



Original Articles

Corbicula fluminea (Corbiculidae, Bivalvia) alters the taxonomic and functional structure of benthic assemblages in neotropical hydropower reservoirs

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ABSTRACT

The objective of this study is to understand how the taxonomic and functional structures of benthic macro-invertebrate assemblages respond to variations in the densities of *Corbicula fluminea*, an invasive species originated in Asia, in neotropical hydropower reservoirs. For that we tested three hypotheses: (1) Sites with higher densities of *C. fluminea* exclude benthic taxa linked to soft substrates and increase the densities of taxa linked to hard substrates. (2) Sites with higher densities of *C. fluminea* support higher diversities than those with natural soft substrates. (3) Higher densities of *C. fluminea* support higher functional diversities than the natural soft substrate sites. Our results show that *C. fluminea* densities are correlated with changes in the taxonomic structure, namely substitution of burrowing taxa for those related to hard substrates, and with increased functional diversity. No taxonomic index showed significant correlation with *C. fluminea* density, but the functional indices (Functional Richness, Functional Dispersion and Rao's Quadratic Entropy) showed significant positive correlations. Our results show that functional traits are more sensitive ecological indicators of biological alteration of physical habitat than those based on taxonomic composition and diversity metrics.

1. 1.Introduction

Ecosystem engineers are species that alter the physical habitat of the ecosystems in which they live and become established (Jones et al., 1994). Ecosystem engineers and the alterations they bring to local habitats are an essential part of ecological processes, such as ecological succession, and they influence species distribution and assemblage taxonomic composition (Oliveira et al., 2011; Zaiko and Daunys, 2015). These effects are especially pronounced when the ecosystem engineers are invasive species, as their presence and density can severely alter other species and ecosystem conditions (Crooks, 2002; Karatayev et al., 2007a; Sousa et al., 2009), including nutrient cycling and energy flux (Linares et al., 2020).

Invasive species are especially common in tropical hydropower reservoirs, where the anthropogenically altered ecological conditions facilitate their introduction and establishment (Linares et al., 2020;

Ricciardi, 2007). Mollusks are one of the most successful groups of freshwater invasive species in reservoirs because their physiological and ecological adaptations confer the capacity to reproduce and generate fertile offspring with a high probability of survival (Jarić et al., 2019; Karatayev et al., 2007b; Zhan et al., 2015).

Among the many invasive species in freshwater ecosystems, *Corbicula fluminea* (Bivalvia, Corbiculidae) is one of the most successful in South America (Darrigran et al., 2020; Labaut et al., 2021; da Rosa and Dantas, 2020). This species was first registered in the La Plata estuary in the 1970's, and now is present in most of the continent's major river systems (Boltovskoy et al., 2009; Cataldo and Boltovskoy, 1998; Darrigran et al., 2020; Reshaid et al., 2017). *C. fluminea* establishment can cause substantial environmental disturbances in natural ecosystems, by displacing native bivalves and other filter-feeders, serving as vectors of parasites, and producing economic losses by biofouling (Cao et al., 2017; Crespo et al., 2015; Sousa et al., 2008). In anthropogenically

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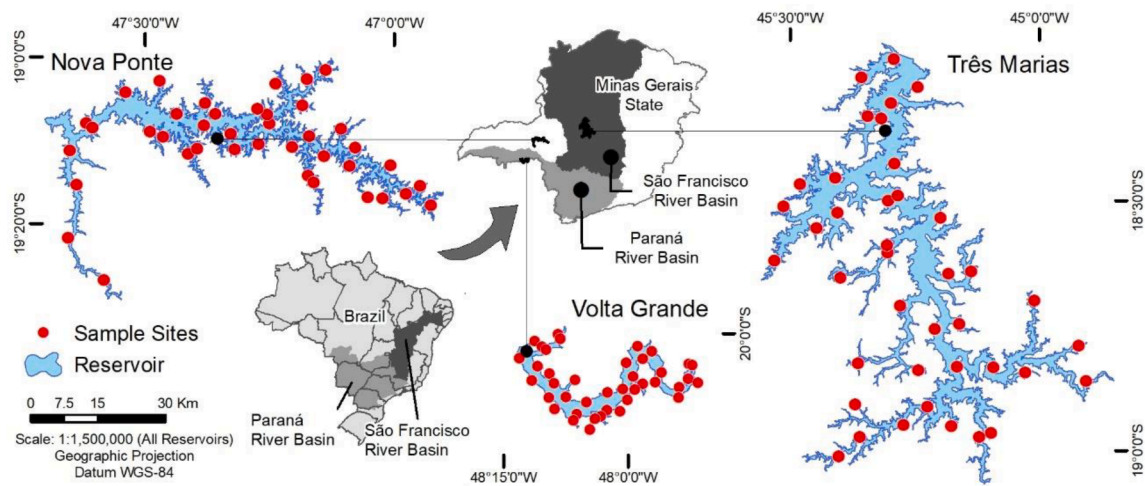


