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RESEARCH ARTICLE

Invasive Asian clam distribution pattern reveals minimal constraints to downstream dispersal and imperceptible ecological impacts

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Abstract

1. The Asian clam *Corbicula fluminea* is an invasive freshwater species that can cause adverse ecological and economic impacts. Information on its dispersal abilities, ecological preferences and impacts may contribute towards the improvement of management strategies, including those relating to regulatory demands such as the European Water Framework Directive (WFD).

2. Both the above perspectives were addressed through inspection of environmental constraints to *C. fluminea* dispersal and impacts in a semi-natural drainage catchment (interconnected system of ditches). Forty sites were surveyed in 2014 to describe the species distribution and to characterize benthic macroinvertebrate communities, water column and sediment physico-chemistry, as well as the hydromorphological conditions.

3. Clams were unevenly distributed in the study area and artificial barriers (dikes) did not prevent downstream dispersal of juveniles. Large variation in clam density (0–3077 clams m^{-2}) could not be explained by physico-chemical or hydromorphological gradients. Although typical clam preference ranges reported in the literature were often exceeded, dense populations were nevertheless observed.

4. Macroinvertebrate community structure suggested associations between the Asian clam and some functional feeding groups. However, the impacts of clams on macroinvertebrate assemblages and ecological quality were negligible, suggesting that contemporary methods designed to comply with the WFD bioassessment scheme may fail to detect important drivers of ecological change in freshwater ecosystems.

5. This study demonstrated the reduced ecological impacts and broad ecological competence of the Asian clam, but also that its spread depends on human vectors. These findings highlight the need to rethink prediction tools supporting preventive measures against the introduction and spread of this invasive bivalve.

KEYWORDS

alien species, benthos, canal, dispersal, ditch, ecological status, invertebrates, stream, Water Framework Directive

1 | INTRODUCTION

The widespread degradation of freshwater ecosystems has been well documented, inspiring regulatory legislation such as the Water Framework Directive (WFD; Directive 2000/60/EC; Council of the European Communities, 2000). The WFD combines ecological assessment of aquatic systems alongside physical and chemical monitoring (Hering et al., 2003). Numerous agents contribute to the degradation

of fresh waters and the spread of non-indigenous invasive species is a major driver of ecological change. They are distinguished as a major threat to aquatic ecosystems, causing biodiversity loss and a range of additional adverse environmental impacts (Pimentel, Zuniga, & Morrison, 2005; Tricarico, Junqueira, & Dudgeon, 2016). Invasive bivalves, in particular, are often considered to be ecosystem engineers by creating and modifying aquatic habitats and transforming resource availability (Sousa, Gutiérrez, & Aldridge, 2009).

The Asian clam *Corbicula fluminea* is considered to be one of the 100 worst invasive species in Europe (Delivering Alien Invasive Species Inventories for Europe [DAISIE], 2008). It has spread from its native range in Southeast Asia to Europe, Africa, North and South America over the last century (Araujo, Moreno, & Ramos, 1993; Clavero et al., 2012; Darrigran, 2002; Phelps, 1994). This bivalve's invasive success stems from its rapid, productive and efficient life-cycle (Aldridge & McMahon, 1978; reviewed in McMahon, 2002), a reproductive system with hermaphroditic potential for self-fertilization and androgenesis (Britton & Morton, 1982; Kraemer & Galloway, 1986), high ecological competence, close association with human activities, wide genetic variability and phenotypic plasticity, and generalist filter-feeding habits (Sousa, Antunes, & Guilhermino, 2008).

The adverse ecological impacts of *C. fluminea* have been widely documented. The invasion by this clam can affect submerged vegetation, phytoplankton, zooplankton, and higher trophic levels (Sousa, Antunes et al., 2008). Dense clam populations have been linked to declines in native bivalves (Darrigran, 2002; Sousa, Antunes et al., 2008; Sousa, Ilarri, Souza, Antunes, & Guilhermino, 2011; Strayer, 1999; Vaughn & Hakenkamp, 2001). Massive Asian clam mortality constitutes a nutrient source promoting water quality degradation (Cherry, Scheller, Cooper, & Bidwell, 2005; Cooper, Bidwell, & Cherry, 2005). Positive impacts of the Asian clam have also been described. Some benthic species can benefit from habitat enrichment by deposition of empty shells (Ilarri, Souza, Antunes, Guilhermino, & Sousa, 2014; Ilarri et al., 2012) and organic matter or nutrients released from the sediments to the water column (reviewed in Vaughn & Hakenkamp, 2001). Conversely, the filtration ability of these clams contributes to significant increases in water clarity (Phelps, 1994). Besides ecological effects, the biofouling activity of the Asian clam can have severe economic impacts. Juveniles are drawn from invaded water bodies and dense populations may accumulate in low-flow areas within freshwater-dependent industries or irrigation settings, often translating into severe economic losses (Mackie & Claudi, 2010; Pimentel et al., 2005; Rosa et al., 2011).

Since dispersal into new habitats is a determinant stage in the invasion process (Davis, 2009), understanding the mechanisms of colonization and the ecological preferences of clams is a key asset for their adequate management (Belz, Darrigran, Netto, Boeger, & Ribeiro, 2012; Hoyer, Schladow, & Rueda, 2015; Kappes & Haase, 2012; Leung et al., 2002). The rapid spread of *C. fluminea* includes human vectors (Brancotte & Vincent, 2002; Britton, 1982; Karatayev, Padilla, Minchin, Boltovskoy, & Burlakova, 2007; Minchin, 2014) and passive transport by waterfowl (Britton, 1982) and fish (Cantanhêde, Hahn, Gubiani, & Fugi, 2008; Gatlin, Shoup, & Long, 2013). However, at the local scale natural dispersal is predominantly achieved by

downstream drift of juveniles (Hoyer et al., 2015; Mouthon, 2003) but it has also been claimed to occur upstream (Voelz, McArthur, & Rader, 1998).

While the interconnectivity of drainage catchments provides favourable conditions for the spread of the Asian clam (Lucy, Karatayev, & Burlakova, 2012), few studies have addressed its dispersal dynamics in such systems (Lucy et al., 2012; Minchin, 2014). Thus, some uncertainties remain regarding facilitating factors and obstacles. For example, the unique ecological conditions of interconnected drainage ditches favour the growth of threatened sphaeriids (Watson & Ormerod, 2005). Also, vegetated waterways can act as a barrier to the downstream dispersal of planktonic larvae of the invasive zebra mussel (Bodamer & Bossenbroek, 2008); such barriers may similarly affect benthic *C. fluminea* juveniles. Where water levels are controlled by dikes, they can pose an additional challenge to dispersal (Gangloff, Hartfield, Werneke, & Feminella, 2011).

