Measuring biodiversity vulnerability in French lakes – The IVCLA index

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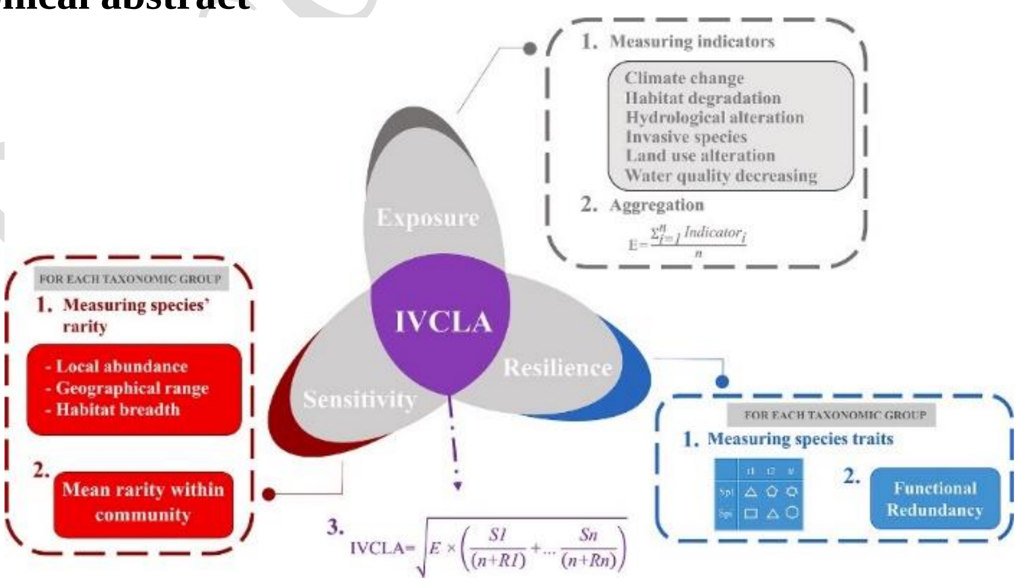
Abstract

Assessing the vulnerability of ecosystems to biodiversity loss has become increasingly crucial in conservation and ecology research. This study proposed a methodology for measuring lake vulnerability to biodiversity loss employing an established framework that combines three components. For this, we measured the resilience (functional redundancy) and sensitivity (an index considering three characteristics of rarity) components for fish and phytoplankton communities. We also measured the exposure component of the main stressors in lakes. We then combined the three components and calculated the vulnerability index (IVCLA) using data from 255 French lakes. We found that all lakes exhibited low levels of resilience, elevated sensitivity regarding average values for fish and phytoplankton groups, and medium exposure to stressors associated with human activities. In addition, there were some discrepancies in resilience and sensitivity patterns between fish and phytoplankton groups, emphasizing the importance of considering information from multiple biological groups when assessing ecosystem vulnerability. Hydrological alterations and low water quality were key stressors related to higher lake vulnerability. Most French lakes have been classified as exhibiting moderate vulnerability. It is crucial to emphasize the potential increase in exposure risks, which could lead to even higher vulnerability levels and, subsequently, biodiversity loss in the future. The IVCLA index offers several advantages, including integrating multiple taxa groups and stressors. We recommend incorporating additional data, such as the resilience and sensitivity of the entire food web, and considering temporal responses to stressors to improve accuracy and predictive power. The IVCLA was developed with the purpose of serving as an effective tool for guiding environmental managers in designing conservation strategies and making informed decisions for lake ecosystems.

Keywords: Risk assessment, Functional traits, Functional redundancy, Rarity, Stressors

Graphical abstract



1. Introduction

Assessing the vulnerability of ecosystems has become increasingly important in conservation and ecology research as it provides valuable information to support management decisions (Weißhuhn et al., 2018). Defining vulnerability levels can help managers identify areas at risk of biodiversity decline due to global changes and implement appropriate conservation strategies (Adger, 2006; De Lange et al., 2010). Despite no consensus, vulnerability is usually measured as combining three components, exposure, sensitivity, and resilience, in a composite index (Füssel, 2007; Weißhuhn et al., 2018). Exposure refers to the nature and degree to which an ecosystem faces a particular or several environmental stressors. Sensitivity is the potential capacity of biodiversity to be affected by stressors, and resilience represents its ability to recover and adapt after a disturbance (Adger, 2006; Baho et al., 2017; Munera-Roldan et al., 2022). Therefore, regarding these three components, a highly vulnerable ecosystem will have high exposure, high sensitivity, and low resilience.

Climate change is among the main stressors of freshwater ecosystems, as it promotes hydrological impacts and water temperature change that can affect organism survival (Heino et al., 2009; Lehtonen, 1996). In lakes, invasive fish species can lead to impacts such as nutrient cycling alteration and loss of indigenous biodiversity via predation, competitive interactions, and pathogens introduction (Collier et al., 2017; Vitule, 2009). Additionally, the human land use around the lake echoes the anthropogenic activities contributing to physicochemical and hydromorphological alterations (Dudgeon et al., 2006). Degradation of the morphological characteristics of habitats, such as reinforcing the littoral zone, also negatively impacts freshwater biodiversity (Feld et al., 2016). This is primarily due to the quality of the littoral zone that plays a crucial role in driving community dynamics of various organisms once the zone harbors a diverse range of resources such as food and refuges (Logez et al., 2016; Vadeboncoeur et al., 2011). Overall, the complex interplay of multiple stressors on lake biodiversity highlights the need for a comprehensive approach to assess ecosystem vulnerability.