Fig. 1. Sampling site locations in Nova Ponte, Volta Grande and Três Marias reservoirs, southeastern Brazil.

altered ecosystems, on the other hand, the ecological response is more nuanced, as *C. fluminea* can become an important factor in the structure and function of the ecosystem and is often associated with increased richness and diversity of benthic macroinvertebrate assemblages in areas where they become established (Darrigran, 2002; Linares et al., 2017; Suriani et al., 2007).

Whereas there are some studies on the effects of *C. fluminea* on the structure and functioning of neotropical freshwater ecosystems (e.g., Ferreira-Rodríguez et al., 2018; Lercari and Bergamino, 2011; Linares et al., 2017), there is still a knowledge gap on how benthic macroinvertebrate assemblages respond to a gradient of density of this species in neotropical reservoirs. Therefore, the objective of this study was to understand the degree to which the taxonomic and functional structures of benthic macroinvertebrate assemblages are associated with variations in *C. fluminea* densities in neotropical hydropower reservoirs. For that

we tested three hypotheses. (1) Sites with higher *C. fluminea* densities have fewer benthic taxa linked to soft substrates and more taxa linked to hard substrates. We predicted that *C. fluminea* densities would be negatively linked to the abundances of soft substrate taxa and positively linked to the abundances of hard substrate taxa. (2) Sites with higher *C. fluminea* densities would support higher taxonomic diversities than those with natural soft substrates. We predicted that diversity metrics (Shannon-Wiener diversity index, Simpson diversity index and Pielou Evenness) would be positively related to *C. fluminea* densities. (3) Sites with higher densities of *C. fluminea* would support higher functional diversities than the natural soft substrate sites. We predicted that functional diversity indices (Functional Richness, Functional Uniformity, Functional Divergence, Functional Dispersion and Rao's Quadrat Entropy) would be positively related to *C. fluminea* densities.

2. Material and methods

2.1. Study area

We collected data from three neotropical hydropower reservoirs (Nova Ponte, Três Marias and Volta Grande; Supplementary Material S1), located in the State of Minas Gerais, southeastern Brazil (Fig. 1). In each reservoir, we defined 40 sampling sites through use of systematic spatially balanced procedures (Macedo et al., 2014; Stevens and Olsen, 2004), focusing on the littoral zone, which is the area with the highest habitat and taxa richness and diversity (Becker et al., 2015; de Moraes et al., 2017; Martins et al., 2015). From a randomly selected point, sampling sites were systematically distributed by dividing the perimeter into equidistant distances from each other (Macedo et al., 2014). In total, we selected 120 sampling sites, 40 in each hydropower reservoir. Sampling occurred in 2009 (Nova Ponte), 2011 (Três Marias), and 2012 (Volta Grande) in April, at the end of the rainy season, ensuring that the reservoirs were at the highest possible water level and consequently with the highest possible habitat diversity (Callisto et al., 2019). All three reservoirs are characterized by fairly similar physical habitat conditions, with oligotrophic waters and homogenous fine sediment substrates, and previous studies have shown that these variables had little effect on the taxonomic structure of the benthic macroinvertebrate assemblages (Martins et al., 2015; Moraes et al., 2016).