This study was conducted in a semi-artificial drainage catchment, where intercommunicating ditches may have facilitated the spread of clams, and where dikes may have inhibited their dispersal. In fact, Asian clam density is highly heterogeneous throughout this system with several ditches remaining free from them, and thus provides an ideal context for exploring the distribution pattern of the clam, and its potential impacts on benthic communities. Furthermore, the catchment structurally typifies irrigation facilities that are widely recognized as susceptible to the fouling activity by Asian clam (Ingram, 1959; Mackie & Claudi, 2010; Prokopovich & Hebert, 1965; Rosa et al., 2011). Thus, interpreting colonization successes and failures in this dynamic context should contribute to management strategies targeted at prevention and control stages.

The primary aim of the present study was (i) to contribute towards a better understanding of *C. fluminea* spread patterns and colonization constraints. To do so, a snap-shot sampling widely covering the catchment was established to characterize water column, benthic compartments and hydromorphology of each site. This also allowed the bioassessment of water quality variation throughout the catchment on the basis of the macroinvertebrate assemblages, thus addressing further research questions on (ii) whether the presence of Asian clams relates to changes in benthic communities, and consequently (iii) if they have impacts on the 'ecological status' of water bodies under the WFD.

2 | METHODS

2.1 | Study area and sampling strategy

This study was carried out in a semi-natural drainage catchment in the Littoral Central region of Portugal (Figure 1), in the hydrographic basin of the River Vouga. It includes a network of interconnected ditches of varying sizes, resembling the structure of agricultural irrigation settings. A series of sequential dikes controls the water level throughout the system.

To represent spatial variation within the catchment, five sub-catchments with different degrees of connectivity were selected for this study, and sampled during late spring 2014 (Figure 1). Sampling
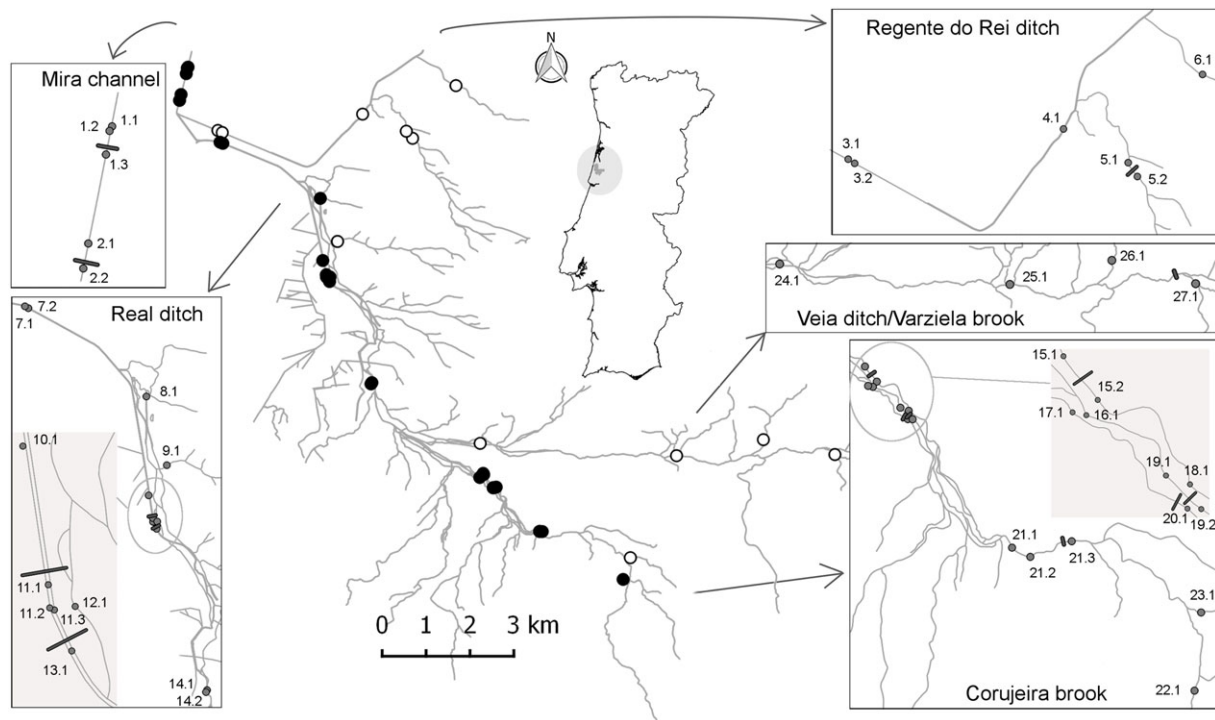
FIGURE 1 Geographic location of 40 study sites in the Littoral Central Portugal. For practical purposes and to improve readability, the study area was artificially divided into five systems, all separately zoomed: Mira channel (MC; five sites); Regente do Rei ditch (RR; six sites); Real ditch (RD; 12 sites); Corujeira brook (CB; 13 sites); Veia ditch and Varziela brook (VV; four sites). Site numbering followed an ascending order from downstream to upstream, and different decimals for a given site designation indicate habitat variants within the same location (e.g. 2.2 was located at the head of a dike and 2.1 downstream of the dike). Sites are represented by symbols, with black and white circles distinguishing invaded and non-invaded sites, respectively, and dikes are represented by bacillary bars

sites were defined within each sub-catchment taking into account site heterogeneity and the occurrence of dikes. In total, 40 sampling sites (Figure 1) were characterized according to (i) water physico-chemistry; (ii) sediment organic burden and particle size distribution; (iii) hydromorphology; (iv) benthic macroinvertebrate community structure; (v) ecological status; (vi) Asian clam density and size structure.

2.2 | Water analysis

Water temperature, pH, dissolved oxygen and conductivity were recorded *in situ* using a multiparameter probe (WTW-Multi3430). Water samples were collected and transported in the dark at 4°C to the laboratory for vacuum filtration through GF/C filters (1.2 μm pore size). The residue was used to quantify total suspended solids (American Public Health Association [APHA], 1995) and Chl *a* content (Lorenzen, 1967). The filtrate was used to quantify coloured dissolved organic carbon (Williamson, Morris, Pace, & Olson, 1999), calcium, alkalinity and hardness by colorimetric analysis (APHA, 1995). Turbidity was indirectly measured according to the absorption coefficient at 450 nm of unfiltered water samples (Brower, Zar, & von Ende, 1998). Total phosphorus and nitrogen content were determined by the tin(II) chloride method (APHA, 1995) and cadmium reduction method (Lind, 1979), respectively, after mineralization of unfiltered samples with potassium persulphate (Ebina, Tsutsui, & Shirai, 1983).

