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WHICH ENVIRONMENTAL FACTORS INFLUENCE THE DISTRIBUTION PATTERNS OF AN ENDANGERED FRESHWATER MUSSEL (*UNIO CRASSUS*)?

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KEYWORDS : Bio-geomorphology ; Habitat modelling ; Freshwater mussel ; *Unio crassus*

ABSTRACT

Freshwater mussels (Bivalvia: Unionida) are valuable components of river ecosystems. Among them, the thick-shelled river mussel (*Unio crassus*) is globally endangered, and its populations are decreasing in many European catchments. Over the last decade, it has become a focal point of environmental conservation programs. A comprehensive understanding of the relationship between the species and its environment is therefore required to optimize those programs. Yet, despite being increasingly studied, freshwater mussel ecological requirements remain complex to establish as they appear to be species- and region-related. We reviewed the potential environmental factors which have been showed to impact freshwater mussels, and therefore possibly *U. crassus*. We compiled datasets of environmental factors and occurrence of *U. crassus* across the study area (Wallonia, Belgium). Logistic regression models were built to identify the main driving factors. Results underscore the predominant significance of hydro-geomorphological variables in shaping distribution patterns. Specific stream power had a significantly negative impact on the distribution of *U. crassus*, while the probability of occurrence increased with catchment area, and with contrasted high and low flows during the year. The high prediction accuracy of the hydro-geomorphological model supports the idea of a considerable influence of hydro-geomorphological habitat on the species. Other parameters are also relevant in predicting mussel distribution, like the percentage of land covered by meadows, elevated heavy metals concentrations and fish richness.

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1. Introduction

Freshwater mussels (Bivalvia: Unionida) are important components of river ecosystems. They provide many benefits for humans and for the biodiversity, including water filtration, nutrient recycling, habitat modification and environmental monitoring (Vaughn, 2018). Among freshwater mussels, 45 % of the species are under threat of extinction (Lopes-Lima et al., 2018), leading to a growing scientific interest in understanding the mechanisms behind the decline (Ferreira-Rodriguez et al., 2019). The causes of the current decrease in freshwater mussel populations are often recognized as multifactorial (Bogan, 1993; Downing et al., 2010; Lopes-Lima et al., 2017). Deterioration and loss of habitats caused by the increasing anthropogenic pressures are major stressors affecting mussels, along with climate and land-use changes, and water pollution degrading river ecosystem (Lopes-Lima et al., 2018; Birk et al., 2020). The response of freshwater mussels to the multiple threats they are facing can vary depending on the species and environ-mental factors, which underscores the necessity of regionally- and species- specific conservation actions (Lopes-Lima et al., 2017; Ferreira-Rodriguez et al., 2019).

The thick-shelled river mussel (*Unio crassus*, Philipsson 1788) is an *endangered* freshwater mussel species. Its decline over the last decades (ca. 45-60 years) is estimated to be over 50 % in Europe, and the decline is expected to continue (Lopes-Lima et al., 2014). More specifically in Belgium, the conservation status of *U. crassus* is qualified as unfavourable to poor according to European Commission criteria of conservation status assessment of species and habitat (DG Environment, 2017). The species is virtually extinct in the north of Sambre and Meuse valley, and the remaining populations are unevenly distributed due to local extinctions in southern catchments (Wallonia). Despite the protection status given by the European Habitat Directive (92/43/CEE), and the national Nature Conservation Law (1973), the health of mussel populations is still decreasing in many catchments. In consequence, *U. crassus* has become a target species of many environmental protection programs. Conservation actions include population reinforcements and habitat preservation or restoration initiatives such as water quality improvement, river meandering or dam removal. Notwithstanding the benefit of such restoration actions, a better understanding of the relationship between *U. crassus* and its habitat is needed to establish costeffective conservation projects and to ensure long-term effectiveness for the species (Lopes-Lima et al., 2017; Chiavacci et al., 2018).

U. crassus is commonly acknowledged as a relatively tolerant species, especially in comparison to other critically endangered species like the pearl mussel (*Margaritifera margaritifera*) (Inoue et al., 2017). *U. crassus* is known to live in rivers from small catchments to large downstream channels, under a rather large range of environmental conditions (Denic et al., 2014; Lopes-Lima et al., 2014; Stoeckl and Geist, 2016; Vaessen et al., 2021) but much remains unknown regarding its distribution drivers. Despite its relative environmental tolerance, the species has vanished from certain catchments. Adults live buried in sediment at the surface of the riverbed and move on relatively short distances for reproduction or in case of disturbance (Vicentini, 2005; Zając and Zając, 2011; Zając et al., 2019). They are vulnerable to perturbations of their habitat due to their limited ability to move and their long lifespan (~30 years) (Zając et al., 2019). Moreover, ecological requirements of the species could vary depending on the catchment, notably because of the peculiar life cycle of unionids mussels. After fertilisation of the eggs in the marsupium of females, they are brooded for 9-35 days (Zając and Zając, 2021). Then small larvae, called glochidia, are expelled with water spurted from female' syphons in the free-flowing water to find a host-fish and attach to its gills or fins to complete their physiological development (Vicentini, 2005; Aldridge et al., 2023). Various fish species are suitable hosts while the preference for certain species seems to be regionally related (Taeubert et al., 2012; Stoeckl et al., 2015). After a few weeks, larvae detach from fish gills and fall on the riverbed where they bury for about two years. Fish migration is therefore the main driver of mussel dispersal, and mussels are highly dependent on the quality of fish populations. Unionids distribution patterns consequently result from host fish distribution and river connectivity (Vaughn and Taylor, 1999; Vaughn and Taylor, 2000; Schwalb et al., 2013; Daniel et al., 2018), but also from hydro-geomorphological characteristics of the stream (Morales et al., 2006; Garcia et al., 2012; Zając et al., 2018; Lopez and Vaughn, 2021) and large-scale factors like climatic variables and land use (Cao et al., 2015; Ferreira-Rodriguez et al., 2019).

