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Interactive effects of land use, river regulation, and climate on a key recreational fishing species in temperate and boreal streams

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Abstract

1. Numerous anthropogenic stressors, including river regulation, excess loadings of nutrients and sediment, channelisation, as well as thermal and hydrological stressors driven by climate change impact riverine ecosystems worldwide. In a time when freshwater degradation and the rate of global warming are faster than ever, understanding the potential interactive effects of local and catchment-scale stressors with large-scale climatic conditions is essential to enhance our ability to plan effective conservation, restoration, and mitigation measures.
2. In this study we analysed a dataset spanning the whole of Sweden using a space-for-time approach to investigate interactive effects of land use, river regulation, and climate on brown trout (*Salmo trutta*) abundance in streams.
3. We found that in warmer regions trout populations were negatively affected in catchments with more intense river regulation by hydropower dams (i.e. ≥10 m^3/km^2 total reservoir storage volume). In such catchments, a 7°C warmer mean summer air temperature was associated with an average between 44% and 83% decline in trout abundance. In catchments with less intense river regulation, trout abundance instead increased moderately with increasing temperature.
4. We also found that brown trout abundance declined with increasing areal extent of urban areas when found in combination with ≥20% agricultural land use. When agricultural land use reached maximum values (84%), brown trout abundance decreased from an average of 13 individuals per 100 m^2 in catchments with no urban areas to values ≤1 in catchments with ≥5% urban land use. Also, brown trout abundance declined with increasing agricultural land use in catchments with ≥3% urban land use.
5. Our study brings innovative empirical evidence of interactive effects between river regulation, land use and climate on brown trout populations. From a management perspective our findings suggest that: (1) restoring natural flows (e.g. through dam removal) and riparian vegetation could mitigate adverse effects of

climate change; and (2) restoration measures that minimise the effects of agriculture and urban land use (e.g. reduction of nutrient levels and restored riparian buffer zones) could help rehabilitate brown trout in catchments with high anthropogenic land use change. However, given the large observed variation between streams, we advise for bespoke management actions stemming from sound knowledge of local habitat conditions and target populations, whenever possible, using an ecosystem management-based approach.

KEYWORDS

brown trout, climate change, dams, multiple pressures, urban area

1 | INTRODUCTION

Riverine ecosystems are extremely rich in biodiversity and provide essential services to society (Strayer & Dudgeon, 2010). However, these ecosystems are threatened by an increasing number of environmental stressors arising from anthropogenic activities, such as river regulation by dams, land-use change (e.g. intense agriculture and urbanisation), and loss of riparian integrity (Foley et al., 2005; Sabater et al., 2018). These activities result *inter alia* in elevated nutrient concentrations, increased erosion, and consequent sediment loadings and pesticide runoff (Meybeck, 2003). Increasingly overlaid on these local and regional changes are further stressors driven by global climate change, including altered thermal and hydrological regimes (Best & Darby, 2020; Vörösmarty et al., 2010). Understanding how freshwater systems respond to the interactive effects of stressors arising not only from human activities at local and catchment scales (Johnson et al., 2017), but also from global climate change is of paramount importance for planning effective conservation and restoration measures (Craig et al., 2017).

Interactions between stressors can give rise to *ecological surprises*, which occur when their combined impacts are not simply additive, and hence difficult to predict from the individual effects of single stressors (Jackson et al., 2016; Townsend et al., 2008). Understanding whether stressors operate independently or interact antagonistically or synergistically is fundamental for managers to decide on the most effective restoration practices and their prioritisation (e.g. which stressor[s] to address, and in what order). For example, restoration of altered river discharge through mandated minimum flows can partly compensate for the negative effects of riparian degradation (Göthe et al., 2019). By contrast, mitigation of abrupt changes in flow velocity due to e.g. daily hydro-peaking can worsen the effects of excessive nutrients, which are otherwise flushed downstream (Bondar-Kunze et al., 2016). A recent review suggests that non-additive responses predominate across aquatic ecosystems (Villar-Argaiz et al., 2018); however, these results mainly come from experimental studies in marine systems and from lakes. In contrast, riverine ecosystems remain relatively understudied in this respect and it is likely that cumulative stressor effects display complex threshold behaviors, where synergism or antagonism may occur at certain values of stressors and initial environmental conditions (Birk et al., 2020; Johnson et al., 2017; Nõges et al., 2016).

Climate change potentially intensifies the effects of human stressors on aquatic ecosystems (França et al., 2020; He & Silliman, 2019). Climate change is predicted to alter variability in thermal mean and extreme values, with implications for many vital biological and ecosystem processes regulated by temperature, such as oxygen consumption, nutrient release from sediment, and in-stream primary and secondary production (Demars et al., 2011; Patrick et al., 2019). Changes in precipitation are also likely to fundamentally impact riverine ecosystems via the alteration of hydrological regimes, which are expected to lead to an increase in the frequency and severity of droughts and floods (Dai, 2013; Truchy et al., 2020). When evaluating ecosystem effects within a multiple stressors framework, evidence is increasing that climate-induced changes can interact strongly with local anthropogenic stressors, e.g. increased nutrient flows (Jeppesen et al., 2010), pollution (Piggott et al., 2015), land use (DeBano et al., 2016; Maloney et al., 2020; Taniwaki et al., 2017), hydromorphological alteration (O'Briain et al., 2019; Tonkin et al., 2018), invasion of non-native species (Lawrence et al., 2014; Schindler, 2001), and overexploitation (Harrod, 2015).

