



HAL
open science

Assessing resilience and sensitivity patterns for fish and phytoplankton in French lakes

Barbbara Silva Rocha, Maxime Logez, Aurélien Jamoneau, Christine Argillier

► To cite this version:

Barbbara Silva Rocha, Maxime Logez, Aurélien Jamoneau, Christine Argillier. Assessing resilience and sensitivity patterns for fish and phytoplankton in French lakes. *Global Ecology and Conservation*, 2023, 43, pp.e02458. 10.1016/j.gecco.2023.e02458 . hal-04177227

HAL Id: hal-04177227

<https://hal.inrae.fr/hal-04177227>

Submitted on 4 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Assessing resilience and sensitivity patterns for fish and phytoplankton in French lakes

Barbbara Silva Rocha^{a,*}, Maxime Logez^b, Aurélien Jamoneau^c, Christine Argillier^a

^a INRAE, Aix Marseille Université, UMR RECOVER, 3275 Route Cézanne, 13182 Aix-en-Provence, France

^b INRAE, RIVERLY, F-69625 Villeurbanne Cedex, France

^c INRAE, EABX, 50 avenue de Verdun, 33612 Cestas, France

ARTICLE INFO

Keywords:

Vulnerability
Functional traits
Functional redundancy
Rarity
Reservoirs

ABSTRACT

Ecosystem vulnerability is crucial information for conservation managers. We assessed the sensitivity and resilience (vulnerability components) patterns of fish and phytoplankton assemblages in French lakes (natural and artificial). We measured resilience (functional redundancy) and sensitivity, an index considering three characteristics of rarity for species. We hypothesized that geographically close lakes have similar resilience and sensitivity for fish assemblages (H1). Then, we tested the correlation between environmental gradients and resilience and sensitivity components, assuming that fish and phytoplankton do not respond similarly to environmental factors and that, consequently, there is no congruence between sensitivity and resilience patterns between of two groups. Also, we tested the hypotheses that species-rich assemblages show higher resilience and sensitivity in French lakes (H2); the highest values of resilience and sensitivity are related to phytoplankton (H3); and assemblages from natural lakes have higher resilience and sensitivity level (H4). We found similar resilience levels in spatially close fish assemblages due to fish dispersal limitations that contributed to create regional patterns in functional structure. Besides, acidity and eutrophication processes are good indicators of sensitivity level for fish. There is a mismatch in resilience and sensitivity levels between fish and phytoplankton, reinforcing importance of using a multi-taxa approach. Also, the components were positively related to taxonomic richness in assemblages showing importance of conserving biodiversity. Finally, we observed higher values of resilience and sensitivity for phytoplankton, as expected for a highly diverse group. Additionally, phytoplankton assemblages in natural lakes showed higher resilience levels than artificial environments, confirming the importance of preserving natural systems to conserve ecosystem functionality.

1. Introduction

Ecosystem vulnerability is a research topic that has gained more attention in the last decades faced to the rapid biodiversity decline promoted by global changes (Weißhuhn et al., 2018). The vulnerability studies estimate the potential for species and/or function loss in ecosystems caused by external impacts (Adger, 2006; Fussler, 2007). This valuable information could be used by conservation managers to develop prioritization and mitigation strategies for threatened ecosystems by human-induced stressors (De Lange et al., 2010). Although there is no clear consensus on the measure of vulnerability in conservation ecology studies, sensitivity and adaptive

* Corresponding author.

E-mail address: barbbara.da-silva-rocha@inrae.fr (B.S. Rocha).

<https://doi.org/10.1016/j.gecco.2023.e02458>

Received 21 December 2022; Received in revised form 21 March 2023; Accepted 3 April 2023

Available online 5 April 2023

2351-9894/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

capacity are considered as two fundamental components of vulnerability (Füssel, 2007; Weißhuhn et al., 2018). The sensitivity estimates the potential magnitude of an impact induced by one or more stressors. Adaptive capacity, also called resilience, represents the ecosystem's capacity to recover and adapt after a disturbance (Adger, 2006; Baho et al., 2017; Munera-Roldan et al., 2022). Considering these two aspects, an environment and the organisms that inhabit it are potentially more vulnerable when they have a high sensitivity and a low resilience capacity to certain perturbations.

In general, most research addressed sensitivity components, whereas studies about resilience capacity are scarce (Angeler et al., 2015; Markovic et al., 2017; Okey et al., 2015; Weißhuhn et al., 2018). The few studies assessing resilience commonly adopt the trait-based approach linked to ecosystem functioning (Angeler et al., 2013; Gladstone-Gallagher et al., 2019; Su et al., 2019). This approach involves using functional redundancy as a proxy for resilience (Angeler et al., 2015; Elmqvist et al., 2003). Functional redundancy measures the degree to which a community is saturated with species possessing similar functional traits and can be calculated as the difference between Simpson's index of species diversity and Rao's quadratic entropy (RaoQ) (de Bello et al., 2007). In this context, a higher redundancy could ensure the ecosystem's resilience capacity after a decline in species diversity promoted by a perturbation due to several species with similar functional attributes/roles (Mouillot et al., 2014; Rosenfeld, 2002). Functional redundancy is a crucial tool in prioritization decisions by managers once it indicates "the lowest threshold" necessary to maintain the integrity of the ecosystem (Bruno et al., 2016; Moreno-García and Baiser, 2021; Rosenfeld, 2002). Therefore, it is crucial to integrate all components of vulnerability for an accurate measure in ecosystems (Markovic et al., 2017; Weißhuhn et al., 2018).

In addition, most previous studies about vulnerability have focused on single (potentially endangered) species facing one main stressor, e.g., climate change (Burthe et al., 2014; Wade et al., 2017). When several species are considered, they generally belong to single taxonomic groups, such as plants (D'Amato et al., 2013) or various vertebrates (Drever et al., 2012; Dufresnes and Perrin, 2015) for terrestrial ecosystems and fish (Nyboer et al., 2019), coral (Kurniawan et al., 2016), and macroinvertebrates (Ippolito et al., 2010) for aquatic ecosystems. However, comparing information about ecosystem vulnerability with multiple taxonomic groups can help to guide conservation efforts more effectively (Markovic et al., 2017; Weißhuhn, 2019). Indeed, the vulnerability level of a specific group can cause cascading effects for other taxonomic groups (Calizza et al., 2015). Also, patterns of vulnerability levels can vary among different taxonomic groups (Arreguín-Sánchez and Ruiz-Barreiro, 2014; Chen et al., 2022; Nevalainen et al., 2019; Teichert et al., 2017). Nonetheless, few studies assess or compare patterns of vulnerability components for more than one taxonomic group in ecosystems.

In freshwater ecosystems, fish and phytoplankton are distinct organisms that support critical ecological roles in providing multiple functions and services (Mota et al., 2014; Naselli-Flores and Padišák, 2022). For instance, fish species contribute to nutrient cycling and represent resources of food, sport, and aesthetic values for humans (Mota et al., 2014). On its turn, phytoplankton produces most of the biosphere oxygen, support most of the primary production, and greatly contributes to ecosystem nutrient cycling (Naselli-Flores and Padišák, 2022). Additionally, fish and phytoplankton occupy distinct extreme positions of freshwater food webs and develop a key role in regulating their structure via top-down and bottom-up effects, respectively (Mota et al., 2014; Naselli-Flores and Padišák, 2022). Therefore, assessing resilience and sensitivity to environmental changes for communities of these two groups is essential to predict the magnitude and prevent future human impacts on biodiversity and freshwater ecosystems' fundamental functions and services (Weißhuhn, 2019; Weißhuhn et al., 2018).

