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

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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

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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.

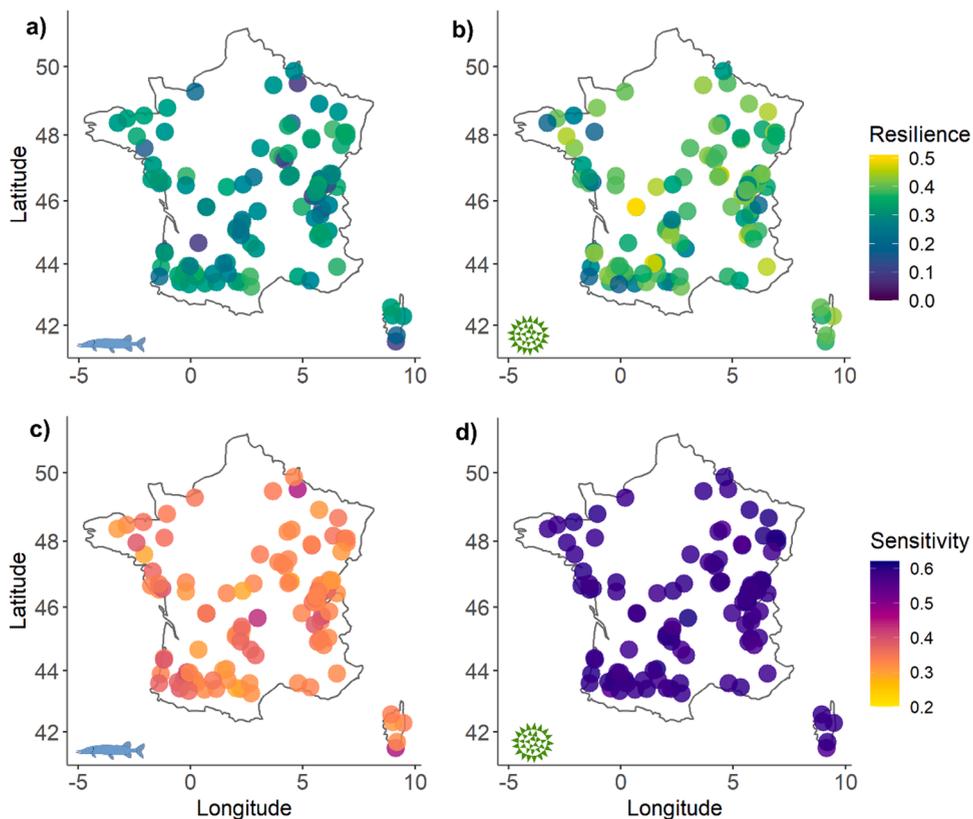


Fig. 1. Maps showing the resilience and sensitivity level regarding fish (panels “a” and “c”) and phytoplankton (panels “b” and “d”) assemblages of 111 French lake ecosystems. To view the legend and color scales for each organism group separately, please refer to Fig. S2.

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 NO_3^- ($\rho = -0.19$, $p = 0.04$) 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,