Hydromorphological stress and habitat degradation are among the most prominent threats to freshwater fish and ecosystems worldwide (Arthington et al., 2016; Rytwinski et al., 2020). Hydromorphological stress comprises all physical alterations to water bodies such as dams, embankments, channelisation and flow regulation, and affect *c*. 40% of European water bodies (EEA, 2018). Sweden has a long history of river regulation, with around 12,000 dams and 2,200 hydropower plants spread over the country, which provide 45% of the national electric power (http://www.energimyndigheten.se/fornybart/vattenkraft/). Damming and altered flow regimes have large impacts on water chemistry, and transport of sediments and organic material, and can lead to higher water temperatures, which increase algal biomass, reduce invertebrate richness and abundance, and negatively impact fish communities (Arthington et al., 2016; Bunn & Arthington, 2002; Rufin et al., 2019; Sabater et al., 2018). Furthermore, by causing fragmentation of habitats within the river network, damming poses a serious threat to migratory fish species, such as salmonids and eels (Brown et al., 2013; Cooper et al., 2017; Tamario et al., 2019; Törnblom et al., 2017).

Habitat degradation is also caused by land-use transformation (Allan, 2004; Price et al., 2019; Urban et al., 2006), which typically involves the increase in areal extent of agricultural and urban areas and the loss of forests and more complex riparian vegetation including trees and large bushes (Kuglerová et al., 2019). Such changes typically lead to increased sediment loads, pesticides and pathogens (Jokinen et al., 2012; Liess & Schulz, 1999), raised water temperature (Piggott et al., 2012), alteration of natural stream flow (Bunn & Arthington, 2002), excess of macronutrients (i.e. phosphorus and nitrogen), and decreased oxygen availability (Winfield, 2015), which in turn affects running water ecosystems including fish communities. There is evidence that urbanisation, agricultural intensification, and water diversion are likely to exacerbate the negative effects of climate change (Mantyka-Pringle et al., 2014; Nelson et al., 2009; Walters et al., 2013; Wooster et al., 2019), which stresses the need for proactive conservation measures. However, the interactive effects of local anthropogenic stressors on stream fish communities, as well as potential interactions with climate change, are only partly uncovered and pose urgent questions that scientists and managers need to address (Maloney et al., 2020; Staudt et al., 2013). Brown trout (*Salmo trutta*) is a cold-water species broadly distributed in boreal streams (Cushing et al., 2006). It is a target of recreational and commercial fishing, as well as of mitigation and restoration policies (Roni et al., 2008; Whiteway et al., 2010). Also, brown trout is a key species for the conservation of the endangered freshwater mussel (*Margaritifera margaritifera*), as it serves as host for the mussel larvae (Clements et al., 2018; Salonen et al., 2017), and is used to indicate the biotic integrity of running waters (Appelberg et al., 2000). Brown trout population abundance is easily measured at shallow stream reaches by standardised electrofishing (CEN, 2003), a method that is extensively used in fish monitoring in Europe, U.S.A., and Canada. Brown trout has a low tolerance to high temperatures (Elliott & Elliott, 2010), and is particularly vulnerable to climate warming and extreme flow conditions, such as low flows and droughts (Burkhardt-Holm et al., 2002; Nicola et al., 2009; Warren et al., 2015). Furthermore, brown trout populations are often migratory (Armstrong et al., 2003; Klemetsen et al., 2003), which makes them particularly susceptible to stress caused by loss of connectivity (Renöfält et al., 2010; Rytwinski et al., 2020).

In this study we used a country-wide dataset of long-time monitoring of stream fish by electrofishing to investigate interactive effects of land use, river regulation, and climate on brown trout populations. Stream flow alteration can intensify the effects of land use and climate change (Lange et al., 2014; Walker et al., 2020), and we expect that river regulation has stronger impacts on brown trout in catchments with larger extent of agricultural and urban areas, and in locations with a warmer and drier climate. Understanding how these interactions between catchment-scale and climate related stressors affect the health of fish populations is critical to the application and prioritising of mitigation and restoration measures (Staudt et al., 2013).

2 | METHODS

2.1 | Electrofishing data

The dataset was extracted from the Swedish Electrofishing RegiSter (SERS), and included data from 11,736 electrofishing sampling occasions conducted between 1980 and 2017 at 2,772 locations in a total of 254 streams across Sweden. Streams were located in 85 catchments with an average size of 275.2 km^2 (*SD* = 663.9, min = 4.5, max = 11,315.0), relatively evenly distributed across the country (Figure S1). Data in SERS are quality assured by using a strict sampling protocol (Bergquist et al., 2014) and posterior quality checks. We selected only streams included in the Swedish Meteorological and Hydrological Institute (SMHI) Vattenwebb (https://www.smhi.se/data/hydrologi/vattenwebb), where electrofishing had included the whole stream width, and in at least three locations per stream, to partition out the variation associated with the random factor *stream*. Streams had a mean width of 8.2 ± 7.9 m (*SD*, Table 1), and stream sampled length 41 ± 24 m (mean ± *SD*). Each location was sampled on average four times in different years (range, 1–38 times, *SD* = 5). Electrofishing was performed by wading mostly between mid-July and October, using DC equipment from Lug AB or BioWave (Biokon). All fish were handled according to ethical approvals (licence number N50/15, Div. Freshwater research), and were returned to the streams alive (Bergquist et al., 2014). Brown trout abundance was estimated through successive removals (usually including three runs) (Bohlin et al., 1989) or, when it was not possible (i.e. <10% of the sampling occasions), from average catch probability (Bergquist et al., 2014), and expressed as estimated number of individuals per 100 m^2. The brown trout caught by electrofishing were mostly juveniles (fry and parr).