2.3 | Sediment analysis

Sediment samples from the top 5 cm were collected for particle size analysis by pooling samples obtained from three to five locations at each site to achieve a composite sample (~500 g) reflecting small-scale patchiness. The samples were transported to the laboratory at 4°C in the dark, sorted to remove debris and oven-dried (70°C for 24 h) before determining organic content by loss-on-ignition (450°C for 6 h; Kristensen & Andersen, 1987). The incinerated samples were used for quantifying fines by wet sieving (≤ 63 μm) with sodium hexametaphosphate (Pope et al., 2000). The retained fraction (> 63 μm) was oven dried and weighed to the nearest 0.01 g; the following fractions were separated in a sieve shaker and weighed: >4000, >2000–4000, >1000–2000, >500–1000, >250–500, >125–250, 63–125 μm. Fractions were converted to the phi scale, and the median, mode and quartile deviation were determined by graphical interpolation of the cumulative particle-size distribution (Pope et al., 2000).

2.4 | Habitat characterization and hydromorphology

Complementary hydromorphological parameters (Raven, Dawson, & Everard, 1998), were recorded: depth; channel and water width; flow velocity, as the mean of three independent measurements at each site with a flow meter (Global water, FP101); presence of different types of macrophytes and presence of filamentous algae; continuity of riparian vegetation on both banks; shading cover of the channel.

2.5 | Macroinvertebrate sampling and analysis

Based on the proportional composition of microhabitats (Hering et al., 2003), benthic macroinvertebrates were collected by kick-sampling from six 1-m transects with a standard hand net (0.30 × 0.30 m; ø 500 μm), using the same sampling effort (in time) across sites.

Macroinvertebrate samples were preserved in 80–90% ethanol until sorting; the organisms then were counted and identified to the lowest practicable taxonomic level, generally the family (Edington & Hildrew, 2005; Elliott & Humpesch, 2010; Hynes, 1993; Pawley, Dobson, & Fletcher, 2011; Sundermann, Lohse, Beck, & Haase, 2007; Tachet, 2000; Wallace, Wallace, & Philipson, 2003). The following macroinvertebrate community metrics were calculated based on family level identification: richness (S), diversity (Shannon's H′) and equitability (Pielou's J′). Three biotic indices were also calculated: (i) EPT, i.e. the number of Ephemeroptera, Plecoptera and Trichoptera taxa; (ii) IBMWP, the sum of pre-defined tolerance (to pollution) scores for each taxon (Alba-Tercedor & Sánchez-Ortega, 1988; Jaímez-Cuéllar et al., 2002); and (iii) IASPT, the average score per taxon, derived from IBMWP.

2.6 | Determination of ecological status

The ecological quality of each sample was determined as an Ecological Quality Ratio (EQR) following the criteria designed to conform to the WFD. For this catchment, EQRs were derived from the multimetric index $IPtl_S$ (South Invertebrate Portuguese Index; INAG, 2009; JRC, 2009):

$IPtl_S$ = 0.4 × S + 0.2 × EPT + 0.2 × (IASPT - 2) + 0.2 × log (sel. EPTCD +1), where S, EPT, IASPT and log (sel. EPTCD +1) are community metrics and biotic indices that must be normalized to corresponding reference values before calculation. The first three metrics were as described above; sel. EPTCD is the sum of abundances of Chloroperlidae, Nemouridae, Leuctridae, Leptophlebiidae, Ephemerellidae, Philopotamidae, Limnephilidae, Psychomyiidae, Sericostomatidae, Elmidae, Dryopidae and Athericidae. EQRs were then calculated by standardizing $IPtl_S$ to the corresponding reference value. Reference values for all metrics were obtained from official guidance documents (INAG, 2009), for rivers from Central Littoral Portugal (INAG, 2008). The following intervals were used to categorize ecological status: 'high', if EQR > 0.74; 'good', if 0.74 > EQR > 0.56; 'moderate', if 0.56 > EQR > 0.37; 'poor', if 0.37 > EQR > 0.19; and 'bad', if EQR < 0.19 (INAG, 2009).

2.7 | Asian clam sampling and processing

Clams were sampled with a Van Veen grab (0.05 m^2). Composite samples were obtained by pooling the content of five grabs (three grabs in sites with exceptionally high clam densities) at each site. After sieving through a 1-mm mesh size bag, clams were counted, and shell lengths were measured with a digital Vernier calliper.

2.8 | Data analysis

Environmental data were compiled into multivariate matrices for: (i) water, (ii) sediment, (iii) hydromorphology, and (iv) biotic (macroinvertebrate metrics) subsets. Principal Component Analysis (PCA) was run within each subset to describe spatial gradients,

centring and standardizing variables to avoid scaling effects (Ter Braak, 1995). Biplots were used to interpret gradients using symmetrical scaling (Gabriel, 2002). Extracted gradients were further analysed by running one-way ANOVA on PCA sample scores of the first two axes to test whether sites invaded by *C. fluminea* differed from non-invaded sites. Correlation analysis was used to explore the association between PCA scores and log density of *C. fluminea*, considering all sites or only invaded sites; this was used to allow the possibility that clams were absent owing to constraints to dispersal, which could cause spurious correlations when all sites are considered. Given that EQRs are integrated indicators of the ecological status of water bodies, they were addressed in the same way as PCA scores.

Detrended Correspondence Analysis (DCA) was used to describe macroinvertebrate community structure, using the untransformed matrix of species abundances (Ter Braak, 1995). One-way ANOVA and correlation analyses were applied as above on the DCA axes scores. As an additional effort to understand the putative effect of clams over macroinvertebrate communities, Canonical Correspondence Analysis (CCA) was conducted (Ter Braak, 1995) on the macroinvertebrate data, using two data matrices as explanatory data: (i) an environmental matrix pooling all environmental variables; (ii) a clam matrix composed of a binomial variable expressing the presence (1) or absence (0) of clams and a continuous log density variable. Manual forward selection of environmental variables was used to reduce the environmental dataset to non-redundant and significant variables (Monte Carlo permutation tests, $P \leq 0.05$). Applying the variation partitioning technique described by Borcard, Legendre, & Drapeau (1992), CCA and partial CCA allowed the amount of variation of the macroinvertebrate dataset to be ascribed to the environmental matrix or to the clam matrix (see other examples in Castro & Gonçalves, 2011; Vidal et al., 2014). These procedures could clarify whether clams might explain some variation in the macroinvertebrate communities, after removing (i.e. partialling out, *sensu* Ter Braak, 1988) confounding environmental influences. CCA models were tested for significance ($P \leq 0.05$) using a Monte Carlo unrestricted permutation test.