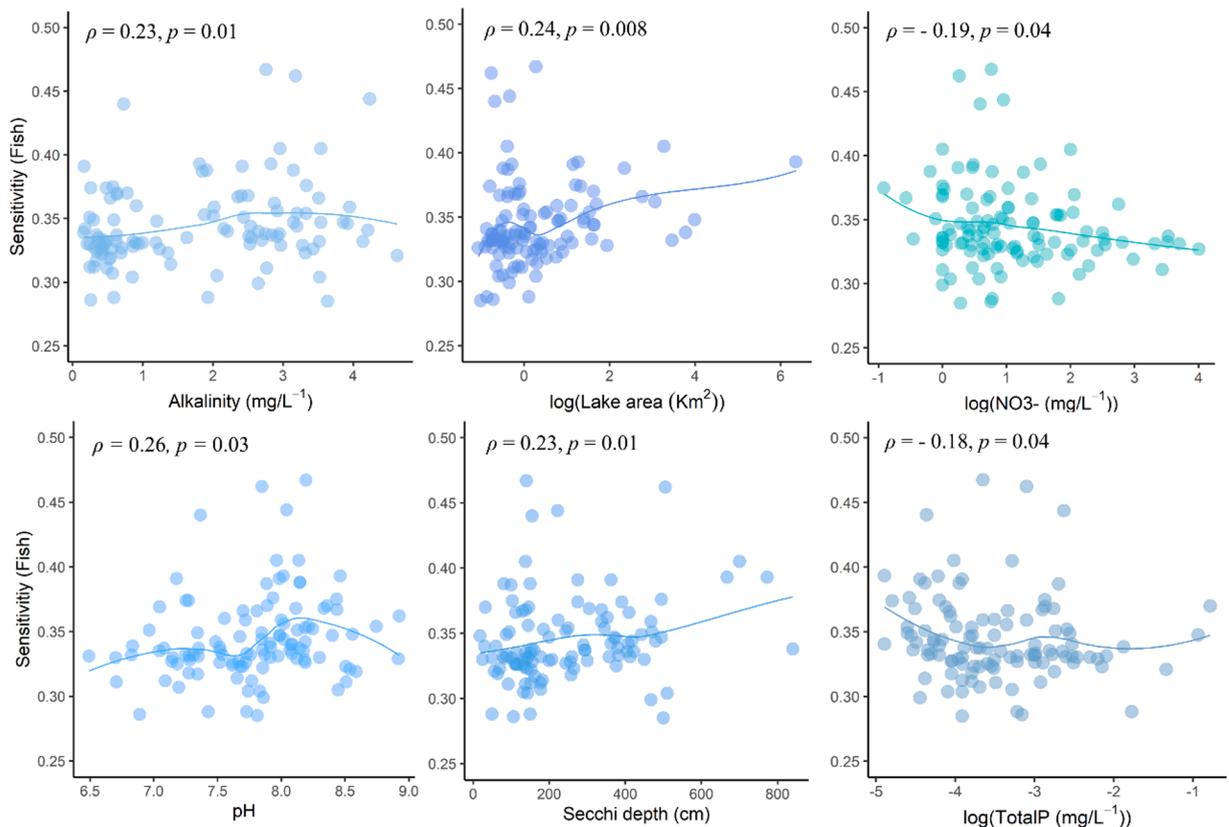


Fig. 2. Plots showing the statistically significant relationships between environmental conditions and sensitivity values for fish communities and the corresponding Spearman's correlation (ρ) and p-value. The lines are a smooth curve computed by the loess method.

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

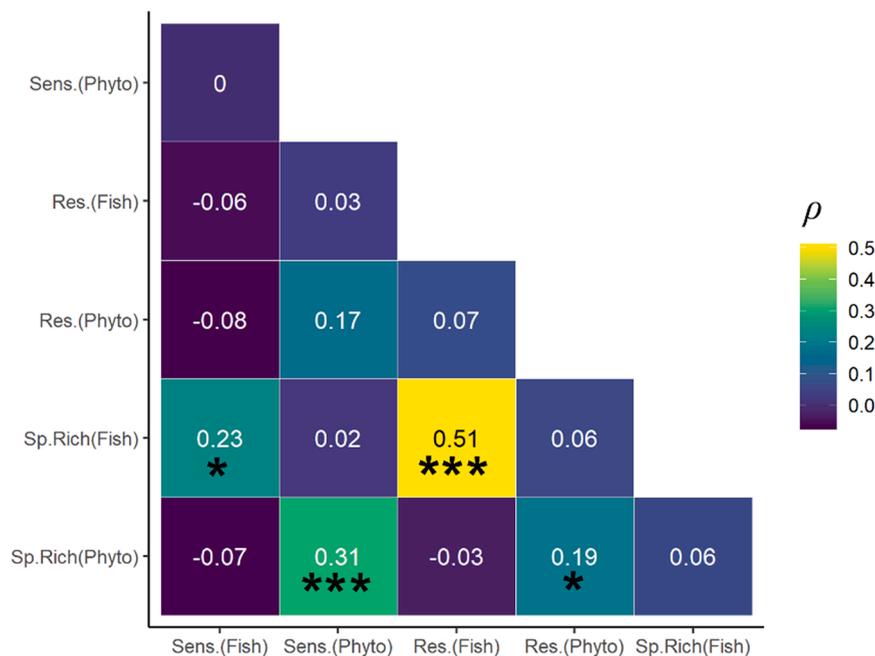


Fig. 3. Spearman's correlation values (ρ) among sensitivity ("Sens."), resilience ("Res.") and species richness ("Sp.Rich") for fish and phytoplankton ("Phyto") assemblages in French lakes. The * (p -value < 0.05) and *** (p -value < 0.001) represent significant correlations between pairs.

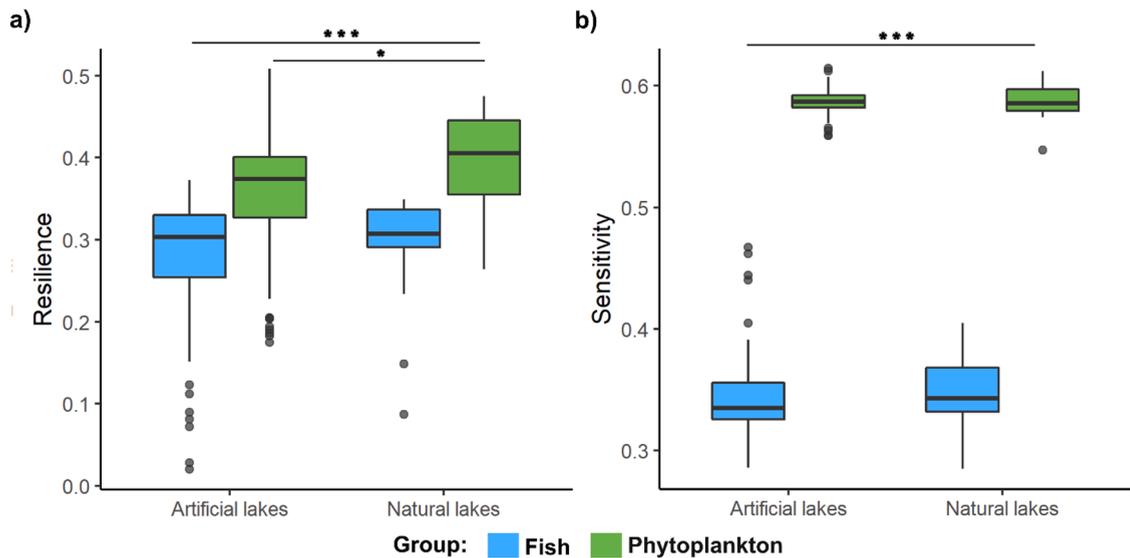


Fig. 4. Boxplot comparing resilience (“a”) and sensitivity (“b”) values for fish and phytoplankton groups regarding observations for all lakes, artificial or natural lakes categories.

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.

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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).

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