2.2 | Data on stressors

Measures of stressors related to river regulation and land use were provided by the SMHI as estimates at catchment scales, as advised by previous studies (Birk et al., 2020; Gergel et al., 2002; Segurado et al., 2013). Variables related to river regulation were extracted through the S-Hype model (HYPE_version_5_10_2, https://vattenwebb.smhi.se/modelarea/) and refers to the period 1990–2013. They were: (1) the average number of dams per 100 km^2 in the catchment; (2) the total reservoir storage volume in the catchment; and (3) the percentage of regulated water volume in the catchment, which was estimated in relation to average yearly water flow at stream mouth (Table 1). These metrics were considered as proxies for flow alteration by dams within the catchment, which according to the Swedish Meteorological and Hydrological Institute has mainly undergone small seasonal changes, while the yearly estimates have remained constant over the last decades. Variables related to land-use stressors were (4) percentage of agricultural land use and (5) percentage of urban land use in the catchment (Table 1), both estimated in 2012. Estimates of agricultural and urban land use have remained

TABLE 1 Variables included in the analyses

Variable type		Variable	Unit	Mean	*SD*
Response		Brown trout	No. per 100 m^2	26	50
Fixed factors	River regulation	Dams	No. per 100 km^2	4	5
		Total reservoir storage volume	m^3	86.81	477.14
		Total reservoir storage volume/area	m^3/km^2	0.89	8.14
		Regulated water volume	%	3.5	8.8
	Land use	Urban land use	%	1.6	2.5
		Agricultural land use	%	12.1	16.6
	Climate	Summer air temperature 1961–1990	°C	15.2	1.0
		Annual precipitation 1961–1990	mm	1,490	534
		Winter air temperature 1961–1990	°C	−5.0	3.7
		Annual temperature	°C	5.4	2.1
	Local environment	Stream wetted width	m	8.22	7.92
		Stream depth	m	0.26	0.11
		Stream section inclination	%	2.9	1.1
		Density of wood pieces	No. per 100 m^2	2	4
		Coverage of underwater vegetation	(Ordinal, from 1 to 3)	1.7	0.9
	Time	Year		2003	9
		Month		8	1
Random factors		Stream			
		Catchment			

Means and standard deviations for continuous variables are given.

stable in Sweden in the recent decades, showing only a minor expansion of urban areas, in a country with a total urban land use of about 2.9% (or 1.2 million hectares, Statistics Sweden, 2019). These were considered *umbrella* variables accounting for several habitat changes, e.g. increased loads of pesticides, nutrients, and fine sediments, hydro-morphological modification, lack of forest cover, and loss of connectivity (Sandin, 2009), but did not include information on the status of local riparian buffers.

2.3 | Climate data

We used a space-for-time approach, whereby the spatial variation in climatic conditions throughout Sweden was used to gain insights into the potential interactive effects of climate change and anthropogenic stressors. A space-for-time approach, despite being commonly used among ecologists when detailed time series are not available, presents a major drawback, which is the risk of detecting responses caused by the spatial variation in the data that is unrelated to temporal changes. We have addressed this aspect by including in the analyses a large number of local environmental variables that are used as covariates to account for between-sites variation, as well as random factors such as catchment and stream to account for unmeasured factors (see below). To capture climatic variation at a country-wide scale, we used *climate normals*, which according to recommendations from the World Meteorological Organization (WMO, 2018), are calculated over a time period of 30 years to reduce year-to-year variability. The normal period considered was 1961–1990, as advised when describing data from the past (WMO, 2018). The variables considered were: (6) mean summer (July) air temperature; (7) mean winter (January) air temperature; and (8) annual precipitation, estimated at the closest meteorological stations to each sampled location (http://www.smhi.se, Table 1). Additionally, we considered (9) annual mean temperature corresponding to all fishing occasions to capture shorter-term and small-scale variation in the temperature regime.

2.4 | Local environmental data

For each sampling location, local environmental parameters were estimated in the field at the time of fish sampling (Table 1), such as: stream wetted width, average stream depth, coverage of underwater vegetation (estimated visually as an ordinal variable with values from 1 to 3), and density of large wood (i.e. number of wood pieces with diameter ≥10 cm and length ≥50 cm per 100 m^2). Stream-bed slope for each location was estimated from maps (1:50 000; Terrängkarta, Lantmäteriet).

2.5 | Data analysis

All analyses were conducted in R 3.3.1 (R Core Team, 2015). To explore the effects of multiple stressors on brown trout abundance, we used general linear mixed models. The most comprehensive model (i.e. *full model*) included catchment-scale variables related to land use, river regulation, and climate, the two-way interactions between those variables, and also local environmental factors. We did not consider higher order interactions, as this would increase the complexity of the model and the chance of Type II errors. The local environmental variables stream wetted width, average stream depth, coverage of underwater vegetation, density of large wood, and stream section inclination are known to affect local brown trout abundance (Donadi et al., 2019; Trigal & Degerman, 2015), and were included as covariates to account for small-scale variation (Table 1). Variation in these local-scale environmental variables is likely to be influenced at least in part by human activities at larger scales. However, we found no significant collinearity between them and the variables related to land use and river regulation (fewer than four variance inflation factors [VIFs], see below), possibly because of a mismatch in the spatial scales (i.e. local vs. catchment scale) of the estimates. Hence, we included them in the models, while recognising that they may partly account for variation caused by unmeasured stressors. Finally, our analyses further included terms for the year and month of the sampling to account for potential within-year variation and temporal shifts in unmeasured factors that could have affected brown trout response (Table 1).

Furthermore, to investigate how much variation in trout abundance was contributed by interactive terms we ran an *additive model*, i.e. including only main effects of explanatory factors. To investigate the contribution of anthropogenic stressors versus local environmental variables we ran a model without land use, river regulation and climate variables (i.e. *local habitat model*), and models where values of land use, river regulation and climate variables were randomised within each variable 1,000 times. We then compared the model fit (via Akaike information criterion [AIC]) and the explanatory power of all models.