2.2. Benthic Macroinvertebrate sampling

In the littoral zone of each site, we sampled benthic macroinvertebrate assemblages by using three Eckman-Birge grabs (0.0675 m² total area). The sediment samples were stored in plastic bags and fixed in

Table 1			
Functional traits and categories used for freshwater macroinvertebrates.			
No.	Functional Traits	No.	Categories
1	Respiration	1	Tegument
		2	Gill
		3	Plastron
		4	Spiracle
2	Locomotion	1	Burrower
		2	Crawler
		3	Attached
		4	Swimmer
		5	Flyer
3	Voltinism	1	≤1 reproductive cycle
		2	>1 reproductive cycle
4	Body flexibility	1	Low < 10°
		2	Moderate > 10–45°
		3	High > 45°
5	Aquatic stages	1	Egg
		2	Larva
		3	Nymph
		4	Adult
6	Adult lifespan	1	Very Short
		2	Short
		3	Long
7	Body shape	1	Streamlined
		2	Flattened
		3	Cylindrical
		4	Spherical
8	Feeding habits	1	Gathering-collector
		2	Shredder
		3	Scraper
		4	Filtering-collector
		5	Predator

10% formalin, then they were washed through a sieve (0.5 mm mesh) with tap water in the laboratory. Benthic macroinvertebrates were identified to the lowest possible level, with most being identified to family. Chironomidae (Insecta, Diptera) individuals were identified to genus and non-native invasive species, namely *Melanoides tuberculata* and *Corbicula fluminea*, to species level. In the neotropics, family level identification is usually the highest possible taxonomic resolution to be achieved for many taxa, due to the huge biodiversity and minimal taxonomic knowledge of most groups. Even when identification to a finer level is possible, it is often too time-intensive to be used in bio-monitoring programs. In addition, many studies have shown that family level identification is able to attain the same accuracy as lower taxonomic level identification in both biomonitoring and ecological studies (Bailey et al., 2001; Buss and Vitorino, 2010; Silva et al., 2016).

All specimens collected were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais. We calculated abundance, taxa richness, Shannon-Wiener diversity index (Shannon, 1948), Simpson diversity index (Simpson, 1949) and Pielou evenness (Pielou, 1966) for each sampling site.

2.3. Functional trait characterization

To characterize the functional structure of the macroinvertebrate assemblages, we produced a trait database comprising eight functional traits and 30 trait categories (Table 1). These functional characteristics were compiled (Supplementary Material S2), first based on neotropical studies (e.g., de Castro et al., 2017; Firmiano et al., 2021; Jovem-Azevêdo et al., 2019; Martins et al., 2021; Tomanova and Usseglio-Polatera, 2007). When functional characteristics were not available for neotropical taxa, we used literature from North America (Pilière et al., 2016; Poff et al., 2006) and Europe (Serra et al., 2016). The categories of characteristics selected involved macroinvertebrate aspects to reflect different environmental conditions, for example food resources, such as phytoplankton and zooplankton. Feeding habits are closely related to the type of resource available, allowing us to infer the cycling of nutrients in ecosystems (Jovem-Azevêdo et al., 2019), important for their functioning. In addition, we included aspects related to life history (e.g., respiration, voltinism and aquatic stages), morphology (body flexibility and body shape) and mobility (locomotion and adult lifespan) of macroinvertebrates.

We used a fuzzy coding approach (Chevenet et al., 1994) to describe the affinity of each taxon for each category within a functional trait. A score was assigned to each taxon for each feature category according to its affinity, ranging from 0 to 3, with 0 - indicating “no affinity”, 1 - indicating “weak affinity”, 2 - indicating “moderate affinity”, and 3 - indicating “strong affinity” (Chevenet et al., 1994). This coding methodology allowed us to compensate for the different types of levels of information available about characteristics of organisms in numerical values. The affinity scores of each taxon for a given trait were standardized so that their sums were equal to 1, ensuring the same weight for each taxon and for each trait in later analyses. Assemblage trait profiles were obtained by multiplying the frequency of each category by the abundances of taxa (Gayraud and Philippe, 2001). This resulted in a trait-by-sites matrix, which contained the abundance of each trait at each site, for subsequent analysis.