In general, most studies assessing vulnerability were developed in the context of climate change (Burthe et al., 2014; Wade et al., 2017). Many authors have focused on assessing species' sensitivity to temperature change, mainly through their tolerance level and the consequences on their distribution range under different scenarios. However, species sensitivity can be measured by several parameters, including their abundance (Baillargeon et al., 2020; Hancock et al., 2020), their physiological responses to water quality degradation (e.g., chemical pollutants; Dvorak et al., 2020), and life history traits (e.g., spawning duration; Nyboer et al., 2019) and even behavioral skills (e.g., dispersal ability and swimming performances) (Hermoso and Filipe, 2021; Louison et al., 2019; Wang et al., 2020). Some of these criteria, such as dispersal ability and genetic factors, are also considered factors of adaptive capacity (Wade et al., 2017). In addition, in the cases where several species were analyzed, they were usually drawn from the same taxonomic group, such as fish (Nyboer et al., 2019; Sievert et al., 2016; Wiedmann et al., 2014) and macroinvertebrate communities (Ippolito et al., 2010).

In these instances, the vulnerability of the communities is often assessed by aggregating sensitivity information related to the species comprising them (e.g., proportion of threatened species or of functional entities, Parravicini et al., 2014; Wiedmann et al., 2014). Furthermore, the functional redundancy, a critical property that contributes to ecosystem resilience (Eisenhauer et al., 2023), can serve as an effective indicator of adaptive capacity of communities (Angeler et al., 2015, 2013; Su et al., 2019). Nevertheless, a multi taxa approach has the potential to yield more practical guidance for conservation efforts to ecosystems once patterns of vulnerability levels vary among taxonomic groups (Chen et al., 2022; Nevalainen et al., 2019; Rocha et al., 2023).

In lake ecosystems, fish and phytoplankton hold distinct positions at opposite ends of the food web and play crucial roles in regulating the structure of these systems through top-down and bottom-up effects, respectively (Mota et al., 2014; Naselli-Flores and Padisák, 2022). Thus, assessing resilience and sensitivity to environmental changes for their communities is essential to predict the magnitude and prevent future human impacts on biodiversity and the lakes' fundamental functions and services (Weißhuhn, 2019; Weißhuhn et al., 2018). In general, lacustrine diversity is essential for maintaining water quality, supporting food provision and recreational activities, and playing crucial roles such as nutrient cycling that underpin these ecosystems' health and ecological integrity (Albert et al., 2021; Reid et al., 2019). Therefore, developing a multi-taxa index is urgently needed to assess and manage lake vulnerability. This is particularly important once the current state of lake ecosystems is concerning, as lakes are exposed to multiple stressors promoted by human activities that can impact their ecological integrity (Bouraï et al., 2020; Heino et al., 2021; Launois et al., 2011).

This study aimed to propose a comprehensive framework to develop a vulnerability index for lake biodiversity loss, combining multiple taxa (fish and phytoplankton) and multiple stressors information. To this end, we used data collected at the French national scale in a harmonized way, i.e., standards of the Water Framework Directive (WFD) monitoring program. Besides determining the vulnerability level for 255 French lakes, we described its main patterns and explored how the components and stressors used to construct it are related. This index is presented as a potential tool for guiding environmental managers in designing conservation strategies and making informed decisions for lake ecosystems.

2. Methods

2.1. Biological data

We used a biological dataset covering 255 French lakes (artificial and natural) sampled between 2006 and 2021 for fish and phytoplankton communities. The fish data were collected following the Norden gillnet standardized protocol (CEN, 2015) 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. Gillnets were placed at different depth strata according to lake bathymetry (<3 m, 3–5.9 m, 6–11.9 m, 12–19.9 m, 20–34.9 m, 35–49.9 m, 50–74.9 m, and >75 m) and random locations overnight for 12 h. The sampling effort was adjusted according to the size and depth of the lake. All sampled fish individuals were identified at the species level, which resulted in 40 species collected. The phytoplankton was sampled using the standardized method following the protocol described in Laplace-Treyture et al. (2009). Four sampling campaigns were conducted, three during the warmer months (from May to October) and one in late winter in each lake. Samplings were made at the deepest point of the lake in the euphotic part of the water column. Phytoplankton taxa (sampled during the four campaigns) were counted following the European Standard NF15204 (CEN-EN 15204). A total of 494 taxa were identified at least at the genus level, i.e., 380 at the species level and 114 at the genus level. For each taxa, the biovolume (in mm^3/l) was calculated with the Phytobs software (Laplace-Treyture et al., 2017), i.e., the abundances weighted by taxa cell biovolume (Derot et al., 2020).

2.2 Functional traits

For each taxonomic group, we selected eight functional traits commonly used in studies assessing functional diversity and representing the species 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, 2021; 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-Treyture et al., 2021; Rimet and Druart, 2018) were: life form, cell biovolume, maximum linear dimension, mixotrophy capacity and flagella, heterocyt, mucilage, and vacuole presence (see Table S2).