Collinearity between predictors was checked by calculating the VIF for each predictor, using a threshold value of 4, and Spearman's rank correlation coefficients. Mean summer air temperature, mean winter air temperature and annual mean temperature were highly correlated (all Spearman's rank correlation coefficients >0.60, p values <0.001), and only mean summer air temperature was therefore retained in the final model. We did this because of its ecological significance, as high temperatures can be deleterious to trout survival (Armstrong et al., 2003), and because it gave a slightly better fit to the data (marginal $r^2 = 0.16$) than mean winter air temperature (marginal $r^2 = 0.15$) and mean annual air temperature (marginal $r^2 = 0.15$). Total reservoir storage volume was divided by catchment area to give a relative estimate of total reservoir storage volume for comparison between catchments of different size (Table 1). This variable, together with stream wetted width, and density of large wood, were log-transformed to reduce skewness. Also, the response variable brown trout abundance was log-transformed to attain normality. The model included a nested random factor *stream* within *catchment* (Table 1), and a symmetrical correlation structure to account for repeated measures so that all sampling events could be included in the analysis. The intraclass correlation, i.e. the correlation between observations coming from the same stream and catchment, was computed following Zuur et al., (2009). Marginal and conditional r^2 values were estimated as described by Nakagawa and Schielzeth (2013). Model validation was performed visually according to standard procedure (Zuur et al., 2009) by plotting residuals against fitted values and against significant explanatory factors, and residual frequency distributions. When interactions between two explanatory factors were found to be statistically significant, we used the R package *ggeffects* 1.0.1 (Lüdecke, 2018) to visualise marginal effects, i.e. the effect of one predictor on the response variable when the other predictors were held constant. The spatial distribution of significant explanatory factors was visualised through maps built with the R package *maps* 3.3.0 (https://CRAN.R-project.org/package=maps). For a map of the spatial distribution of the response variable brown trout abundance across Sweden, see Donadi et al., (2019).

3 | RESULTS

We found that mean summer air temperature interacted synergistically with total reservoir storage volume to affect trout populations (*full model*, $F = 4.94$, $df = 4{,}098$, p value $=0.026$, Table 2, Figure 1). Trout abundance decreased with warmer temperature in catchments with larger total reservoir storage volume, while it increased with warmer temperature in catchments with smaller total reservoir storage volume (Figure 1). The relationship between trout abundance and summer air temperatures shifted from positive to negative when total reservoir storage volume was close to 10 m^3/km^2, and became steeper the larger the total reservoir storage volume. Our model predicted that a 7°C difference corresponded to an average 44% decline in trout abundances in catchments with total reservoir storage volume of 10 m^3/km^2, and to an average 83% decline in catchments with a total reservoir storage volume of 100 m^3/km^2, which is comparable with the maximum value of 92 m^3/km^2 observed in our data. However, while our analysis revealed that climate effects could depend on the intensity of river regulation, predictions of absolute values of brown trout abundance from our model should be made with caution especially at the lower end of our temperature gradient, where replicates were few (see the large 95% confidence intervals in Figure 1).

The observed pattern was not driven by collinearity between summer air temperature and total reservoir storage volume (VIFs < 4, Table S1), and summer air temperatures did not differ on average in catchments with more or less intense river regulation (Figure S2). At a national scale, the highest summer temperatures are found in the south of Sweden, and the medium and high values of total reservoir storage volume (≥ 10 m^3/km^2) are found in the south and central Sweden (Figure 2).

We also found that in catchments with lower agricultural land use ($\leq 10\%$), trout abundance slightly increased with increasing urban areas ($F = 5.43$, $df = 1{,}155$, $p = 0.020$, Table 2, Figure 3), while in catchments with higher agricultural land use ($\geq 20\%$), trout

TABLE 2 Estimates from the *full model* of the effects on brown trout (*Salmo trutta* L.) abundance of multiple stressors and their interactions, as well as environmental covariates

Explanatory factors	*F*-value	*p*-value	Slope	*SE*
Dams	0.008	0.931	−0.007	0.086
Total reservoir storage volume (log)	4.680	**0.031**	1.146	0.530
Regulated water volume	3.175	0.075	−0.143	0.080
Urban land use	0.001	0.978	−0.013	0.459
Agricultural land use	2.871	0.090	−0.086	0.051
Summer air temperature 1961–1990	1.094	0.296	−0.055	0.052
Annual precipitation 1961 – 1990	0.358	0.550	−0.007	0.012
Stream wetted width (log)	57.845	**<0.001**	−0.388	0.051
Stream depth	158.958	**<0.001**	−0.712	0.057
Stream section inclination	12.622	**<0.001**	0.040	0.011
Density wood pieces (log)	43.740	**<0.001**	0.139	0.021
Coverage of underwater vegetation	3.286	0.070	0.014	0.021
Year	4.700	**0.030**	0.002	0.008
Month	1.638	0.201	−0.009	0.007
Dams * total reservoir storage volume (log)	1.245	0.265	−0.010	0.009
Dams * regulated water volume	0.794	0.373	0.001	0.001
Dams * urban land use	0.299	0.584	0.002	0.004
Dams * agricultural land use	1.953	0.163	−0.001	0.001
Total reservoir storage volume (log) * regulated water volume	0.003	0.960	2×10^{-04}	0.003
Total reservoir storage volume (log) * urban land use	0.181	0.671	0.023	0.053
Total reservoir storage volume (log) * agricultural land use	0.061	0.805	−0.001	0.005
Regulated water volume * urban land use	1.378	0.241	−0.009	0.008
Regulated water volume * agricultural land use	0.146	0.702	-4×10^{-04}	0.001
Agricultural land use * urban land use	5.434	**0.020**	−0.003	0.001
Summer air temperature 1961–1990 * dams	0.006	0.941	-4×10^{-04}	0.006
Summer air temperature 1961–1990 * total reservoir storage volume (log)	4.940	**0.026**	−0.078	0.035
Summer air temperature 1961–1990 * regulated water volume	3.215	0.073	0.010	0.005
Summer air temperature 1961–1990 * urban land use	0.023	0.879	0.004	0.028
Summer air temperature 1961–1990 * agricultural land use	4.174	0.061	0.007	0.003
Annual precipitation 1961–1990 * dams	0.562	0.454	0.001	0.002
Annual precipitation 1961–1990 * total reservoir storage volume (log)	0.127	0.721	−0.002	0.006
Annual precipitation 1961–1990 * regulated water volume	0.488	0.485	0.001	0.001
Annual precipitation 1961–1990 * urban land use	0.118	0.731	0.001	0.003
Annual precipitation 1961–1990 * agricultural land use	0.992	0.319	−0.001	0.001

Note: Significant *p*-values ($\alpha < 0.05$) are indicated in bold.

