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A multifaceted index of population health to detect risk-prone populations and underlying stressors in wildlife

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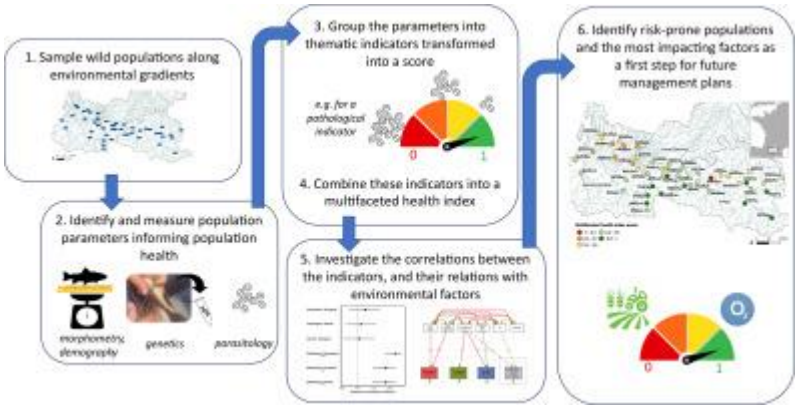
Abstract :

Local declines of wild populations represent the most visible part of biodiversity loss, and their detection often relies on long-term surveys. An alternative to identify risk-prone populations is to use indicators informing on their general health (i.e., their general fitness and ability to cope with changing environment) based on simple and complementary parameters estimated from snapshot sampling. However, most studies on wildlife population health focus on one or only a few parameters, yielding potentially biased conclusions for conservation. Here, we developed a multifaceted index of population health by combining 3 complementary indicators, namely pathological, ecological, and genetic indicators, based on an integrative approach traditionally used to assess ecosystem multifunctionality. We investigated their complementarity and relevance for detecting brown trout (Salmo trutta) risk-prone populations at a large spatial scale, and the underlying environmental stressors. The multifaceted health index properly represented the individual indicators' complementary information. It identified a cluster of moderately risk-prone populations and raised the alarm for one population. Each indicator was individually associated with distinct environmental stressors relevant for brown trout requirements. The multifaceted health index highlighted surrounding agricultural land and oxygen concentration as the most impacting environmental factors for the general health and sustainability of brown trout populations. The implementation of such integrative index can be transferred to a wide range of species and contexts. This index therefore provides to environmental managers and conservationists a snapshot and easily operated tool to identify risk-prone populations and areas to restore or conserve.

Graphical abstract



Highlights

► We propose a multifaceted index to assess wildlife populations health. ► This index combines three individual pathological, ecological, and genetic indicators. ► Each individual indicator was associated with distinct environmental stressors. ► The multifaceted health index identified the most impacting environmental stressors. ► This approach efficiently highlighted the most risk-prone populations in the area.

Keywords : Population demography, Sustainability, Biological indicator, Parasitology, Genetics, Environmental variability

Abbreviations:
MFI: multifaceted indicator of population health
PI: pathological indicator
EI: ecological indicator
GI: genetic indicator

1. Introduction

By altering environmental conditions and biotic interactions, global change is threatening many plant and animal species, thereby increasing their risk of extinction (Radchuk et al., 2019; Spooner et al., 2018; Thomas et al., 2004). Species extinction is systematically preceded by the decline in abundance of local populations, which actually represents the most important and visible part of the global biodiversity loss (Collen et al., 2011; Hughes et al., 1997). Local declines of populations may therefore serve as early warning signals (EWS) for managers to mitigate the aftermaths of global change (Drake & Griffen, 2010). However, characterizing these declines requires long-term surveys of populations' abundance that are labor-intensive and still scarce in wild populations (Atkinson et al., 2006).

Monitoring indicators informing the general health of populations may be a relevant alternative to long-term surveys to infer their ability to cope with new environmental conditions (Stephen, 2014), and to identify risk-prone populations (Clements & Ozgul, 2016; Goff et al., 2020). The general health of populations is here defined as their general status (i.e., fitness) and their demo-genetic sustainability over short- to long-term periods (Hoban et al., 2013; Kophamel et al., 2021). Population health is therefore intrinsically multifaceted, and it can be informed by multiple indicators (generally genetic, phenotypic, or demographic information), measured during snapshot sampling events. For example, a decrease in the mean body size of whales appeared as a good EWS of local populations' declines (Clements et al., 2017). Similarly, intraspecific genetic diversity (or related indices such as effective population sizes) informs on the adaptive potential of populations in changing environments (Hoban et al., 2013; Lande & Shannon, 1996). Likewise, pathogenic infection can represent a silent threat to population fitness by provoking sudden mortality under new environmental conditions (Valenzuela-Sánchez et al., 2017). Hence, a thorough monitoring of wildlife populations' characteristics informing their general health may help noticing EWS and setting pro-active management decisions.