2.3. Resilience component

We calculated the functional redundancy metric to represent the resilience level for fish and phytoplankton communities (De Bello et al., 2007). The functional redundancy 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). We used the traits and abundance (for fish) or total biovolume (i.e., cell biovolume times abundance; for phytoplankton) matrices to calculate this metric. We measured functional redundancy values for each taxonomic group separately, using the "rao.diversity" function from the R package SYNCSA (Debastiani and Pillar, 2012).

2.4. Sensitivity component

To represent sensitivity in communities, we used species rarity information. Rare species are expected to present a higher vulnerability to extinction (Gaston and Kunin, 1997; Purvis et al., 2000) due to their low abundance, narrow distribution, and low environmental tolerance.

Consequently, they are more sensitive to the impacts of environmental changes promoted by natural or human-induced disturbances (Caro, 2010; Foden et al., 2013; Leitão et al., 2016). To represent community sensitivity, we adapted a recent integrative index developed by Leitão et al. (2016). 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 maximum number of sampled individuals or biovolume observed in lakes where the species occurred for fish or phytoplankton, respectively (Leitão et al., 2016; Maciel, 2021). We measured the GR by calculating the area (km^2) of the minimum convex polygon encompassed by the outermost limits of occurrence of each species 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 length 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 community, 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” (R package sp; Pebesma et al., 2012), “projection” (R package raster; Hijmans et al., 2015), “spTransform” (R package rgdal; Bivand et al., 2015) and “gArea” (R package rgeos; Bivand et al., 2017). The HB, as previously applied by Burner et al. (2022), was represented by a co-occurrence based habitat specialist-generalist score developed by Fridley et al. (2007) and Manthey and Fridley (2009). In short, this method considers the empirical observation that habitat specialist species would co-occur with a smaller subset of species than the habitat generalists (Fridley et al., 2007). To calculate habitat specialist-generalist score (ranging between 0 and 1) for each species, we used the multiple Simpson similarity index (Baselga et al., 2007).

In order to decrease the magnitude across LA and GR values, we standardized them between 0 and 1 by dividing them by the respective maximum value observed over all species for LA and all lakes for GR (i. e., the total area of French lakes assessed, Flather and Sieg, 2007). In addition, we down-weighted each metric by its correlation with the two others (Kark et al., 2002) to consider the degree of dependence between them. Finally, all metrics were integrated into a single index (here called sensitivity index, SI) for a species i, which is calculated as

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

where the values wLA, wGR and wHB 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 (wLA) we used the equation

$$wLA = \frac{1}{2} + \left[\frac{1 - |r_{LAGR}|}{2}\right] + \left[\frac{1 - |r_{LAHB}|}{2}\right]$$

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 and 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 (for fish and phytoplankton separately) at the assemblage level by calculating the mean of all SI_i values for species co-occurring in each lake.

2.5. Exposure component

To represent the exposure component, we measured information for six general environmental stressors promoted by human activities. These stressors include water quality and habitat degradation, hydrological alteration, climate change, presence of non-native species, and other human land use alteration in the catchment.

2.5.1. Water quality degradation

To measure the stressor related to water quality, we first collected information about eight physicochemical parameters in each lake. We considered: alkalinity, dissolved oxygen concentration (DO), suspended materials (MIS), nitrates and nitrites concentrations (i.e., NO_3^-, NO_2^-), pH, Secchi depth (i.e., water transparency), and total phosphorus concentration (TotalP, see Table S3). All parameters were measured at the deepest point of the lakes according to national standards (MEDDE, 2012; AFNOR, 2015). To summarize information about all parameters, we used the site score values provided by the two first PCA axes (PCA1 and PCA2; 45 % of explanation) constructed using all physicochemical variables. In some cases, the fish and phytoplankton data sampling of the focus lake was not conducted in the same year. Therefore, to build the PCA axes, we used two values for each environmental condition for each lake (values collected during the closest sampling date of fish and phytoplankton samplings). After, we calculated the mean score value on each axis for each lake. Lakes showing greater scores in PCA1 (hereafter PC1_WQ) showed higher acidity (lower pH and alkalinity), lower DO. Lakes with greater score in PCA2 (hereafter PC2_WQ) showed less acidity but greater productivity process with greater values of NO_3^-, NO_2^- and MIS (Fig. S1). We were able to calculate water quality information for 252 lakes. We used the function “prcomp” to run the PCA analysis.

2.5.2. Habitat degradation

To measure habitat degradation extent, we selected nine variables representing mainly loss of habitat diversity and complexity in lake-shores, as described in Carriere et al. (in press). The variables describing lakeshore structure were bank artificialization and compaction, erosion, absence of riparian vegetation, and change in aquatic vegetation. The alteration of the substrate was described by sand dumping, gravel dumping, material extraction from the lakeshore, and siltation (Table S3). We then determined a single value for habitat degradation stressor by combining the values of the nine variables using the "one-out, all-out" (OOAO) approach, as applied by Carriere et al., in press. This principle states that when multiple metric values are considered within a multimetric indicator, the one with the lowest value, signifying the most significant impact, is employed to portray the overall condition of the water body (European Communities, 2005). Initially, all selected variables varied between 0 and 1, in which lakes holding a value of 0 show the lowest habitat quality (see more details in Carriere et al., in press). Therefore, in order to 1 represent the lowest habitat quality in lakes, we inverted the variable's sense by subtracting the observed value from 1. We could measure habitat degradation information for 204 lakes with the available data.