3 | RESULTS

The Asian clam was unevenly distributed across the study area (Figure 2). Sub-catchments RR and VV were completely free from the clam, while the remaining sub-catchments showed wide variation in clam density (4.1–3076.9 clams m^{-2}). The absence of clams in sites 9.1 and 23.1 is notable, given that these sites are integrated in highly invaded sub-catchments RD and CB; both these clam-free sites are in tributaries of the main ditch. Overall, most of the sites supported populations of small individuals (shell length < 20 mm). In the lower reaches (see MC and sites 7.1 and 7.2), the smallest, hence youngest, individuals (shell length < 5 mm) dominate; in upstream sites smaller individuals are rare.

3.1 | Variation of *C. fluminea* distribution with respect to environmental gradients

Sediments were generally homogeneous across the study area (Figure 3a; Table S2). Although PC1 and PC2 reflected particle size and

FIGURE 2   Total density of *Corbicula fluminea* in 40 study sites (in log scale). Stacked bars are used to provide information on shell length classes found at each sampled site. The bars were ordered from the most downstream locations in MC system to the most upstream locations in VV system (see Figure 1 for the system definition). The grey vertical lines indicate the relative position of the main dikes throughout the catchment
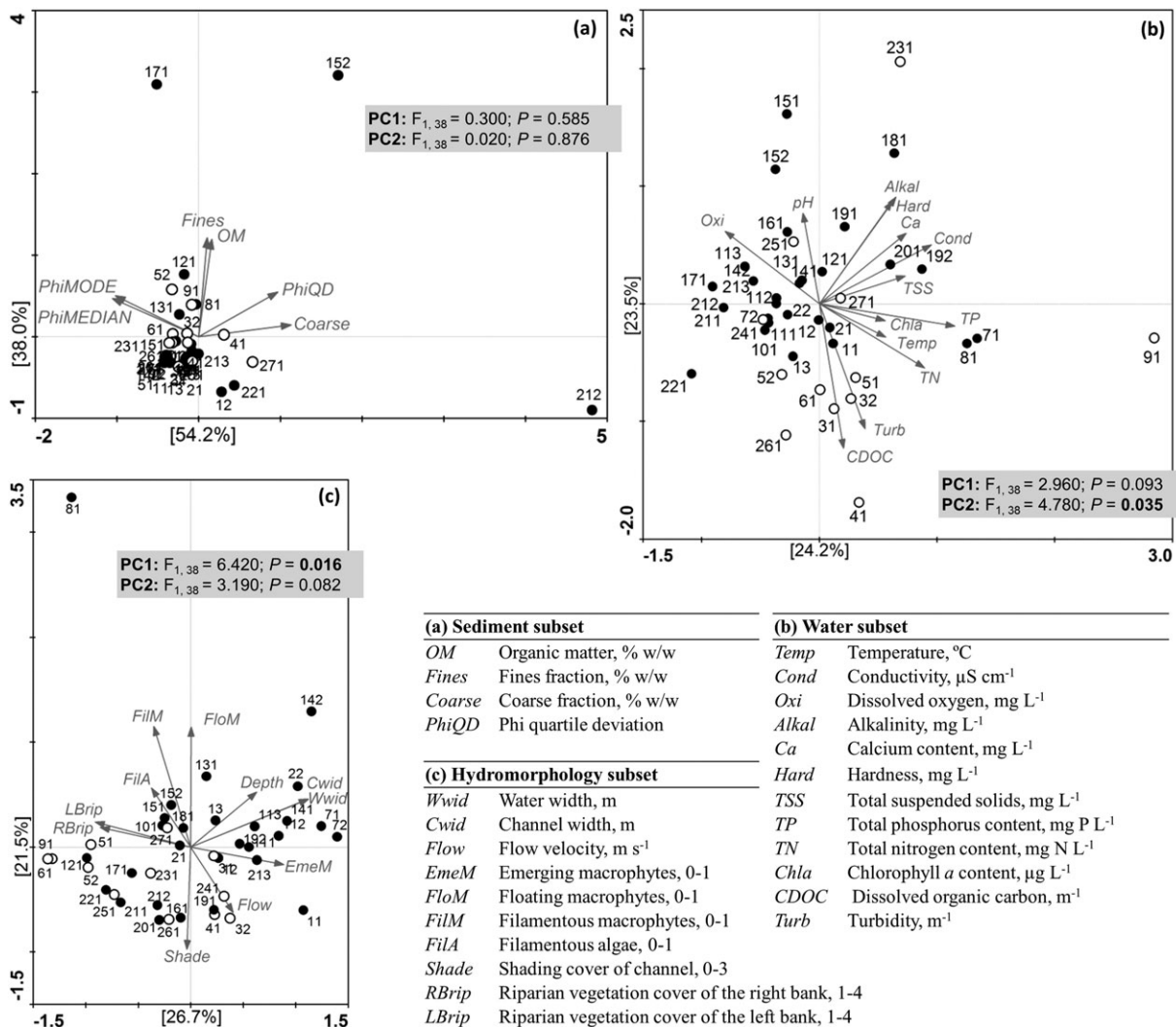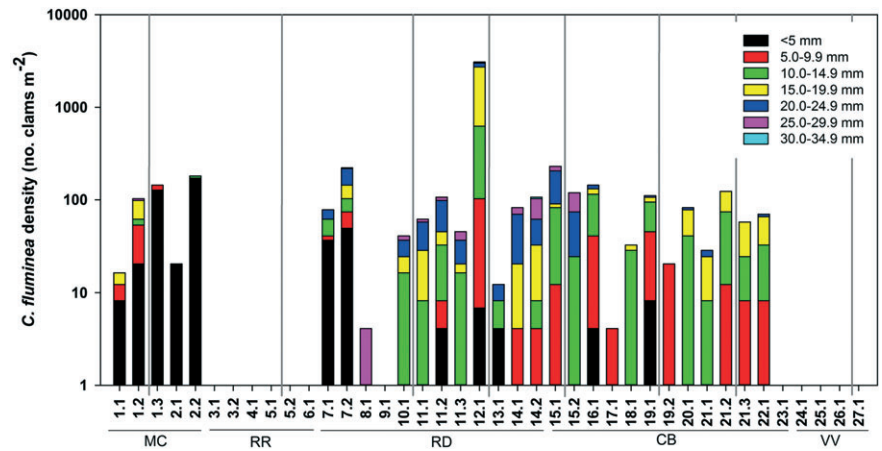