Previous literature have frequently explored the relationship between patterns in the level of resilience or sensitivity and the spatial distribution (Tracy et al., 2022), environmental conditions (Alther et al., 2019) or even the species diversity information in freshwater systems (Lamothe et al., 2018; Pelletier et al., 2020). For instance, studies evidenced similar resilience and sensitivity for spatially close freshwater assemblages of large-sized organisms such as fishes (Sievert et al., 2016). This is because these organisms have lower dispersal ability when compared to microorganisms, and lakes' spatial configuration can generate strong regional patterns in taxonomic and functional facets for this group (Beisner et al., 2006; Van Looy et al., 2019). Additionally, conservation studies test abiotic factors as predictors of resilience and sensitivity once they are related to important aspects driving biodiversity patterns, such as resource availability and habitat quality (Poole, 2002; Van Looy et al., 2019; Xue et al., 2018). Finally, fish and phytoplankton species-rich assemblages usually have a high functional redundancy (Kruk et al., 2017; Teichert et al., 2017) and an important number of sensitive species (e.g., rare, endemic, specialist; Ai et al., 2013; Kruk et al., 2017). Therefore, high species richness is expected to help ensure the maintenance of ecosystem functions in the case of species extinction due to impacts of human disturbance (i.e., insurance effect of biodiversity; Yachi and Loreau, 1999).

The type of ecosystem assessed is also important when investigating vulnerability components (Arreguín-Sánchez and Ruiz-Barreiro, 2014). In freshwaters, for example, the different kinds of water body systems (e.g., lake vs. river) can display different patterns of vulnerability levels due to the influence of their specific environmental characteristics (e.g., habitat and food availability, Teichert et al., 2017). However, according to our knowledge, the differences between natural and artificial environments have never been studied when assessing lake vulnerability. Artificial lakes, such as reservoirs, are usually more recent and less stable human-made environments that commonly have characteristics such as high nutrient and sediment input that contribute to an increase in turbidity and productivity level (Hayes et al., 2017, p. 4; Launois et al., 2011). Also, artificial lakes usually have shorter water residence times and higher water level fluctuation that mainly affect the habitats in the littoral zone (Borics et al., 2003; Kimmel and Groeger, 1984). These environmental characteristics act as filters for reducing species and functional diversity as more sensitive fish and phytoplankton species may be extirpated (Logez et al., 2016; Stević et al., 2013; Várbíró et al., 2017).

The present study aimed to assess the resilience and sensitivity (vulnerability components) patterns of fish and phytoplankton assemblages in French lake ecosystems. For this, we used functional redundancy and a rarity index (adapted from Leitão et al., 2016) to present resilience and sensitivity, respectively. Among the assessed patterns, we first searched for geographical patterns in the spatial distribution of sensitivity and resilience values for the two taxonomic groups across the country. Because patterns in fish biodiversity

are strongly influenced by regional processes such as dispersal (Beisner et al., 2006), we hypothesized that geographically close lakes have similar resilience and sensitivity for fish assemblages (H1). We then tested the correlation between environmental gradients and resilience and sensitivity components, assuming that fish and phytoplankton do not respond similarly to environmental factors and that, consequently, there is no congruence between sensitivity and resilience patterns between the two groups. Additionally, we tested correlation patterns among resilience, sensitivity and species richness for each taxonomic group. We hypothesized that species-rich assemblages show higher resilience and sensitivity in French lakes (H2). Compared to fish, phytoplankton is a higher diverse group in which several sensitive species are expected to co-exist and provide redundant functions (Borics et al., 2020; Logares et al., 2015). In addition, phytoplankton species have shorter generation times and greater metabolic rates, which can provide a faster and stronger recovery capacity after environmental changes (Downing and Leibold, 2010). Therefore, we also hypothesized that the highest values of resilience and sensitivity are related to the phytoplankton group (H3). Finally, because natural lakes are environments expected to present more sensitive species and redundant functions than artificial lakes (Kimmel and Groeger, 1984), we hypothesized that assemblages from natural lakes have higher resilience and sensitivity level (H4).

2. Methods

2.1. Biological and environmental data

We used a biological dataset, for fish and phytoplankton, sampled in 111 French lakes (26 natural and 85 artificial lakes) between 2008 and 2011. The fish data were collected following the Norden gillnet standardized protocol (CEN, 2005) during the summer period between June and October. This protocol used multi-mesh gillnets (30 m length and 1.5 m height) with 12 different panels of mesh sizes ranging from 5 to 55 mm knot-to-knot. They were set overnight (12 h) at random locations in different depth strata, and the sampling effort was adjusted to lake depth and area. All sampled fish individuals were identified at the species level. A total of 40 fish species were collected. The phytoplankton data was sampled using the standardized method following the protocol of Laplace-Treytore et al. (2009). Four sampling campaigns, three during the warmer months (i.e., May to October) and one in late winter, were performed in each lake. Samplings were collected at the deepest point in the euphotic part of the water column. Phytoplankton taxa were counted following the European Standard NF15204 (CEN-EN 15204). A total of 662 taxa were identified at least at the genus level, i.e., 519 species and 143 genera. For each taxa, we then calculated the biovolume (in mm^3) with the Phytobs software (Laplace-Treytore et al., 2017), i.e., the abundances weighted by taxa cell biovolume (Derot et al., 2020). We also determined the species richness of fish and phytoplankton assemblages.

We collected 11 environmental parameters in each lakes (Table 1). Six of them were related to the physicochemical environment: water temperature, alkalinity, nitrate concentration (NO_3^-), pH, secchi depth (a proxy for turbidity) and total phosphorus concentration (TotalP). The others were hydromorphological parameters: lake area (positively correlated with lake volume and mean depth), littoral artificialization (LitArt), littoral erosion (LitEro), riparian vegetation loss (RipVegLoss) and upstream volumes retained (VolRet). We did not include altitude as an environmental parameter as it strongly correlates to water temperature and TotalP in our dataset. The water temperature value was represented by the annual mean epilimnion temperature modeled for each lake (Prats and Danis, 2019; Sharaf et al., 2023). The parameters alkalinity, NO_3^- , pH, secchi depth, and TotalP were measured at the deepest point of the lakes according to national standards (MEDDE, 2012; Afnor, 2015). We considered information of these variables for samplings occurring during the years 2006 and 2015, i.e., the closest year when compared to biotic sampling events. We obtained mean values for these parameters regarding the integration of vertical profiles zone and four seasonal campaigns (Koenings and Edmundson, 1991; Pourriot and Meybeck, 1995)

LitArt, LitEro, RipVegLoss are morphological variables related to the suitability of the littoral zone in lakes. This zone influences the community dynamics of different biological groups in aquatic ecosystems because of its high diversity of habitats and resources (e.g., food and refuges; Logez et al., 2016; Schmieder, 2004; Zohary and Ostrovsky, 2011). The LitArt represents the proportion of the lakeshore presenting artificial structures constructed to avoid erosion process or for recreational purposes, which can decrease natural

Table 1

List of environmental parameters selected to represent lake's water quality and habitat suitability for fish and phytoplankton organisms. Units, mean, minimum and maximum values are presented for each parameter. The parameters were pH, total phosphorus concentration ("TotalP"), nitrate concentration (" NO_3^- "), secchi depth, water temperature ("Water temp."), alkalinity, lake area, littoral artificialization (LitArt), littoral erosion (LitEro), riparian vegetation loss (RipVegLoss) and upstream volumes retained (VolRet).

Group	Variable	Unit	Mean	Minimum	Maximum
Water quality	pH	-	7.79	6.49	8.92
	TotalP	mg/L	0.04	0.01	0.45
	NO_3^-	mg/L	5.04	0.09	55
	Secchi depth	cm	244.50	18.7	840
	Water temp.	$^{\circ}\text{C}$	13.88	9.23	18.25
	Alkalinity	mg/L	1.77	0.16	4.63
Habitat suitability	Lake area	km^2	8.38	0.34	577.12
	LitArt	-	0.88	0.21	1
	LitEro	-	0.98	0.76	1
	RipVegLoss	-	0.72	0.03	1
	VolRet	-	0.93	0.03	1

habitat and resource availability in the littoral zone. The LitEro represents the lakeshore's proportion with erosion due to different human activities that can promote higher sedimentation, nutrient delivery, and habitat modification in the lakes. The RipVegLoss represents the lakeshore's proportion without riparian cover, indicating weak stability of banks (against erosion), low resource availability, and a decrease in the depuration process. In addition, the VolRet variable is a hydrological parameter related to the level of water retention in the catchment area (due to the presence of a dam upstream). It indicates changes in the hydrological regime, residence time, and indirect chemical concentrations in lakes. All above-cited hydromorphological metrics represents the habitat suitability for species from 0 (more habitat suitability) to 1 (less habitat suitability). More details are provided in (Carriere et al. 2023).