The relationship between freshwater mussels and environmental factors is clearly established. However, many factors have showed ability to influence freshwater mussel occurrence. For instance, flow regimes and stream discharge (Peterson et al., 2011; Daniel et al., 2018; Dascher et al., 2018), host fish richness and abundance (Vaughn and Taylor, 2000; Schwalb et al., 2013; Daniel et al., 2018) were found to be correlated with habitat suitability of freshwater mussels. Stream size, channel morphology, bed stability and grain size also have a demonstrated effect on mussel populations (Strayer, 1993; McRae et al., 2004; Gangloff and Feminella, 2007; Daniel and Brown, 2013; Cao et al., 2015; Pandolfo et al., 2016; Key et al., 2021). Concerning land use, the proportions of urban area, of agricultural land and of forest in the catchment were found relevant for mussel abundance (Burlakova et al., 2011; Daniel and Brown, 2013; Cao et al., 2015; Pandolfo et al., 2016; Daniel et al., 2018). Nevertheless, mussel species do not respond uniformly to environmental factors (Haag, 2012; Rzymski et al., 2014; Inoue et al., 2017), and the various methods, species, spatial scales, and geomorphological contexts makes it difficult to generalize results across scales, regions, and species. Therefore, we investigated regional distribution to determine which environmental factors influence the presence of *U. crassus* in Wallonia (Belgium) using a modelling-based approach. Modelling techniques have been increasingly used for explaining and predicting species occurrence, including those of freshwater mussels. Moreover, the integration of spatial data enables the identification of priority areas for conservation and restoration efforts to be made. Such techniques allow narrowing the ecological requirements of a species and the coupling of catchment- and reach-scale variables have demonstrated high predictive power (McRae et al., 2004; Newton et al., 2008; Cao et al., 2015).

To address regional knowledge gaps of the habitat of *U. crassus*, the influence of multi-scale environmental variables, namely hydrological, geomorphological, human-related variables, water chemistry, pollutants concentration, and biotic variables on the occurrence of *U. crassus* was investigated. We first reviewed the potential factors which have been shown to have an impact on the presence of *U. crassus*. Second, we compiled datasets incorporating these factors and the

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occurrence of *U. crassus* across the study area (Wallonia, Belgium). Third, we identified key variables most strongly associated with the distribution pattern of *U. crassus* using logistic modelling. Statistical analyses were conducted on three subsets of variables: hydro-geomorphological, physico-chemistry of water including potentially harmful chemicals and land use, and biotic variables.

We hypothesized that (i) the minimal ecological requirements of *U. crassus* could be defined by hydro-geomorphological characteristics of the streams, (ii) if there are any regional differences of occurrence due to distinct geological structure, they could be identified by proxy factors like pH, conductivity and calcium contents in water, (iii) acute and diffuse pollutions would be limiting factors for *U. crassus* presence, and (iv) host fish population abundance is directly linked to *U. crassus* presence.

2. Methods

2.1. STUDY AREA

The study was conducted in Belgium over the Wallonia Region, the southern part of Belgium (Fig. 1). In total, 93 sites were considered. Their locations were chosen because of available data, with no regards to the presence nor the absence of *U. crassus* at those locations. Most of them are situated at, or close to, gauging stations from the hydrological monitoring networks of the SPW - MI & SPW ARnE (Walloon Public Service). They are distributed in 68 rivers from three main international catchments (Meuse, Scheldt, Rhine). The sites encompass a broad range of conditions as they are located in different natural sub-regions characterized by distinct geological, hydrological, and climatic features. Natural regions, due to their geological substratum, are characterized by different sedimentary and hydrology conditions in their catchments (Petit, 1995). Ardenne region, which reckons 53 % of the sites, is characterized by Palaeozoic substratum which is impervious schisto-sandstones. The Fagne-Famenne region (12 % of the study sites) is characterized by soft shales from the Upper Devonian. The Condroz region displays a typical Appalachian landscape and gathers 9 % of the sites. Depressions are made of Carboniferous limestone and Upper Devonian sandstones are found on the ridges. In Lorraine (8 % of the sites), sandy-loaded rivers flow on various substratum from Triassic and Lower Jurassic. Rivers in Hainaut region (7 %), and in the Brabant region (4 %), developed in silty area and Loessic sandy cover, respectively. Hesbaye region (4 %) is an agricultural plateau formed by a thick layer of loess with Cretaceous chalk underneath in the eastern part. The Entre-Vesdre-et-Meuse region (4 %), to the north-east of Ardenne region, contains Devonian rocks and Cretaceous deposits. Annual rainfalls are between 700 mm and 800 mm in westernmost Wallonia, where altitude ranges from 100 m to 300 m above sea level, and they can add up to 1400 mm in Upper Belgium (Erpicum et al., 2018).

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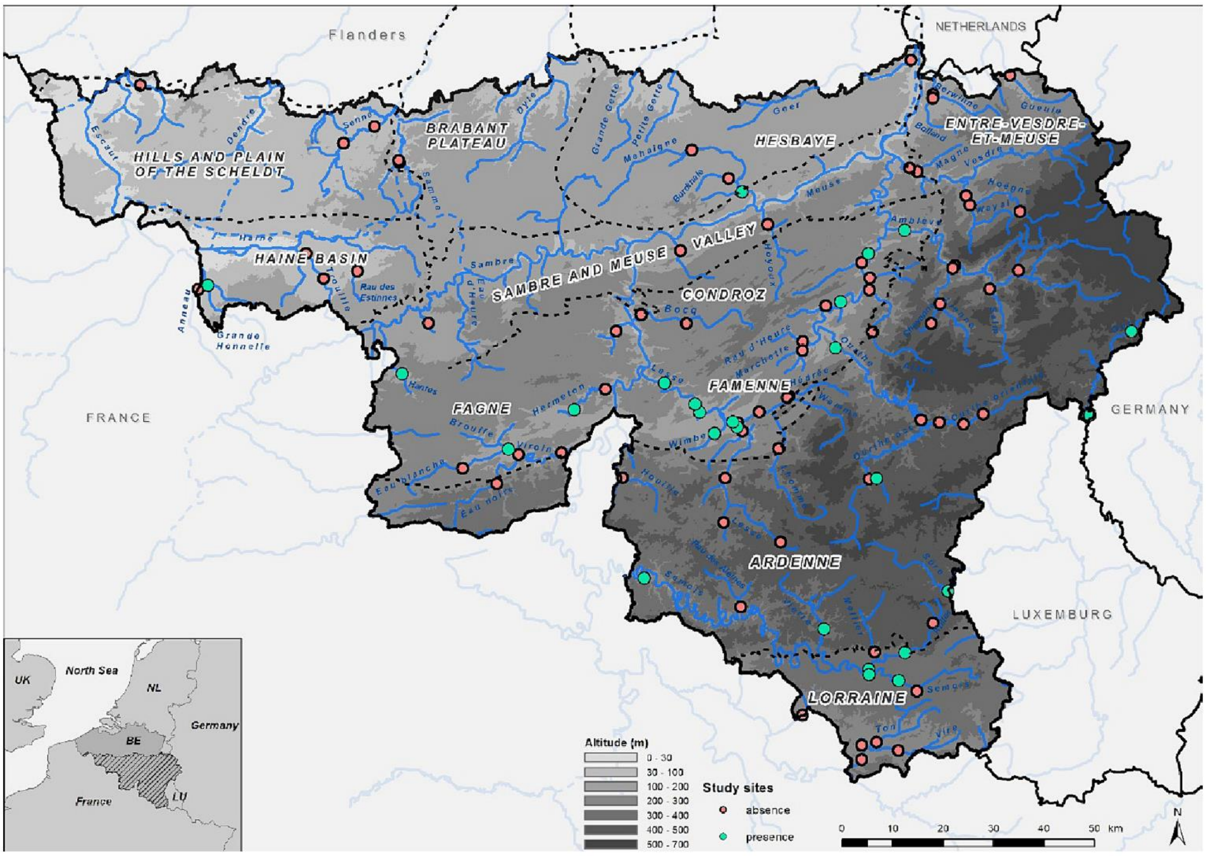
Figure 1. *Natural regions of Wallonia with sampling locations*