Functional diversity (FD) was evaluated by applying five complementary indices that measure different aspects of taxa in functional space: Functional Richness, Functional Uniformity, Functional Divergence (Villéger et al., 2008), Functional Dispersion (Laliberté and Legendre, 2010) and Rao's Quadratic Entropy (Botta-Dukát, 2005). (1) Functional Richness (FRic) represents the volume of the functional space (convex hull), occupied by the species of an assemblage (Villéger et al., 2008). (2) Functional Uniformity (FEve) is a measure of regularity with which the functional trait space is occupied by the abundance of species in an assemblage (Villéger et al., 2008). (3) Functional Divergence

(FDiv) analyzes how functionally dispersed the most abundant species are in an assemblage within the functional trait space (Villéger et al., 2008). (4) Functional Dispersion (FDis) represents the average distance of each species in the space of functional characteristics from the centroid of all species in the assemblage, weighted by relative abundance (Laliberté and Legendre, 2010). (5) Rao's Quadratic Entropy (Rao's Q) is defined as the expected dissimilarity between two individuals of a given assemblage in the space of functional characteristics weighted by their relative abundances (Botta-Dukát, 2005).

All functional diversity index calculations were performed using the dbFD function of R software (R Core Team, 2015) of the FD package (Laliberté and Legendre, 2010). A distance matrix was obtained with the functional trait data, using the Gower distance (Gower, 1966), from which we extracted via Principal Coordinate Analysis (PCoA) the first two axes, used together with the taxa abundance matrix to estimate functional diversity indices (Schleuter et al., 2010). We maintained the first two axes of the PCoA after testing (Supplementary Material S3) the quality of the functional space (Maire et al., 2015).

2.4. Data analyses

To test our first hypothesis, we performed Threshold Indicator Taxa Analysis (TITAN) to detect change points in the macroinvertebrate taxa responses to *C. fluminea* density. TITAN combines change point and indicator species analyses to detect abrupt changes in the abundance and frequency of taxa along the *C. fluminea* density gradient, and uses bootstrap resampling (1000 permutations) to create 95% confidence intervals (Baker and King, 2010). Change points indicate where along the continuum of a disturbance variable that various taxa in a response assemblage begin to appear (z +) or disappear (z-).

To test if sites with higher densities of *C. fluminea* supported higher taxonomic diversities than those with natural soft substrate, we ran generalized linear models (GLMs). In doing so, we used the macroinvertebrate diversity variables (Shannon-Wiener diversity, Simpson diversity, Pielou evenness) versus the density of *C. fluminea*. The GLMs used Gaussian distribution (Ives and Freckleton, 2015) and to determine if the variables showed positive or negative correlations from the deviations from the *C. fluminea* densities, we then calculated Pearson correlations (r) for all models. All analyses were done using R software version 3.5.1 (R Core Team, 2015).

To test if higher densities of *C. fluminea* supported higher functional diversities than the natural soft substrate sites, we ran generalized linear models (GLMs). In doing so, we used the macroinvertebrate functional diversity variables (Functional Richness, Functional Uniformity, Functional Divergence, Functional Dispersion and Rao's Quadratic Entropy) versus the densities of *C. fluminea*. The GLMs used Gaussian distribution (Ives and Freckleton, 2015). To determine if the variables showed positive or negative correlations from the deviations from the *C. fluminea* densities, we then calculated Pearson correlations (r) for all models. These analyses also were done using R software version 3.5.1 (R Core Team, 2015).

Because site locations may result in a lack-of-independence (or spatial autocorrelation) among our sites, we performed a Moran's I test for spatial autocorrelation (Lecocq et al., 2019; Smeraldo et al., 2020). To do so, we used the residuals of our tested models using the spdep package (version 1.1.2; Bivand and Wong, 2018) in R (R Development Core Team, 2015). No tested model indicated spatial autocorrelation (Supplementary Material S4).