2.2. Functional traits

For each taxonomic group, we selected eight functional traits commonly used in studies assessing functional diversity and representing the ecological roles in ecosystems and the response of species to environmental changes (Borics et al., 2020; Derot et al., 2020; Litchman and Klausmeier, 2008; Martini et al., 2021; Stefani et al., 2020; Truchy et al., 2015). For the fish group, the selected traits extracted from literature (Froese, 2009; Schmidt-Kloiber and Hering, 2015) were: body size, fecundity, feeding substrate, longevity, parental care, spawning substrate, trophic guild, and thermal tolerance (see their ecological importance in table S1). For phytoplankton, the traits selected from specific literature (Abonyi et al., 2018; Borics et al., 2020; Klais et al., 2017; Laplace-Tretyure et al., 2021; Rimet and Druart, 2018) were: biological form, cell biovolume, flagella, heterocyst, maximum linear dimension, mixotrophy, mucilage, and vacuole (see details in table S2).

2.3. Assemblage resilience

As a proxy of resilience level, we measured the functional redundancy for fish and phytoplankton groups following de Bello et al. (2007). This metric represents how a community is "saturated" with similar traits and considers the difference between taxonomic diversity (Simpson's index) and trait diversity (Rao's quadratic entropy). Considering this aspect, it was possible to identify the variation in functional redundancy of assemblages with the same level of trait diversity but distinct levels of taxonomic diversity (or vice versa). To measure functional redundancy, we used the Gower's distance among species according to the selected traits and the abundance (for fish) or total biovolume (i.e., cell biovolume times abundance for phytoplankton) matrices. We calculated functional redundancy values for each taxonomic group separately, using the function "rao.diversity" from the package SYNCSA (Debastiani and Pillar, 2012).

2.4. Assemblage sensitivity

We assumed that rare species are expected to have a higher vulnerability to extinction (Gaston and Kunin, 1997; Purvis et al., 2000). This is because these species show low abundance, narrow distribution and environmental tolerance and, consequently, are more sensitive to impacts of environmental changes promoted by natural or human-induced disturbances (Caro, 2010; Foden et al., 2013; Leitão et al., 2016). Therefore, we adapted a recent integrative index developed by Leitão et al. (2016) to represent community sensitivity. This index combines complementary information about the rarity characteristics of each species, i.e., local abundance (LA), geographical range (GR) and habitat breadth (HB) as proposed by (Rabinowitz, 1981). A combination of these three facets of rarity is essential for better evaluating species vulnerability to extinction (Tóth et al., 2022).

To represent the LA we used the mean number (based on the multiple lake samplings) of sampled individuals or biovolume in lakes where the species occurred for fish or phytoplankton, respectively (Leitão et al., 2016). We measured the GR by calculating the area (km²) of the minimum convex polygon encompassed by the outermost limits of each species' occurrence regarding their distribution on sampled lakes. For species recorded only in one lake, the GR was measured as the area of the lake. For species recorded in two lakes, we considered the polygon area in which sides are the mean extension of the two lakes and the distance between them. Restricting the GR estimates to our data allowed us to draw the environmental context in which species occur in French lakes. Also, for the phytoplankton group, it helped to deal with the lack of data about range distribution for most species in the literature. To measure GR, we used the functions: "SpatialPoints", "spDists" (package sp; Pebesma et al., 2012), "projection" (package raster; Hijmans et al., 2015), "spTransform" (package rgdal; Bivand et al., 2015) and "gArea" (package rgeos; Bivand et al., 2017). The HB was represented by the "tolerance" metric from "Outlying Mean Index" analyses (Dolédéc et al., 2000). Using the HB metric, it was possible to measure the species-specific niche breadth relative to the available niche space from the multidimensional space of all lakes' environmental characteristics. To calculate the HB, we used the function "niche" from the package ade4 (Chessel et al., 2009; Thioulouse et al., 2018) using the 11 environmental variables described previously. Before estimating HB values, all the environmental variables were log-transformed.

To decrease the magnitude across values, the three metrics, LA, GR, and HB, were log-transformed and standardized between 0 and 1 (Leitão et al., 2016). We also down-weighted each metric by its correlation with the two others (Kark et al., 2002) to consider the degree of dependence between them. We then integrated the three metrics in a single index (here called sensitivity index, SI) for a species *i*, which is calculated as

$$SI_i = 1 - \left(\frac{[(LA_i \bullet wLA) + (GR_i \bullet wGR) + (HB_i \bullet wHB)]}{2(wLA + wGR + wHB)} \right)$$

where the values w_{LA} , w_{GR} , and w_{HB} represent the weighting parameters, i.e., the degree of independence of each metric from the others. To calculate, for example, the weighting parameter for local abundance (w_{LA}) we used the equation

$$w_{LA} = \frac{1}{2} + \left[\left(\frac{1 - |r_{LAGR}|}{2} \right) \right] + \left[\left(\frac{1 - |r_{LAHB}|}{2} \right) \right]$$

in which r_{LAGR} represents the Pearson's correlation coefficient between LA and GR and r_{LAHB} represents the Pearson's correlation coefficient between LA and HB.

The SI_i values vary between 0: the potential value reached by the less sensitive species (i.e., most common, locally abundant with a large niche breadth); and 1: the potential value reached by the most sensitive species (i.e., rarer, less abundant with a small niche breadth). This way, it was possible to compare SI values between the two taxonomic groups (Leitão et al., 2016). Finally, we measured the sensitivity index at the assemblage level by calculating the mean of all SI_i values for species co-occurring in each lake.

2.5. Statistical analyses

To examine if sensitivity and resilience for fish and phytoplankton assemblages show geographical patterns and test the hypothesis that the closest lakes have similar resilience and sensitivity for fish assemblages (H1), we applied Mantel tests (Mantel, 1967). More specifically, we calculated Mantel tests between Euclidean distance matrices for resilience and sensitivity metrics and the geographic distance matrix for lakes by applying the Spearman's correlation and 9999 permutations (Legendre and Legendre, 2012). When significant correlations were observed, we also performed a partial mantel test to assess the relationship between the distance matrices for resilience and sensitivity metrics and the lakes geographic distance matrix, while controlling for potential environmental conditions spatially structured (i.e., Euclidean distance among the 11 selected environmental variables). Mantel and partial mantel tests were applied using the vegan package (Oksanen et al., 2020).

To test the correlation between resilience and sensitivity components and environmental gradients (i.e., the 11 selected environmental conditions) and the level of congruence for these components when comparing fish and phytoplankton groups, we ran Spearman's correlation analyses. In addition, to test the hypothesis that species-rich assemblages show higher resilience and sensitivity in French lakes (H2), we also conducted Spearman's correlation analyses among resilience, sensitivity, and species richness. For this, we used information for each taxonomic group separately.