2.2. DATA COMPILATION

A dataset of 38 environmental variables (explanatory variables) and the occurrence of *U. crassus* (response variable) was compiled (Table 1). The explanatory variables were selected according to a literature review. We assembled biotic, hydro-geomorphological, physicochemical and landscape data. *U. crassus* occurrence were obtained from the SPW - DEMNA surveys carried out within the European strategy of nature conservation program (SPW, 2021) and according to our own observations. When no presence data were available, visual surveying was conducted. To do this, the same observer surveyed a 20-50 m long section (downstream or upstream of the station, depending on the site configuration) for 20 min with underwater viewing scope and used tactile sampling in the soft substrate deposits. If no individual was found, the banks were prospected for dead shells as a double check for absence. A single living individual found counts as presence for the study site. Most of the sites needed prospection for presence and 69 sites were surveyed during August 2020, of which 11 were found positive. Host fish data was obtained from the SPW - DEMNA surveys (SPW, 2021).

Physicochemical variables were collected as part of the SPW surface water quality monitoring network (SPW, 2020 Fig. S1). We used median values for the period 2005-2020 rather than means owing to highly skewed distributions. Median area-specific sediment yields (SSY) were calculated at watershed scale while looking for regional differences and were interpolated using the inverse

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distance weighting method for Wallonia and value at each study site was extracted from the resulting raster (Van Campenhout et al., 2022). Landscape human-related variables were either calculated or extracted from GIS layers. Land cover data is from Copernicus Global Land Service (Buchhorn et al., 2020) and has a global resolution of 100 m. The data were reclassified in 6 classes: coniferous forest, deciduous or mixed forest, meadows, agricultural area, urban area, and another class regrouping the permanent water bodies and bare lands. The percentage occupied by each class was calculated for each catchment. The latter was not considered in the statistical analysis given the low occurrence of this class (0 % of appearance in average; max of 0.6 %). Population density was

downloaded from SPW Geoportal (SPW, 2021). The original qualitative data was coded in 8 classes of number of inhabitants per 500 m radius, ranging from 10 to 50 inhabitants to 1001 to 2000 inhabitants. The areas with < 10 inhabitants per 500 m radius are not mapped because of privacy law. We transformed the variable into a quantitative one by taking the centre of each class and gave the value of 5 to areas with no data since it was not possible to differentiate areas with < 10 inhabitants from the areas with no inhabitant.

Hydro-geomorphological features were collected from a dataset originally compiled by Petit et al. (2005) and completed by field measurement or computed from GIS layers from the SPW Geoportal (SPW, 2021). Channel width at bankfull stage was computed by averaging distances between top of the left and right banks of 10 cross-section profiles extracted from Lidar digital elevation model (DEM) of Wallonia. The DEM has a spatial resolution of 1 m, planimetric accuracy is < 1 m, and the altimetric accuracy is about 0.12 m (SPW Geoportal, 2023). Water surface gradient (slope) was calculated on field during high flow and/or using high water marks and completed by calculations with LIDAR on a distance that depends on the width (at least 14 times). Wolman grain size analyses (Wolman, 1954) were performed on riffles to obtain median grain size (D50). Hydrological data used to compute Q_{355}, the ratio of extreme monthly coefficients (Cm ratio) and number of days below Q_{355} in 2020 was downloaded from the website of the hydrological monitoring networks of the Walloon Public Service for the period 2010-2020 (SPW, 2023). The Q_{355} corresponds to the 10th lower value of discharge happening 10 days by year on average. It was calculated by ordering daily flow values by year, then averaging the 10^{th} smaller values of each year for a gauging station. The Cm ratio is obtained by calculating monthly coefficients (Cm), which are average monthly flows divided by the average annual flow, the maximal monthly coefficient is then divided by the minimal monthly coefficient. Q_{355} values were normalized by catchment area. The number of days below the Q_{355} for a dry year (2020) was used to highlight rivers which could be more sensitive to prolonged dry and hot period, resulting in extreme low flows. Specific stream power at bankfull discharge (ω_{Qb}) was calculated using the Bagnold equation (Bagnold, 1966, 1977). Bankfull discharge values used to compute specific stream power are from Van Campenhout et al. (2020) and completed with field observation during floods.

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Table 1. *Descriptive statistics of the tested environmental variables (mean, standard deviation, median and minimum and maximum values). For hydrological and physicochemical data, years give the period covered by the surveys. For each environmental variable, most relevant references mentioning effect of the environmental variable on U. crassus or on other freshwater mussel species are given.*

