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Food-web energy fluxes, energy transfer efficiency, and diversity respond distinctively to pollution and water diversion in rivers

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Abstract

1. Water diversion and pollution are two pervasive stressors for river ecosystems that often co-occur. The individual effects of both stressors on river communities and energy transfer across the food webs are well described; however, how they interact remains unknown. We hypothesised that low-to-moderate nutrient pollution gradient would cause a mild increase in invertebrate driven herbivory and water diversion a strong reduction in detritivory, whereas their joint effect would reduce invertebrate abundance and diversity, as well as total energy fluxes (from basal resources to invertebrates and fish). We also expected a shift in body size spectra slope with increased energy transfer between trophic levels with moderate pollution, but not with water diversion.

2. To test these hypotheses, we selected four rivers across a range of nutrient pollution levels (a proxy of water quality) subject to similar water diversion schemes and compared food webs upstream and downstream of their diversion weirs.

3. Both stressors changed the availability of basal food resources. Nutrient pollution induced changes in the green food web (i.e., biofilm-based) by enhancing biofilm stocks, whereas water diversion affected the brown food web (i.e., detritus-based) by decreasing stocks of detritus.

4. The propagation of the effects to higher trophic levels differed with each stressor: pollution increased the homogeneity of community within the reach, whereas water diversion made communities more heterogeneous. Moreover, pollution induced changes within omnivores, increasing herbivory and carnivory, whereas diversion reduced the total energy fluxes through a decrease in detritivory, especially with pollution.

5. Although most of the variables studied seemed to be more sensitive to water diversion, pollution often accentuated the response, being the interaction between both stressors more explanatory than any of the two stressors on its own.

6. The effects of water diversion on diversity and energy flow through food webs are more detrimental to moderately polluted rivers than to systems with high quality water.

7. We show that the use of tools merging knowledge on trophic relationships among species and their metabolic requirements enables disturbances to be detected that would otherwise go unnoticed.

1 | INTRODUCTION

The increase of human population and the intensification of their activities have raised water demand (Ripple et al., 2017). In Europe, for instance, the impact of human activities on rivers is severe (Tockner et al., 2021), as, in order to satisfy the demand of water for agriculture, industry and domestic use (Albert et al., 2021), rivers are increasingly being regulated by barriers that store and divert water flows (Belletti et al., 2020). These structures have multiple effects on ecosystems. The barriers themselves disturb the dispersion of aquatic organisms across the fluvial network (Jones et al., 2020), which affects community structure (Munasinghe et al., 2021). Additionally, water diversion driven by these infrastructures can modify environmental conditions through narrowing wetted channel, reducing flow velocity and water depth and altering water physico-chemistry (Dewson et al., 2007a), which leads to changes in community abundance and diversity (Munasinghe et al., 2021). Water diversion can also alter the availability of basal resources (Power et al., 2013), for instance reducing the stock of coarse detritus, which is retained in the impoundments (Schmutz & Moog, 2018) and transported through diversion canals (Arroita et al., 2015). This might have special importance in forested rivers, where detritus is the main energy source (Zhang et al., 2019) since primary production is usually limited by canopy cover (Bernhardt et al., 2018) and nutrients (Elser et al., 2007). Thus, here, the main source of energy and nutrients is detrital organic matter colonised by microbes (Marks, 2019), which means that the brown food web (i.e. detritus-based) dominates over the green food web (i.e. biofilm-based).

River ecosystems often face multiple stressors simultaneously (Sabater et al., 2018), which may interact in contrasting ways (Jackson et al., 2016; Orr et al., 2020) depending on the interaction strength and the direction of the interaction (Piggott et al., 2015). One of the most pervasive stressors in freshwater ecosystems is pollution (Reid et al., 2019), which most often manifests interactively with other stressors (Dolédec et al., 2021), degrading further the water quality and ecosystem status (Lemm et al., 2021). Chemical pollution might have contrasting effects on ecosystems depending on the composition of pollutants (Flores et al., 2014), the level of dilution in the receiving water bodies (Carey & Migliaccio, 2009) and the target organisms (Artigas et al., 2014). In addition, depending on

their individual effects on biota, some compounds are simply toxic (Patel et al., 2020; Vasilachi et al., 2021), whereas others, such as nutrients, subsidise biological activity at low concentrations, but reduce it at high concentrations (Carey & Migliaccio, 2009). Algae, in particular, increase in abundance at moderate concentrations of nutrients (Keck & Lepori, 2012), which can have important consequences on food webs, as these organisms offer higher-quality food than detritus (Brett et al., 2017).

In addition to altering the food basis to invertebrate production, water diversion and pollution can directly alter the composition and structure of invertebrate communities (Munasinghe et al., 2021) and hence they may impact ecosystem functioning by changing food webs (de Guzman et al., 2021). Water diversion and pollution may also modify organismal body size, a predictor of the position species occupy in the food web (Woodward et al., 2005). Some mechanisms responsible for changes in body size include increases of pollution tolerant taxa (Peralta-Maraver et al., 2019) or decreases in abundance of large organisms due to water abstraction (Boddy et al., 2020). These changes can modify the slope of the relationship between abundance and body mass (i.e., size spectrum), which can be interpreted as a change in the efficiency of energy transfer along food webs (Woodward et al., 2005). Additionally, alterations in diversity and composition of food webs, may also lead to changes in energy fluxes along food webs, leading to alterations in ecosystem functions such as herbivory, detritivory, or carnivory (Barnes et al., 2018).

Isolated effects of water diversion and pollution on food web structure have been previously documented (e.g. Boddy et al., 2020; Mor et al., 2019). However, there are few studies assessing the combined effects of these two stressors on the organisation of food webs and on ecosystem functioning. In a previous study, when addressing the interactive effects of these stressors we observed that water diversion and pollution affected food webs through bottom-up mechanisms (i.e., resource supply controlled) inducing alterations in the brown and in the green food web (de Guzman et al., 2021). However, de Guzman et al.'s (2021) study, based on stable isotopic analyses, was conducted with a subset of the food webs comprising only about 20% of the total taxa in the original communities. This simplification of the food webs disregards the diversity and the trophic links between all the different taxa, thus ignoring emergent properties that show up when studying the entire complexity of food webs

(de Jonge et al., 2019). In the current study, we address the effects of these stressors with emphasis on the structure of food webs and on bioenergetics. We focus on different diversity metrics at various spatial scales to detect structural responses to these stressors and their interaction. Besides, we create an updated matrix of trophic links from available literature and own findings and join it with the current knowledge of the metabolic requirements of species using a recent modelling approach (Barnes et al., 2018; Gauzens et al., 2019; Jochum et al., 2021), we estimate the effects of these stressors on the energy fluxes of food webs. Additionally, we use individual body size information to infer alterations of energy transfer efficiency in the food webs.