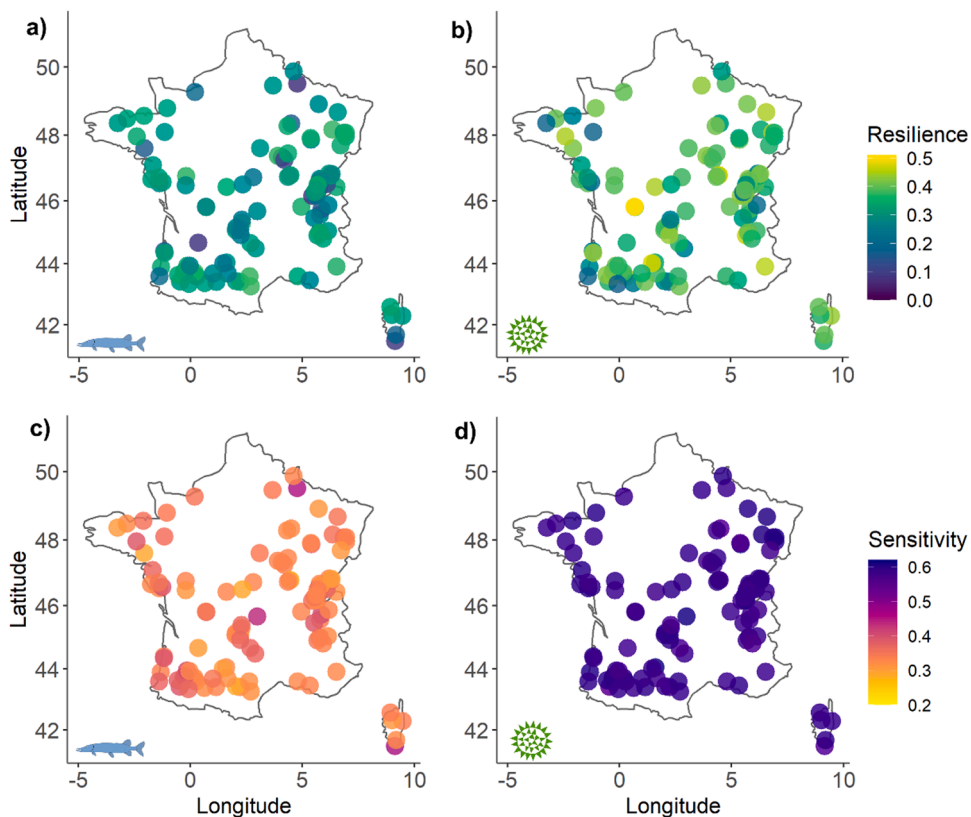


Fig. 1. Maps showing the resilience and sensitivity level regarding fish (panels “a” and “c”) and phytoplankton (panels “b” and “d”) assemblages of 111 French lake ecosystems. To view the legend and color scales for each organism group separately, please refer to Fig. S2.

To test the hypotheses that the highest values of resilience and sensitivity are related to the phytoplankton group (H3) and that assemblages from natural lakes have higher resilience and sensitivity level (H4), we used beta regression analysis (Ferrari and Cribari-Neto, 2004). Beta regression was applied once resilience and sensitivity ranged from 0 to 1, i.e., proportional data (Geissinger et al., 2022). For this, we constructed two models that considered the resilience and sensitivity values for all taxonomic groups as response variables, respectively. The predictor variables were the organism group (i.e., fish or phytoplankton) and the type of lake (artificial or natural) as a nested variable for the observations of each organism group. We ran models using the function “betareg” from betareg package (Zeileis et al., 2016).

3. Results

We found a significant weak correlation considering the distances in functional redundancy for fish assemblages and the geographical distances between lakes (Mantel test, $r = 0.118$, $p = 0.004$; partial Mantel test, $r = 0.163$, $p = 0.001$). This means that some fish assemblages in geographically close lakes have similar resilience levels (Fig. 1a). On the other hand, no significant correlation was observed regarding the resilience level in phytoplankton assemblages (Mantel test, $r = -0.007$, $p = 0.566$) or the sensitivity values considering fish ($r = 0.047$, $p = 0.113$) and phytoplankton ($r = -0.011$, $p = 0.618$) groups.

Regarding the relationship with the vulnerability metrics and environmental gradients, we observed a positive correlation of fish sensitivity with lake pH ($\rho = 0.26$, $p = 0.03$), lake area ($\rho = 0.24$, $p = 0.008$), alkalinity ($\rho = 0.23$, $p = 0.01$), secchi depth ($\rho = 0.23$, $p = 0.01$) and a negative correlation with NO₃⁻ ($\rho = -0.19$, $p = 0.04$) and TotalP ($\rho = -0.18$, $p = 0.04$), Fig. 2. The correlation between environmental conditions and resilience in fish assemblages was not statistically significant. Besides, we did not find any significant correlation between environmental conditions and the values of resilience and sensitivity for phytoplankton (Table S3).

We found no significant correlations between fish and phytoplankton groups considering functional redundancy and sensitivity values, evidencing an incongruence in their patterns (Table S3). Considering each taxonomic group separately, we found a significant positive correlation between species richness and the functional redundancy and sensitivity index in assemblages. More specifically, higher species richness is related to higher functional redundancy in fish ($\rho = 0.51$, $p < 0.001$) and phytoplankton ($\rho = 0.19$, $p < 0.05$) assemblages. Also, higher species richness is related to higher sensitivity in fish ($\rho = 0.23$, $p < 0.05$) and phytoplankton ($\rho = 0.31$, $p < 0.001$) assemblages (Fig. 3).

Phytoplankton assemblages showed higher resilience and sensitivity when compared to fish (Tables S5 and S6; Fig. 4). In addition,

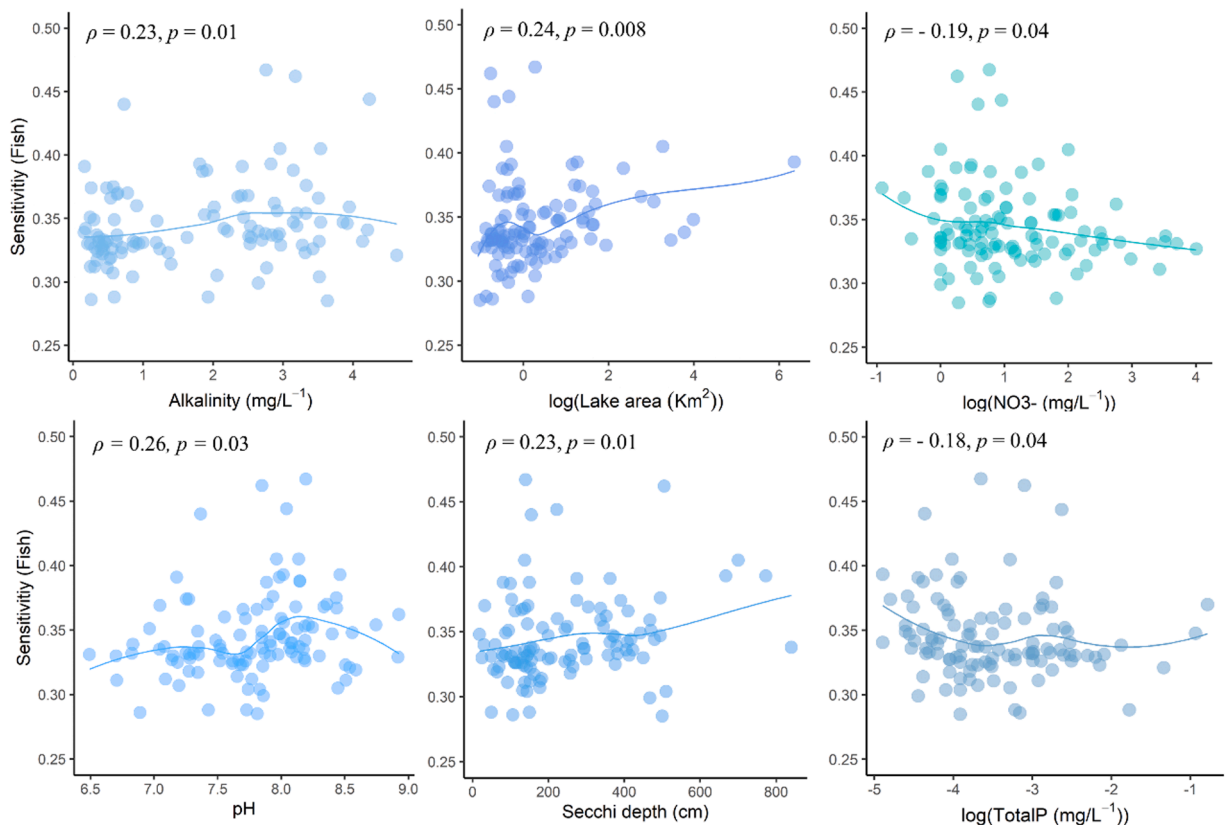


Fig. 2. Plots showing the statistically significant relationships between environmental conditions and sensitivity values for fish communities and the corresponding Spearman's correlation (ρ) and p-value. The lines are a smooth curve computed by the loess method.

we observed significant higher values of resilience in phytoplankton assemblages from natural lakes compared to reservoirs (Table S5; Fig. 4a). The sensitivity values did not significantly vary between the lake types (artificial and natural) within each taxonomic group (Table S6, Fig. 4b).