2.5.3. Hydrological alteration

To represent the hydrological alteration stressor in lakes, we also used the OOAO approach, considering the five hydrological variables described in Carriere et al. (in press). The variables were tributary changes, flow obstacles (provided by dams or weirs), water abstraction, upstream water impoundment, and bank concreting (related to lower bank permeability; see Table S3). In order to the value 1 represent the highest hydrological alteration level, we inverted the variable's sense by subtracting the observed value from 1. We were able to calculate hydrological alteration information for 204 lakes.

2.5.4. Climate change

To represent climate change stressor, we calculated the slopes of daily epilimnion temperature (provided by Sharaf et al., 2023) variation across the past 48 years until the sampling date of our biological data. The 48-year time frame was selected to encompass the temporal range of data available in Sharaf et al. (2023). To capture the long-term trends in temperature changes, we used the non-parametric Theil-Sen estimator and the "TheilSen" function from the 'openair' package (Carslaw and Ropkins, 2012) as previously applied in Lopez et al. (2019). This non-parametric method was chosen because it is robust to outliers and does not assume a particular distribution for the data, which is suitable for non-normally distributed data. The slopes obtained ranged from 0.01 °C/day to 0.06 °C/day and positive values indicate an increase in temperature over time in the lakes. We were able to calculate climate change information for 242 lakes.

2.5.5. Presence of non-native species

To represent non-native species pressure, we used the sum of the relative abundance of all non-native fish species occurring in each lake. We considered as non-native only those species whose native range distribution does not include any French freshwater ecoregion (Abell et al., 2008). To determine if species were non-native, we used information from literature, i.e., INPN (Inventaire national du Patrimoine naturel; http://inpn.mnhn.fr) and Keith et al. (2011). The 16 non-native species observed were: *Ameiurus melas*, *Carassius auratus*, *Carassius carassius*,

Carassius gibelio, *Cyprinus carpio*, *Gambusia affinis*, *Hypophthalmichthys molitrix*, Lep*omis gibbosus*, *Micropterus salmoides*, *Neogobius melanostomus*, *Oncorhynchus mykiss*, *Ponticola kessleri*, *Pseudorasbora parva*, *Salvelinus alpinus*, *Salvelinus fontinalis* and *Salvelinus namaycush*. We were able to calculate non-native species information for all 255 lakes. Information about non-native species of phytoplankton is not available. Therefore, this stressor was not considered for the phytoplankton biological element in the present study.

2.5.6. Human land use alteration in the catchment

To represent human land use alteration, we calculated the change in the percentage of non-natural areas in the lake catchment between 2000 and 2018. For this, information from Corine Land Cover database (CLC; Büttner et al., 2004) for France was used (available online; https://www.statistiques.developpement-durable.gouv.fr/corine-land-cover-0). The non-natural area considered were the CLC categories: (1) artificial territories and (2) agricultural territories (without grasslands, i.e., code 23) (Bouraï et al., 2020; Launois et al., 2011). The extent of land alteration was quantified as a percentage, with higher values indicating an increase in non-natural areas within the lake catchment resulting from human activities during the specified period. We were able to calculate land-use change information for 251 lakes.

2.5.7. Aggregation of all stressors

For the water quality stressor, we considered the two PCA axes obtained to represent it. Thus, we obtained seven variables (i.e., indicators) representing the six stressors (i.e., water quality and habitat degradation, hydrological modification, climate change, the introduction of non-native species, and human land-use alteration) considered for exposure components (Appendix 1). All indicators were first rescaled to values ranging between 0 and 1 using maximum value transformation (Weißhuhn, 2019). We then aggregated all stressor indicators in a unique exposure metric based on the arithmetic mean (Alexandrakis and Poulos, 2014; Tonmoy et al., 2014). More specifically, the exposure metric was calculated with the equation

$$\text{Exposure} = \frac{\sum_{i=1}^{n} Indicator_i}{n}$$

where n is the total number of indicators considered to calculate exposure, and Indicator_i represents each indicator from 1 to n.

Several aspects can support the choice for this aggregation approach. First, we aimed the production of an overall exposure metric in which each stressor has equal importance to exposure degree. In addition, it decreases subjectivity in weighting the potential effect of stressors regarding an ecosystem composed of ecologically distinct organisms (Villa and McLeod, 2002). Finally, this kind of aggregation allowed us to calculate the exposure for all lakes, even in cases where information for some indicators was unavailable.

2.6. Aggregation of vulnerability components

Finally, to measure the vulnerability index (IVCLA) of all 255 lakes, we aggregated the sensitivity and resilience (for each taxonomic group) and the exposure components using a numerical approach. For this, we modified a commonly applied formula for the vulnerability index (Hamidi et al., 2020; Li et al., 2018; Weißhuhn et al., 2018) to accommodate different organism groups:

$$IVCLA = \sqrt{E \cdot \left(\frac{S_1}{(n + R_1)}\right) + \cdots + \left(\frac{S_n}{(n + R_n)}\right)}$$

where E represents the exposure metric, the S_1 and R_1, and the S_n and R_n represent the resilience and sensitivity metrics for the first and last organism groups, respectively. The n represents the number of organism groups (i.e., 2) considered in the index measurement.

2.7. Exploratory analyses

The resilience, sensitivity, and exposure components and the IVCLA index were also classified into five categories to simplify the interpretation and facilitate communication with a broader audience. The classes and the respective range of values were: very low (0–0.2), low (>0.2–0.4), medium (>0.4–0.6), high (>0.6–0.8), and very high (>0.8–1). It is worth noting that the resilience and sensitivity values considered for classification were the mean values between the fish and phytoplankton taxonomic groups.