Wildlife population health is multifaceted and encompasses several intrinsic parameters such as ecological (e.g. population abundance, body condition), genetic (e.g. genetic diversity) or pathological (e.g. pathogen infection) parameters, which are complementary and influenced by multiple environmental factors (Stephen, 2014). Most studies on wildlife population health focus on one or only a few parameters. However, when interpreted independently, these indicators can yield opposite conclusions, and therefore potentially biased outcomes for wildlife population management. For instance, a population can show high local abundance, making it resilient to stochastic demographic fluctuations but a low level of genetic diversity, leaving it vulnerable under fluctuating environmental conditions (Maebe et al., 2019). Similarly, pathogen infection may differently affect a genetically diversified or an inbred host population (King & Lively, 2012). In addition, different indicators might be differently modulated by environmental factors. For example, an increase in temperature may benefit individual growth, while favoring pathogen development detrimental to individual fitness and population health, so that the use of multiple indicators may better capture the global impact of environmental stressors. Besides, the combination of several indicators into a single index of population general health could buffer potential uncertainties related to the measurement of each individual indicator. Therefore, more integrative studies incorporating several indicators are needed to grasp the multiple dimensions of wild population health.

This query is timely because recent advances in field and laboratory techniques enable the development of such integrative indicators. For instance, remote sensing mapping landscape types (Skidmore, 2003) or molecular tools assessing genetic diversity and environmental DNA quantifying the abundance of species (Bohmann et al., 2014; Hoban et

al., 2013) offer new non-invasive monitoring tools to address this challenge while minimizing the impact on sampled populations. Building on such new field and molecular techniques, this study aims at developing a multifaceted index of population health (MFI) combining individual indicators related to the pathological, ecological, and genetic status of populations. The construction of this MFI is inspired from studies measuring ecosystem multifunctionality by synthetizing multiple ecosystem functions into a single score (e.g. Manning et al., 2018). We first tested the covariation between each component indicator and their covariation with the MFI to investigate their complementarity or redundancy for informing population general health. We then tested the link between each of these indicators and potential natural and anthropogenic environmental stressors to identify the most impacting for population health.

We focused on populations of a common freshwater fish, the brown trout *Salmo trutta*, that has important economic, cultural and recreational values (Unfer & Pinter, 2018). This species is highly sensitive to environmental stressors such as water warming and chemical alterations (Eklöv et al., 1999; Elliott & Elliott, 2010). We sampled populations along a large spatial gradient associated with water physicochemical variations. For each population, we quantified 3 component indicators informing on their pathological, ecological and genetic status and combined them into a MFI. Our final aims were to identify low-health populations that are the most risk-prone and likely to decline in the sampled area, and the underlying environmental factors. We expected the component indicators to provide complementary information, revealed by a weak covariation among them within populations. Consequently, combining these indicators into a MFI should provide a better assessment of population health and its underlying environmental factors. We thus predicted a tighter association between environmental factors and the MFI relative to each individual component indicator.

2. Methods

2.1. Brown trout sampling

We developed the MFI in brown trout populations because the ecology of this salmonid fish is well known. This species is particularly sensitive to water temperature and quality (Elliott, 1994), so that water characteristics may be tightly associated with population health. We sampled 46 wild populations experiencing a wide range of environmental conditions in southern France, at the foothills of the Pyrenean mountains (Fig. 1, Table A1). During summer 2019, we electro-fished up to 20 individuals per site (when local abundances allowed it), representing 865 sampled brown trout in total (Table 1, Table A1). We targeted juveniles (mean size ± SD 75±14mm), corresponding mainly to young-of-the-year (0+) fish because it is the most sensitive stage to environmental stressors and pathogen infection, and the most abundant cohort. After manipulations (see hereafter), we released the fish alive into their sampling sites. Authorizations to sample brown trout were provided by the Directions Départementales des Territoires of Ariège, Haute-Garonne and Hautes-Pyrénées respectively.

2.1.1. Pathological indicator (PI)

The PI focused on the most impacting pathogen for brown trout in our study area: the myxozoa *Tetracapsuloides bryosalmonae.* This pathogen is the causative agent of the proliferative kidney disease (PKD), an emerging disease that has been increasingly reported during the last two decades, in Europe and North America. PKD can cause up to 100% mortality during severe outbreaks, especially in young-of-the-year cohorts, representing a threat for infected populations (Okamura et al., 2011).

We assessed the infection by *T. bryosalmonae* and its load in sampled fish using a non-lethal method developed in Duval et al. (2021) quantifying the DNA of pathogen excreted in the fish urine, considered as a proxy for the level of kidney infection. After

capture, the fish recovered for 30min, and were placed individually into plastic bottles with 1.2L of commercial mineral water for 1h to let time for the infected fish to excrete pathogen spores or DNA through urine. Then, we used a Vampire sampler® to filter 1L of the water and extracted DNA from 1.2µm filters. Lastly, we used specific droplet digital PCRs (ddPCRs) to quantify *T. bryosalmonae* DNA (see Duval et al. (2021) for the complete procedure). Population infection prevalence is the number of positive individuals for *T. bryosalmonae* DNA detection divided by the number of sampled individuals. The fish pathogen load corresponds to the concentration of *T. bryosalmonae* DNA divided by the time of excretion and the fish body mass to correct for variation in urine excretion (Hunn, 1982).

