our results showed a negative effect of human use (recreational fishing, presence of water sport, or stocking) on functional (ecological and morphological) richness. This loss in richness can suggest that anthropogenic disturbances can lead to similar responses of assemblages and modify assemblage rules. On the contrary, hydro-morphological alterations only negatively affected phylogenetic richness but positively morphological richness. The negative effect of hydro-morphological alterations on fish richness has been showed in large rivers in a previous study but the different facets of diversity and the relative importance of this effect in comparison with other environmental drivers such as climatic ones were not investigated (Schinegger et al., 2013; Schmutz et al., 2015, 2016). The negative effect of non-native species on morphological diversity showed higher morphological diversity in native assemblages compared to complete ones. Similar results have been observed in comparable ecosystems. In fish, some studies showed a higher diversity of traits in non native species, suggesting that being functionally different could be one reason of their invasion success (Angulo-Valencia et al., 2022; Takács et al., 2021). In aquatic plants in China, Wang et al. (2021) showed an increase of plant functional diversity with a high degree of invasion of a non-native species. Moreover, the negative effect of some environmental drivers on morphological richness observed on native assemblages only disappeared when considering complete assemblages, but it was not the case for ecological and phylogenetic richness. Non-native species bring new morphological diversity and traits but these traits are not related to new ecological functions, suggesting ecological redundancy.

Moreover, our results showed contrasted responses depending on the component considered. Indeed, we detected low effect of disturbances on evenness, even if we observed an effect of all anthropogenic disturbances on morphological evenness. Morphological evenness differed between native and non-native species suggesting "a false compensation" since non-native and native species do not have equivalent functional roles within assemblages, which could have strong consequences for the maintenance of assemblages (Sobral et al., 2016). Moreover, results showed higher significant effects of some environmental factors such as mean temperature or mean rainfall on phylogenetic, morphological, and ecological indices than species richness. Then, the direction of the relationship between environmental factors and diversity was different between species richness and other indices. It is especially true for temperature seasonality for which a positive relationship was observed with species richness whereas negative ones were observed for almost all indices. This result suggests that integrating new facets of biodiversity, in addition to species richness, which is currently used in conservation studies, strongly enhances the assessment of management decisions (Fleishman et al., 2006; Hillebrand et al., 2018; Hurlbert & Jetz, 2007). Our study brings new insights since it highlighted that the type of anthropogenic pressures might be taken into consideration by planners and conservation managers in the prioritization of some sites, when facets are not congruent, because different types of biodiversity are more sensitive than others to different anthropogenic impacts. For instance, Cadotte and Tucker (2018) highlighted an approach of prioritizing sites which maximize 80%–85% of the upper values indices for each facet. The strongest anthropogenic impact in a given site might inform which index constitutes the most useful and sensitive indicator for management of biodiversity. For instance, the focus might be on functional diversity (ecological and morphological) when considering sites impacted by hydro-morphological pressures, whereas combining phylogenetic and functional diversity indices would be helpful in identifying sites impacted by human use.

CONCLUSION

Our study highlighted that the type and the level of disturbances could induce different responses, sometimes antagonistic and could differently affect the diversity and the structure of assemblages in freshwater fish. Consequently, these results revealed the importance of integrating a multifaceted approach to assess the responses of assemblages to multiple and different types of anthropogenic disturbances, which might be taken into account to better understand community-level responses to anthropogenic pressures and help guide priorities in conservation planning. Moreover, results showed that indices presented in this study constitute interesting complementary indicators to ones previously developed for fish in the assessment of local anthropogenic pressures but also climatic factors, including evolutionary history of species but also their functional characteristics.

ACKNOWLEDGMENTS

We are indebted to the French Biodiversity Office (OFB) for providing fish data. We are grateful to Nicolas Charpin for morphological measurements. Jessica Côte was funded by OFB. EDB lab was supported by "Investissement d'Avenir" grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Côte, 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.22263373. Data about life history traits were downloaded from Fishbase (https://www.fishbase.se/search.php) searching for "name of the species," the literature for all the species. Worldclim database was downloaded from https://www.worldclim.org/ by searching for "historical climate data" and then "bioclimatic variables". IPR+ database was downloaded from https://naiades.eaufrance.fr/ by searching for "accès aux données" and then "France entière" and "Hydromorphologie". Abundances OFB database was downloaded from https://naiades.eaufrance.fr/ by searching for "accès aux données" and then "France entière" and "Hydrobiologie".

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Côte, Jessica, Nicolas Poulet, Laurence Blanc, and Gaël Grenouillet. 2023. "Disentangling the Effects of Different Human Disturbances on Multifaceted Biodiversity Indices in Freshwater Fish." *Ecological Applications* 33(4): e2845. https://doi.org/10.1002/eap.2845