The numerator degree of freedom is 1 for all factors, and the denominator degrees of freedom is 1,155 and 4,098 for variables estimated respectively at the scale of catchments and locations.

abundance decreased with increasing urban areas. For values of agricultural land use comparable to the maximum of 84% observed in our dataset, our model predicted a decline from *c*. 13 individuals per 100 m^2 in catchments with no urban areas, to 1 or no individuals in catchments with more than 5% urban land use. (Figure 3). For constant values of urban land use, the interaction shows negative effects of agricultural land use on brown trout abundance when urban land use is above 3%, but mild positive effects below this value. These synergistic effects of land use are more likely to occur in the south and central parts of Sweden, where relatively high urban and agricultural land use often co-occur (Figure 4).

Annual precipitation, as well as number of dams per 100 km^2, and percentage of regulated water volume were not associated with significant main or interactive effects on trout abundance. Wetted width and average depth were the local environmental covariates that explained most variation in trout abundances, both showing

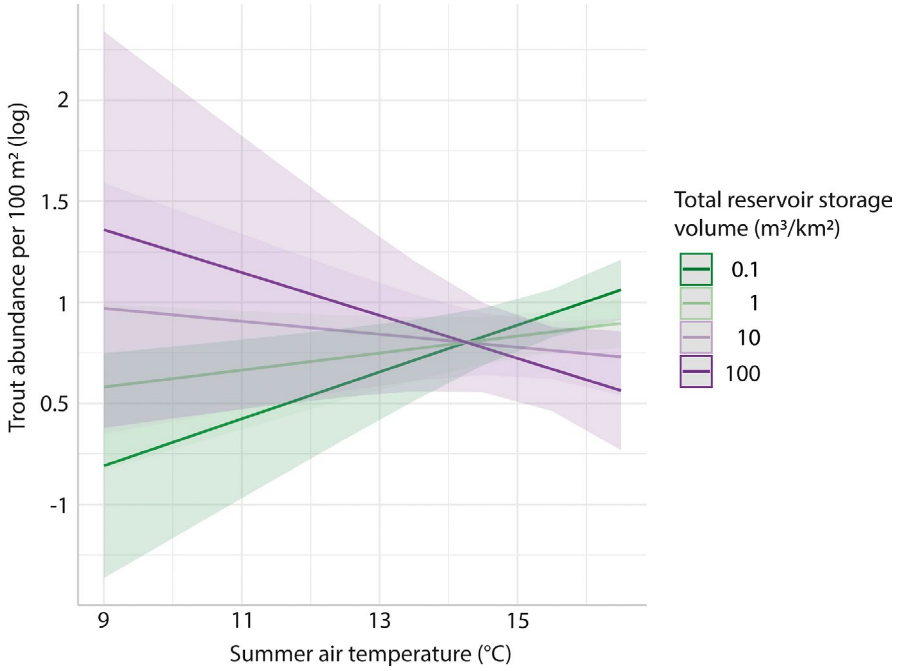

FIGURE 1 Interactive effects of summer air temperature and total reservoir storage volume on brown trout (*Salmo trutta* L.) abundance as predicted by the *full model*. Lines of different colours show marginal effects of increasing summer air temperature in catchments with different total reservoir storage volume. Shaded areas show 95% confidence intervals. Note the log unit on the y axis

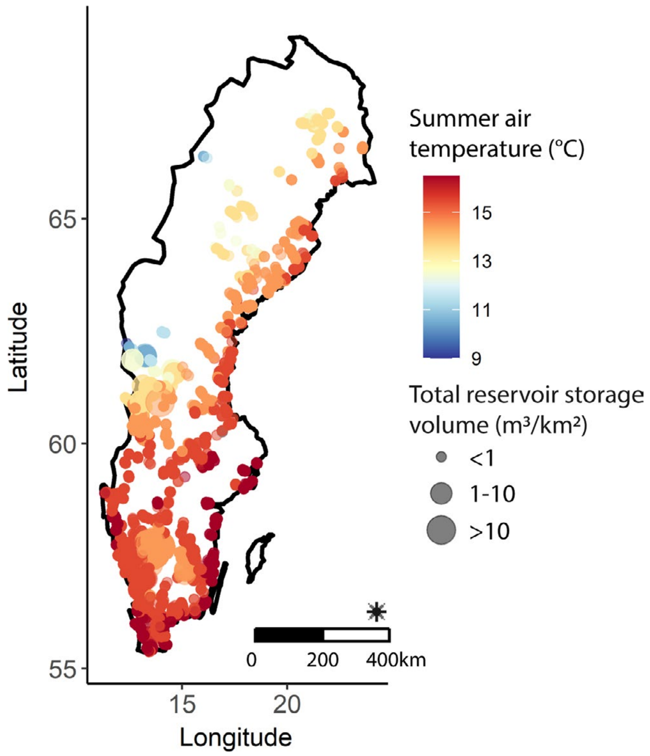

FIGURE 2 Map of Sweden showing summer air temperature as colour of the dots and total reservoir storage volume as size of the dots

inverse relationships (Table 2). Furthermore, trout abundance increased with increasing density of large wood, and, to a minor extent, with steeper stream section inclination and year (Table 2).