We scaled the infection prevalence and the mean pathogen load in each population into scores ranging between 0 (the population with the highest prevalence or highest mean pathogen load) and 1 (the population with the lowest prevalence or lowest mean pathogen load), with the R *scales* package (Wickham & Seidel, 2020). We averaged these two scores and rescaled the mean between 0 and 1 to build the PI. Populations with the lowest pathogen prevalence and load were considered the healthiest from a pathological point of view.

2.1.2. Ecological indicator (EI)

The EI is based on the population density and the fish mean body condition. We estimated fish density at each site as the number of juveniles caught per minute through single-pass electrofishing surveys ("catch-per-unit-effort", CPUE, Kruse et al., 1998). After the urine excretion step (2.1.1.), we anaesthetized each fish with benzocaine, measured and weighed them to the nearest mm and 0.1g respectively. We calculated fish body condition (K) according to equation (1) (Fulton, 1904), with W as fish mass in g, and L as fish length in cm.

$$(1) \qquad K = \frac{W}{L^3} \times 100$$

As for the PI (2.1.1.), we scaled the mean body condition and fish density into scores between 0 and 1, averaged them and rescaled the mean to build the EI. Populations with the highest density of juveniles and the highest mean body condition were considered the healthiest from an ecological point of view (Lobón-Cerviá, 2005; Robinson et al., 2008).

2.1.3. Genetic indicator (GI)

We fin-clipped each fish for genetic analyses and stored the fins in 70% ethanol. The LGC® Group (UK) used the KASPar allele-specific fluorescent genotyping system to genotype each individual at 175 SNPs, among which 158 were confidently genotyped (Table A2). These included 141 SNPs evenly spread on the brown trout linkage genetic map from Saint-Pé et al. (2019), as well as 17 SNPs from Ahmad et al. (2018), identified as candidate loci in the resistance/tolerance to the infection by *T. bryosalmonae*. To ensure the reliability of the genotyping, we duplicated 17 individuals that indicated a 0.2% error in scoring (5 mismatches in 2584 comparisons). To identify potential genotyping errors, we ran Hardy-Weinberg equilibrium tests with the *genepop* package (Rousset, 2008). We removed from the analyses 6 loci that departed from the equilibrium in 5 to 22 populations (Table A2) and 7 individuals that did not amplify properly so that 152 loci and 858 individuals were genotyped.

The GI is based on the effective population size (N_e), a measure of population sustainability (Waples & Do, 2010) and the mean multilocus heterozygosity (*MLH*), a genomic inbreeding estimator often positively correlated with individual fitness in wild populations (Hansson & Westerberg, 2002). We computed the *MLH* with the package *inbreedR* (Stoffel et al., 2016). We computed populations' N_e with the linkage disequilibrium

method (Waples & Do, 2007) in NeEstimator 2.1 (Do et al., 2014) with a lowest allele frequency of 0.05. These values were logged to homogenise variance.

As for the other indicators (2.1.1., 2.2.2.), we scaled *MLH* and N_e into scores between 0 and 1, averaged them and rescaled the mean to build the GI. Populations with the highest N_e and *MLH* harbor higher genetic variation, enhancing their response to environmental changes and reducing their sensitivity to genetic stochasticity, so that they were considered the healthiest from a genetic point of view (Evans & Sheldon, 2008; Palstra & Ruzzante, 2008).

2.1.4. Multifaceted health index

We then calculated the MFI of each population by combining these 3 component indicators. We averaged the PI, EI and GI, before rescaling the mean between 0 and 1 to obtain the final MFI.

2.2. Environmental data

To investigate the impact of natural and anthropogenic factors on these different indicators, we measured key environmental factors (Table 1). Brown trout is highly sensitive to temperature, oxygen concentration, pH and conductivity (Elliott, 1994). Therefore, we recorded water temperature in each site every 4h between July and August 2019 with a HOBO® logger and we acquired O_2 concentration, pH, and specific conductivity through snapshot measures with the In-Situ® Aqua TROLL 500 Multiparameter Sonde in August 2020. In addition, we quantified PO_4^{3-}, NO_2^- and NO_3^- concentrations in the water reflecting water eutrophication, based on 50mL samples collected in May 2020 at the Laboratoire Ecologie Fonctionnelle et Environnement according to the ISO 15681-2 and ISO 13395 norms, respectively.

We estimated the percentage of agricultural land in a 2km buffer around each site with the CORINE Land Cover 2018 dataset (European Environment Agency), as it represents the main anthropogenic pressure in the sampled area. We also used the QGIS software (2022) to estimate the distance from the source and the altitude of the sampled sites. We expected that the general health of brown trout populations would be lower in the warmest waters with the lowest oxygen concentration, the highest values of eutrophication and the highest surfaces of agricultural land in their surroundings (Jonsson et al., 2011; Molony, 2001).

2.3. Statistical analyses

We conducted the statistical analyses in the R environment (R 4.0.3, R Core Team 2020).

2.3.1. Covariance between the indicators

We quantified the covariance between the PI, EI and GI and with the MFI respectively using pairwise Spearman correlation tests with Holm's correction for multiple inference (n=6 pairs of indicators) from the *RcmdrMisc* package (Fox, 2020). A positive and significant correlation between two indicators would indicate that they co-vary and support redundant information.