Thus, the aim of our study is to assess the isolated and interactive effects of water diversion and water pollution on the structure of communities and on the patterns of energy transfer across food webs. We hypothesise that (Figure 1):

1. Low-to-moderate nutrient pollution will reduce α diversity through a loss of pollution-sensitive taxa, but will subsidise biofilm and invertebrate density, especially herbivores, resulting in a global increase in energy flux and the abundance of larger individuals, which will create shallower slopes in size spectra.
2. Diversion linked to weirs will reduce the amount of coarse detritus downstream, which will in turn reduce invertebrate density, detritivory, and energy fluxes through food webs. Size spectra slopes will remain unaltered by weirs due to the unchanged resource quality but the intercept will decrease linked to the reduced amount of resources and densities.
3. Water diversion will override the effects of pollution, as diversion strongly reduces detritus (i.e. the main food resource) downstream, while pollution will cause a moderate increase in biofilm, leading to a decrease in invertebrate density and energy fluxes and a shift in size spectra with larger individuals and reduced abundances.

2 | MATERIALS AND METHODS

2.1 | Sampling design and study sites

We selected four rivers within the northern Iberian Peninsula (Urumea, Leitzaran, Kadagua and Deba; Table S1, Figure S1), which differed in their ecological status and water quality (URA, 2017a, 2017b). Water quality ranged from high to moderate according to the local water monitoring agency, who regularly measures the levels of nutrients, heavy metals, and other organic chemical compounds in water (URA, 2017b), and none of the selected rivers showed a poor ecological status (URA, 2017a). The cover and maturity of the riparian forests also differed between rivers (higher in Urumea and Leitzaran than in Kadagua and Deba), which was inversely related to the degree of urbanisation (Table S1). The four rivers had a similar water diversion scheme, consisting of a weir (3–6.5 m high,

FIGURE 1 Conceptual figure of the proposed hypotheses: H1 refers to the hypothesis regarding pollution, H2 refers to water diversion, and H3 refers to the interaction between both stressors. Control reach and diverted reach are the sampling sites above and below the weirs. Low pollution and moderate pollution is a simplification of the pollution gradient. The brown and green circles represent detritus and biofilm in each food web, primary consumers are represented in yellow, omnivores in pink and carnivores in red. Arrows between nodes indicate the link and the thickness represents the strength of the relationship. The slope in body mass–abundance size spectra from Control–Low pollution site is redrawn in a lighter colour in the other biplots as reference.
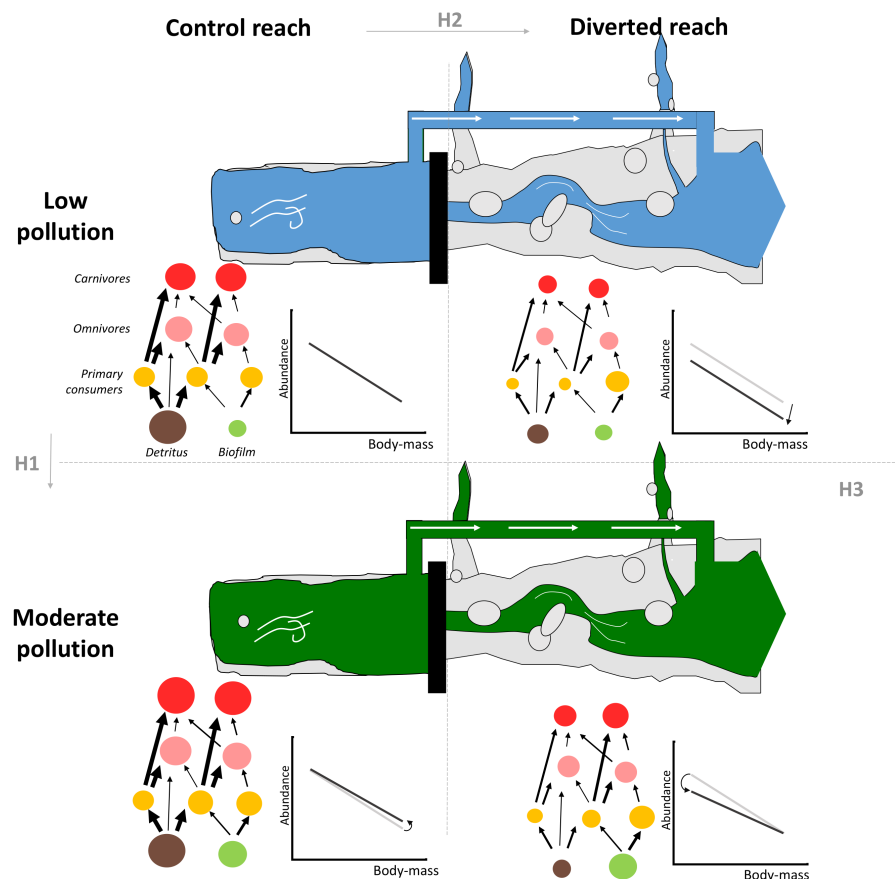
Figure S1) and a canal that can divert up to 90% of the monthly average river flow to hydropower plants. We defined two 100m-long reaches in each river: a control reach upstream from the stagnant water retained by the weir and a diverted reach in the bypassed section downstream from the weir, but below the direct effect of the water spillage.

2.2 | Water and site characteristics

Water characteristics did not differ between reaches (Table S2), although they differed among rivers, establishing a gradient of pollution. According to this gradient (represented in our study by the total dissolved nitrogen [TDN] gradient, which ranged from 0.85 to 1.94 mg N/L), Urumea was the least polluted river, followed by Leitzaran and Kadagua, with Deba being the most polluted. The gradient correlated with the concentrations of most solutes, pH, conductivity, and temperature (Table S2).