Our *full model* including catchment-scale factors and their interactions had a better model fit and a higher explanatory power (AIC = 4,875, marginal r^2 = 0.16) compared to the *additive model* (AIC = 5,288, marginal r^2 = 0.12), and the *local habitat model* (AIC = 5,239, marginal r^2 = 0.07). The marginal r^2 of the models resulting after randomising land use, river regulation and climate variables 1,000 times was on average 0.07 (±0.0006 *SD*; 0.066 min, 0.68 median, 0.071 max). The conditional r^2 was 0.82, indicating that the random factors *catchment* and *stream* explained most of the variation in trout abundance. The intraclass correlation was 0.15 at catchment level, and 0.43 at stream level, which indicates large variation between streams and relatively low variation between catchments.

4 | DISCUSSION

Our results highlight the potential effects of interactions between future temperature increases and additional anthropogenic stressors on trout abundance in streams. The ICPP scenario RCP8.5 predicts that Sweden will undergo an increase in mean summer air temperature of between 3 and 6°C in the next 100 years. According to our findings this may correspond to a decrease in trout density of 57%–78% in catchments with intense river regulation. Among the variables related to river regulation, total storage volume was the most important factor in explaining variation in brown trout density. The number of dams per 100 km^2, although it could be a good proxy for the loss of connectivity, may be less representative for hydropower activities, because many dams are not used for hydropower production, or are run-of-river dams, i.e. the river is not regulated to the same extent as rivers with an impoundment hydropower plant (large reservoirs). Surprisingly, the percentage of regulated water volume in relation to the annual mean flow had less explanatory power than total reservoir storage volume. This could be because the variable poorly captured the high temporal and spatial variability of flow regulation, as large fluctuations often occur

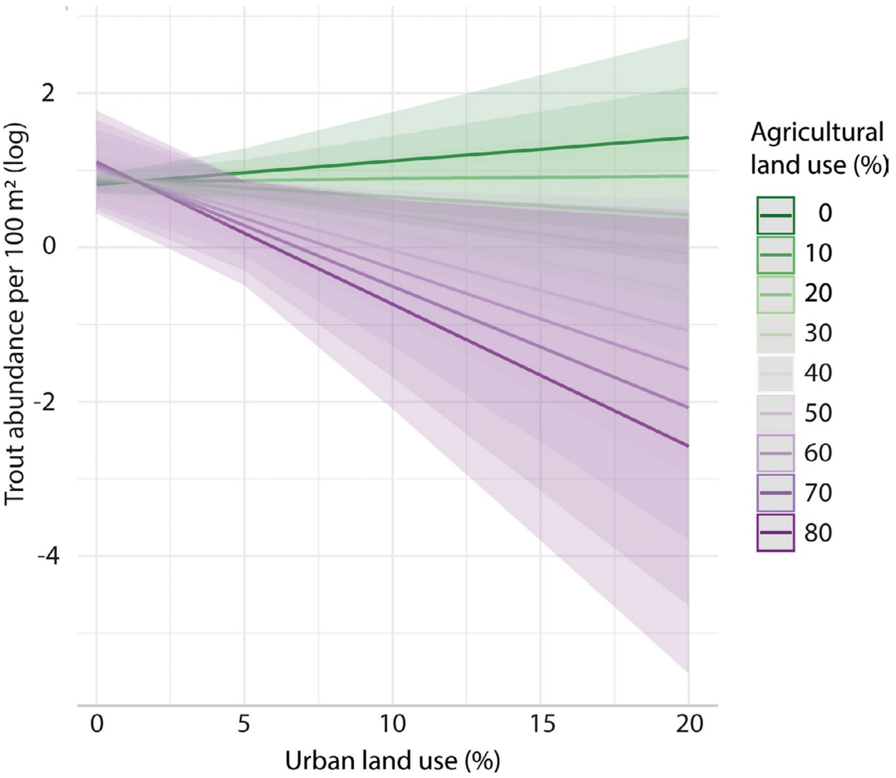

FIGURE 3 Interactive effects of urban and agricultural land use on brown trout (*Salmo trutta* L.) abundance as predicted by the *full model*. Lines of different colours show marginal effects of increasing urban land use in catchments with different agricultural land use. Shaded areas show 95% confidence intervals. Note the log unit on the y axis

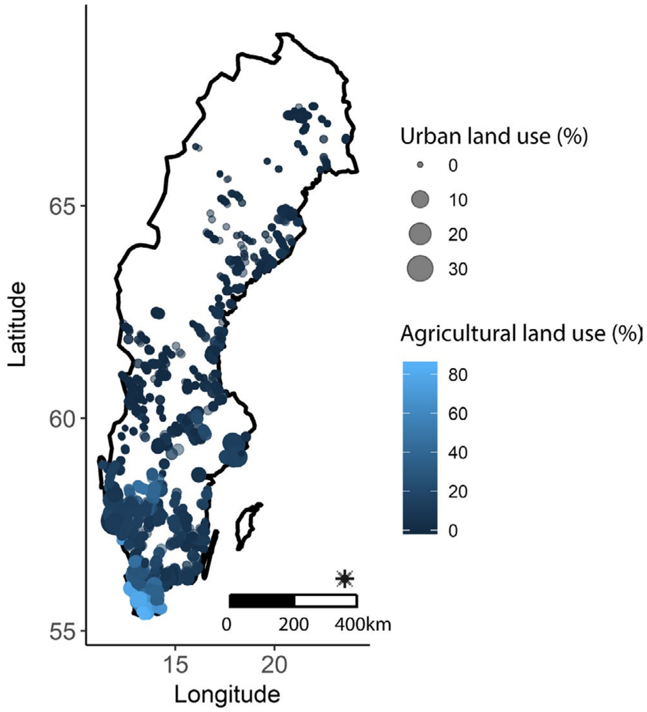

FIGURE 4 Map of Sweden showing agricultural land use as colour of the dots and urban land use as size of the dots