2.3.2. Impacts of the environmental factors on the indicators and multifaceted health index

To investigate the impacts of the environmental factors on the component indicators and the MFI, we used a redundancy analysis (RDA) with the *vegan* package (Oksanen et al., 2020). This analysis is a constrained form of principal component analysis which explains a set of response variables (here the indicators) by a set of explanatory variables (here the

environmental factors). We assessed the validity of the RDA through an analysis of variance (ANOVA, 999 permutations).

Additionally, we ran path analyses to outline the statistically significant relationships between the environmental factors and the indicators while taking into account the inter-dependence of the environmental factors, using the *lavaan* (Rosseel, 2012) and *semPlot* (Epskamp et al., 2019) packages. We added and removed incrementally the links between the variables, only keeping significant relationships until reaching the lowest Akaike's Information Criterion (AIC), together with a non-significant Chi² p-value (>0.05), a Comparative Fit Index (CFI) >0.95 and a Root Mean Square Error of Approximation (RMSEA) <0.05 (Hu & Bentler, 1999; Rigdon, 1996). Because the MFI was highly correlated with the component indicators, we ran two path analyses separately: one including the 3 component indicators and one including only the MFI. However, as the covariations among environmental factors remained the same, we joined both analyses for graphical representation.

3. Results

3.1. Covariance between the component indicators and with the multifaceted index

The PI, EI and GI did not significantly covary (Spearman correlation tests and adjusted Holm's p-values; PI *vs.* EI, r=0.14, 95% CI -0.16 to 0.41, P=1; PI *vs.* GI, r=0.06, 95% CI -0.23 to 0.34, P=1; GI *vs.* EI r=0.03, 95% CI -0.26 to 0.32, P=0.1; Fig. A2). In addition, each of the 3 component indicators were significantly and positively correlated to the MFI (Spearman correlation tests; MFI *vs.* PI r=0.69, 95% CI 0.50-0.82, P<0.001; MFI *vs.* EI, r=0.52, 95% CI 0.27-0.70, P=0.001; MFI *vs.* GI, r=0.52, 95% CI 0.27-0.70, P=0.001; Fig. A2). These correlation coefficients did not differ significantly among them (95% CI overlap among the coefficients, Fig. A2), hence indicating that the 3 component indicators equally contributed to the MFI.

3.2. Effect of environmental factors on the indicators

The highest MFI scores were mostly located upstream and closer to the Pyrenean mountains, whereas the lowest scores were found further downstream, with a specific cluster in the western part of the studied area (Fig. 1). This spatial pattern was also detectable with the PI but not with the EI and GI (Fig. A1). The population with the lowest MFI score was BAUSou, which had a low score for each component indicator (Fig. 1, Fig. A1).

The ANOVA confirmed the validity of the RDA (df=9, F=3.11, P=0.001). The global variance of the indicators' scores (component and MFI) constrained by the environmental factors was of 43.71%, including 39.93% explained by the two first axes (Fig. 2). The PI was negatively associated with the mean summer water temperature and the NNO_2-NNO_3 concentration (Fig. 2), suggesting that fish in colder and less eutrophicated water were less frequently and severely infected by *T. bryosalmonae*. The EI was poorly defined by both axes, and thus poorly explained by the measured environmental factors (Fig. 2). The GI was positively associated with the distance from the source, and negatively with the percentage of agricultural land, suggesting that fish further downstream and in less agricultural areas had a better genetic status. The MFI was strongly and negatively associated with the percentage of agricultural land, and positively associated with the O_2 concentration. Overall, the first axis was positively related to high scores for all the indicators, therefore the populations on the left part of the plot were identified as the less healthy and the most likely to decline (Fig. 2).

The path analyses for the component indicators (χ^2=20.68, df=19, P=0.36; CFI=0.99; RMSEA=0.04) and the MFI (χ^2=6.070, df=7, P=0.53; CFI=1; RMSEA=0) both met the

validation requirements. Consistently with the RDA, they revealed statistically significant relationships between some environmental factors and the indicators, while evaluating the covariances between environmental factors, i.e., considering their non-independence (Fig. 3). For instance, the concentration of NNO_2-NNO_3, the percentage of agricultural land and the mean summer water temperature were positively correlated: agricultural sites were thus warmer and more eutrophicated. The mean summer temperature and the percentage of agricultural land were negatively correlated with the altitude, implying that warm agricultural sites were mostly located at low altitudes. After considering the environmental factors covariations, the PI was negatively associated with the nutrient concentration and the mean water temperature (Fig. 3, see Fig. A3 for a visual representation). The EI was negatively associated with the percentage of agricultural land, as was the GI which was additionally positively associated with the distance from the river source (Fig. 3, see Fig. A3 for a visual representation). The set of measured environmental factors explained a consistent part of the variance of the PI and the GI (R^2=0.45 and R^2=0.37, respectively), but barely explained the variance in the EI (R^2=0.09, Fig. 3). The path analysis run separately for the MFI identified a positive relationship with the O_2 concentration and a strong negative relationship with the percentage of agricultural land (Fig. 3, see Fig. A4 for a visual representation). The MFI had the highest percentage of variance explained by the model (R^2=0.55, Fig. 3).