Additionally, to evaluate the differences in resilience and sensitivity between fish and phytoplankton groups, we used a Mann–Whitney–Wilcoxon test with the function "wilcox.test". Finally, we ran Spearman's correlations to explore the relationships among patterns of all stressors composing the exposure component with the biotic components (resilience and sensitivity for fish and phytoplankton) and the final value of vulnerability for each lake. All the analyses were performed in the R Statistical Software Environment (R Core Team, 2021). The R code is available as a supplementary file (Appendix 2).

3. Results

In the fish taxonomic group, we observed mean values of 0.27 and 0.54 for resilience and sensitivity components. For the phytoplankton, the corresponding values were higher, i.e., 0.32 (Mann-Whitney $U_{Resilience} = 15{,}110$, $p \leq 0.001$) and 0.74 (Mann-Whitney $U_{Sensitivity} = 1737$, $p \leq 0.001$) (Fig. 1a and b and Appendix 1). Regarding the exposure component, we found a mean value of 0.33, in which the lowest and highest exposure values observed were 0.15 and 0.54 (Fig. 1c).

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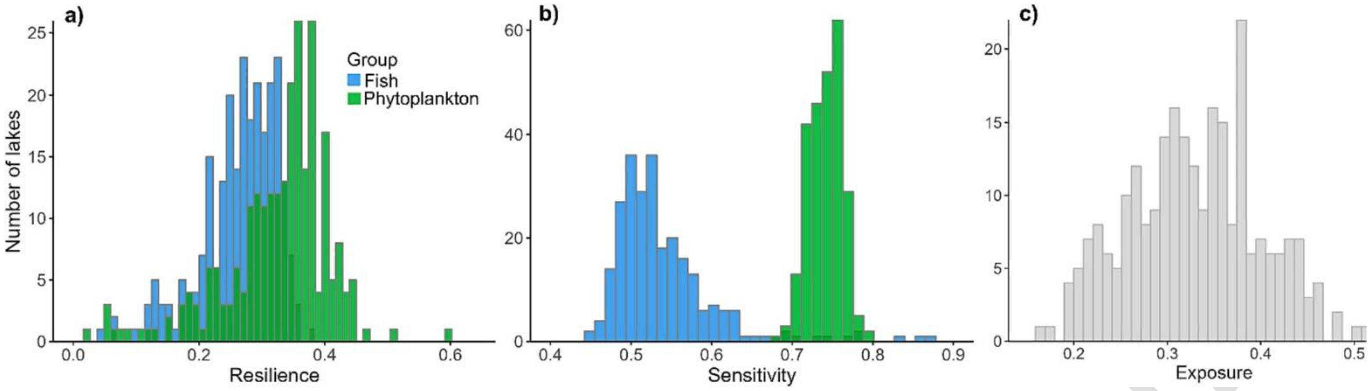

Fig. 1. Histogram of values for the three assessed components resilience (panel "a"), sensitivity (panel "b"), and exposure (panel "c") on 255 French lakes sampled between 2006 and 2021.

When we categorized the values of all components (Fig. 2), most of the lakes we studied (99 %, $n = 253$) showed a low or very low level of resilience based on the average value for both taxonomic groups. Most lakes demonstrated a high level of sensitivity (95 %, $n = 243$), again based on the mean for both groups. We also observed that a smaller number of lakes (0.02 %, $n = 7$) exhibited the lowest level of exposure to the selected stressors.

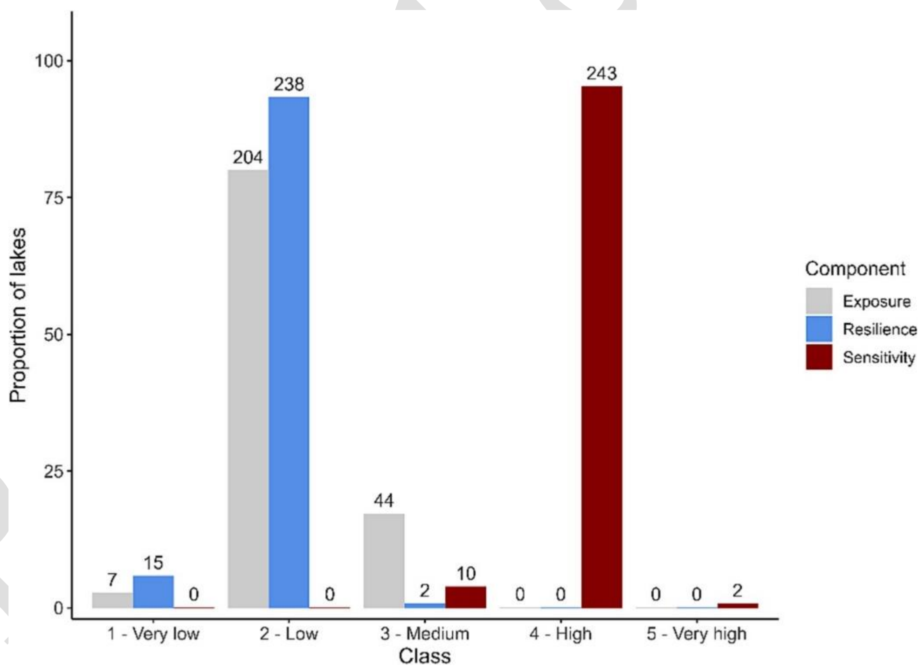

Fig. 2. Graphs showing the proportion and number of lakes ($N = 255$) according to each component values (exposure, mean resilience and mean sensitivity) and each class of vulnerability level, i.e., very low (0–0.2), low (>0.2–0.4), medium (>0.4–0.6), high (>0.6–0.8) and very high (>0.8–1).