several times a day. To pinpoint the exact mechanisms behind the observed patterns is, however, not an easy task, as river regulation affects trout density in manifold ways. Loss of connectivity can prevent migrating populations from reaching upstream areas, while long-lasting or permanent flow reduction can reduce habitat availability downstream, possibly below the critical size for brown trout population survival (Törnblom et al., 2017). Also, hydropeaking produces large and rapid shifts in flow, which can results in stranded fish along the shores (Hunter, 1992) and dewatered spawning areas when flow is abruptly reduced (Young et al., 2011), and flushing of fish juveniles and eggs downstream when the flow is abruptly increased (Saltveit et al., 1995). Many of these effects could be exacerbated by a warmer climate, as suggested by our findings. Higher temperature could hence lead to longer periods of desiccation in the by-passed river channels downstream of hydropower reservoirs (Poole & Berman, 2001; Renöfält et al., 2010; Vander Vorste et al., 2020), diminished access to thermal refugia (Fullerton et al., 2018), reduced oxygen concentration in the hyporheic zone, which will affect both trout reproduction as well as invertebrates communities (Calles et al., 2007), and increased water temperatures caused by the release of warm surface waters from hydropower reservoirs and small dams (Lessard & Hayes, 2003; Zaidel et al., 2021). Also, a warmer climate can favour the arrival of invasive species, potentially exacerbating predation and competition on brown trout populations (Daufresne & Boët, 2007; Dibble et al., 2020; Wenger et al., 2011).

Although the effects of flow alteration on stream habitat and biota caused by hydropower dams have been extensively investigated (Bunn & Arthington, 2002; Poff et al., 1997), effects on fish populations are more elusive. For example, a recent meta-analysis could not detect any significant effects of flow regulation on fish density, possibly due to the paucity of studies available (Sabater et al., 2018). Another reason could be that researchers have overlooked the potential interactions between stressors. In our analysis, total reservoir storage volume showed a positive main effect on trout abundance, which was caused by few replicates in catchments with intense river regulation, where relatively high trout abundance was found. This would point to the wrong conclusions if interactive effects were not considered and supports the importance of adopting a multiple stressor framework when assessing environmental impacts. A recent modelling study has found that future (warmer) temperatures, together with changes in water storage, may favour the expansion of warm-water non-native species at the expenses of native species, as some parts of the river basin get warmer (Dibble et al., 2020). Another study has shown that river regulation for hydropower interacts with local anthropogenic stressors, such as loss of connectivity and riparian degradation, to affect fish community diversity and composition in bypassed reaches downstream of dams (Göthe et al., 2019). The authors show that, when the water flow is reduced, brown trout is replaced by fish species with opportunistic traits (e.g. omnivory, high fecundity, short life span, and small size), such as European perch (*Perca fluviatilis* L.) and common roach (*Rutilus rutilus* L.). Although we did not find significant interactive effects of river regulation and land use change, our study brings novel empirical evidence that river regulation potentially interacts with increased temperatures to affect native fish populations. Together with others, we underline the importance of explicitly considering potential synergies of anthropogenic stressors in combination with climate change to assess human impacts on natural ecosystems and implement effective conservation and mitigation policies (Brook et al., 2008; Lemm et al., 2020; Staudt et al., 2013).

Climate change is predicted to worsen water stress in many regions of the world by altering thermal and hydrological regimes (Palmer et al., 2008). While we found that warmer summer temperature interacted with river regulation to negatively affect brown trout populations at a country-wide scale, we did not detect any clear effects of precipitation. This could be due to the fact that annual precipitation, the variable considered in the analyses, was too coarse to capture the occurrence of droughts and low flow events (Patrick et al., 2019; Truchy et al., 2020). In Sweden, increases in run-off are expected in the north, which will increase the potential for hydropower production, whereas run-off decreases are expected in the southern part of the country (Andréasson et al., 2004). At the same time, the demand for hydropower may grow with the efforts made by Sweden and many other countries of phasing-out fossil fuels (Green & Staffell, 2016; Zarfl et al., 2014). Within the EU, the new Directive on the promotion of the use of energy from renewable sources (European Commission, 2018) sets a binding target for the EU countries of at least 32% renewable energy in gross final energy consumption by 2030. In such a scenario, it could be essential to implement measures that can counteract cumulative effects of flow alteration and climate change; for example, the reintroduction of natural flooding patterns and environmental flows from hydropower reservoirs that mimic natural hydrological regimes, the restoration of riparian vegetation and lateral connectivity, and the increase in the amount of, and access to, thermal refugia (Myers et al., 2017; Palmer et al., 2008; Renöfält et al., 2010).

We found that brown trout in general benefitted from higher summer temperatures in the catchments with low flow regulation, which were present throughout the country. Our finding suggests that: first, natural flow regimes may help buffer potential negative effects of climate warming, especially in the south of Sweden where temperature are higher; and second, that moderate climate warming may not be deleterious on its own for brown trout in boreal regions. Previous studies have found that brown trout populations have declined with increasingly warmer climates in e.g. Spain (Almodóvar et al., 2012), New Zealand (Scott & Poynter, 1991); and Switzerland (Burkhardt-Holm et al., 2002), while a study conducted in Iceland showed a positive temperature-driven trend (O'Gorman et al., 2016). These different patterns may be due to the fact that growth of young stream-living brown trout occurs in the range of circa 3–19°C, with an optimum around 13°C (Elliott & Elliott, 2010; Elliott & Hurley, 2000), which means that climate warming may be especially critical at the southern edge of brown trout global geographic distribution, rather than in boreal regions. Hence, we expect the direction and magnitude of climate effects on trout abundance to vary between the northern cooler and southern warmer regions of Sweden, but also because of the effects of small-scale factors, e.g. types and integrity of riparian vegetation, amount of dead woody debris, and levels of groundwater input (Sandin & Johnson, 2004), and catchment-scale anthropogenic stressors, e.g. river regulation (this study). We should further note that in our study we did not look at variation in trout biomass and mean size. O'Gorman et al. (2016) found positive effects of higher temperatures in Icelandic streams on brown trout biomass and growth rate, but not on mean size, whereas a recent study in central Europe has shown that warming causes physiological stress that induces a diminished growth in brown trout, and possibly a faster development of pathogens (Borgwardt et al., 2020). For brown trout as well as other fish species, integrated responses to climate change that include multiple (fish) metrics and account for local and regional variation remain therefore a subject worth further investigation.