Variable	Units	Mean	Standard deviation	Median	Range	Date	Source	References
Hydro-geomorphological subset (n = 69)								
Catchment area	km^2	295	358	147	10–1607		LHGF[a]	Gangloff and Feminella, 2007; Cao et al., 2015; Tonkin et al., 2015
Channel width	m	15.5	9.4	13.3	2.7–62.3		LHGF	Gangloff and Feminella, 2007
Local slope	m.m^{-1}	0.0044	0.0038	0.0031	0.0008–0.0255		LHGF	Cao et al., 2015
Specific Stream power	W.m^2	63	46	51	6–263		LHGF	Layzer and Madison, 1995; Pandolfo et al., 2016
Characteristic low-flow discharge (Q_{355})	m^3.s^{-1}.km^{-2}	1.6	1.1	1.4	0.2–6.8	2010–2020	LHGF	Daniel et al., 2018
Ratio of extreme monthly coefficients (Cm ratio)	–	9.6	4.7	10.2	1.7–22.5	2010–2020	LHGF	Di Maio and Corkum, 1995; Lopez and Vaughn, 2021
Numbers of days below Q_{355} in 2020	–	69	25	69	0–172	2020	LHGF	Chiavacci et al., 2018
Median grain size (D_{50})	mm	51	28	50	0.03–128	–	LHGF	McRae et al., 2004; Brainwood et al., 2008; Daniel and Brown, 2013
Biotic subset (n = 68)								
Phoxinus phoxinus biomass	kg.ha^{-1}	14.36	21.54	9.06	0–141	2007–2019	SPW - DEMNA[b]	Taeubert et al., 2012
Cottus gobio biomass	kg.ha^{-1}	10.57	12.48	6.12	0–67	2007–2019	SPW - DEMNA	Taeubert et al., 2012
Squalius cephalus biomass	kg.ha^{-1}	25.56	42.77	3.67	0–198	2007–2019	SPW - DEMNA	Taeubert et al., 2012
Total biomass of fish (all species)	kg.ha^{-1}	155	116	127	0–656	2007–2019	SPW - DEMNA	Taeubert et al., 2012
Number of fish species	–	10	4	10	0–19	2007–2019	SPW - DEMNA	Taeubert et al., 2012; Chiavacci et al., 2018
Physico-chemical and land use subset (n = 81)								
Total N	mgN.l^{-1}	3.8	1.8	3.2	0.2–8.4	2005–2020	SPW - DGARNE[b]	Wang et al., 2007; Barák et al., 2022
Cadmium	µg.l^{-1}	0.06	0.12	0.03	0.005–0.76	2005–2020	SPW - DGARNE	Bogan, 1993; Hansten et al., 1996
Chromium	µg.l^{-1}	0.52	0.34	0.4	0.25–2.7	2005–2020	SPW - DGARNE	Rzymski et al., 2014
Conductivity at 25 °C	µS.cm^{-1}	389	260	299	52–1031	2005–2020	SPW - DGARNE	Burlakova et al., 2011; Johnson et al., 2014
Copper	µg.l^{-1}	1.45	1.32	1.2	0.4–12	2005–2020	SPW - DGARNE	Hansten et al., 1996; Wang et al., 2007; Markich, 2017; Timpano et al., 2022;
BOD5	mg.l^{-1}	1.37	0.77	1	0.55–5.85	2005–2020	SPW - DGARNE	
Glyphosate	µg.l^{-1}	0.06	0.14	0.03	0.025–1.127	2007–2019	SPW - DGARNE	Bringolf et al., 2007; Annett et al., 2014
Nickel	µg.l^{-1}	1.9	1	1.8	0.3–5	2005–2020	SPW - DGARNE	Markich, 2017; Timpano et al., 2022
Nitrates	mgN.l^{-1}	3.16	1.43	2.88	0.25–7.53	2005–2020	SPW - DGARNE	Douda, 2010; Moore and Bringolf, 2018
pH	–	7.8	0.34	7.84	5.525–8.34	2005–2020	SPW - DGARNE	Wang et al., 2007; Burlakova et al., 2011
Total P	mgP.l^{-1}	0.13	0.14	0.07	0.01–0.752	2005–2020	SPW - DGARNE	Strayer, 2014; Bartsch et al., 2017; Barák et al., 2022
Lead	µg.l^{-1}	0.95	1.19	0.7	0.3–10.56	2005–2020	SPW - DGARNE	Markich, 2017
Potassium	mg.l^{-1}	3.1	2.12	2.5	0.25–14.15	2005–2020	SPW - DGARNE	Wang et al., 2018; Wang et al., 2023
Oxygen saturation	%	91.3	6.1	93	68–99	2005–2020	SPW - DGARNE	Ganser et al., 2015; Barák et al., 2022
Sodium	mg.l^{-1}	15.19	14.39	10.75	2.5–87.7	2005–2020	SPW - DGARNE	Gillis, 2011; Pandolfo et al., 2012
Sulfates	mg.l^{-1}	29.83	34.67	15.8	6.4–169.2	2005–2020	SPW - DGARNE	Mount et al., 2016; Erickson et al., 2017
Zinc	µg.l^{-1}	14.47	44.5	7	5–403	2005–2020	SPW - DGARNE	Hansten et al., 1996; Markich, 2017; Timpano et al., 2022
Calcium	mg.l^{-1}	54.26	43.02	37	2.2–138.1	2005–2020	SPW - DGARNE	Mount et al., 2016; Erickson et al., 2017
Land cover - Coniferous forest	%	11	12	9	0–54	2019	Copernicus Global Land Service	Burlakova et al., 2011; Cao et al., 2015
Land Cover - Deciduous & mixed forest	%	43	18	42	7–88	2019	Copernicus Global Land Service	Burlakova et al., 2011; Cao et al., 2015
Land Cover – Meadows	%	13	7	12	0–38	2019	Copernicus Global Land Service	
Land Cover - Agricultural area	%	29	21	20	0–82	2019	Copernicus Global Land Service	Cao et al., 2015; Pandolfo et al., 2016
Land Cover - Urban area	%	4	4	3	0–17	2019	Copernicus Global Land Service	Daniel et al., 2018
Sediment yields	t.km^{-2}an^{-1}	42.5	38.7	31.7	8–268	1996–2018	LHGF	Johnson et al., 2014
Population density	inhab/ 500 m	307	372	175	5–1500	2019	SPW - Metawal	Burlakova et al., 2011

[a] LHGF: Hydrology and fluvial geomorphology laboratory (ULiège - Department of Geographic Sciences, UR SPHERES).
[b] SPW: Public Services of Wallonia.

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2.3. STATISTICAL ANALYSES

We used logistic regression models including linear effects of the explaining factors, with variable selection to identify the environmental factors responsible of the current distribution of *U. crassus*. Logistic models have an efficient theoretical background and are largely accepted as a suitable and well-established method for species distribution modelling (Pearce and Ferrier, 2000). An overview of the collinearity of the selected variables was obtained using correlation matrix (Fig. S2). We used the dredge function of the R package MuMIn (Barton, 2022) for automated model selection, which allows to deal with multicollinearity. We used the Akaike information criterion corrected for degrees of freedom (AICc), a maximum of 5 effects per model and 0.05 as critical level of significance. As some data were not available for each site, the initial dataset contained missing values. We split it in three subsets of explaining factors to retain as much sites as available. We grouped factors related to hydro-geomorphology, to physico-chemistry and land use, and to biotic data and we identified one model per subset. The selected models were validated by testing them against their null model using the likelihood ratio test (LRT) viewed as a test of significance of all the coefficients. For model evaluation, we computed the Area under the ROC curve (AUC) and the true skill statistic (TSS). The AUC were obtained by boostrapping. We split the resampled datasets in training (2/3) and validating (1/3) datasets. The first ones were used to reparametrize the models and the second ones to independently obtain the AUC. The mean values of the AUC were computed thanks to the normalization suggested by Zhou et al. (2002). AUC values between 0.7 and 0.8 are acceptable (better agreement than random), values between 0.8 and 0.9 are excellent, and value over 0.9 are considered as outstanding (Hosmer Jr et al., 2013). A TSS value of 1 indicates perfect agreement and values equal to or less than zero indicate a performance no better than random (Allouche et al., 2006). We used sensitivity equals specificity to select the cutting levels and to compute the confusion matrices. Additionally, we computed McFadden's (1974) pseudo-R- squared for insights on the ratio of information gained with the predictors. Odds ratio (OR) were computed to estimate the effect of the increase of one-unit in explanatory variable on the response variable. The 95 % confidence intervals are also presented as an estimation of the precision of the OR. Confidence interval containing 1 attests of a statistically non-significant predictor. OR smaller than 1 implies a negative relationship between the explanatory variable and the response variable, while OR > 1 indicates a positive relationship. OR cannot be compared in-between models.