2.3 | Sampling and sampling processing

The food webs of the eight study sites (four rivers × two reaches) were sampled during late spring of 2018. The largest flow differences between upstream and downstream reaches from weirs occur in this period of the year because discharge tends to baseflow but diversion canals are still active. In summer, further reductions of precipitation and river discharges forces hydropower to stop to maintain ecological flows.

2.3.1 | Biofilm, benthic organic matter, and macroinvertebrates

Autotrophic biofilm (hereafter biofilm) biomass was estimated by means of a field fluorometer (Bentho Torch, bbe-Moldaenke, Germany) on 18 cobbles per reach. Additionally, we collected nine benthic Surber samples (surface of 0.09 m², mesh of 0.5 mm) from random points in each reach. For each sample, we gathered the organic matter retained on an 8-mm sieve to obtain the ash free dry mass (by drying at 70°C for 72 hr and ashing the material at 500°C for 8 hr). Macroinvertebrates collected in a 0.5-mm sieve were preserved in 96% ethanol. In the laboratory we sorted, identified to the lowest possible taxonomic level following Tachet et al., 2010 (mostly to genus-level except for some Diptera identified to subfamily level, Heptageniidae to family level and Annelida to subclass level), and counted them to obtain population densities. In addition, we measured the body length of up to 30 randomly selected individuals of each taxon in every sample (except for oligochaetes, planarians, and leeches, which were not measured) with a binocular microscope (Leica M165FC, Wetzlar, Germany) equipped with a Leica DFC310FX camera using Leica Application suite V4 software program (LAS V4.1). Total body

length was considered as the distance from the anterior part of the head to the posterior part of the last abdominal segment excluding antennae and cerci. For gastropods, we measured the maximum length of the shell (Meyer, 1989), and for crustaceans of the genus *Echinogammarus*, the dorsal length of the first abdominal segment to posteriorly obtain body length (Flores et al., 2014). We did not correct length measurements for potential effects of storage in ethanol. We obtained individual body mass (mg dry mass) using published length–mass relationships (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Burgherr & Meyer, 1997; Larrañaga et al., 2009; Meyer, 1989; Stoffels et al., 2003).

2.3.2 | Fish

We conducted fish samplings along the reaches (sampled surface area from 385.3 to 1731.6 m²) by depletion electrofishing with a backpack-electrofishing unit (Hans Grassl IG2002/D30, Schönau am Königssee, Germany). Stop-nets were set at the upstream and downstream ends of the reaches and multiple runs were made until the depletion of the captures (Lobón-Cerviá, 1991). All fish were anaesthetised with MS-222, identified, counted and weighed to the nearest g. We converted wet mass into dry mass through conversion factors published in www.fishbase.se. The study was approved by the Ethics Committee for Animal Welfare of the University of the Basque Country (reference: CEBA M20/2016/135).

2.3.3 | Invertebrate diversity

We estimated invertebrate taxa diversity through Hill numbers (i.e. number equivalent, ^qD [Jost, 2006]) with the entropart package for R (Marcon & Hérault, 2015). We used Hill numbers of order 0 (^0D, species richness, which is insensitive to the abundance of individuals of each taxon, highlighting the response of rare taxa), 1 (^1D, the exponential of Shannon's entropy, which weighs each taxon according to its log-transformed abundance), and 2 (^2D, inverse of Simpson concentration, which weighs each taxon according to its abundance, highlighting the response of dominant taxa) (Jost, 2006). We computed α diversity per sample in each reach for the three Hill number orders and β diversity among samples within each reach for orders 0 and 1 of diversity measures. Beta diversity (D_β) for the diversity orders (q) 0 and 1 was transformed from β entropy (H_β) considering also α entropy (H_α) as described in Marcon and Hérault (2015):

$$^qD_\beta = e_q^{\frac{^qH_\beta}{1-(q-1)^qH_\alpha}} \tag{1}$$

2.3.4 | Food webs and energy fluxes

We constructed local food webs (nine replicates per river and reach, one per Surber collected) joining information of every resource,

benthic invertebrate and fish captured. For every invertebrate taxon in each sample, we calculated mean body mass from the individual masses measured and estimated the total biomass. In the case of fish, we estimated the total biomass of each species at each sample ($0.09\,m^2$ Surber sample) assuming a homogeneous distribution of fish along the reach. Additionally, we estimated total metabolic rate for each invertebrate and fish taxon based on individual metabolic rate, calculated for each individual using an allometric equation derived from Gillooly et al. (2002):

$$X = \exp\left((a \cdot \ln(BM) + x_0) + E/kT\right) \qquad (2)$$

where X is the metabolic rate (in watts, W), a is the allometric exponent (0.71), BM is the body mass (g), E is the activation energy (0.63 eV), k is the Boltzmann's constant ($8.62 \cdot 10^{-5}$ eV/K), T is the temperature (K), and xo is a normalisation factor (17.17 for invertebrates and 18.47 for fish) (Brown et al., 2004). We gathered mean daily T of the 190 days before the sampling date in each reach by means of water level dataloggers (Solinst Levelogger Edge 3001; Solinst Canada Ltd., Georgetown, USA). In the case of biofilm, we used the average biomass per cobble surface to estimate total biomass in each sample. Fine detritus was a scarce basal resource with a heterogeneous distribution along the reach and was not quantified; instead, it was equalled to the mean biofilm biomass values.