4. Discussion

We developed an easy-to-build operational multifaceted index informing on the general health of wild populations, as a first management step to identify risk-prone populations and guide conservation priorities. To that end, we combined indicators of population pathological, ecological, and genetic status into a multifaceted health index (MFI) by adapting a framework traditionally used to assess ecosystem multifunctionality. We showed that the 3 component indicators measured in brown trout populations did not covary, suggesting that they carry non-redundant and complementary information on population health. The MFI equally synthetized their information and enhanced the detection of risk-prone populations. The component indicators were associated with different environmental stressors, and the MFI highlighted the most important stressors regarding the populations' general health, which can help prioritizing conservation actions.

4.1. Identifying risk-prone populations

The pathological, ecological, and genetic indicators (PI, EI and GI, respectively) did not covary, indicating that they carry complementary information regarding population health. For instance, the population ARRGou showed a good GI suggesting a high adaptive potential, but its PI and EI were weak. The discrepancy between indicators illustrates the need for a more integrative index to get reliable insights of populations' general health. The combination of the indicators into a MFI therefore enhanced the accuracy of health assessment and ultimately classified ARRGou as a moderately risk-prone population.

This is especially true because the 3 component indicators equally contributed to the MFI, indicating that each indicator was accurately represented by the MFI. The MFI identified a cluster of populations with low scores in the north-western part of the studied area, in which especially one population (BAUSou) showed a high risk of decline. Congruently, we observed that its density has decreased markedly in 2020 (data not shown). This particular case illustrates the potential of the MFI to detect early warning signals of populations' declines (Clements & Ozgul, 2016; Drake & Griffen, 2010), even though further temporal surveys would be needed to validate this hypothesis.

4.2. Identifying underlying environmental stressors

We further showed that the component indicators were influenced by different environmental factors. We found associations between the indicators and the environmental factors tested that were mutually coherent and consistent with the biological requirements of brown trout, hence comforting the robustness of the multifaceted index.

For instance, the PI decreased with increasing nutrient concentration and water temperature. This result is consistent with *T. bryosalmonae* life cycle: increased water temperature favors its multiplication and transmission as well as the growth of its main host, a bryozoan, that is also favored by increasing concentration in nutrients, which in turn increases the available niche for the pathogen (Okamura et al., 2011).

Likewise, the GI increased with increasing distance from the source, following the prediction that genetic diversity usually increases downstream in riverine fish (Paz-Vinas et al., 2015), and decreased with increasing percentage of agricultural land. In addition, we found that our agricultural sites were warmer and more eutrophicated (3.2.). Since high concentration in nutrients, high temperature and low oxygen concentration are unfavorable conditions for brown trout survival and reproduction (Burkhardt-Holm & Scheurer, 2007; Elliott & Elliott, 2010), large agricultural surroundings may thus be associated with a rapid decline in the population demographic performance, ultimately decreasing its genetic diversity, as observed in other aquatic species (Blum et al., 2012; Nicol et al., 2017).

The EI also decreased with the percentage of surrounding agricultural land, but this indicator was globally poorly explained by the measured environmental factors.

The MFI was better explained by the measured environmental stressors than the 3 individual indicators, showing its relevance in indicating the most impacting factors for brown trout populations' health, i.e., the percentage of agricultural land and the oxygen concentration in the water. Consistently, the populations identified as the most likely to decline had the highest percentages of agricultural land in their surroundings. This corroborates the negative impact of agricultural land on the density and production found in other wild salmonid populations (Jonsson et al., 2011; Vondracek et al., 2005).

Lastly, an important advantage of the MFI is that it revealed the most impacting environmental stressors among those measured, including both the direct and indirect impacts of other environmental factors as revealed by the path analysis. Indeed, this integrative MFI approach showed that the presence of agricultural land was the main driver of low population health, combined with low oxygen concentration. Investigating the impact of environmental factors on the different facets of population health could enhance existing knowledge on the species' ecological niche and tolerance ranges (Sax et al., 2013) and help refining management practices.

4.3. Implementation and implications for wildlife conservation

This study shows how integrating different facets of health at the intraspecific level can improve risk assessment in wild populations, which is a major target for managers and stakeholders. Biological indicators combining multiple parameters at different scales of the ecosystem (communities, species, populations, genes) generally outperform single-parameter indicators (Alric et al., 2021; Friberg, 2014). Our MFI likewise demonstrated that the combination of several indicators appears wiser to limit the individual indicators' imperfections. Nonetheless, some individual parameters must be interpreted cautiously. For instance, a low genetic diversity could merely reveal past demographic history rather than the consequence of a recent contemporary stress (Matocq & Villablanca, 2001), and the body condition may misleadingly reflect individual health as it can be density-dependent or associated with some diseases (Bruneaux et al., 2017). This implies that the use of an

integrative index should not impede complementary analyses of the individual parameters to ensure that some important information is not lost during the process, blurring special patterns (e.g., especially alarming pathological or genetic status).