4. Discussion

This paper investigated patterns of sensitivity and resilience of fish and phytoplankton assemblages in French lakes. We found that fish assemblages in geographically closer lakes have similar resilience levels. Thus, this result suggests that regional processes help predict resilience patterns for this taxonomic group. Some spatial factors, such as increased connectivity for closer freshwater systems, can shape similar patterns in fish functional diversity for a specific region (Manfrin et al., 2020). In fact, Mehner et al. (2021) have previously found that closer European lakes have similar species. This is mainly because larger aquatic organisms, such as fish, have low dispersal ability and are influenced by lake connectivity (Strecker et al., 2011; Zarnetske et al., 2017). In addition, the post-glacial colonization process helps to explain the similar regional patterns in fish diversity in temperate freshwaters (Dias et al., 2014). Because we did not find a spatial structure for sensitivity, our hypothesis (H1) that the closest lakes have similar resilience and sensitivity for fish assemblages was not supported by the data.

Moreover, we observed that higher sensitivity level in fish assemblages was related to lakes presenting lower acidity, nutrient concentration, turbidity and larger sizes. Lakes showing an accumulation of nutrients and smaller sizes are frequently associated with the eutrophication process, a major anthropogenic pressure for freshwater ecosystems (Leng, 2009). Therefore, our findings suggest that French lakes exhibiting higher acidification and eutrophication levels are associated with the presence of more tolerant and less specialized fish. Additionally, we observed an incongruence in resilience and sensitivity between the fish and phytoplankton groups. As we expected, this mismatch reflects the different roles of spatial and environmental factors driving assemblage structure for fish and phytoplankton organisms. This result suggests that studies focusing on just one group are missing crucial and complementary information related to organisms developing distinct and important functional roles in ecosystems.

According to our results, fish and phytoplankton assemblages become more resilient and sensitive as species richness increases in French lakes, corroborating our H2. Firstly, the pattern found for resilience reinforces the insurance effect of diversity buffering potential loss of functions promoted by human disturbances in assemblages from French lakes. This pattern is consistent with the results of Teichert et al. (2017) for fish assemblages. It also goes in accordance with previous literature in which the taxonomic richness of freshwater organisms was found to be a good indicator of resilience and stability in ecosystems (Mykrä et al., 2011; Van Looy et al., 2019). Besides, previous studies also demonstrated that more diverse assemblages are more likely to have rare species or more specialized species (i.e., sensitive) in fish and phytoplankton assemblages (Kruk et al., 2017; Pompeu et al., 2021). Finally, our findings suggest that species richness is a better predictor than spatial or environmental factors for the resilience and sensitivity level of aquatic species assemblages. However, other processes linked to biotic interactions are reported as contributing to drive taxonomic and functional structure of temperate assemblages (Comte et al., 2016; Kruk et al., 2017). Thus, future studies should explore the



Fig. 3. Spearman's correlation values (ρ) among sensitivity ("Sens."), resilience ("Res.") and species richness ("Sp.Rich") for fish and phytoplankton ("Phyto") assemblages in French lakes. The * (p -value < 0.05) and *** (p -value < 0.001) represent significant correlations between pairs.

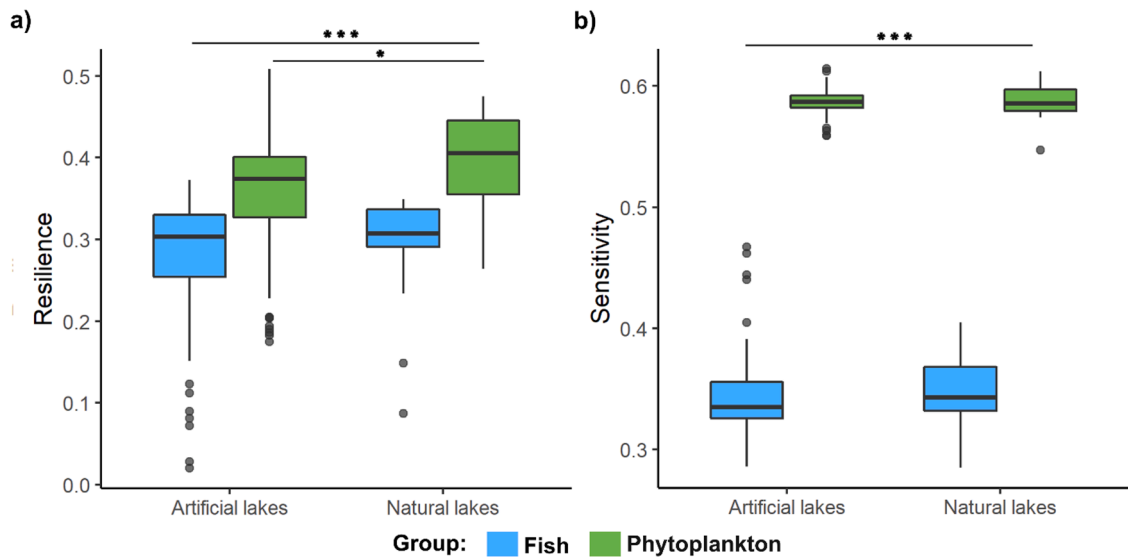


Fig. 4. Boxplot comparing resilience (“a”) and sensitivity (“b”) values for fish and phytoplankton groups regarding observations for all lakes, artificial or natural lakes categories.

relationship between biotic interaction and sensitivity and resilience patterns.

Phytoplankton assemblages showed higher sensitivity and resilience levels than fish in French lakes, corroborating our H3. The lower resilience capacity for fish assemblages is mainly due to lower species richness and the strong negative influence of biotic interactions on functional redundancy in French lakes, as already reported by literature (Comte et al., 2016; Teichert et al., 2017). In addition, phytoplankton is represented by smaller organisms with shorter generation times and greater metabolic rates, providing faster response and greater adaptation capacity (i.e., resilience) after disturbance (Jackson et al., 2021). Yet, the greater sensitivity level in phytoplankton assemblages can be explained by lower mean values for all three components of the rarity index, i.e., abundance, range distribution, and niche breadth (see values for each sensitivity component in Fig S1). Assemblages of microscopic organisms are known as “rare biosphere” in literature because most species present low abundance (Jousset et al., 2017; Logares et al., 2014). In addition, Roubeix et al. (2016) showed that phytoplankton species distribution in French lakes is strongly constrained by a combination of spatial process (i.e., migration) and environmental filtering acting on species with different tolerances for nutrient concentration, assuming a low range distribution.

Moreover, our results also suggested that resilience and sensitivity decrease along trophic levels in ecosystems once they are higher for producers (phytoplankton). Recently, Siqueira et al. (2022) showed that the assemblage’s stability decreased with trophic levels in freshwater systems. It is important to highlight that if the sensitivity index is high for most phytoplankton assemblages, some lakes presenting low redundancy must be of greater vulnerability to human disturbances. Considering the cascading effect (Power, 1992; Strong, 1992), the negative impacts of disturbances on vulnerable phytoplankton assemblages could indirectly affect fish or other organism groups from higher trophic levels that contribute to crucial functions in lake ecosystems. Thus, it is urgent to measure vulnerability components regarding multi-taxa information for ecosystem conservation studies. Going further, a solution to consider the indirect effect of species interactions from other trophic levels (magnitude of trophic cascade on the ecosystem) could be to evaluate measures of vulnerability components for food webs in ecosystems. Studies assessing freshwater food web vulnerability are still scarce and should be explored in future research (see Calizza et al., 2015).

According to our results, phytoplankton assemblages from artificial lakes showed less resilience, i.e., the capacity to adapt and recover after impacts of human disturbances, compared to natural lakes. This finding is related to characteristics of artificial lakes, which are human-created environments where environmental conditions have the potential to negatively affect species diversity and redundancy. More specifically, artificial lakes and particularly reservoirs can have lower habitat diversity promoted by several factors, such as high water level fluctuations (Kimmel and Groeger, 1984), low water residence time, and low age (Irz et al., 2006). In fact, Várbró et al. (2017), revealed that high habitat diversity allows the coexistence of more species holding different functional traits, consequently increasing functional redundancy in temperate reservoirs. Additionally, the lower residence time and age of artificial systems and the more disturbed environmental conditions (e.g., eutrophication and water mixing) reduce functional redundancy by extirpating species and altering functional composition in assemblages (Graco-Roza et al., 2021; Philippot et al., 2021; Várbró et al., 2017). As we did not find a difference in values between observations from natural and artificial lakes when considering the other components, our hypothesis that assemblages from natural lakes have higher resilience and sensitivity level (H4) was not supported by the data.