To estimate energy fluxes between nodes of local food webs, we used an adapted food-web energetics approach (Barnes et al., 2018; Gauzens et al., 2019; Jochum et al., 2021) by means of the *fluxweb* package (Gauzens et al., 2019). This approach uses allometric scaling laws to quantify metabolic rates (Brown et al., 2004). The model assumes a steady-state system, where the energetic losses of nodes in each food web, estimated by metabolic rate of consumer j (X_j) and predation on consumer j by higher trophic levels (k), need to be balanced by the energetic gains defined through resource consumption and assimilation (Barnes et al., 2018; O'Neill, 1969). The flux of energy $F_{i,j}$ from resource i to consumer j was calculated as:

$$\sum_i \varepsilon_{ij}F_{ij} = X_j + \sum_k W_{jk}F_k \qquad (3)$$

where ε_{ij} is the efficiency in which consumer j assimilates the energy consumed from resource i. Energy fluxes to each consumer are defined as $F_{ij} = W_{ij}F_j$, where F_j is the sum of all ingoing fluxes to consumer j and W_{ij} is the proportion of F_j obtained from resource/prey i, after scaling consumer preferences w_{ij} to the biomass (B) of the different resources/preys as:

$$W_{ij} = \frac{w_{ij}B_i}{\sum_k w_{kj}B_k}. \qquad (4)$$

For that, an adjacency matrix with possible trophic links among all taxa present in our study and feeding preferences for each possible food resource was created based on the predator–prey links observed in the literature (Gray et al., 2015; Tachet et al., 2010) and on

our own gut content findings from previous experiments (See supplementary dataset at figshare). Three trophic groups were considered based on feeding preferences: primary consumers (feeding on basal food resources), omnivores (feeding on basal food resources and preys), and carnivores (feeding on preys). For carnivore taxa we assumed that preferences were equally distributed among prey species. For omnivore invertebrates and primary consumers, w values were given following preferences in Tachet et al. (2010), where traits related to consumed food are quantified using affinity scores between 0 and 5. For omnivores, affinity scores related to predation were equally distributed among prey species. For cannibalistic species, we set the preference for cannibalism to 0.01 in the adjacency matrix to minimise the amount of energy a consumer could ingest from its own biomass. Assimilation efficiencies (ε) for the consumption of food resources were calculated following Lang et al. (2017):

$$\varepsilon = e^{\varepsilon'} \cdot e^{E \frac{T-T0}{kTT0}} / \left(1 + \left(e^{\varepsilon'} \cdot e^{E \frac{T-T0}{kTT0}}\right)\right) \qquad (5)$$

where ε' is a normalisation constant for assimilation efficiency (−1.670 for detritivory, 0.179 for herbivory and 2.260 for carnivory), E is the activation energy (0.164 eV), k is the Boltzmann's constant and T is the temperature (K) and T_0 the temperature normalised to 20°C.

We calculated whole food-web energy flux as the sum of energy fluxes within each local food web (each Surber sample). Additionally, we quantified three consumption pathways summing the outgoing fluxes from each food resource: herbivory (consumption of biofilm), detritivory (consumption of coarse and fine detritus), and carnivory (consumption of animals) in the entire food web and within each trophic group (primary consumers, omnivores, and carnivores) of each local food web.

2.3.5 | Body size spectra

We constructed size spectra for the entire community (including invertebrate and fish), and for primary consumers, omnivores, and carnivores, separately. We used body mass of the measured (invertebrates) and weighed (fish) organisms. Since the log-transformed length values followed a normal distribution, we obtained body mass of the remaining non-measured invertebrates by means of the *truncnorm* package (Mersmann et al., 2018), based on the mean, standard deviation, minimum, and maximum values of each taxon in each sample. We used animals with body mass higher than 0.1 mg to construct the size spectrum, since organisms with lower weight are assumed to be underrepresented as they can be washed through the 0.5-mm mesh sieves (Gruenert et al., 2007). We divided the total range of body mass ($\log_{10}BM$) values into seven logarithmic bins of the same width and regressed density of organisms (N; $\log_{10}N$) against the centre of the bin (White et al., 2008). The creation of these bins allowed using body mass as a covariate in the analyses. The number of bins influences the estimated regression coefficients, so the same number of bins was used in each community to allow the comparison of slopes and intercepts between reaches.

2.4 | Data analyses

We conducted all the statistical and data analyses using R software, version 3.6.0. (R Core Team, 2019). We performed linear models by including reach as factor, pollution (TDN) as covariate and their interaction as sources of variation. Some variables were log-transformed to fulfil the requirements for linear models. We avoided non-linear models as we considered four values in the covariate (pollution) not to be enough for reliable discrimination between linear and non-linear curve fitting (Jenkins & Quintana-Ascencio, 2020). We repeated all the analysis considering River as factor instead of pollution as covariate to test for pairwise differences between reaches within each river through post hoc analysis using *t*-statistic (Multcomp package, Hothorn et al., 2008). For details regarding the collected data and the code used, see de Guzman et al. (2023).

3 | RESULTS

3.1 | Pollution increased basal food resources, but not the total energy flux along the food web

Moderate pollution increased biofilm biomass along the pollution gradient ($F_{1,140} = 26.11$, $p < 0.001$; Figure 2, Table 1), most clearly at low pollution (low TDN). Coarse detritus also increased with pollution, although not as clearly as biofilm ($F_{1,68} = 5.51$, $p = 0.022$; Figure 2, Table 1). Taxon richness, Shannon diversity, and Simpson diversity at α scale and invertebrate density were not affected by pollution (Figure 3, Table 1); however, β diversity for taxon richness and Shannon diversity decreased with it ($F_{1,284} = 23.64$, $p < 0.001$ and $F_{1,284} = 29.6$, $p < 0.001$ respectively; Figure 3, Table 1). Mean body mass of primary consumers and omnivores increased with pollution ($F_{1,888} = 4.35$, $p = 0.037$ and $F_{1,727} = 5.74$, $p = 0.017$; Figure S2, Table S3), as well as estimated metabolic rate and biomass of omnivores ($F_{1,727} = 18.73$, $p < 0.001$ and $F_{1,727} = 13.32$, $p < 0.001$) and metabolic rate of carnivores ($F_{1,328} = 4.7$, $p = 0.031$). Neither total energy fluxes along food webs nor

any consumption pathway varied with pollution (Figure 4, Table 1); however, herbivory and carnivory driven by omnivores increased along the pollution gradient ($F_{1,68} = 12.47$, $p = 0.001$ and $F_{1,68} = 6.57$, $p = 0.013$; Figure S3, Table S3). The size spectra of the entire community and of each trophic group did not change with pollution (Figure 5, Table 2).

3.2 | Water diversion effects on community structure and energy fluxes were exacerbated with pollution

Water diversion had important effects at the base of the food web as it reduced coarse detritus stock by a 26.1% on average from control to diverted river sections ($F_{1,68} = 7.69$, $p = 0.007$; Figure 2, Table 1). Biofilm biomass was unaffected by diversion ($F_{1,140} = 0.1$, $p = 0.747$, Figure 2, Table 1). However, interactive effects between both stressors were not observed for the stock of basal food resources (Figure 2, Table 1).