Importantly, the implementation of such integrative health indexes is highly flexible depending on management objectives as they can be built from a wide variety of parameters depending on the particularities of the studied systems. In this study, the parameters chosen were relevant for the brown trout, and easily implemented in the field, which improves the operationality of this index by managers and stakeholders. In other studies or species, additional indicators could be integrated such as physiological parameters (e.g. haematocrit, oxygen consumption, Bruneaux et al., 2017; cortisol, Sadoul & Geffroy, 2019), telomere length informing on the exposure to environmental stressors (e.g. in Dupoué et al., 2017), or demographic parameters (e.g. population age structure, Hixon et al., 2014; sex ratio, Le Galliard et al., 2005). Furthermore, our PI focused on the most threatening pathogen for our populations, but it could be accommodated to other pathogens and even to a wider community of pathogens so as to more realistically reveal the stresses imposed by pathogens. For instance, high sequencing throughput methods can be developed to screen the entire community of parasites infecting individuals, as it has been done for Chinook salmon (*Oncorynchus tshawytscha*) (Bass et al., 2017). The PI could be applied to mammal or avian species, based on fecal pathogen eggs counts (Kumar et al., 2019) or pathogen identification in the blood (Anjos et al., 2021). The MFI tested in our study could thus be applied to a wide range of species and ecosystems, and therefore help wildlife managers in prioritizing conservation measures into a wide variety of ecological contexts.

The implications of this new index are multiple. First, to understand how this MFI could guide species and habitat conservation actions, a parallel can be drawn with the community indicators of river quality (López-López & Sedeño-Díaz, 2015). For instance, the Fish Index, developed at the European scale, uses information from fish assemblages to assess the water quality of rivers (Pont et al., 2007). These indicators are very useful to assess the environmental quality of rivers at large spatial scales, but may be too coarse to compare sites with similar species composition. For instance, brown trout is the main species contributing to fish biomass in many mountainous areas in Europe, so that a community indicator based on fish assemblage does not allow the assessment of habitat quality. In these cases, gaining information at the *intraspecific level* is more appropriate to estimate the variation in habitat quality and identify potential key environmental stressors. Our indicator is therefore extremely valuable for indicating population and habitat qualities of ecosystems with dominant species, which is actually the norm rather than an exception in many areas in the World (Avolio et al., 2019). Focusing on the dominant species conservation may therefore benefit the whole ecosystem through conservation measures enhancing the habitat quality, corresponding to the concept of umbrella species (Roberge & Angelstam, 2004). Second, since it is based on the assessment of a single species, our indicator is also extremely useful for managers focusing on emblematic (or economically important) species for which specific actions are often needed.

4.4. Conclusions

The development of multifaceted health indexes brings more integrative insights on wildlife population health and potential risk of decline in changing environments. The development of such indexes is timely as cutting-edge field and molecular technologies enable digging into complex processes at the intraspecific level along fine gradients of anthropogenic perturbations. Moreover, non-invasive methods now enable to sample at wider geographic scales and a high number of populations, while minimizing the time spent on the field and the

395 impact on the sampled populations. The framework used in this study could thus be
396 transferred to a wide range of species and different component indicators, as a tool to
397 anticipate wildlife populations' declines and to guide future management decisions. An
398 important perspective would be to normalize this index according to reference populations (as
399 in Pont et al., 2007), which would undoubtedly ease its interpretation and implementation. We
400 hope that our work will motivate researchers to improve this tool and make it operational for
401 managers and stakeholders.

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Tables

Table 1: Summary of the measures in the 46 sampled brown trout populations, see Table A1 for details on each population.

Type of parameter	Method	Measure	Range	Mean	SD
Sampled individuals	Count	Number of brown trout sampled (N)	10-20	19	3
Environmental factors	GIS software	% Agricultural land in a 2km buffer	0-89	49	24
		Altitude (m)	232-844	447	136
		Distance from source (km)	3-105	28	21
	HOBO logger	Mean summer temperature (°C)	12.3-19.4	16	1.9
	Ponctual dosage	PO_4^{3-} (µg/L)	0-205	58	55
		NNO_3^- NNO_2^- (µg/L)	0-2440	747	661
	Ponctual measure (InSitu)	pH	7.7-8.7	8.3	0.2
		Conductivity (µs/cm)	24-460	216	117
		O_2 concentration (mg/L)	8.5-11.4	9.8	0.5
Pathological indicator	Parasite DNA detection in fish urine	Infection prevalence (%)	0-100	30	40
		Parasite DNA excretion (copies/µL/g/min)	0-17	2	3.6
Ecological indicator	Measures in the field	Condition factor	1.05-1.43	1.24	0.08
		Brown trout density (N/min)	0.12-2.40	0.89	0.52
Genetic indicator	SNPs	MLH[a]	0.13-0.21	0.17	0.02
		N_e [b]	6-681	138	174