In conclusion, our study has implications for better assessing vulnerability components in freshwater ecosystems. The study found that fish assemblages in geographically closer lakes have similar resilience levels. Therefore, focusing on groups of lakes with similar fish populations and resilience levels can be a more efficient and effective way to conserve fish and their ecosystems than targeting

individual lakes. Lower sensitivity in fish assemblages was associated with lakes experiencing processes such as acidification and eutrophication. This information highlights the importance of considering exposure to stressors related to these processes when assessing the vulnerability index in French lakes. We emphasize the importance of integrating data from different organism groups in the development of a vulnerability index for aquatic or other ecosystems. This strategy will provide a more accurate assessment that managers can use to make informed decisions when prioritizing conservation efforts and mitigating impacts on these ecosystems. In addition, we emphasize the importance of using biodiversity as an indicator of resilience capacity and sensitivity in freshwater lake ecosystems. A better understanding of resilience and sensitivity component patterns is essential to avoid poor management decisions about ecosystem conservation. Finally, using a multi-taxa approach, we provided a framework to assess and compare information about resilience and sensitivity components. However, the degree and nature of exposure to impacts induced by stressors (e.g., climate change, species invasion, habitat loss) that represent the exposure component are still needed as a next step to develop a vulnerability index for lake ecosystems.

Ethics Statement

The study was carried out under compliance with relevant laws and guidelines and was approved by the INRAE-CIRAD-IFREMER-IRD ethics committee.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The authors do not have permission to share data.

Acknowledgements

We would like to thank everyone who participated in data collection and management, especially Nathalie Reynaud and Alexandra Carriere. The authors also thank Pierre Alain Danis and Najwa Sharaf for their valuable help with temperature data. Finally, we thank Christophe Laplace-Treyture for help with phytoplankton data.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02458](https://doi.org/10.1016/j.gecco.2023.e02458).

References

- Abonyi, A., Horváth, Z., Ptačnik, R., 2018. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. *Freshw. Biol.* 63, 178–186.
- Adger, W.N., 2006. Vulnerability. *Glob. Environ. Change* 16, 268–281.
- Ai, D., Chu, C., Ellwood, M.F., Hou, R., Wang, G., 2013. Migration and niche partitioning simultaneously increase species richness and rarity. *Ecol. Model.* 258, 33–39.
- Alther, R., Thompson, C., Lods-Crozet, B., Robinson, C.T., 2019. Macroinvertebrate diversity and rarity in non-glacial Alpine streams. *Aquat. Sci.* 81, 1–14.
- Angeler, D.G., Allen, C.R., Johnson, R.K., 2013. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. *J. Appl. Ecol.* 50, 572–584.
- Angeler, D.G., Baho, D.L., Allen, C.R., Johnson, R.K., 2015. Linking degradation status with ecosystem vulnerability to environmental change. *Oecologia* 178, 899–913.
- Arreguín-Sánchez, F., Ruiz-Barreiro, T.M., 2014. Approaching a functional measure of vulnerability in marine ecosystems. *Ecol. Indic.* 45, 130–138.
- Baho, D.L., Allen, C.R., Garmestani, A.S., Fried-Petersen, H.B., Renes, S.E., Gunderson, L.H., Angeler, D.G., 2017. A quantitative framework for assessing ecological resilience. *Ecol. Soc. J. Integr. Sci. Resil. Sustain.* 22, 1–17.
- Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., Longhi, M.L., 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* 87, 2985–2991.
- Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Rouault, E., Bivand, M.R., 2015. Package ‘rgdal’. *Bind. Geospatial Data Abstr. Libr. Available Online* <https://cran.r-project.org/web/packages/rgdal/index.html> Accessed 15 Oct. 2017.
- Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K.O., Bivand, M.R., 2017. Package ‘rgeos’. *Compr. R Arch. Netw. CRAN*.
- Borics, G., Tóthmérész, B., Grigorszky, I., Padišák, J., Várbíró, G., Szabó, S., 2003. Algal assemblage types of bog-lakes in Hungary and their relation to water chemistry, hydrological conditions and habitat diversity. In: *Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages*. Springer, pp. 145–155.
- Borics, G., Bácsi, I., Lukács, B.A., Botta-Dukát, Z., Várbíró, G., 2020. Trait convergence and trait divergence in lake phytoplankton reflect community assembly rules. *Sci. Rep.* 10, 1–11.
- Bruno, D., Gutiérrez-Cánovas, C., Velasco, J., Sánchez-Fernández, D., 2016. Functional redundancy as a tool for bioassessment: A test using riparian vegetation. *Sci. Total Environ.* 566, 1268–1276.
- Burthe, S.J., Wanless, S., Newell, M.A., Butler, A., Daunt, F., 2014. Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. *Mar. Ecol. Prog. Ser.* 507, 277–295.
- Calizza, E., Costantini, M.L., Rossi, L., 2015. Effect of multiple disturbances on food web vulnerability to biodiversity loss in detritus-based systems. *Ecosphere* 6, 1–20.