In addition, diversion itself did not affect α diversity, in terms of richness, Shannon or Simpson diversity (Figure 3). Together with pollution, however, diversion increased taxon richness in control reaches along the gradient of pollution, whereas it showed a significant decrease in diverted reaches ($F_{1,68} = 10.25$, $p = 0.002$ and $F_{1,68} = 25.51$, $p < 0.001$; Figure 3, Table 1), a trend mainly created by the most polluted river. By contrast, β diversity for taxon richness was higher in diverted than in control reaches ($F_{1,284} = 37.05$, $p < 0.001$; Figure 3, Table 1), suggesting that diversion increased the heterogeneity of community composition across samples. Moreover, the overall effect of diversion on invertebrate density was negative ($F_{1,68} = 18.49$, $p < 0.001$; Figure 3, Table 1), mainly due to the strong effect in the most polluted river ($F_{1,68} = 25.51$, $p < 0.001$).

Regarding fish, assemblage was the same in upstream and downstream reaches in each river, densities in diverted reaches were higher than in control ones in three out of four rivers, but biomass and average body mass were larger in two out of four rivers (Table S4). Water diversion did not affect mean body mass of none
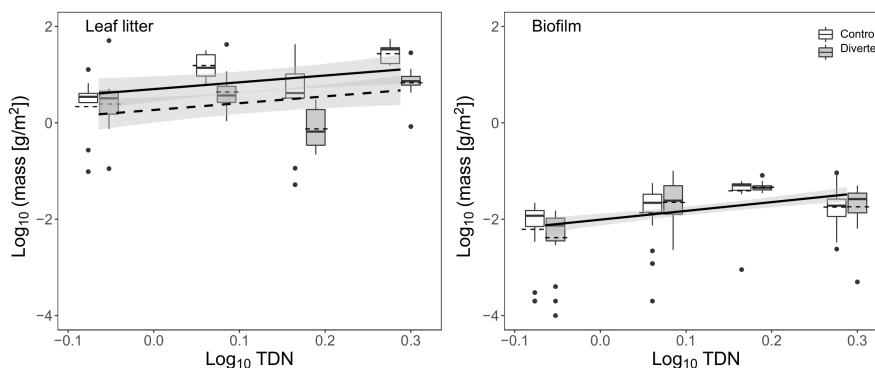

FIGURE 2 Resource abundance in the studied reaches (white for control; grey for diverted): leaf litter and biofilm represented along the pollution gradient. The box plots show the median, the interquartile range and the tails of the distribution. Dashed lines represent the mean value. A single black regression line is represented when only the total dissolved nitrogen (TDN) gradient was significant and black regression lines (solid line for control; dashed line for diverted) are drawn when the effect of the diversion differed. Bands around the line represent the 95% confidence interval.

TABLE 1 Linear model results comparing stock of basal resources, invertebrate density and diversity, and energy fluxes throughout food webs between control and diverted reaches along the pollution gradient (Log$_{10}$TDN).

	Log$_{10}$TDN			Reach			Log$_{10}$TDN:Reach		
	F	p	Coeff.	F	p	Coeff.	F	p	Coeff.
Stock of basal resources									
Coarse detritus[†]	5.51	**0.022**	2.33	7.69	**0.007**	−0.43	2.36	0.13	
Biofilm[†]	26.11	**<0.001**	1.62	0.10	0.747		0.31	0.577	
Invertebrate community descriptors									
Taxon richness									
Alpha	0.39	0.533		2.73	0.103		10.25	**0.002**	−24.46
Beta	23.64	**<0.001**	−0.20	37.05	**<0.001**	0.05	3.22	0.074	
Shannon diversity									
Alpha	0.01	0.939		0.01	0.937		0.63	0.429	
Beta	29.60	**<0.001**	−0.26	2.53	0.113		2.04	0.154	
Simpson diversity									
Alpha	0.0002	0.989		0.06	0.805		0.69	0.408	
Invertebrate density[†]	2.99	0.088		18.49	**<0.001**	−0.25	25.51	**<0.001**	−2.29
Energy fluxes									
Total fluxes[†]	0.14	0.714		6.02	**0.017**	−0.45	12.73	**<0.001**	−4.97
Herbivory[†]	0.39	0.533		0.30	0.587		4.24	**0.043**	−3.43
Detritivory[†]	0.11	0.739		6.86	**0.011**	−0.46	13.88	**<0.001**	−5.03
Carnivory[†]	0.94	0.335		0.05	0.822		9.97	**0.002**	−5.93

Note: '†' indicate log$_{10}$ transformed variables. Bold values indicate statistical significance ($p < 0.05$). Coefficients are shown for significant responses and consider pollution gradient (Log$_{10}$TDN) and Control reaches as reference in all cases.

Abbreviation: TDN, total dissolved nitrogen.

of the three trophic groups (Figure S2, Table S3), but with increasing pollution, mean body mass of primary consumers decreased in diverted reaches ($F_{1,888} = 5.29$, $p = 0.022$; Figure S2, Table S3). Diversion decreased estimated total metabolic rate of every trophic group (Table S3, Figure S2), and together with pollution, it was reduced for primary consumers, while it increased for carnivores ($F_{1,888} = 5.93$, $p = 0.015$ and $F_{1,328} = 9.08$, $p = 0.003$ respectively, Figure S2, Table S3). In addition, total biomass of carnivores increased with diversion ($F_{1,328} = 6.56$, $p = 0.011$, Figure S2, Table S3) and it decreased in diverted reaches with increasing pollution for primary consumers ($F_{1,888} = 15.96$, $p < 0.001$).