FIGURE 3   Ordination (PCA) biplots representing the distribution of 40 study sites according to the (a) sediment, (b) water, (c) hydromorphology subsets. Grey arrows represent environmental gradients and, on the bottom right corner, the abbreviations used for the variables and corresponding units are shown. Site scores are represented by black (invaded) and white (non-invaded) circles; for clarity, site numbering was simplified (for example, site 1.1 reads here as 11). The percentage of variance explained by PC1 (horizontal axis) and PC2 (vertical axis) was added to the corresponding axis in each diagram within square brackets. One-way ANOVA summaries comparing invaded and non-invaded sites by PCA scores are displayed in each biplot within grey-shadowed frames

organic load, respectively, dense clustering of sample scores close to the origin was observed (Figure 3a). Sediments were mostly composed of coarse- and medium-granule sand, with low particle sorting (phi QD).

Sites 15.2, 17.1 and 21.2 were a notable exception, with a higher percentage of fines, coarse particles and/or organic matter content. Sediment characteristics were weak predictors of Asian clam distribution

(no distinction between invaded and non-invaded sites was found – see ANOVA summary in Figure 3a). Moreover, sediments did not constrain clam density as suggested by the absence of significant correlations between density records and PC1 or PC2 (Table 1).

The physico-chemistry of water samples (raw data in Table S1) showed heterogeneity across the catchment (Figure 3b), with differential scores relating to mineralization (conductivity, hardness) and organic load (TN, CDOC, turbidity). Grouping of sites according to the presence or absence of clams (Figure 3b) was supported by significantly lower PC2 scores for non-invaded sites (ANOVA summary in Figure 3b). This suggests that the clams were generally more common at sites with higher dissolved oxygen levels, higher pH and mineral-rich waters, whereas they were not present in the more turbid and carbon-rich waters. Asian clam density was only partially dependent on water physico-chemistry, as indicated by the significant correlation between density and PC2 scores for all sites but not for invaded sites (Table 1).

The hydromorphology of the catchment also indicated heterogeneity (Figure 3c; Table S3), with a marked contrast between wider or deeper ditches, where emergent macrophytes were present (right side of diagram), and narrower or shallower ditches, where riparian cover was greater (left side of diagram). Sites with higher cover of filamentous and floating-leaved macrophytes were those where emerging macrophytes were practically absent and where shading was lower (see opposing vertical gradients in Figure 3c). The primary gradient was related to the distribution of clams, as revealed by a significant distinction of PC1 scores between invaded and non-invaded sites (ANOVA summary in Figure 3c); it was also significantly correlated with *C. fluminea* density, but only when all sites were considered (Table 1). In fact, clams occur across the entire environmental gradient (black circles in Figure 3c), but were less frequent in shallower and narrower ditches.

3.2 | Impact of *C. fluminea* on ecological status and benthic communities

The biotic subset (Table S4) revealed an ecological quality gradient ranging from high to low scores in biotic index values (primary axis;

TABLE 1 Summary of the correlation analyses between log density of *C. fluminea* (considering all sites or only the invaded sites) and the PCA scores (PC1 and PC2) from the environmental and biotic subsets, or the DCA scores from the macroinvertebrate community ordination. Significant correlations are shown in bold

	All sites Pearson coeff.	*P*	Invaded sites Pearson coeff.	*P*
Sediment PC1	0.145	0.371	0.144	0.464
Sediment PC2	−0.057	0.727	−0.170	0.388
Water PC1	−0.291	0.068	−0.163	0.408
Water PC2	0.355	**0.025**	0.211	0.282
Hydromorphology PC1	0.375	**0.017**	0.107	0.586
Hydromorphology PC2	0.116	0.475	−0.288	0.137
Biotic metrics PC1	0.036	0.824	−0.123	0.534
Biotic metrics PC2	−0.076	0.639	−0.044	0.824
Macroinvertebrates Axis 1	0.187	0.253	0.463	**0.015**
Macroinvertebrates Axis 2	0.104	0.529	−0.190	0.342

Figure 4a) and in abundance and unevenness of samples (secondary axis; Figure 4a). Ecological quality metrics were poorly related to clam distribution, as confirmed by the absence of significant differences between invaded and non-invaded sites (ANOVA summary in Figure 4a), and by the lack of significant correlation between PC scores and clam density (Table 1). Also, no significant correlations between EQR scores and clam density were found, either considering all sites ($r = -0.065$; $P = 0.691$) or when restricted to invaded sites ($r = 0.052$; $P = 0.793$). Sites with clam densities >100 individuals m^{-2} were consistently representative of almost the entire range of EQR classifications (poor–good; Figure 4b); in addition, the ecological status of several non-invaded sites was classified as bad (25.1) and poor (3.1–5.1; 27.1). This was reinforced by the absence of significant differences in EQR scores between invaded and non-invaded sites (ANOVA: $F_{1, 38} = 0.37$; $P = 0.535$).

Despite the environmental heterogeneity of the catchment, macroinvertebrate community structure was comparatively homogeneous, resulting in dense clustering of DCA sample scores (Figure 5a). Invaded **F5** and non-invaded sites were not distinct ecologically (ANOVA summary in Figure 5), suggesting that clam presence tends not to constrain other benthic invertebrates. Similar evidence is suggested by CCA, with environmental variables such as oxygen, TN, TP, flow, depth, Chl *a*, filamentous algae, SST, shade, channel width, phiQD and organic matter being more important in explaining macroinvertebrate variation than clam presence or density (Table 2). Overall, environmental data explained 65.5% of the variation while clam contribution was negligible (2.9%, and non-significant). The intersection of both explanatory datasets explained 7.1% of the total variation, with 24.5% remaining unexplained.

In contrast, clam density in invaded sites was significantly correlated with axis 1 DCA scores (Table 1), corresponding to a moderate association ($r = 0.463$; Figure S1) between these variables. It is represented by increasing *C. fluminea* densities from the left to the right side of the sample scatterplot (Figure 5a); higher *C. fluminea* densities were therefore associated with taxa on the right side of the species scatterplot (Figure 5b). Functionally, these taxa include scraper grazers (e.g. Hydroptilidae, Limnephilidae) and collector gatherers (e.g. Beraeidae, Elmidae, Ephemerellidae, Hydrobiidae, Psychomyiidae). On the other hand, predators (e.g. Atyidae, Ceratopogonidae, Erpobdellidae, Glossiphoniidae) and shredders (e.g. Anthomyiidae, Asellidae) were more common on the opposite side of the biplot (Figure 5b), generally corresponding to sites with lower clam density.