In addition, when comparing patterns of classes for resilience and sensitivity between fish and phytoplankton, some lakes with low or high values for phytoplankton were not consistently found to have the same categories for the fish group (Tables 1 and 2).

Table 1. Percentage and number (in parentheses) of lakes classified in each category of resilience level considering fish and phytoplankton. The categories were (very low = “VL”, low = “L”, medium = “M”, high = “H”, very high = “VH”). Values in bold indicate the proportion of lakes where both taxonomic groups exhibited congruence in their assigned classes.

		Phytoplankton resilience				
		VL	L	M	H	VH
Fish resilience	VL	**1.6 (4)**	9.8 (25)	1.6 (4)	0 (0)	0 (0)
	L	7.1 (18)	**68 (174)**	11.8 (30)	0 (0)	0 (0)
	M	0 (0)	0 (0)	**0 (0)**	0 (0)	0 (0)
	H	0 (0)	0 (0)	0 (0)	**0 (0)**	0 (0)
	VH	0 (0)	0 (0)	0 (0)	0 (0)	**0 (0)**

Table 2. Percentage and number (in parentheses) of lakes classified in each category of sensitivity level for fish and phytoplankton. The categories were (very low = “VL”, low = “L”, medium = “M”, high = “H”, very high = “VH”). Values in bold indicate the proportion of lakes where both taxonomic groups exhibited congruence in their assigned classes.

		Phytoplankton sensitivity				
		VL	L	M	H	VH
Fish sensitivity	VL	**0 (0)**	0 (0)	0 (0)	0 (0)	0 (0)
	L	0 (0)	**0 (0)**	0 (0)	0 (0)	0 (0)
	M	0 (0)	0 (0)	**0 (0)**	87.8 (224)	0 (0)
	H	0 (0)	0 (0)	0 (0)	**11 (28)**	0 (0)
	VH	0 (0)	0 (0)	0 (0)	1.2 (3)	**0 (0)**

The average vulnerability value (IVCLA) observed in lakes was 0.43, with a range from 0.3 to 0.6 (Fig. 3a). Among the total lakes assessed, 55 % (n = 142) exhibited a vulnerability higher than the mean observed (Appendix 1). When we classified the IVCLA values into different categories, we found that 70 % (n = 179) of lakes exhibited medium level of vulnerability (Fig. 3b).

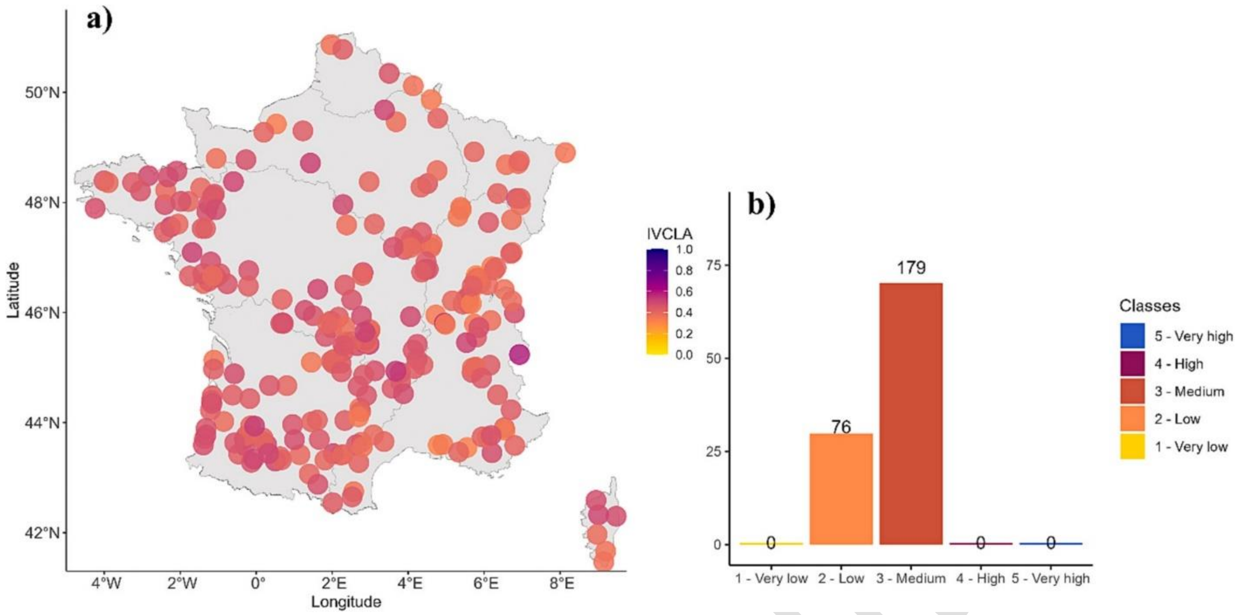

Fig. 3. IVCLA values for the 255 French lakes sampled between 2006 and 2021 (panel "a") and the proportion and number of lakes classified in five categories (panel "b"); i.e., very low (0–0.2), low (>0.2–0.4), medium (>0.4–0.6), high (>0.6–0.8) and very high (>0.8–1).