Regarding energy fluxes, diversion generally decreased total fluxes and detritivory ($F_{1,68} = 6.02$, $p = 0.017$ and $F_{1,68} = 6.86$, $p = 0.011$ respectively; Figure 4, Table 1), mainly because of the strong effect in the most polluted river ($F_{1,68} = 12.73$, $p < 0.001$ and $F_{1,68} = 13.88$, $p < 0.001$ respectively; Figure 4, Table 1). The decrease in detritivory with diversion was a consequence of the decrease in detritivory driven by primary consumers ($F_{1,68} = 8.70$, $p = 0.004$ Figure S3, Table S3). Additionally, interactive effects between pollution and diversion decreased detritivory in primary consumers and omnivores along the pollution gradient ($F_{1,68} = 17.35$, $p < 0.001$ and $F_{1,68} = 9.88$, $p = 0.002$ respectively; Figure S3, Table S3). Interactive effects of pollution and water diversion also decreased herbivory and carnivory ($F_{1,68} = 4.24$, $p = 0.043$ and $F_{1,68} = 9.97$, $p = 0.002$ respectively; Figure 4, Table 1). This was explained by the decrease in

herbivory driven by primary consumers and omnivores ($F_{1,68} = 5.07$, $p = 0.028$ and $F_{1,68} = 4.14$, $p = 0.046$ respectively; Figure S3, Table S3) and by carnivores ($F_{1,68} = 32.85$, $p < 0.001$, Figure S3, Table S3).

Finally, the energy transfer efficiency (slope of the size spectra) of the entire community or of the three trophic groups did not differ between reaches; not even with increasing pollution (Figure 5, Table 2). Nonetheless, diversion had an overall negative effect on the intercept of primary consumers ($F_{1,48} = 16.71$, $p < 0.001$; Figure 5, Table 2) again mainly due to the strong decrease in the most polluted river (Log$_{10}$TDN:Reach interaction: $F_{1,48} = 27.70$, $p < 0.001$, Table 2).

4 | DISCUSSION

Water diversion reduced the abundance of detritus, whereas nutrient pollution promoted biofilm production. These changes at the base of the brown and green food webs propagated to higher trophic levels.

4.1 | Pollution increased the stock of basal food resources, but did not alter energy transfer

Biofilm biomass increased along our pollution gradient, as it tends to do with moderate nutrient concentrations (Ardón et al., 2021).
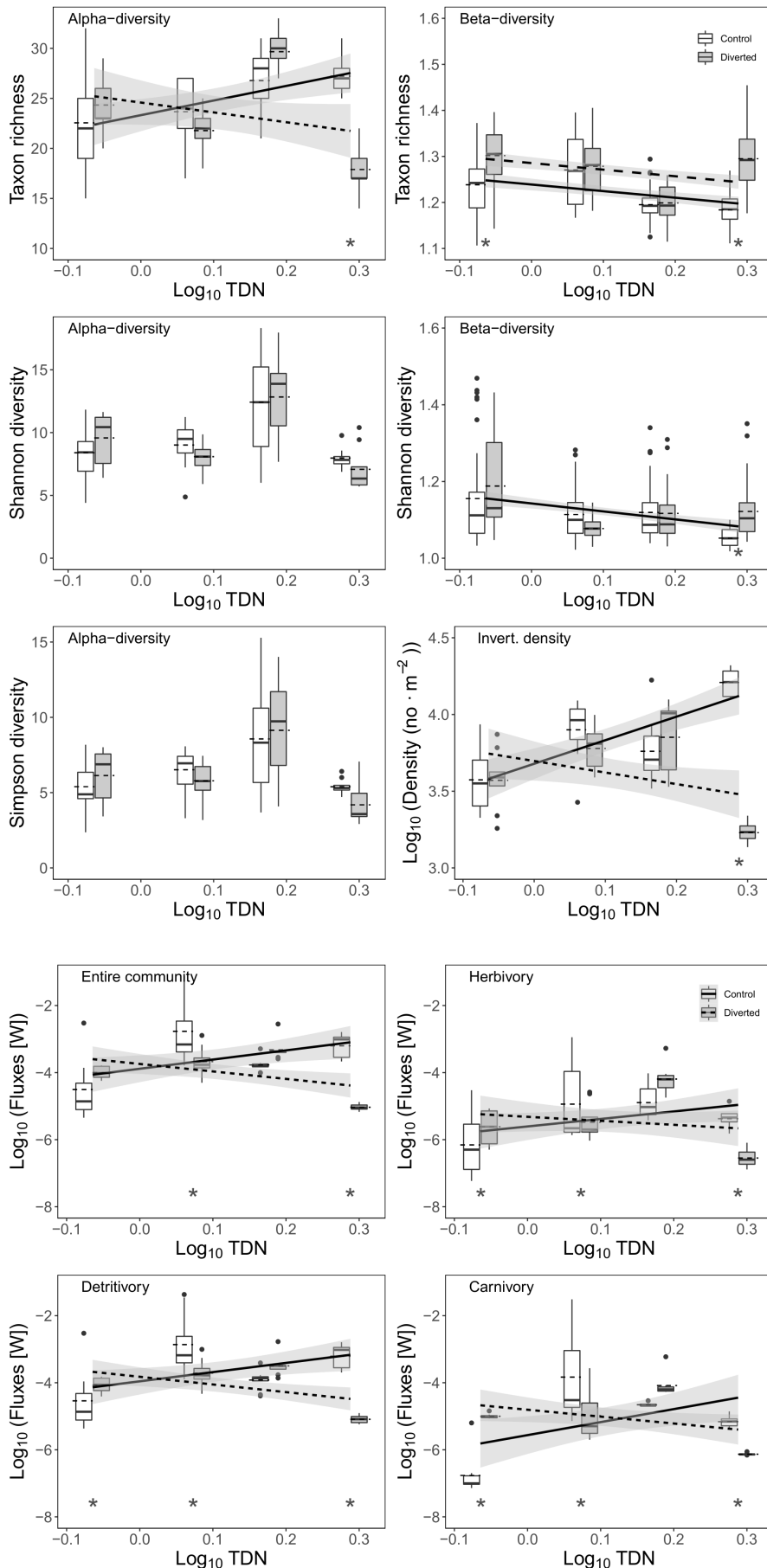
FIGURE 3 Diversity and density of macroinvertebrate assemblage in the studied reaches (white for control; grey for diverted): α and β diversity for taxon richness, α and β diversity for Shannon diversity, α diversity for Simpson diversity and density. The box plots show the median, the interquartile range and the tails of the distribution. Dashed lines represent the mean value. A single black regression line is represented when only the total dissolved nitrogen (TDN) gradient was significant and black regression lines (solid line for control; dashed line for diverted) are drawn when the effect of the diversion differed. Bands around the line represent the 95% confidence interval. Significant differences between the control and diverted reaches within each river are marked with an asterisk.