4 | DISCUSSION

The spatial distribution pattern of Asian clams in the catchment studied suggests the downstream connectedness of populations. Asian clam was absent from entire sub-catchments, as well as upstream ditches within heavily invaded sub-catchments. This primarily confirms passive downstream dispersal of smaller individuals with the water current, which is recognized as the main mechanism for local dispersal of *C. fluminea* in both lotic and lentic systems (Hoyer et al., 2015). Passive transport upstream by animal vectors or human activities appears to be limited in this catchment, despite its recognized
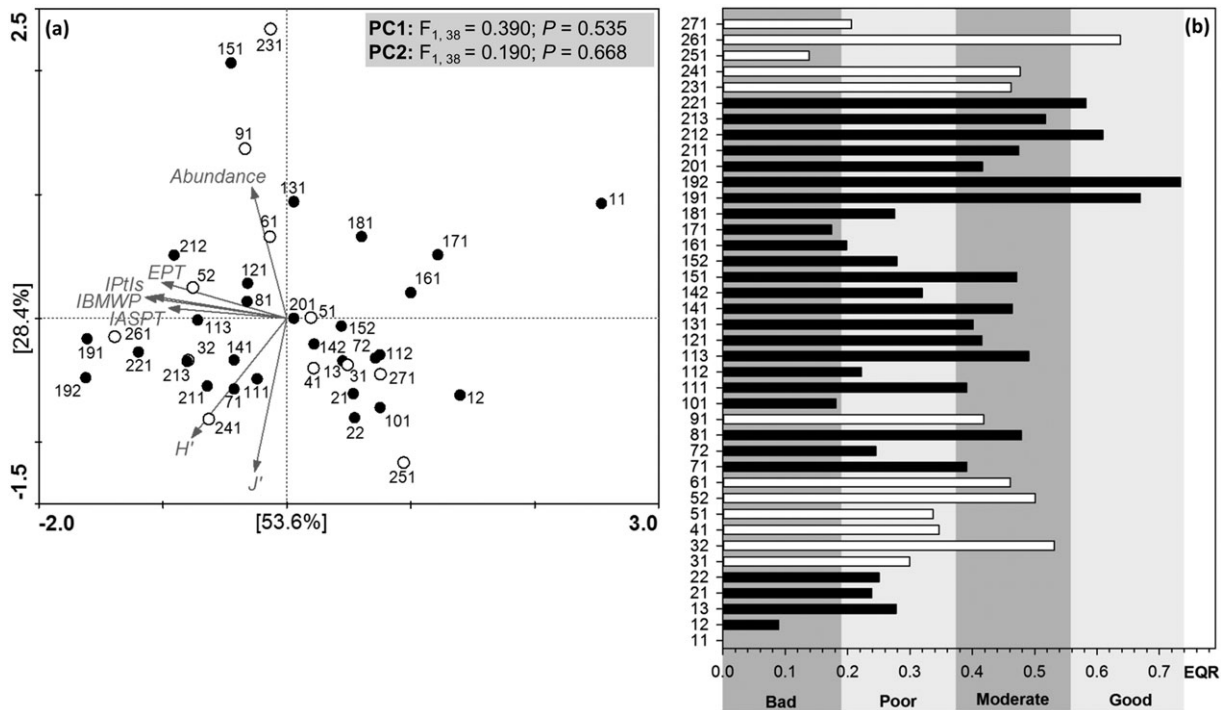
FIGURE 4 Ordination (PCA) biplot showing the distribution of 40 study sites according to biotic metrics derived from the macroinvertebrate community (a), and resulting EQR calculated for all sampled sites (b). Black and white circles (panel a) or bars (panel b) distinguish invaded and non-invaded sites, respectively, and grey arrows in (a) represent environmental gradients. As in Figure 3, site numbering was simplified for clarity, percentage of variance explained by axis is given and the ANOVA summary is displayed (significance of the comparison between invaded and non-invaded sites)
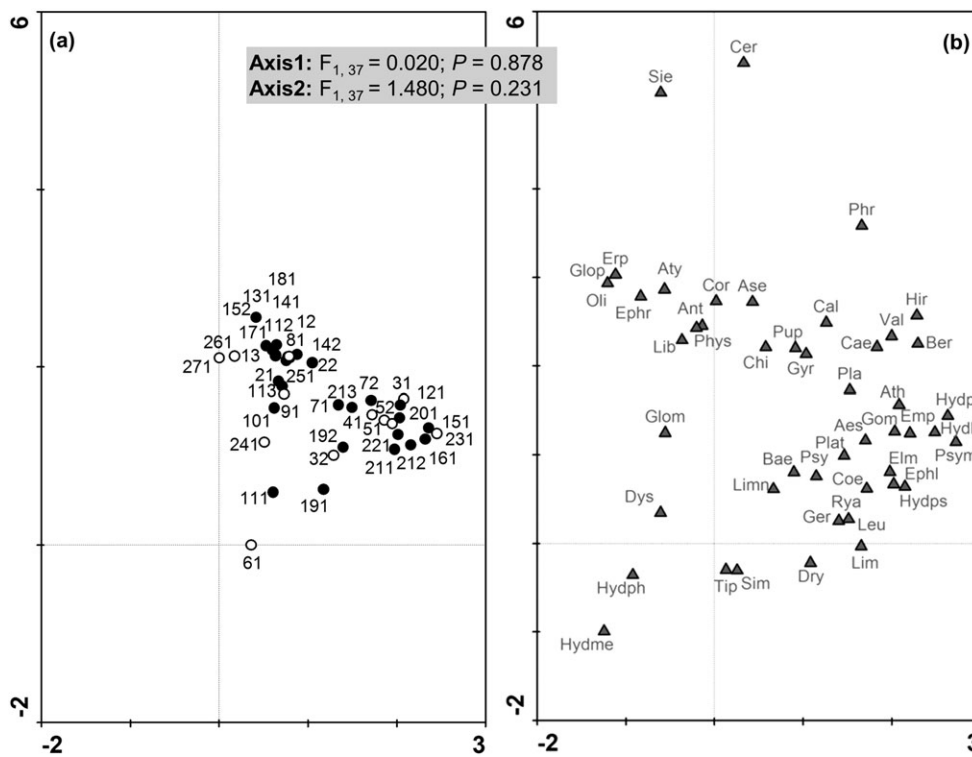