3. Results

We collected a total of 3003 benthic macroinvertebrates divided among 43 taxa (Supplementary Material S1). The *C. fluminea* density in the sampled sites varied between 0 and 1644 individuals/m², with a mean value of 476.54 individuals/m² for the 38 sites with the presence of the species. TITAN analysis detected 12 benthic macroinvertebrate

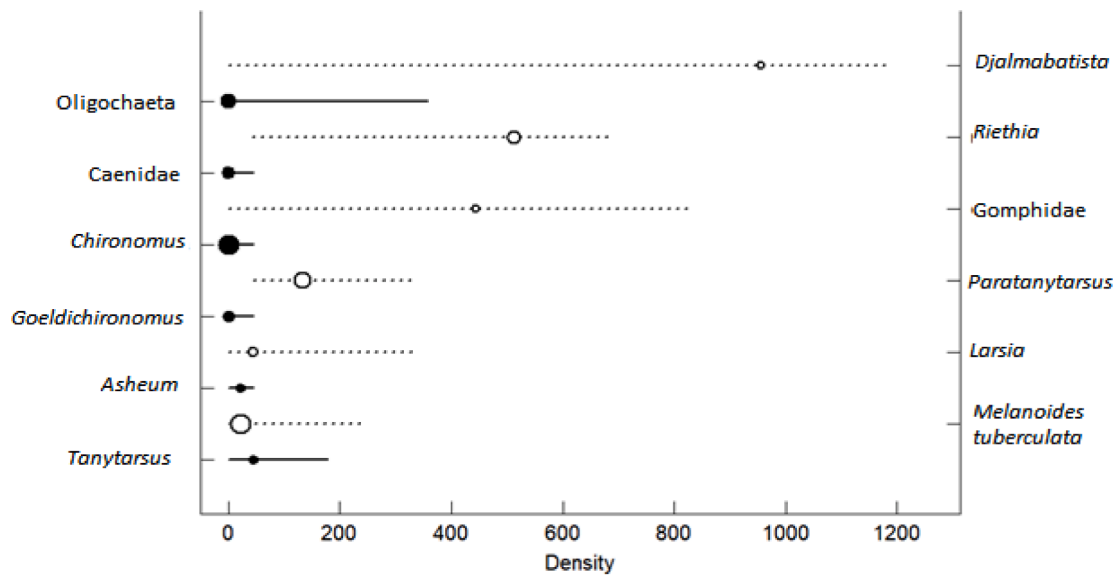


Fig. 2. Robust indicator taxa identified by TITAN in response to *Corbicula fluminea* density. Lines (solid or dashed; Z- and Z+ respectively) represent 95% confidence intervals of observed change points (black or open circles; Z- and Z+ respectively).

Table 2

Benthic macroinvertebrate assemblage Shannon-Wiener diversity, Simpson diversity, and Pielou evenness correlations with *Corbicula fluminea* density.

Variable	<i>p</i>	<i>F</i>	Pearson <i>r</i>
Shannon-Wiener	0.8711	0.0264	−0.016
Simpson	0.8996	0.016	−0.012
Pielou	0.09337	2.8657	−0.004

Table 3

Macroinvertebrate Functional Richness (Fric), Functional Uniformity (Feve), Functional Divergence (Fdiv), Functional Dispersion (Fdis) and Rao's quadratic entropy (Rao's Q) correlations with *Corbicula fluminea* density. Values in bold represent significant correlations.

Variable	<i>p</i>	<i>F</i>	Pearson <i>r</i>
Fric	0.01002	6.8998	0.26
Feve	0.0636	3.521	−0.19
Fdiv	0.2396	1.4002	0.12
Fdis	< 0.001	19.819	0.41
Rao's Q	< 0.001	24.025	0.45

taxa with a significant response (purity and reliability ≥ 0.95) to *C. fluminea* densities (Fig. 2). Caenidae (Ephemeroptera), *Asheum* (Chironomidae, Diptera), *Chironomus* (Chironomidae, Diptera), *Goeldichironomus* (Chironomidae, Diptera), *Tanytarsus* (Chironomidae, Diptera) and *Oligochaeta* (Clitellata) were significantly less abundant (Z-). On the other hand, *Djalmabatista* (Chironomidae, Diptera), *Riethia* (Chironomidae, Diptera), *Paratanytarsus* (Chironomidae, Diptera), *Larsia* (Chironomidae, Diptera), Gomphidae (Odonata) and *Melanoides tuberculata* (Thiaridae, Gastropoda) were significantly more abundant (Z+).