- Caro, T., 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press.
- Carriere, A.M.-J., Reynaud, N., Gay, A., Baudoin, J.-M., Argillier, C., 2023. LHYMO: A new WFD-compliant multimetric index to assess lake hydromorphology and its application to French lakes. *Eartharxiv*. <https://doi.org/10.31223/X5FT0Q>.
- CEN, 2005. Water Quality—Sampling of Fish with Multi-mesh Gillnets (EN 14757: 2005).
- Chen, Y., Xiong, K., Ren, X., Cheng, C., 2022. An overview of ecological vulnerability: A bibliometric analysis based on the Web of Science database. *Environ. Sci. Pollut. Res.* 29, 12984–12996.
- Chessel, D., Dufour, A.-B., Dray, S., 2009. Analysis of ecological data: exploratory and euclidean methods in environmental sciences. Version 14–14 2 Oct. 2010 1 4 11.
- Comte, L., Cucherousset, J., Boulétreau, S., Olden, J.D., 2016. Resource partitioning and functional diversity of worldwide freshwater fish communities. *Ecosphere* 7, e01356.
- D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecol. Appl.* 23, 1735–1742.
- de Bello, F., de Leps, J., Lavorel, S., Moretti, M., 2007. Importance of species abundance for assessment of trait composition: An example based on pollinator communities. *Community Ecol.* 8, 163–170.
- De Lange, H.J., Sala, S., Vighi, M., Faber, J.H., 2010. Ecological vulnerability in risk assessment—a review and perspectives. *Sci. Total Environ.* 408, 3871–3879.
- Debastiani, V.J., Pillar, V.D., 2012. SYNCSA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics* 28, 2067–2068.
- Derot, J., Jamoneau, A., Teichert, N., Rosebery, J., Morin, S., Laplace-Treytoure, C., 2020. Response of phytoplankton traits to environmental variables in French lakes: new perspectives for bioindication. *Ecol. Indic.* 108, 105659.
- Dias, M.S., Oberdorff, T., Huguény, B., Leprieux, F., Jézéquel, C., Cornu, J.-F., Brosse, S., Grenouillet, G., Tedesco, P.A., 2014. Global imprint of historical connectivity on freshwater fish biodiversity. *Ecol. Lett.* 17, 1130–1140.
- Dolédéc, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: a new method. *Ecology* 81, 2914–2927.
- Downing, A.L., Leibold, M.A., 2010. Species richness facilitates ecosystem resilience in aquatic food webs. *Freshw. Biol.* 55, 2123–2137.
- Drever, M.C., Clark, R.G., Derksen, C., Slattery, S.M., Toose, P., Nudds, T.D., 2012. Population vulnerability to climate change linked to timing of breeding in boreal ducks. *Glob. Change Biol.* 18, 480–492.
- Dufresnes, C., Perrin, N., 2015. Effect of biogeographic history on population vulnerability in European amphibians. *Conserv. Biol.* 29, 1235–1241.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1, 488–494.
- Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. *J. Appl. Stat.* 31, 799–815.
- Foden, W.B., Butchart, S.H., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* 8, e65427.
- Froese, R., 2009. FishBase. World wide web electronic publication. [Httpwww.fishbase.org](http://www.fishbase.org).
- Füssel, H.-M., 2007. Vulnerability: a generally applicable conceptual framework for climate change research. *Glob. Environ. Change* 17, 155–167.
- Gaston, K.J., Kunin, W.E., 1997. Rare—common differences: an overview. In: Kunin, W.E., Gaston, K.J. (Eds.), *The Biology of Rarity*, Biol. Rarity, 17. Springer, Dordrecht, pp. 12–29.
- Geissinger, E.A., Khoo, C.L., Richmond, I.C., Faulkner, S.J., Schneider, D.C., 2022. A case for beta regression in the natural sciences. *Ecosphere* 13, e3940.
- Gladstone-Gallagher, R.V., Pilditch, C.A., Stephenson, F., Thrush, S.F., 2019. Linking traits across ecological scales determines functional resilience. *Trends Ecol. Evol.* 34, 1080–1091.
- Graco-Roza, C., Soininen, J., Correa, G., Pacheco, F.S., Miranda, M., Domingos, P., Marinho, M.M., 2021. Functional rather than taxonomic diversity reveals changes in the phytoplankton community of a large dammed river. *Ecol. Indic.* 121, 107048.
- Hayes, N.M., Deemer, B.R., Corman, J.R., Razavi, N.R., Strock, K.E., 2017. Key differences between lakes and reservoirs modify climate signals: a case for a new conceptual model. *Limnol. Oceanogr. Lett.* 2, 47–62.
- Hijmans, R.J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Lamigueiro, O.P., Bevan, A., Racine, E.B., Shortridge, A., 2015. Package 'raster.' R Package 734.
- Ippolito, A., Sala, S., Faber, J.H., Vighi, M., 2010. Ecological vulnerability analysis: a river basin case study. *Sci. Total Environ.* 408, 3880–3890.
- Irz, P., Odion, M., Argillier, C., Pont, D., 2006. Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs? *Aquat. Sci.* 68, 109–116.
- Jackson, M.C., Pawar, S., Woodward, G., 2021. The temporal dynamics of multiple stressor effects: From individuals to ecosystems. *Trends Ecol. Evol.* 36, 402–410.
- Jousset, A., Bienhold, C., Chatzinotas, A., Gallien, L., Gobet, A., Kurm, V., Küsel, K., Rillig, M.C., Rivett, D.W., Salles, J.F., 2017. Where less may be more: How the rare biosphere pulls ecosystems strings. *ISME J.* 11, 853–862.
- Kark, S., Mukerji, T., Safriel, U.N., Noy-Meir, I., Nissani, R., Darvasi, A., 2002. Peak morphological diversity in an ecotone unveiled in the chukar partridge by a novel Estimator in a Dependent Sample (EDS). *J. Anim. Ecol.* 71, 1015–1029.
- Kimmel, B.L., Groeger, A.W., 1984. Factors controlling primary production in lakes and reservoirs: a perspective. *Lake Reserv. Manag.* 1, 277–281.
- Klais, R., Norros, V., Lehtinen, S., Tamminen, T., Olli, K., 2017. Community assembly and drivers of phytoplankton functional structure. *Funct. Ecol.* 31, 760–767.
- Koenings, J.P., Edmundson, J.A., 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. *Limnol. Oceanogr.* 36, 91–105.
- Kruk, C., Segura, A.M., Costa, L.S., Lacerot, G., Kosten, S., Peeters, E.T., Huszar, V.L., Mazzeo, N., Scheffer, M., 2017. Functional redundancy increases towards the tropics in lake phytoplankton. *J. Plankton Res.* 39, 518–530.
- Kurniawan, F., Adrianto, L., Bengen, D.G., Prasetyo, L.B., 2016. Vulnerability assessment of small islands to tourism: The case of the Marine Tourism Park of the Gili Matra Islands, Indonesia. *Glob. Ecol. Conserv.* 6, 308–326.
- Lamothe, K.A., Alofs, K.M., Jackson, D.A., Somers, K.M., 2018. Functional diversity and redundancy of freshwater fish communities across biogeographic and environmental gradients. *Divers. Distrib.* 24, 1612–1626.
- Laplace-Treytoure, C., Barbe, J., Dutartre, A., Druart, J.C., Rimet, F., Anneville, O., 2009. Protocole standardisé d'échantillonnage, de conservation, d'observation et de dénombrement du phytoplancton en plan d'eau pour la mise en œuvre de la DCE: version 3.3. 1. Irstea.
- Laplace-Treytoure, C., Hadoux, E., Plaire, M., Dubertrand, A., Esmieu, P., 2017. PHYTOBS v3. 0: Outil de comptage du phytoplancton en laboratoire et de calcul de l'IPLAC.
- Laplace-Treytoure, C., Derot, J., Prévost, E., Le Mat, A., Jamoneau, A., 2021. Phytoplankton morpho-functional trait dataset from French water-bodies. *Sci. Data* 8, 1–9.
- Launois, L., Veslot, J., Irz, P., Argillier, C., 2011. Selecting fish-based metrics responding to human pressures in French natural lakes and reservoirs: Towards the development of a fish-based index (FBI) for French lakes. *Ecol. Freshw. Fish.* 20, 120–132.
- Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. B Biol. Sci.* 283, 20160084.
- Leng, R., 2009. The impacts of cultural eutrophication on lakes: A review of damages and nutrient control measures. *Freshw. Syst. Soc.* 20, 37–38.
- Litchman, E., Klausmeier, C.A., 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Syst.* 39, 615–639.
- Logares, R., Audic, S., Bass, D., Bittner, L., Boutte, C., Christen, R., Claverie, J.-M., Decelle, J., Dolan, J.R., Dunthorn, M., 2014. Patterns of rare and abundant marine microbial eukaryotes. *Curr. Biol.* 24, 813–821.
- Logares, R., Mangot, J.-F., Massana, R., 2015. Rarity in aquatic microbes: Placing protists on the map. *Res. Microbiol.* 166, 831–841.
- Logez, M., Roy, R., Tissot, L., Argillier, C., 2016. Effects of water-level fluctuations on the environmental characteristics and fish-environment relationships in the littoral zone of a reservoir. *Fund. Appl. Limnol.* 189, 37–49.