FIGURE 4 Energy fluxes of river food webs and functions in the studied reaches (white for control; grey for diverted): fluxes throughout the entire food web and herbivory-, detritivory-, and carnivory-related fluxes. The box plots show the median, the interquartile range and the tails of the distribution. Dashed lines represent the mean value. A single black regression line is represented when only the total dissolved nitrogen (TDN) gradient was significant and black regression lines (solid line for control; dashed line for diverted) are drawn when the effect of the diversion differed. Bands around the line represent the 95% confidence interval. Significant differences between the control and diverted reaches within each river are marked with an asterisk.

FIGURE 5 Size spectra for entire community, primary consumers, omnivores, and carnivores. Circles represent control reaches and squares diverted reaches. Regression lines are derived from the linear models. A single regression line is represented when only differences along body mass were significant and two regression lines (solid line for control; dashed line for diverted) are drawn when the effect of the diversion was significant. Note that the interaction pollution: reach was also significant in primary consumers, but only effect of diversion is shown.
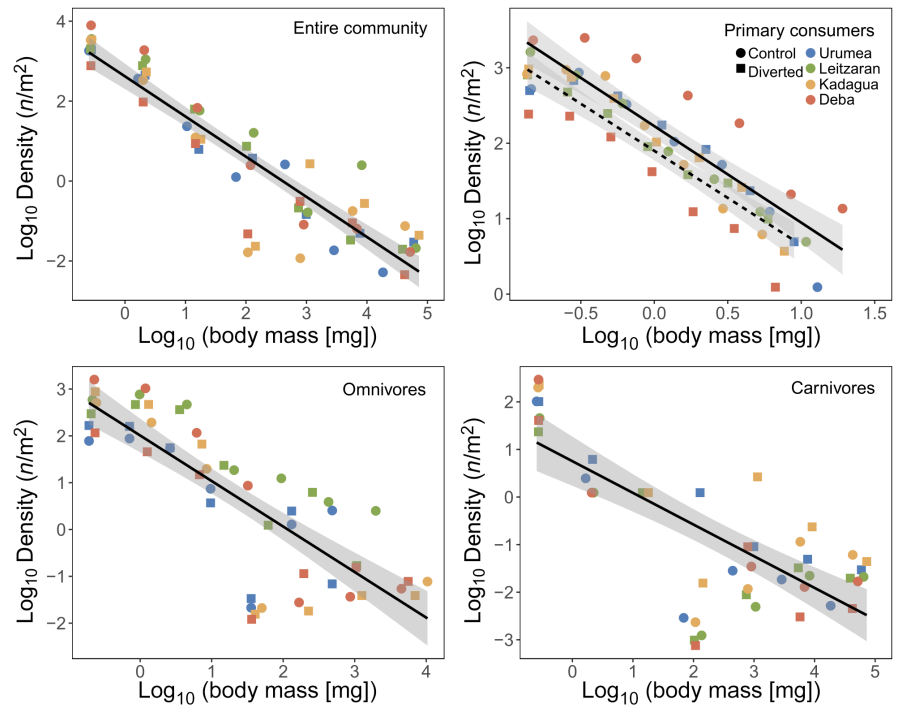
This result suggests that the beneficial effects of nutrients overrode the harmful effects of other compounds in our systems (Rosi et al., 2018). Although the relative abundance of biofilm (i.e. a high quality resource) over detritus did not increase along the pollution gradient, we expected an increase of the nutritional quality of both types of basal food resources as in previous studies (Evans-White & Halvorson, 2017; von Schiller et al., 2007). The increase in nutritional quality, together with the increase of the abundance of both basal resources, can explain the increase of abundance of macroinvertebrates, also common in other studies (Cross et al., 2006; García et al., 2017). Increases in the body size of primary consumers have also been linked to enhanced resource quality (García et al., 2017); however, the increases in body mass observed in our study could be attributed either to resource quality or quantity variations. Additionally, pollution can reduce α diversity (Johnson et al., 2013) as sensitive species might disappear (Cortelezzi et al., 2013) and lead to the homogenisation of assemblages (Johnson & Angeler, 2014). In our experiment, β diversity for taxon richness and for Shannon diversity were reduced with pollution leading to more homogeneous communities; however, the tendency to increase α diversity demonstrated that our gradient of pollution only ranged from low-to-moderate.

We expected pollution to increase energy fluxes, as enhanced nutrient concentration rises detritus quality (Cross et al., 2003) and biofilm biomass (Brett et al., 2017), and can thus potentially sustain a higher production of primary consumers (McCutchan & Lewis, 2002). Moreover, the preference of consumers for biofilm over detritus typically causes shifts from the brown to the green pathway as a response to nutrient enrichment (Bumpers et al., 2017). However, in our study, omnivores increased herbivory, but we did not observe either a general increase in the energy fluxes or an increment of the green pathway with pollution.

We further predicted the slope of size spectra to become shallower along the pollution gradient, as the increase of the quality of basal food resources (Evans-White & Halvorson, 2017) usually increases the efficiency of trophic transfer (Mulder & Elser, 2009), with large individuals becoming relatively more abundant in the most polluted sites. However, we observed that pollution did not alter size spectra, suggesting that communities shaped their taxonomic and internal energy pathways, but without overall changes in energy transfer efficiency due to pollution.

4.2 | Pollution accentuated the response of food webs to water diversion

The combined effects of water diversion and pollution on food webs are poorly known (e.g. de Guzman et al., 2021). However, some studies have addressed the combined effects of flow reduction and nutrient enrichment (Lange et al., 2014; Matthaei et al., 2010), which are also consequences of water diversion and pollution. While Matthaei et al. (2010) observed larger effects with flow reduction and Lange et al. (2014) reported a stronger effect of nutrient enrichment through farming intensity, in our study, we observed that pollution accentuated the response of food webs to water diversion.

Water diversion has been linked to a decrease of detritus stock in diverted reaches (Martínez et al., 2013) as a consequence of retention in the impoundments (Schmutz & Moog, 2018) and of diversion towards canals (Arroita et al., 2015). Less known is the effect of diversion on biofilm, although it tends to be favoured by high flow velocity (Matthaei et al., 2010) as nutrient exchange is enhanced (Dewson et al., 2007b). Thus, in our study, we expected diversion

TABLE 2 Linear model results comparing size spectra between control and diverted reaches along the pollution gradient (Log_{10}TDN).