Moreover, we noticed interesting patterns when assessing correlations between stressors and the IVCLA and its component values (Fig. 4). Among these correlations, fish sensitivity was the component more negatively related to a greater number of stressors, i.e., climate change, human land-use alteration, and water quality. In addition, all stressors are at least correlated to one component of the IVCLA index. The PC1_WQ axis followed by human land use alteration were the indicators presenting the strongest correlations with the resilience and sensitivity of fish and phytoplankton. We also found a positive and significant correlation between the IVCLA values and almost all stressors (except the PC2_WQ variable), even if no clear correlation was observed between the four biological components and the stressors. Still, lakes presenting higher vulnerability were more significantly related to higher stress promoted by hydrological alteration (ρ = 0.59, $p \leq$ 0.001) and water quality degradation (PC1_WQ variable, ρ = 0.39, $p \leq$ 0.001). The PC1_WQ variable mentioned is related to higher acidity (lower pH and alkalinity) and lower DO.

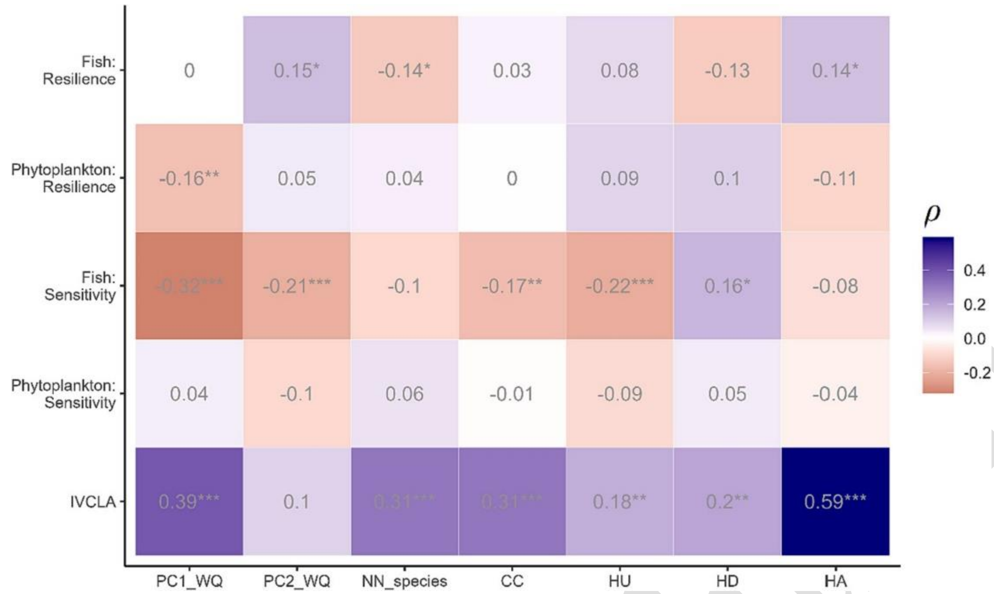

Fig. 4. Spearman's correlation values among all stressors considered to construct the exposure component (x-axis) and the resilience, sensitivity, and IVCLA values (y-axis) of the 255 French lakes sampled between 2006 and 2021. The stressors assessed were: water quality degradation "WQ", the presence of non-native species "NN", climate change "CC", human land-use "HU", habitat degradation "HD", and hydrological alteration "HA". The * (p-value <0.05), ** (p-value < 0.01), and *** (p-value < 0.001) represent the significance of the correlations between pairs.

4. Discussion

We proposed a new lake's vulnerability index (IVCLA) to measure the ecosystem vulnerability to biodiversity loss that integrates information for two taxonomic groups and multiple stressors. With the present index, we were able to effectively capture valuable information on the resilience and sensitivity patterns of the ecologically distinct fish and phytoplankton taxonomic groups that play equally crucial roles in providing functions and services to the ecosystem. Additionally, we integrated exposure magnitude regarding the contribution of the main stressors linked with the main human activities threatening lake ecosystems.

We observed that nearly all lakes lacked minimum exposure levels, highlighting the potential for negative impacts from at least one of the evaluated assessed stressors on these waterbodies. Urgent action is needed to address these stressors, i.e., water quality and habitat degradation, hydrological alteration, climate change, species invasion, and land-use alteration, and implement conservation measures to safeguard species and functional diversity in French lakes. Furthermore, it is concerning that most lakes exhibited moderate levels of vulnerability, indicating a considerable risk of biodiversity loss. This finding alarms the trend toward a potential increase in vulnerability levels responding to ongoing global changes and indicates the need for further investigation in other regions.

Moreover, most lakes displayed low or very low resilience and high sensitivity values. The greater values regarding mean resilience and sensitivity are mainly related to phytoplankton rather than fish. Rocha et al. (2023) have already found higher values of resilience and sensitivity for this taxonomic group when compared to fish communities in French lakes. This is because phytoplankton communities mainly comprise rare species (i.e., sensitive species) that present microscopic sizes, with short generation times and high metabolic rates, which may provide faster response and greater adaptation capacity against stressors (i.e., resilience). However, the finding of incongruity between the classes of resilience and sensitivity for fish and phytoplankton reinforces the importance of incorporating information from both taxonomic groups in accurately assessing the vulnerability of lakes.