[a] Multilocus heterozygosity

[b] Effective population size

Figures

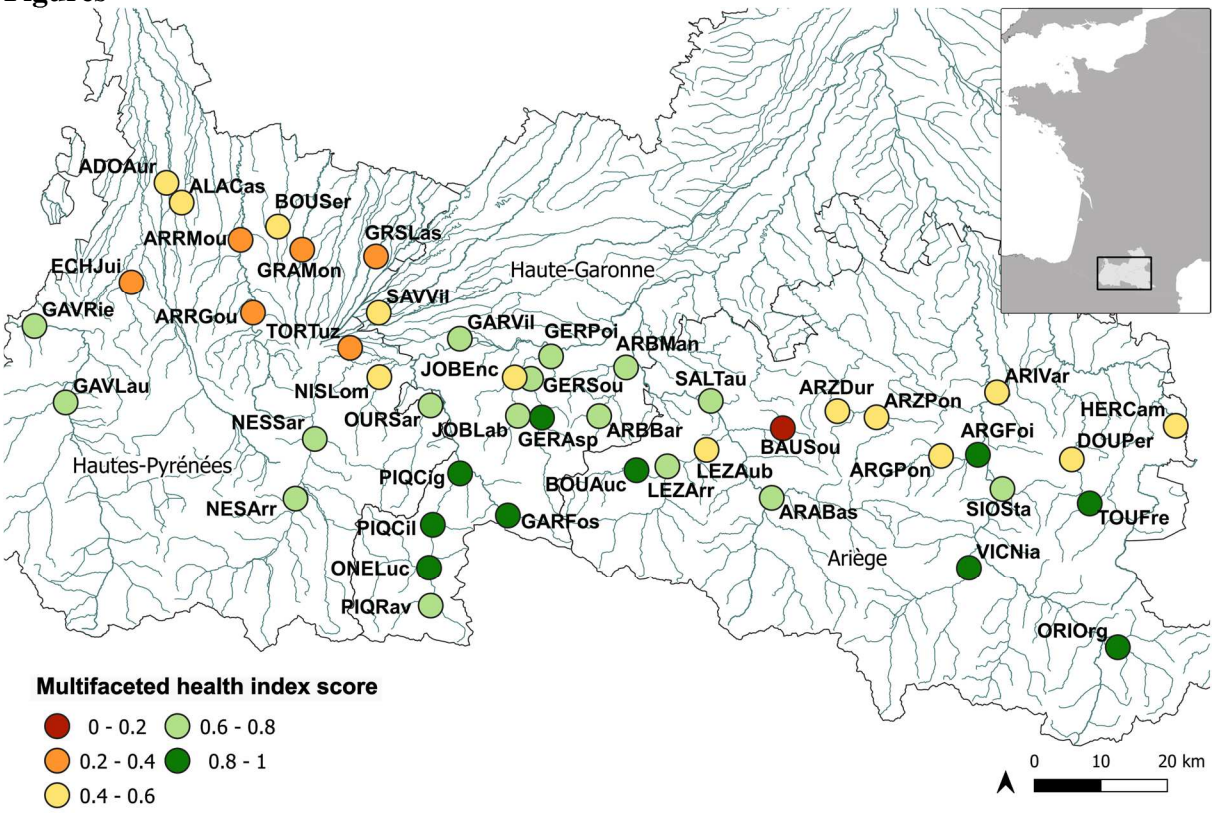

Figure 1. Map of the 46 sampled populations and their multifaceted health index. Dark red represents the populations with a low multifaceted health index score, and dark green the populations with a high score. The inset map shows the location of the studied area, in Southern France at the foothill of the Pyrenees. Codes for the sampled sites (in bold) and departments (standard police) are indicated.