FIGURE 5 Ordination (DCA) scatterplots representing the distribution of 40 study sites according to the abundance of macroinvertebrate families; to facilitate visualization, sample scores are shown as circles in panel (a) separately from taxon scores as triangles in panel (b). Black and white circles in panel a) distinguish invaded and non-invaded sites, respectively. As in previous figures, site numbering was simplified for clarity and the ANOVA summary is displayed (significance of the comparison between invaded and non-invaded sites). Macroinvertebrate abbreviations in panel (b) can be found in Table S5. Site 1.1 was excluded from the analysis because there were no taxa other than Corbiculidae

TABLE 2 CCA summary applied to the macroinvertebrates dataset, showing partitioning of variation between 'environment' and 'clam' data (presence and abundance). For each explanatory dataset, full and partial models are shown, as well as their significance (Monte Carlo permutation test, $P \leq 0.05$). Partial models represent the variation due to one subset after excluding the shared component of variation with the other subset

Source of variation	Eigenvalue	Total inertia (total variation)	F	P	Proportion of variance explained
Environment	1.675	2.307	5.8	0.002	72.6%
Environment | clam	1.510	2.307	5.3	0.002	65.5%
Clam	0.231	2.307	2.0	0.062	10.0%
Clam | environment	0.066	2.307	1.4	0.100	2.9%

importance (Hubenov, Trichkova, Kenderov, & Kozuharov, 2013; Schmidlin & Baur, 2007). In fact, these populations were apparently unable to actively disperse upstream (Voelz et al., 1998); this may be a feature of populations in this catchment, whose juveniles apparently lack typical mucous threads (Rosa et al., 2014) that assist associated dispersal (McMahon, 1983; Prezant & Chalermwat, 1984). In addition, the role of dikes as barriers to the spread of invasive species has been suggested (Gangloff et al., 2011; Rahel & Olden, 2008) but this preventive effect was not apparent in the present study. Young clam populations were found in lower reaches of the catchment and, in general, no discontinuities across dikes were found considering the size class structure of pre- and post-dike populations; this signals the ability to cross the barrier by young, lighter juveniles suspended in the overflow.

Given that dikes did not seem to act as a barrier to clam dispersal, the environmental heterogeneity of the catchment was expected to play a role in defining the invasion dynamics, yet sediment features were not a major determinant of clam distribution and density. Although Asian clam generally prefers finer sediments (Cooper, 2007; Lucy et al., 2012; Schmidlin & Baur, 2007), coarse- or medium-granule sand substrates dominate this catchment, lending support to an affinity for coarser substrate that has been documented elsewhere (Leff, Burch, & McArthur, 1990). Other studies have found no feasible correlations between *C. fluminea* population parameters and physico-chemical habitats, including substrate type (Boltovskoy, Correa, Cataldo, Stripeikis, & Tudino, 1997; Gangloff et al., 2011). An association with sediment organic load was also expected, given *C. fluminea* feeding strategies (Reid, McMahon, Foighil, & Finnigan, 1992). A short, low-range gradient in sediment organic matter limits interpretation, as well as the fact that richer sediments (sites 12.1, 15.1 and 17.1) were either severely or mildly invaded by the Asian clam. Conversely, clear positive correlations between clam distribution and sediment organic load have been reported from systems with similar and larger gradients in organic load (Sousa, Antunes, & Guilhermino, 2006; Sousa, Rufino, Gaspar, Antunes, & Guilhermino, 2008), while other studies showed no significant correlation (Boltovskoy et al., 1997). The interplay between filter-feeding, with consequent deposition of unassimilated organic material (faeces and pseudofaeces) in the sediment, and pedal-feeding that promotes removal of organic material from sediments (Hakenkamp & Palmer, 1999; Karatayev, Burlakova, & Padilla, 2005; Phelps, 1994; Sousa et al., 2009; Vaughn & Hakenkamp, 2001), might help to explain the ambiguous role of organic matter load as a descriptor of Asian clam distribution in invaded systems.

Unlike sediment, water physico-chemistry and channel hydromorphology influenced the distribution of clam density, but they

did not clearly separate invaded and non-invaded sites. A notable exception was the non-invaded RR sites with distinct water physico-chemistry (3.1–6.1; Figure 3b), i.e. with lower mineralization, pH and dissolved oxygen but higher organic load. However, the absence of clam cannot be explained by comparing the values for these variables (Table S1) and *C. fluminea* tolerance ranges. Water mineral content can constrain the establishment of Asian clam owing to the requirement for shell production. For example, Sousa, Rufino et al. (2008) reported positive correlations between water hardness and the density of *C. fluminea*, although their hardness values were lower than those observed in the present study for non-invaded water bodies; indeed, the ranges found in the present study for hardness and calcium content were within the optimal range for *C. fluminea* establishment (Ilarri & Sousa, 2012). Also, pH was higher than the lower limit of tolerance of 5.6 (Karatayev et al., 2005), while dissolved oxygen was above levels limiting growth (1–3 mg L^{-1}; Belanger, 1991) and high potential for massive invasion (Ilarri & Sousa, 2012). Upper tolerance limits to dissolved organic carbon or turbidity for the Asian clam are high (Ilarri & Sousa, 2012); thus, these parameters should not explain the absence of the species from RR sites. The relationship between nutrient load and *C. fluminea* distribution was also not clear since high nutrient levels were found both in invaded and non-invaded sites; in fact, this relationship is still poorly understood (Nakamura & Kerciku, 2000; Pigneur et al., 2014). These findings add weight to the hypothesis that sites without *C. fluminea* are like this because clams have not yet reached there rather than because of unfavourable environmental conditions.