	Entire community			Primary consumers			Omnivores			Carnivores		
	F	p	Coeff.	F	p	Coeff.	F	p	Coeff.	F	p	Coeff.
Body mass	271.58	**<0.001**	-1.05	363.31	**<0.001**	-1.29	104.98	**<0.001**	-0.89	55.04	**<0.001**	-0.71
Log_{10}TDN	0.18	0.669		0.08	0.773		0.004	0.950		0.00	0.999	
Reach	0.26	0.611		16.71	**<0.001**	-0.33	2.13	0.151		0.69	0.411	
Body mass:Log_{10}TDN	0.001	0.970		0.55	0.461		1.25	0.270		0.01	0.926	
Body mass:Reach	0.43	0.517		0.08	0.785		0.20	0.658		0.08	0.779	
Log_{10}TDN:Reach	1.22	0.274		27.70	**<0.001**	-3.20	0.30	0.586		2.34	0.134	
Body mass:Log_{10}TDN:Reach	0.13	0.721		1.81	0.185		2.11	0.153		0.04	0.840	

Note: Bold values indicate statistical significance ($p < 0.05$). Coefficients are shown for significant responses and consider pollution gradient (Log_{10}TDN) and Control reaches as reference in all cases.

Abbreviation: TDN, total dissolved nitrogen.

to reduce biofilm biomass. Nonetheless, we detected no effect of water diversion on biofilm biomass across the range of pollution, suggesting minimal effects of diversion on water velocity and nutrient exchange rate.

The effects of water diversion on consumer abundances and diversity were more complex. A decline in invertebrate density with flow reduction has been reported elsewhere (Martínez et al., 2020; Matthaei et al., 2010), but our study adds that this negative effect is more common in the polluted rivers, showing signs of an intensification of diversion effects with pollution. Similarly, other studies have shown that water diversion reduces local diversity (Munasinghe et al., 2021), due to the reduced habitat diversity (Cazaubon & Giudicelli, 1999). In our study, we demonstrate that α diversity is negatively affected by diversion only interactively with pollution, as the reduction was only obvious in the most polluted river. Moreover, we expected diversion to homogenise the habitat and reduce β diversity, but we observed the contrary: diversion increased compositional β diversity across samples. One possible explanation is the common pattern of β-diversity reduction with decreasing abundance (Stier et al., 2016). However, this could only play a role in the most polluted river, in which invertebrate density was clearly reduced. The most likely explanation is that water level variations are much larger in the diverted reaches, as they endure much lower discharges than the reaches above the weirs, but suffer similar floods as the diverted canals get overflown. Thus, diversion can originate patches of very different inundation history (Bunn & Arthington, 2002) and, consequently, more dynamic benthic migration patterns and higher β diversities (Vallefuoco et al., 2022). Pollution is not expected to be relevant for this mechanism, which is in line with the observed lack of interaction between diversion and pollution when explaining β diversity. Regarding fish, the presence of the same species in the studied upstream and downstream reaches, with higher densities in most of the diverted sites, also suggest that water diversion did not cause a strong impact on fish assemblages. This is not unexpected, as previous studies report that diversion reduces fish abundance and richness as a consequence of reduced longitudinal connectivity, altered flow regimes and degraded habitats (Kuriqi et al., 2021), but also showed weak negative effects compared to nutrient enrichment (Lange et al., 2014).

Different properties of the communities were shaped by both stressors studied, but the slope of the size spectra, and thus, the energy transfer efficiency, remained unchanged, which denotes communities adapted to the conditions in their environment by adjusting diversity and energy fluxes, but ultimately maintaining the size structures comparable to reference systems (Petchey & Belgrano, 2010). Nevertheless, energy fluxes of different types of consumers responded to the interaction of pollution and water diversion. Fluxes through herbivory, detritivory, and carnivory, and consequently through the entire community, were reduced by diversion in the most polluted river, but increased in the less polluted one. Interestingly, the response of energy fluxes to perturbations suggests a fit to the intermediate disturbance hypothesis (Connell, 1978) but for functioning instead of diversity, as the fluxes

are inhibited by diversion in the most polluted river (as expected from the response of abundance), but they are stimulated in the less polluted river. This stimulus can also be linked to the slight increase of α diversity with water diversion. Ultimately, both the increment of energy fluxes and the lack of response of the rest of the variables suggests the less polluted rivers to be more resistant to water diversion. Nevertheless, we need to bear in mind that this interpretation is based on a rather small number of systems, which makes it impossible to test for hump-shaped responses that supporting the intermediate disturbance hypothesis would need.

5 | CONCLUSIONS

In the current study, both low-to-moderate nutrient pollution and water diversion independently affected different features of food webs: pollution modified the green food web and diversion the brown food web. Although the size structure of the community was not affected, both pollution and diversion modified the diversity and energy fluxes. Most interestingly, the interaction between both stressors was more explanatory than any of the two stressors on its own, with pollution exacerbating the negative effect of water diversion. Our study illustrates the complexity of the responses of biological systems when multiple stressors act simultaneously and suggests that water diversion can have slighter consequences when it does not happen in conjunction with water pollution. Current knowledge on trophic links between species and metabolic requirements of organisms offer promising tools to detect anthropogenic disturbances that can otherwise go unnoticed.

AUTHOR CONTRIBUTIONS
Conceptualisation: A.E., A.L., D.v.S., and J.M.G. Developing methods and conducting the research: I.d.G., A.E., A.L., D.v.S., J.M.G., and A.V.P.C. Data analysis and interpretation: I.d.G., A.L., and J.M.M. Preparation of figures and tables: I.d.G. Writing: I.d.G., A.L., J.M.M., A.E., D.v.S., J.M.G., and A.V.P.C.

CONFLICT OF INTEREST STATEMENT
Authors declare that there is no conflict of interest regarding the material discussed in the manuscript.

DATA AVAILABILITY STATEMENT
The original data that supports the findings of this study and the code used for the main analyses are openly available in Figshare and GitHub: https://figshare.com/s/c01f99343e3eb84b4346.

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