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3. Results

3.1. HYDRO-GEOMORPHOLOGICAL DATASET

After data cleaning, the hydrogeomorphology dataset contained 69 observations with the 8 explaining variables (Table 1), divided in 21 *U. crassus* presences and 48 absences. The 8 tested variables were: catchment area, bankfull width of the stream, median grain size (D_{50}) of the riverbed, local slope of the river stretch, specific stream power, Q_{355}, number of days below the Q_{355} for the year 2020, and Cm ratio (Table 1).

The logistic regression model highlighted the significantly positive effect of the catchment area and of the Cm ratio, and the negative effect of the specific stream power at bankfull discharge (Table 2, Fig. 2). The AUC attests of an outstanding predictive capacity at distinguishing presence from absence.

Table 2. *Summary and evaluation of the logistic regression model of the presence of U. crassus with the selected hydro-geomorphological variables. OR: Odds ratios; CI: confidence intervals (2.5 %-97.5 %).*

	OR	CI	Z value	*p*-value
Intercept	0.1138	0.0103–0.8479	−1.980	0.0477
Catchment area	1.0051	1.0024–1.0089	3.111	0.0019
Cm ratio	1.2289	1.0713–1.4515	2.716	0.0066
Specific stream power	0.9530	0.9142–0.9834	−2.618	0.0088

Likelihood ratio test deviance = 34.8; ddl = 3, p-value $<$ 0.0001; AUC = 0.91; TSS = cutting level = 0.27; McFadden's pseudo R-squared = 0.41.

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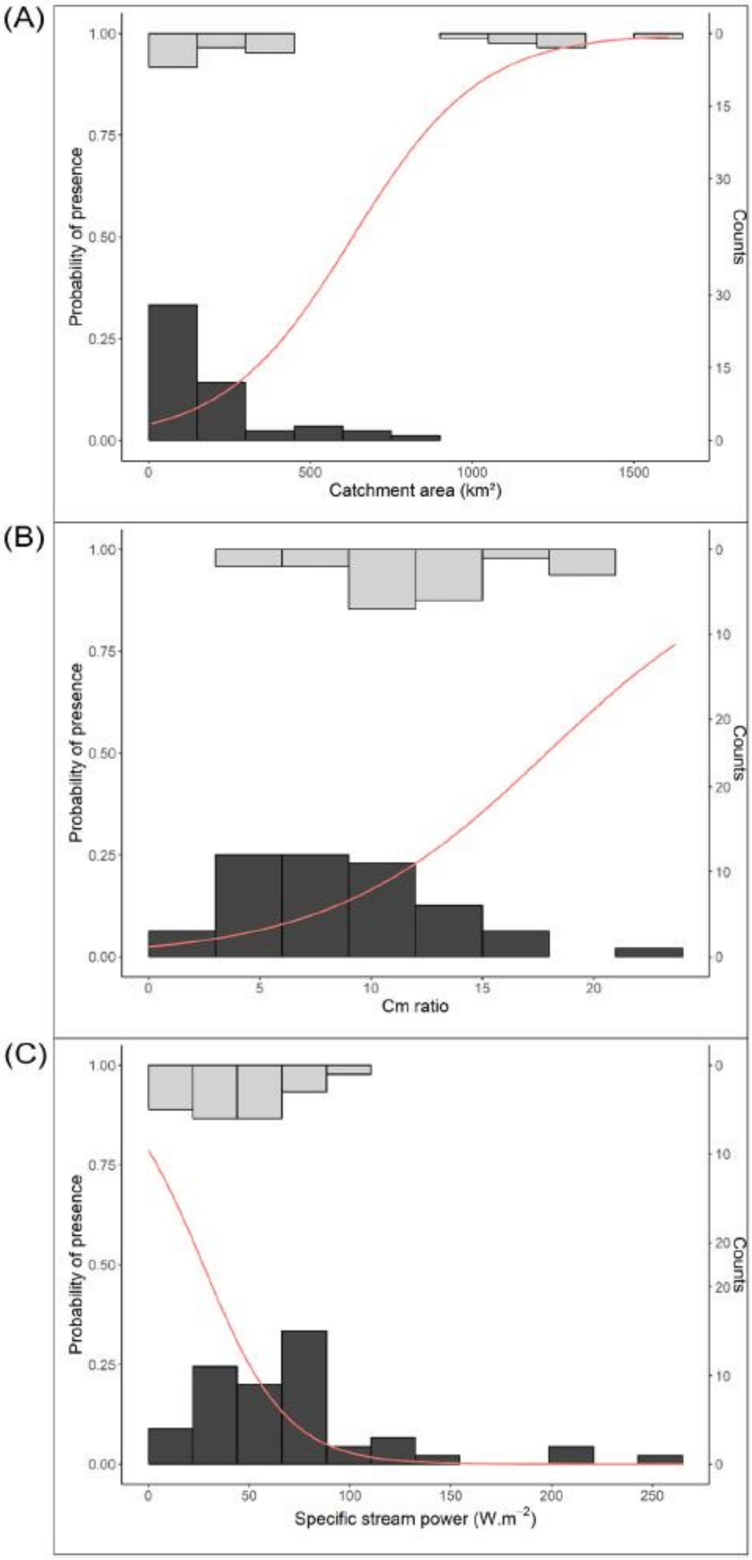
Figure 2. *Ecological responses of Unio crassus : probability of presence (curve) as a function of (A) watershed area, (B) Cm Ratio, (C) specific stream power, and distribution of the presences (upper histogram) and absences (lower histogram) according to the explaining variables of the hydro-geomorphological model (Table 2).*



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3.2. BIOTIC DATASET

After data cleaning, the biological dataset contained 68 observations for 5 variables (Table 1), divided in 16 *U. crassus* presences and 52 absences. The 5 tested variables were: the abundance of host fish (i.e. bullhead, minnow, and chub), the total fish biomass per hectare, and the total number of fish species in the catchment.

The logistic regression model underlined the significantly positive effect of the total number of fish species (Table 3, Fig. 3). The AUC attests of a better than random agreement at distinguishing between presence and absence.