Clam distribution was weakly associated with channel hydromorphology, with an apparent preference of clams for deeper and wider ditches, although an incipient depth gradient was also apparent (range: 0.10–0.80 m). *Corbicula fluminea* populations are found across an extended depth range (shallow–24 m; Minchin, 2014). The preference for wider channels might be related to the avoidance of shaded areas linked to lower water temperatures (*C. fluminea* prefers warmer waters; Simard et al., 2012). The environmental gradient found for flow was wider, but did not correspond to any clear clam preference pattern – both running and standing waters can sustain clam populations with density records of more than 100 individuals m^{-2} (Table S3). Similarly, Boltovskoy et al. (1997) and Gangloff et al. (2011) found no correlations between flow and *C. fluminea* distribution in invaded systems. Furthermore, while some studies evidenced higher clam density in lotic vs. lentic systems (Karatayev et al., 2005; Lucy et al., 2012), others demonstrated lower success of the clam in colonizing turbulent waters (Schmidlin & Baur, 2007). The response of clams to flow conditions has been

concomitantly related to the systems' productivity (Karatayev et al., 2005; Pigneur et al., 2014; Schmidlin & Baur, 2007), and dispersal (Eng, 1977; Hoyer et al., 2015). The limited range of spatial variation of resource variables in the catchment studied may have acted as confounding factors, preventing clear identification of differential preferences. Although in the present study neither macrophytes nor filamentous algae seem to deter the Asian clam, this contrasts with evidence from the literature. For example, Karatayev, Burlakova, Kesterson, & Padilla (2003) found non-overlapping distribution of Asian clam and submerged waterthyme, which was linked to oxygen depletion below the macrophyte bed (*C. fluminea* is intolerant to even moderate hypoxia; Matthews & McMahon, 1999); no oxygen limitation was found within the study area (Table S1). It is also reasonable to hypothesize that seasonal exudates from some macrophytes have the potential to promote segregation via allelopathic interference (Stamp, 2003); however, the sampling surveys were not designed to capture this phenomenon.

Environmental variables were the major descriptors of macroinvertebrate distribution, rather than the presence or density of clams. This implies that there is apparently no impact of Asian clams on benthic communities in this catchment, unlike those documented in other studies (see below). However, an association between the clam and scraper-grazers and collector-gatherers was apparent. Other studies have reported positive correlations between Asian clam density and macroinvertebrates in general or with particular groups (Howard & Cuffey, 2006; Ilarri et al., 2012; Sampaio & Rodil, 2014; Schmidlin, Schmera, & Baur, 2012; Soucek, Schmidt, & Cherry, 2001). The presence of clams can favour other invertebrates by contributing to the organic enrichment of the benthic compartment (Sousa et al., 2009). On the other hand, shell deposition by dense populations represents major structural changes to the benthic substrate, resulting in increased provision of novel substrata for attachment and refuge (Bódis, Tóth, Szekeres, Borza, & Sousa, 2014; Gutierrez, Jones, Strayer, & Iribarne, 2003; Schmidlin et al., 2012; Sousa et al., 2009). Amphipods and chironomids can be favoured by both clam-related organic material and sediment restructuring (Ilarri et al., 2012, 2014; Sampaio & Rodil, 2014; Werner & Rothhaupt, 2008). Gastropods have been positively associated with Asian clam on the basis of shell use as refuge and as surfaces for scraper-grazing and oviposition (Ilarri et al., 2012; Sampaio & Rodil, 2014). Although a part of the benthic biota can be favoured by Asian clam, concurrent detrimental effects in the native trait spectrum (Strayer, 2012) should not be disregarded. For example, increase in the density of native clams was observed after experimental dredging to remove *C. fluminea* in Lake Tahoe (Wittmann et al., 2012). Several studies have more directly demonstrated strong relationships between the establishment of *C. fluminea* and a decline in native bivalves (Ilarri et al., 2012; Sousa et al., 2011). These latter contribute to the typical molluscan diversity of valuable wetland systems and drainage catchments (Herzon & Helenius, 2008; Prezant & Chapman, 2004). Such a risk to native molluscan diversity was not observed in the present study as no bivalves other than *C. fluminea* were found. Gastropods were generally rare, except for Hydrobiidae, which were abundant and widespread, possibly as the result of unmonitored diffuse pollution sources that could favour tolerant taxa (such as Hydrobiidae; SNIFFER, 2007).

Similarly to the structure of the macroinvertebrate community, ecological water quality (*sensu* WFD) appeared to be largely unaffected by *C. fluminea*. A notable case was site 12.1, which supports a highly dense, stable population (Rosa et al., 2014). At this site, ecological quality was moderate, and there were few invaded or non-invaded sites that scored higher. These inconsistencies suggest that integrative water quality metrics can be relatively insensitive to the impact of an invasive species, supporting the need for integrating any specific descriptor for alien species within the assessment methods – see an overall context for this perspective in Tricarico et al. (2016). It is also worth noting the strong effect that *C. fluminea* may have on benthic bacteria and periphyton communities through its pedal-feeding activity, the latter being a key component of biological quality assessment, *sensu* WFD. Therefore, the potential nuisance effects of *C. fluminea* should be studied further with enhanced emphasis on specific indicator biota.

Asian clam invasion has been mostly studied in directional, continuous lotic systems, or relatively isolated lentic water bodies. This study concerned dispersal constraints and the impacts of clam invasion in a catchment resembling agricultural drainage ditches, where a sequential dike system is used to control water levels. Drainage ditches are among the most extensive freshwater habitats in agricultural areas and low lands (Verdonschot, Keizer-Vlek, & Verdonschot, 2011), providing food supply and adequate niches for diverse aquatic biota (often including rare species) and performing connectivity functions within intensively managed, and often dry, croplands (reviewed by Herzon & Helenius, 2008). These attributes emphasize the ecological value of drainage ditches and highlight the need for comprehensive knowledge of the dynamics and impacts of invasive species, so that appropriate management and conservation strategies can be implemented in such non-natural habitats.

Overall, the results suggest minimal constraints to dispersal and the broad ecological competence of the clam. It appears that (i) clams spread only in areas where accidental or deliberate introductions have occurred in the past; (ii) clam dispersal is mostly driven by downstream drift; (iii) dikes do not prevent dispersal but they may act as a population bottleneck favouring the transport of smaller clams. These observations reinforce the relevance of pest management measures focused at preventing new human-driven introduction of invasive bivalves (see Tricarico et al. (2016) for a review on the European policy and recommendations for alien species management). They also raise the possibility of developing biological control strategies based on predation on young populations (Pereira et al., 2016) that might be especially applicable downstream of dikes. There were only mild associations of Asian clam distribution with the environmental variables, and the patterns observed were often inconsistent with reported ecological preferences of the species. Considering that tolerance ranges and ecological preferences are used as descriptors of the invasion risk by Asian clam (Mackie & Claudi, 2010), these results highlight the need to rethink early-warning systems available to manage the threat. Clams also showed no major effects on the biological water quality or on benthic macroinvertebrate assemblages. Perhaps this was because the invasion is recent and still within a lag phase (Rosa et al., 2011), or because the system studied is so modified that the effects of *C. fluminea* on sensitive native species are otherwise

eclipsed. Either way, this outcome (a less 'sexy' one, according to Strayer, 2012) contributes to reducing the bias of meta-analyses that summarize invasion impacts; these integrative studies are often derived from the literature, where idiosyncratic contexts of severe impacts of invasive species tend to be over-emphasized.

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