We found that resilience and sensitivity for fish and phytoplankton are related to lakes affected by various stressors incorporated in the exposure component. This means that, in the most exposed lakes, we found few specialist species (i.e., few rare species) and/or few species displaying similar functions (i.e., low resilience). Therefore, the threat of disturbances in reducing freshwater biodiversity and consequently decreasing communities' capacity to adapt seems to be an ongoing process. In addition, the decrease in water quality associated with acidification and eutrophication processes seems to exert an important role in driving patterns of resilience and sensitivity for fish and phytoplankton communities, which is in line with previous literature (Borics et al., 2021; Brucet et al., 2013). However, the contribution of most stressors regarding levels of the different IVCLA components (i.e., resilience and sensitivity for fish and phytoplankton) reinforces the importance of integrating all stressors' information for a holistic measurement of the exposure component. We found that increased hydrological changes (e.g., flow obstacles and upstream water impoundment), besides the acidification process and reduced dissolved oxygen, are good indicators of higher vulnerability to biodiversity loss in French lakes. Interestingly, while above cited stressors demonstrated a positive correlation with the IVCLA index, suggesting their potential as threats to less resilient and more sensitive lakes, other stressor (i.e., PC2_WQ) has not evidenced a clear relationship. This finding suggests imbricated impacts of various stressors that must be more investigated. It also highlights the complex and multifaceted nature of lake vulnerability and the value of this new index in lake management.

The IVCLA offers several advantages over other approaches for assessing lake vulnerability, in addition to integrating multiple taxa groups and stressors (Adger, 2006). For instance, it uses functional redundancy and species rarity information as indicators of resilience and sensitivity, respectively. These relatively simple metrics allow us to compare and use ecologically distinct taxonomic groups. In addition, it seems more accurate to represent general responses to disturbance or functions provided by all communities than when considering a specific trait and its expected response to several different stressors. However, we are aware that the index naturally relies on certain limitations. For example, the sampling method applied for fish may have led to an underestimation of species rarity in the lakes studied. Future research should explore alternative, more comprehensive sampling approaches to select all species (including the rarest) in the environment. Additionally, we used all available environmental information that efficiently represents the stressors according to the literature.

Nonetheless, information regarding some complex stressors (e.g., habitat degradation and hydrological alteration) was unavailable for some lakes, and the exposure component was measured without considering them. Including these stressors in the future could result in a variation in the exposure level and probably modify the results of the correlations obtained with the biological components.

Moreover, several steps can be taken further to improve the accuracy and usefulness of the index. To enhance its accuracy, we suggest short-term steps, including information about the resilience and sensitivity of the entire food web, which would consider the complex biotic interactions in lakes (Rocha et al., 2023). Additionally, future studies could consider modeling various scenarios for potential changes in stressors to determine the sensitivity of the tool and its ability to predict future vulnerabilities accurately. In the long term, once the IVCLA methodology has been applied and refined, we will be able to validate its effectiveness in assessing lake vulnerability and identify areas for improvement. For instance, information about the temporal responses of communities to environmental stressors will allow us to assess and aggregate the effect of stressor interactions, a necessary (but complex to measure) aspect to take into account in risk models (Markovic et al., 2017). Finally, we decided to show the patterns of IVCLA based on their absolute values. However, it is also possible to standardize these values to provide an overview of the relative vulnerability in the context of the lakes under interest.

5. Conclusion

In conclusion, our study proposed a new framework for measuring lake vulnerability, integrating information from different taxonomic groups and multiple stressors. Using the IVCLA index, we found that most French lakes displayed low to medium exposure, high sensitivity and low resilience levels. In addition, negative relationships between the resilience and sensitivity patterns for both taxonomic groups and the different stressors highlight the ongoing process of reducing freshwater biodiversity due to negative disturbances. The IVCLA offers several advantages over other approaches to assess lake vulnerability regarding multiple stressors according to its current biodiversity status. Moreover, it holds the potential to serve as an effective tool for identifying sites that need ecological improvement. This tool can provide valuable guidance to environmental managers in making decisions that encompass reducing the effects of local stressors, enhancing ecosystem resilience, and implementing other conservation strategies.

CRediT authorship contribution statement

BSR: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **CA**: Funding acquisition (equal); Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting); Supervision (supporting); **AJ and ML:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **CLT and NR**: Data curation (equal); Methodology (supporting); Writing– review and editing (supporting).

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

Biological data (fish and phytoplankton) and physico-chemical data (i.e., dissolved oxygen DO, MIS, NO3-, NO2-, pH, secchi depth, and TotalP) are available on NAIADES web site (http://www.naiades. eaufrance.fr/). Other environmental data like alkalinity are available on the data plateform of Pole ECLA (http://geo.ecla.inrae.fr/). The variables bank artificialization and compaction, erosion, absence of riparian vegetation, change in aquatic vegetation, tributary changes, flow obstacles (provided by dams or weirs), water abstraction, upstream water impoundment, and bank concreting are openly available on recherche.data.gouv.fr at https://doi.org/10.57745/S3IFUR. The water temperature data is available online at https://doi.org/10.57745/O. All stressor indicators estimated and the code to calculate the final IVCLA index are available as supplementary materials.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.168205.

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