Table 3. *Summary and evaluation of the logistic regression model of the presence of U. crassus with the selected biotic variables. OR: Odds ratio; CI: confidence intervals (2.5 %-97.5 %).*

	OR	CI	Z value	p-value
Intercept	0.0248	0.0021–0.1792	−3.303	0.001
C. gobio abundance	0.9568	0.8868–1.0108	−1.343	0.179
Number of fish species	1.2947	1.1056–1.5650	2.949	0.003

Likelihood ratio test deviance = 13.2, ddl = 2, p-value 0.001; AUC = 0.79; TSS = cutting level = 0.25; McFadden's pseudo R-squared = 0.18.

Figure 3. *Ecological response of Unio crassus : probability of presence (curve) as a function of the number of fish species in the catchment, and distribution of the presences (upper histogram) and absences (lower histogram) according to the explaining variables of the biotic model (Table 3).*

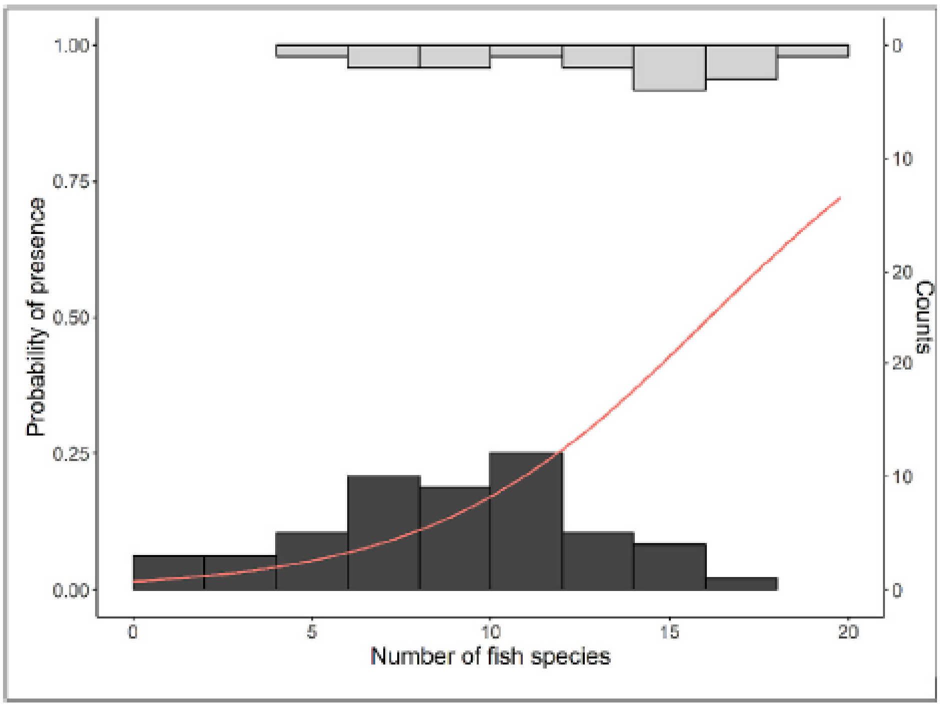

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Table 4. *Summary and evaluation of the logistic regression model of the presence of U. crassus with the selected physicochemical variables. OR: Odds ratios; CI: confidence intervals (2.5 %-97.5 %).*

	OR	CI	Z value	p-value
Intercept	0.3838	0.0309–7.3900	−0.689	0.4910
% of meadows	1.1488	1.0536–1.2718	2.936	0.0033
Chromium concentration	0.0335	0.0001–1.2845	−1.383	0.1666
Zinc concentration	0.7111	0.5200–0.8947	−2.501	0.0124
Lead concentration	19.986	0.9229–614.07	1.836	0.0664

Likelihood ratio test deviance = 23.78, ddl = 4, p-value <0.0001; AUC = 0.85; TSS = cutting level = 0.32; McFadden's pseudo R-squared = 0.25.

3.3. PHYSICOCHEMICAL AND LAND USE DATASET

After data cleaning, the physicochemical and land use dataset contained 81 observations for the 25 explaining variables, divided in 22 *U. crassus* presences and 59 absences. The 25 tested variables were: land cover proportion in the watershed split in five classes (see Methodology), population density in a radius of 500 m, sediment yields, total nitrogen, total phosphorus, concentration in extractible cadmium, chromium, copper, nickel, lead, zinc, potassium and sodium, concentration in calcium, sulfate, nitrate, glyphosate, oxygen saturation, the 5-day biochemical oxygen demand (BOD), conductivity at 25 °C, and pH in the water column.

The logistic regression model highlighted the significantly negative effect of the concentration in zinc, and the significantly positive effect of the proportional area covered by meadows (Table 4, Fig. 4). The AUC attests of an excellent predictive capacity at distinguishing between presence and absence of the species based on the selected variables.