Our study showed combined negative effects of urban and agricultural land use on brown trout populations. Alteration of environmental conditions following land use change, such as increased sedimentation and algal production, contaminant pollution, deteriorated oxygen conditions, higher water temperatures due to the loss of riparian vegetation (Allan, 2004) can all negatively affect brown trout populations. Previous studies have shown that stream habitat conditions and biota respond nonlinearly to gradients of increasing anthropogenic land use, often supporting thresholds in the range of 10%–20% for urban land use, and of 30%–50% for agricultural land use (see references in Allan, 2004). These studies, however, did not consider interactive effects, which can reveal more complex responses to combined stressors (e.g. contrasting effects, conditionality), and lower threshold values than expected when considering only main effects. Trout abundance decreased with urban land use when agricultural land use was ≥20%, and decreased with agricultural land use when urban land use was >3%. These are relatively low values and should serve as warnings for managers working with land-use development plans. From a restoration perspective, measures that buffer the effects of agriculture and urban land use, such as reduction of nutrient levels, and stream and riparian restoration, may be highly effective rehabilitation strategies for the biota (Burdon et al., 2020; Mantyka-Pringle et al., 2016).

The positive effects on brown trout abundance of urban land use in catchments with little agriculture (≤10%), and of agricultural land use in catchments with fewer urban areas (≤3%) is in line with positive responses of primary producers and macroinvertebrates to moderate increases in nutrients, light, and water temperature at low anthropogenic land use intensity (Price et al., 2019; Quinn, 2000). However, we should note that in our dataset estimates of land use were given at the catchment scale and may deviate from local conditions at sites where brown trout were sampled. Hence, the observed patterns could reflect a *spatial legacy effect* of land use at catchment scale, which is caused for example by the transport of nutrients across the river network and which depends on the network structure (Helton et al., 2017). Negative responses of ecosystem variables to agricultural and urban land use may thus dominate at local scales (Kuemmerlen et al., 2019), but may be obscured by the fact that many of the sampled locations were located in areas with minimal human impacts. Finally, we also considered the role of confounding (i.e. collinear) factors, specifically, if higher agricultural and/or urban land use at lower latitudes (or altitudes) could explain the patterns observed. We rejected this hypothesis as, first, at lower latitudes or altitudes the full ranges from high to low values of agricultural and urban land use were well covered, and second, such a correlation would not explain the interactive effects of agricultural and urban land use on trout abundance. However, given that we had relatively fewer samples with relatively high urban land use, we cannot exclude that a bias might have been introduced by an increase in trout abundance following more frequent restoration measures nearby urban areas.

Our study highlights a strong relationship between trout abundance and stream identity. The random factors stream and catchment explained most of the variation, as indicated by the high conditional r^2 (i.e. 0.82). The marginal r^2 was 0.16 in the *full model*, which was 4 and 9 units higher compared to the r^2 of the *additive model* and the r^2 of the *local habitat model*. The significance of the stressors and their interactions is supported by the large (>300 units) differences in AIC scores between the models, yet our predictors explained a relatively small part of the overall variation in trout abundance. This could be due to missing covariates describing local habitat differences and/or poor estimates of existing ones (e.g. river regulation and land use variables were estimated at catchment scales and may not be representative of local conditions). Riverine ecosystems are typically characterised by high small-scale habitat heterogeneity and frequent stochastic processes (Thorp et al., 2006). Our dataset spanned the whole of Sweden and hence included very different environmental conditions, and we acknowledge that we may have missed relevant factors explaining local variation. For example, the extent and diversity of riparian vegetation, which were not assessed in our study, have extensive effects on ecosystem functioning (Burdon et al., 2020). Riparian vegetation can benefit salmonids in several ways, e.g. by reducing summer water temperatures (Broadmeadow et al., 2011; Johnson & Almlöf, 2016; Justice et al., 2017) and fine sediment loads (Stanford et al., 2020), by increasing macroinvertebrate abundance (Dala-Corte et al., 2020), and by mitigating adverse impacts of agricultural diffuse pollution (Turunen et al., 2021). Also, we lacked data on oxygen availability and toxic compounds, which can interact with other stressors and jeopardise the health of fish populations and freshwater ecosystems at both small and large spatial scales (Lemm et al., 2020; Malaj et al., 2014). Hence, given the large variation between streams, our results should be interpreted with caution when applied at local scales. In this respect, we echo the conclusions of Birk et al., (2020), saying that rivers exhibit complex and site-specific stressor interactions due to their large habitat heterogeneity and, possibly, to the exposure to several (here unmeasured) hydrological and morphological stressors. Our findings of interactive effects between river regulation, land use, and climate on brown trout populations should therefore be regarded as a warning about potentially meaningful stressor interactions. However, we advise for bespoke management actions stemming from sound knowledge on local habitat conditions, target populations, and river connectivity. Last but not least, an improved understanding of the mechanisms through which multiple stressors impact riverine ecosystems is fundamental to identify the causal links between drivers of changes and responses, and thus design effective management and restoration actions in the face of current and future threats.

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DATA AVAILABILITY STATEMENT

All data are available at the SERS SLU repository (https://www.slu.se/institutioner/akvatiska-resurser/databaser/elfiskeregistret/), and at the SMHI Vattenwebb (https://www.smhi.se/data/hydrologi/vattenwebb, https://vattenwebb.smhi.se/modelarea/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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