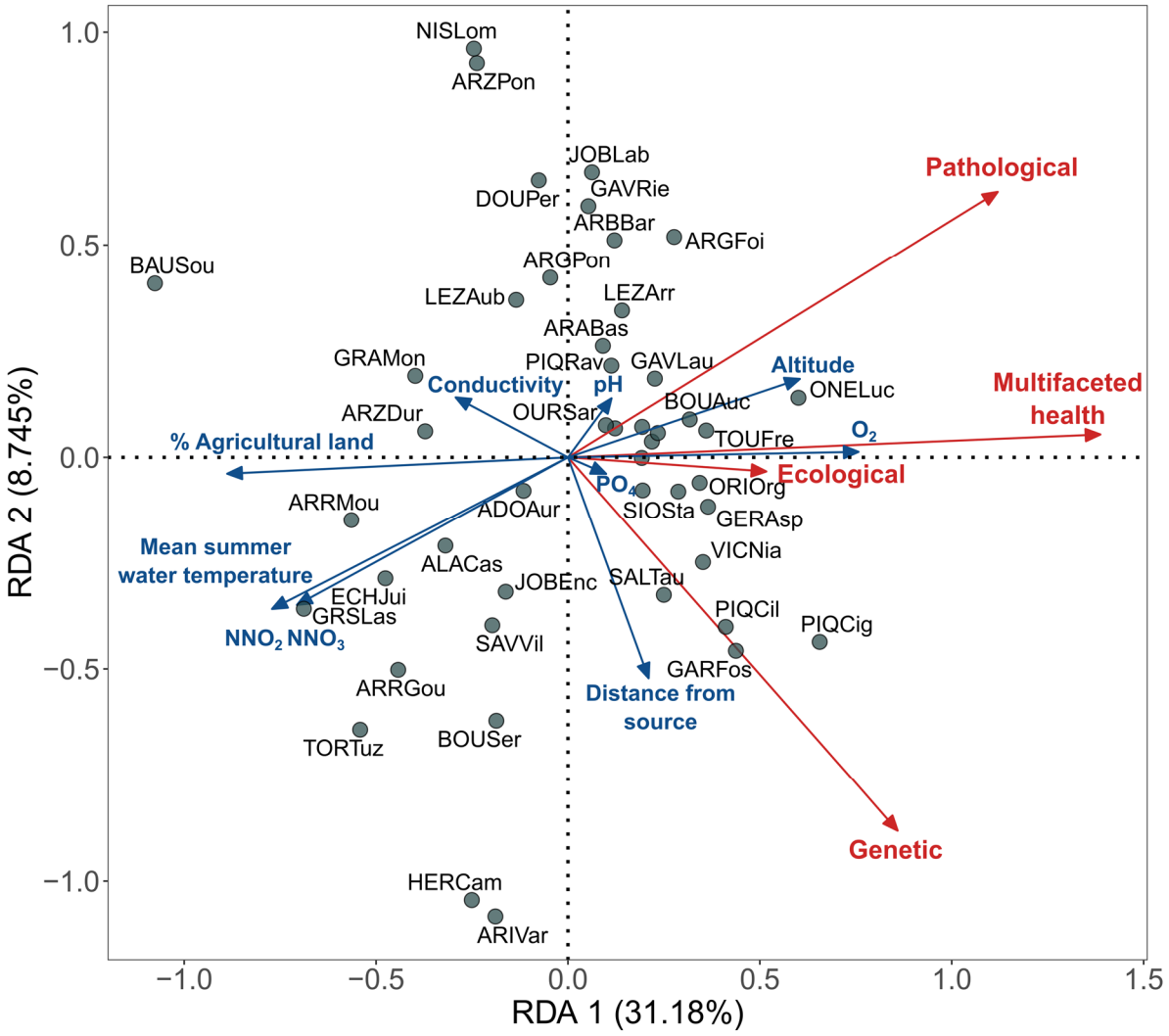

Figure 2. Biplot of the redundancy analysis showing the relation between the indicators (response variables, in red) and the environmental factors (explanatory variables, in blue). Dots represent the sampled populations together with their code.

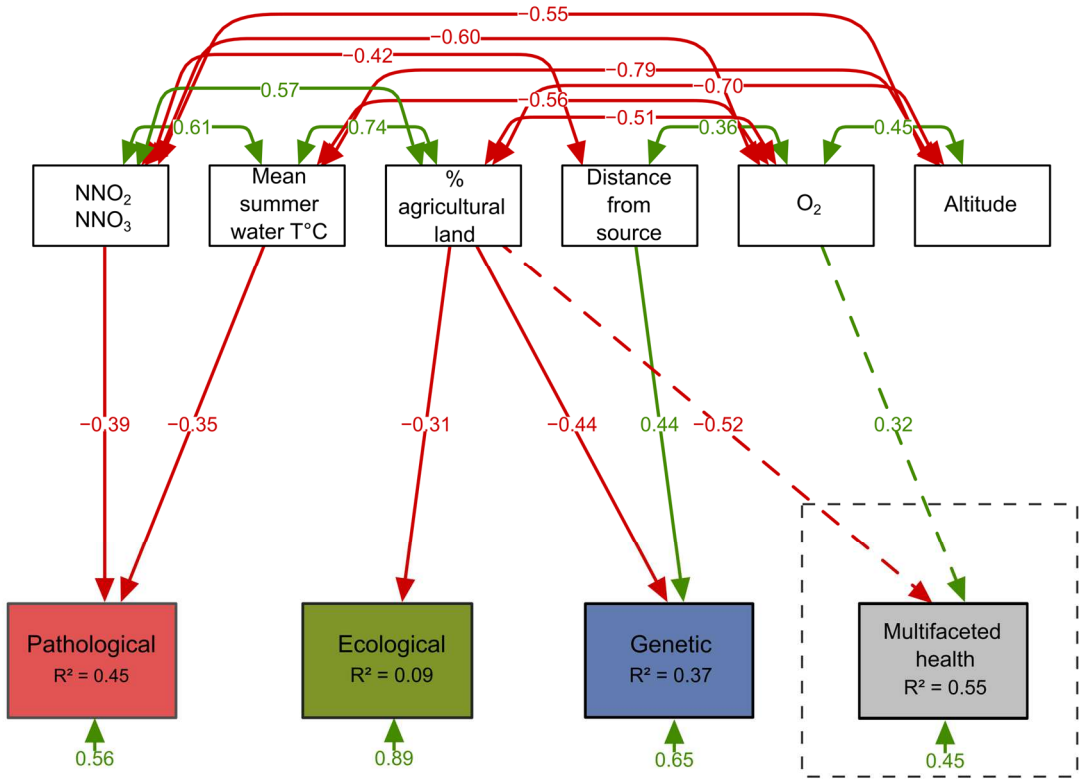

Figure 3. Plot of the best path analyses explaining the 3 indicators and the multifaceted health index. Plain arrows represent the impact of the environmental factors on the indicators, and double arrows represent the covariations between the environmental factors. Dotted arrows towards the multifaceted health index and the dotted rectangle indicate that this variable was part of a different analysis but represented on the same figure for the sake of clarity (see 2.3.2.). Red arrows represent negative relationships and green arrows represent positive relationships, and the estimates are indicated. All the relationships represented on the graphic are statistically significant (see Table A3 for details). T°C: temperature.