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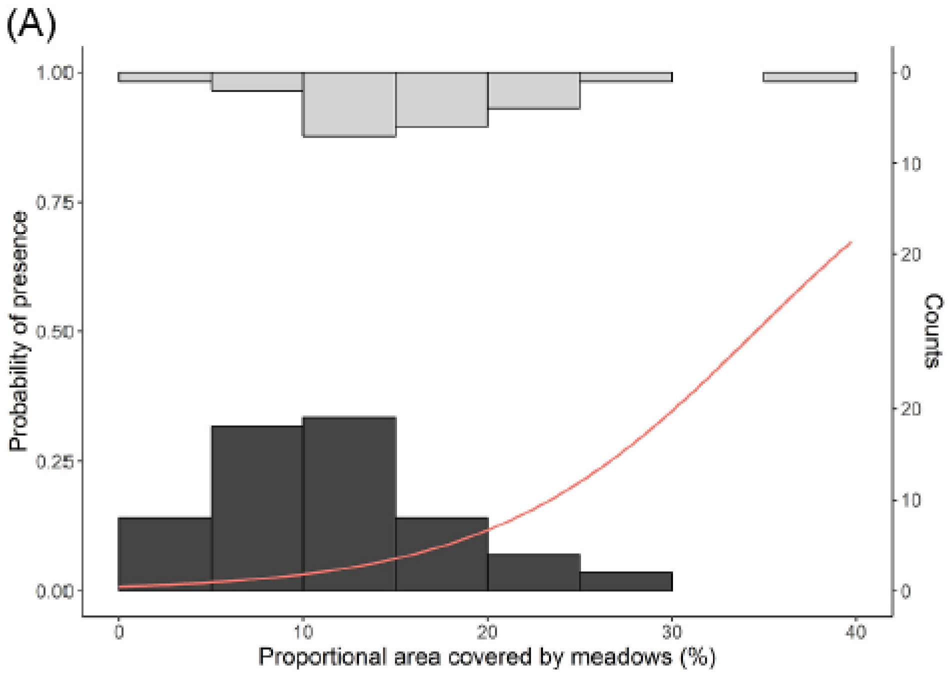
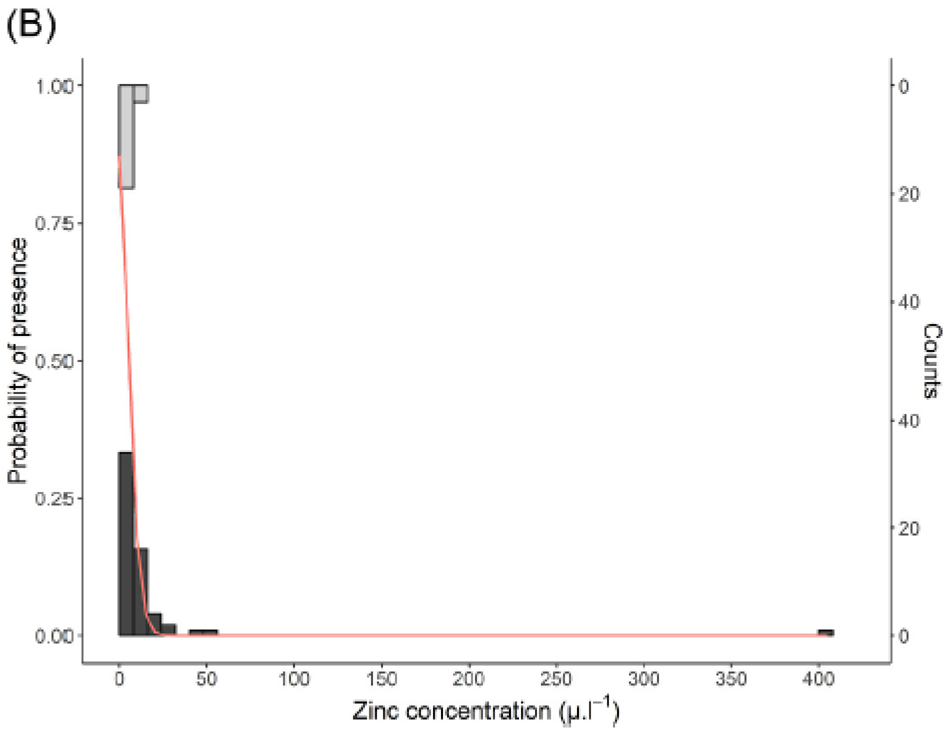
Figure 4. *Ecological response of Unio crassus: probability of presence (curve) as a function of (A) the proportional area covered by meadows, (B) Zinc concentration, and distribution of the presences (upper histogram) and absences (lower histogram) according to the explaining variables of the physicochemical and land use model (Table 4).*





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4. Discussion

Literature analysis showed that many environmental factors can influence the thick-shelled river mussel. To investigate the fundamental ecological requirements of this species, hydro-geomorphological, biotic, and physicochemical variables were selected for this analysis based on available data. The three sets of variables proceed as successive filtering to eventually define the ecological niche of the species. We supposed that the hydro-geomorphological model stresses the ability of the streams to provide minimal ecological requirements for *U. crassus* and its host fish. The biotic model highlights the need of *U. crassus* for a diversity of host fish populations, and results of the physicochemical model confirm that human perturbations could be a limiting factor for *U. crassus* presence. It is to note that despite the usefulness of modelling technique, it is limited to the data it was trained with, and we cannot exclude that some relevant variables were not considered.

In the hydro-geomorphological model, the catchment area, the specific stream power, and the Cm ratio have significant effects and give a high prediction accuracy. We found a positive effect of the flow variability (Cm ratio) on the probability of presence of *U. crassus*, meaning that the probability of presence increases when the difference between high- and low-flows is more pronounced. Yet, literature review of flow variability effects on the probability of presence of mussels showed discrepancies. Mussel abundance will usually increase with flow stability, but, for some Unionidae, flow variability can increase the probability of presence (Di Maio and Corkum, 1995). Although this could be surprising, response to flow variability is likely species-specific (Lopez and Vaughn, 2021). For example, it has been demonstrated that floods imperilled freshwater pearl mussels (Hastie et al., 2000; Hastie et al., 2003), while Zając et al. (2019) observed little impact on *U. crassus* mortality. In their study, many mussels were displaced by the flood, but found alive up to 50 m downstream (Zając et al., 2019). Moreover, specific low- and high-flow characteristics may be important to explain variations in basin-scale fish species richness (Iwasaki et al., 2012). The positive correlation between the size of the drainage basin and the probability of presence of *U. crassus* is not surprising as it has already been evidenced for other species. Ford et al. (2016) have shown that mussel diversity and abundance increased with stream size, probably because larger streams provide attenuated flood events and lower thermal fluctuations. In a similar way, Daniel et al. (2013) found that the stream order is positively correlated with freshwater mussel species richness, which they attributed to a reduced habitat disturbance along with lower current velocity and increase of fine sediments. In their review, Lopez and Vaughn (2021) also highlighted the clear positive link between mussel presence and increase of stream order or longitudinal distance from headwaters. These authors hypothesized that it expresses the fact that the risk of local extinction for mussels is lower in large rivers. Stream hydro-geomorphological characteristics change along the longitudinal gradient, underlying the ecological and morphological continuity between upstream and downstream (Vannote et al., 1980). From upstream to downstream, rivers usually become wider and deeper, temperature as well as food availability increase, while slope and grain size decrease providing an enhanced diversity of habitat (Leopold and Maddock, 1953; Gordon et al., 2004). Therefore, progressive modifications in habitat characteristics provide to *U. crassus* different food re-sources, variance in survival of glochidia due to water temperature increases, and a more diverse accessibility