- Manfrin, A., Bunzel-Drüke, M., Lorenz, A.W., Maire, A., Scharf, M., Zimball, O., Stoll, S., 2020. The effect of lateral connectedness on the taxonomic and functional structure of fish communities in a lowland river floodplain. *Sci. Total Environ.* 719, 137169.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res* 27, 209–220.
- Markovic, D., Carrizo, S.F., Kärcher, O., Walz, A., David, J.N., 2017. Vulnerability of European freshwater catchments to climate change. *Glob. Change Biol.* 23, 3567–3580.
- Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B.E., Bittner, L., Castella, E., 2021. Functional trait-based approaches as a common framework for aquatic ecologists. *Limnol. Oceanogr.* 66, 965–994.
- Mehner, T., Argillier, C., Hesthagen, T., Holmgren, K., Jeppesen, E., Kelly, F., Krause, T., Olin, M., Volta, P., Winfield, L.J., 2021. Model-based decomposition of environmental, spatial and species-interaction effects on the community structure of common fish species in 772 European lakes. *Glob. Ecol. Biogeogr.* 30, 1558–1571.
- Moreno-García, P., Baiser, B., 2021. Assessing functional redundancy in Eurasian small mammal assemblages across multiple traits and biogeographic extents. *Ecography* 44, 320–333.
- Mota, M., Sousa, R.G., Araújo, J., Braga, C., Antunes, C., 2014. Ecology and conservation of freshwater fish: Time to act for a more effective management. *Ecol. Freshw. Fish.* 23, 111–113.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl. Acad. Sci.* 111, 13757–13762.
- Munera-Roldan, C., Colloff, M.J., Locatelli, B., Wyborn, C., 2022. Engaging with the future: Framings of adaptation to climate change in conservation. *Ecosyst. People* 18, 174–188.
- Mykrä, H., Heino, J., Oksanen, J., Muotka, T., 2011. The stability–diversity relationship in stream macroinvertebrates: Influences of sampling effects and habitat complexity. *Freshw. Biol.* 56, 1122–1132.
- Naselli-Flores, L., Padišák, J., 2022. Ecosystem services provided by marine and freshwater phytoplankton. *Hydrobiologia* 1–16.
- Nevalainen, M., Vanhatalo, J., Helle, I., 2019. Index-based approach for estimating vulnerability of Arctic biota to oil spills. *Ecosphere* 10, e02766.
- Nyboer, E.A., Liang, C., Chapman, L.J., 2019. Assessing the vulnerability of Africa's freshwater fishes to climate change: a continent-wide trait-based analysis. *Biol. Conserv.* 236, 505–520.
- Okey, T.A., Agbayani, S., Alidina, H.M., 2015. Mapping ecological vulnerability to recent climate change in Canada's Pacific marine ecosystems. *Ocean Coast. Manag.* 106, 35–48.
- Pebesma, E., Bivand, R., Pebesma, M.E., RColorBrewer, S., Collate, A.A.A., 2012. Package 'sp.' *Compr. R Arch. Netw.*
- Pelletier, M.C., Ebersole, J., Mulvaney, K., Rashleigh, B., Gutiérrez, M.N., Chintala, M., Kuhn, A., Molina, M., Bagley, M., Lane, C., 2020. Resilience of aquatic systems: Review and management implications. *Aquat. Sci.* 82, 1–25.
- Philippot, L., Griffiths, B.S., Langenheder, S., 2021. Microbial community resilience across ecosystems and multiple disturbances. *Microbiol. Mol. Biol. Rev.* 85, e00026–20.
- Pompeu, P.S., de Carvalho, D.R., Leal, C.G., Leitão, R.P., Alves, C.B.M., Braga, D.F., Castro, M.A., Junqueira, N.T., Hughes, R.M., 2021. Sampling efforts for determining fish species richness in megadiverse tropical regions. *Environ. Biol. Fishes* 104, 1487–1499.
- Poole, G.C., 2002. Fluvial landscape ecology: Addressing uniqueness within the river discontinuum. *Freshw. Biol.* 47, 641–660.
- Pourriot, R., Meybeck, M., 1995. *Limnologie générale*.
- Power, M.E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73, 733–746.
- Prats, J., Danis, P.-A., 2019. An epilimnion and hypolimnion temperature model based on air temperature and lake characteristics. *Knowl. Manag. Aquat. Ecosyst.* 420, 8.
- Purvis, A., Jones, K.E., Mace, G.M., 2000. Extinction. *BioEssays* 22, 1123–1133.
- Rimet, R., Druart, J.-C., 2018. A trait database for Phytoplankton of temperate lakes. *Ann. Limnol. - Int. J. Lim.* 54, 18.
- Rabinowitz, D., 1981. Seven forms of rarity. *Biol. Asp. Rare Plant Conserv.*
- Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. *Oikos* 98, 156–162.
- Roubeix, V., Danis, P.-A., Feret, T., Baudoin, J.-M., 2016. Identification of ecological thresholds from variations in phytoplankton communities among lakes: Contribution to the definition of environmental standards. *Environ. Monit. Assess.* 188, 1–20.
- Schmidt-Kloiber, A., Hering, D., 2015. www.freshwaterecology. Info—an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecol. Indic.* 53, 271–282.
- Schmieder, K., 2004. European lake shores in danger—concepts for a sustainable development. *Limnologica* 34, 3–14.
- Sharaf, N., Prats, J., Reynaud, N., Tormos, T., Peroux, T., Danis, P.-A., 2023. A long-term dataset of simulated epilimnion and hypolimnion temperatures in 401 French lakes (1959–2020). *Earth Syst. Sci. Data Discuss.* 1–16.
- Sievert, N.A., Paukert, C.P., Tsang, Y.-P., Infante, D., 2016. Development and assessment of indices to determine stream fish vulnerability to climate change and habitat alteration. *Ecol. Indic.* 67, 403–416.
- Siqueira, T., Hawkins, C.P., Olden, J., Tonkin, J., Comte, L., Saito, V.S., Anderson, T.L., Barbosa, G.P., Bonada, N., Bonecker, C.C., 2022. Ecological stability propagates across spatial scales and trophic levels in freshwater ecosystems.
- Stefani, F., Schiavon, A., Tirozzi, P., Gomarasca, S., Marziali, L., 2020. Functional response of fish communities in a multistressed freshwater world. *Sci. Total Environ.* 740, 139902.
- Stević, F., Mihaljević, M., Špoljarić, D., 2013. Changes of phytoplankton functional groups in a floodplain lake associated with hydrological perturbations. *Hydrobiologia* 709, 143–158.
- Strecker, A.L., Olden, J.D., Whittier, J.B., Paukert, C.P., 2011. Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecol. Appl.* 21, 3002–3013.
- Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73, 747–754.
- Su, G., Villéger, S., Brosse, S., 2019. Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. *Glob. Ecol. Biogeogr.* 28, 211–221.
- Teichert, N., Lepage, M., Sagouis, A., Borja, A., Chust, G., Ferreira, M.T., Pasquaudo, S., Schinegger, R., Segurado, P., Argillier, C., 2017. Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. *Sci. Rep.* 7, 1–11.
- Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., Pavoine, S., 2018. Multivariate analysis of ecological data with ade4.
- Tóth, R., Czeglédi, I., Takács, P., Tedesco, P.A., Erős, T., 2022. Taxonomic rarity and functional originality of freshwater fishes and their responses to anthropogenic habitat alterations. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 32, 484–494.
- Tracy, E.E., Infante, D.M., Cooper, A.R., Taylor, W.W., 2022. An ecological resilience index to improve conservation action for stream fish habitat. *Aquat. Conserv. Mar. Freshw.* 32, 951–966.
- Truchy, A., Angeler, D.G., Sponseller, R.A., Johnson, R.K., McKie, B.G., 2015. Linking biodiversity, ecosystem functioning and services, and ecological resilience: Towards an integrative framework for improved management. In: *Advances in Ecological Research*. Elsevier, pp. 55–96.
- Van Looy, K., Tonkin, J.D., Flourey, M., Leigh, C., Soininen, J., Larsen, S., Heino, J., LeRoy Poff, N., Delong, M., Jähnig, S.C., 2019. The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. *River Res. Appl.* 35, 107–120.
- Várbíró, G., Görgényi, J., Tóthmérész, B., Padišák, J., Hajnal, É., Borics, G., 2017. Functional redundancy modifies species–area relationship for freshwater phytoplankton. *Ecol. Evol.* 7, 9905–9913.
- Wade, A.A., Hand, B.K., Kovach, R.P., Luikart, G., Whited, D.C., Muhlfeld, C.C., 2017. Accounting for adaptive capacity and uncertainty in assessments of species' climate-change vulnerability. *Conserv. Biol.* 31, 136–149.
- Weißhuhn, P., 2019. Indexing the vulnerability of biotopes to landscape changes. *Ecol. Indic.* 102, 316–327.

- Weißhuhn, P., Müller, F., Wiggner, H., 2018. Ecosystem vulnerability review: Proposal of an interdisciplinary ecosystem assessment approach. *Environ. Manag.* 61, 904–915.
- Xue, Y., Chen, H., Yang, J.R., Liu, M., Huang, B., Yang, J., 2018. Distinct patterns and processes of abundant and rare eukaryotic plankton communities following a reservoir cyanobacterial bloom. *ISME J.* 12, 2263–2277.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* 96, 1463–1468.
- Zarnetske, P.L., Baiser, B., Strecker, A., Record, S., Belmaker, J., Tuanmu, M.-N., 2017. The interplay between landscape structure and biotic interactions. *Curr. Landsc. Ecol. Rep.* 2, 12–29.
- Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., Rocha, A.V., Zeileis, M.A., 2016. Package betareg. R. Package 3.
- Zohary, T., Ostrovsky, I., 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters* 1, 47–59.