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to host fish. Our results support a negative influence of the specific stream power on the probability of presence of *U. crassus*. Specific stream power corresponds to the amount of energy developed by the river for the bankfull discharge. It is function of river slope, discharge, and width (Bagnold, 1966, 1977). Likewise, previous studies found a negative correlation between mussel occurrence and density and stream power or other related hydraulic variables (Layzer and Madison, 1995; Allen and Vaughn, 2010; Lopez and Vaughn, 2021). Similarly, Zając et al. (2018) and Cao et al. (2015) found the slope to be negatively correlated with mussel abundance as well as mussel species richness. It is hypothesized that when river energy is higher, mussels, along with their host fish, need hydraulic refuges (Strayer, 1999). Moreover, the specific stream power value is linked to the magnitude of sediment transport (rolling) (Houbrechts et al., 2006), and the depth of active layer (Houbrechts et al., 2012), which has a direct influence on sedentary living species. In rivers with concave longitudinal profile, the specific stream power is generally correlated with catchment area through discharge and longitudinal slope. In headwaters, the steep slope but low discharge leads to moderate stream power. According to this distribution model of stream power, mid-sized rivers (100-500 km^2) display the maximal specific stream power (Ferguson, 1981). Downstream, despite the increase in discharge, the specific stream power decreases as the slope decreases as a negative exponential function of the distance (Knighton, 1998), and the width increases. In Wallonia and especially Ardennes, high heterogeneity in hydroclimatic conditions and relief may be observed. Indeed, most of the Ardennian rivers present a knickpoint in their longitudinal profile due to tectonic uplift of the Ardennian massif (Demoulin, 1998). As they originate from plateaus, which are tertiary erosion areas, Ardennian rivers display a gentle slope upstream which then steeply increases, producing a maximum in specific stream power at knickpoints. Specific stream power in those rivers do not follow the normal pattern of distribution, and that is maybe why catchment area was also retained in the model despite theorical correlation. The two variables are complementary when considering regional differences. However, both variables could also have an influence on mussels even in a "normal pattern", but one of the two variables may not be selected because of collinearity.

Regarding the biotic model, fish richness (i.e., the number of fish species) has a positive effect on the presence of U crassus. Vaughn and Taylor (2000) found a positive correlation between mussel richness and fish richness. Fish species richness increases with catchment area and the concomitant increase of habitat availability (Oberdoff et al., 1995). Nevertheless, this relationship is region-specific because it relies on basin features. Otherwise, our data do not show high correlation between fish richness and catchment area (R^2 = 0.2). Therefore, we consider the two significant variables (catchment size and fish richness) as two independent explanation of *U. crassus* presence. Nevertheless, fish richness could be seen as a confounding effect, because of the peculiar life cycle of freshwater mussels which require host fish for their development. Unexpectedly, our analysis did not show an effect of P. phoxinus whereas a study carried out in Wallonia demonstrated that this species was the main host fish species infested by unionids glochidia and the most common in unionids (Stoeckle et al., 2019). Also, an additional element must be considered. The muskrat (*Ondatra Zibethicus*) is present in nearly every watershed in Wallonia and is recognized as a predator of *U. crassus* and known to cause dramatic damage to mussel populations (Zahner-Meike and Hanson, 2001). For now, monitoring of muskrat populations mainly relies on voluntary civic participation, so data is not equally distributed on the territory. As a result, muskrat population data could not be included in this study but should definitively be kept in mind when considering *U. crassus* populations conservation.

Finally, the physicochemical and landcover model highlighted the significant positive effect of the proportion of area occupied by meadows in the catchment and the negative effect of Zn concentration. The proportion of area occupied by meadows is negatively correlated with agricultural land use and other associated environmental factors namely, sediment yield, total phosphorus, calcium, and glyphosate. We hypothesized that this variable holds for a good quality indicator. Meadows could play a role of buffer between the river and the rest of the basin. Moreover, it is linked to semi-natural banks and food availability for the mussels (Grunicke et al., 2023). Significant efforts have been made to improve the quality of the water since the implementation of the Water Framework Directive (WFD - 2000/60/EC), which could explain that very few pollutant parameters were significant for the presence/absence of the species. Indeed, past mining activities in Wallonia are responsible for contamination of river and overbank sediments by toxic metals. Pb—Zn mining activities in drainage basins, especially in the east of Belgium, have led to increase in metals concentration in rivers by bank erosion and overflowing (Swennen et al., 1994). The maximal Zn concentration in our data was observed in the Geul river, which is especially known for high contamination by heavy metals due to former Pb—Zn mining activities (Swennen et al., 1994). It should be noted that even if not statistically significant, the two other variables kept in the model are heavy metal concentrations (i.e. Pb and Cr), indicating that contaminating activities like mining and steelworks could have caused local extirpation of the species in Wallonia. More than a century ago, authors had already noted that pollution from industries like papermills, steel mills, etc. were implicated in the destruction of the freshwater bivalve fauna (e.g. Ortmann, 1909, 1918; in Bogan, 1993). Metal mixtures can exert a combined negative effect on freshwater mussels, especially when they have the same toxic mode of action (Timpano et al., 2022). For example, a mixture of Cu, Ni and Zn has been demonstrated to have greater impact on the growth rate of mussels than metals alone, which suggest for the authors that the current regulatory limits based on single-metal toxicity may be insufficient for mussel protection (Timpano et al., 2022). Moreover, concentration in humic acids in water could increase the toxicity of Zn on Unionidae glochidia but decrease the toxicity of other metals like Cd and Cu (Hansten et al., 1996). Rivers with the highest Zn values in our dataset (Geul, Hoëgne and Vesdre) originate in a region of plateaus characterized by peatlands and moors, which give humic acids to the water. Finally, it is to note that substances toxicity varies with water hardness and pH (Wang et al., 2007; Markich, 2017) but, despite this correlation, neither pH, nor conductivity or calcium, were retained by the selection algorithm.

The results of the three models are complementary and they should not be analyzed independently. We demonstrated that hydro-geomorphological characteristics of the streams are the best predictors of *U. crassus* presence in Wallonia, which highlights the pertinence of considering the longitudinal gradient of river for *U. crassus* habitat. Previous work had already stressed how river longitudinal profile underlie biotic communities in general (Vannote et al., 1980), and especially fish populations (Huet, 1954) as well as *U. crassus* (Zając et al., 2018). Physico-chemistry of the river also changes along this gradient (water temperature, pH, chemicals concentration...), along with land

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use in the floodplain. Consequently, effect of environmental variables should always be seen through the first "filter of geomorphology" as it acts as the primary driver.

5. Conclusion

This paper presents a comprehensive study of the regional habitat of *U. crassus* in Belgium. Our results indicate a predominant significance of the hydro-geomorphological variables to explain the occurrence of *U. crassus*. Specific stream power at bankfull discharge decreases the probability of presence of *U. crassus*, while the probability increases with catchment area. Furthermore, *U. crassus* is more often found in rivers with pronounced differences between high- and low flows. Despite having a lower prediction accuracy, fish richness and proportional area covered by meadows in the catchment are positively significant for the occurrence of *U. crassus*. On the contrary, heavy metals loads in water column, especially Zn, decrease the probability to find the species. We believe that these results underscore the critical role played by hydro-morphology in the sustainment of good ecological status of water bodies, and that river hydro-morphological quality should be considered to maximize effectiveness of freshwater conservation programs. Never-theless, the chemical quality of water should always be a fundamental preoccupation as some pollutants like heavy metals can remain harmful in the ecosystem for a very long time.

Appendix A. Supplementary data

Supplementary data to this article can be found online at

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