Results for taxonomic and functional diversities differed. No taxonomic diversity metrics (Shannon-Wiener index, Simpson index, Pielou evenness) showed significant correlation with *C. fluminea* densities (Table 2). Regarding functional diversity metrics (Table 3), Functional Richness (Fric; $p = 0.01$, $F = 6.90$), Functional Dispersion (Fdis; $p < 0.001$, $F = 19.82$) and Rao's Quadratic Entropy (Rao's Q; $p < 0.001$, $F = 24.02$) showed significant positive correlations with *C. fluminea* densities. On the other hand, Functional Uniformity (Feve; $p = 0.06$, $F = 3.52$) and Functional Divergence (Fdiv; $p = 0.24$, $F = 1.40$) showed no significant correlations.

4. Discussion

C. fluminea changes the substrate of sites where its population is established, especially in high densities, because its shells accumulate into a hard tridimensional substrate (Darrigran et al., 2020; Sousa et al., 2008; Werner and Rothhaupt, 2007). These ecological effects can be especially dramatic in the littoral areas of hydropower reservoirs that are characterized by unconsolidated, undifferentiated soft substrates (de Moraes et al., 2017; Martins et al., 2015). Our results show that the densities of *C. fluminea* populations can be an important driver for the taxonomic composition and functional structure of benthic macroinvertebrate assemblages in hydropower reservoirs.

We found that all benthic taxa that showed a negative correlation with *C. fluminea* density were characterized as burrowers (Firmiano et al., 2021; Martins et al., 2021). Thus, the physical environment changes associated with this invasive ecosystem engineer are deleterious to this locomotion mode of some other benthic macroinvertebrates. Because of the accumulation of living individuals and their shells, higher densities of *C. fluminea* can hinder the access of burrowing taxa to soft substrates, therefore limiting their access to food items and shelter from predators (Hakenkamp et al., 2001; Ward and Ricciardi, 2007).

Some taxa had a positive relation (Z+) with the biologically altered complex habitat created by *C. fluminea*, which can provide microhabitats and food items that would not be easily available in reservoirs (de Moraes et al., 2017; Linares et al., 2020; Martins et al., 2015). South American native freshwater communities usually lack powerful benthic suspension feeders that can provide a direct link between benthic and water column components of the ecosystem, a role that *C. fluminea* assumes especially in lentic ecosystems like reservoirs (Crespo et al., 2015; Dias et al., 2014; Sousa et al., 2008). Previous studies using thermodynamic indicators showed that *C. fluminea* provides a strong link to production in the water column and the benthic habitat in neotropical reservoirs, increasing the complexity of benthic macroinvertebrate assemblages (Linares et al., 2019, 2018, 2017).

The functional diversity effects that we found may also be a result of *C. fluminea* altering the complexity of the substrate as an ecosystem engineer. Increased physical habitat heterogeneity increases benthic macroinvertebrate assemblage functional diversity (Milesi et al., 2016), which is supported by the positive correlation between *C. fluminea* density and Functional Richness (Fric). The significant results of Functional Dispersion (Fdis) and Rao's quadratic entropy (Rao's Q) show that

another component of functional diversity, the functional dissimilarity of the individuals of the assemblage, showed significant positive correlation with *C. fluminea* density (Mouchet et al., 2010). This result suggests that the sites altered by the invasive bivalve have a wider range of microhabitat that can be exploited by different taxa with different traits (Karadimou et al., 2016). These results also suggest that functional indicators are more sensitive to physical habitat alterations than taxonomic indicators, since the latter failed to detect those variations in our study.

5. Conclusions

Our results show that densities of invasive *Corbicula fluminea* are important drivers for the taxonomic and functional structure of benthic macroinvertebrate assemblages in neotropical hydropower reservoirs. They also show that ecological indicators based on functional traits are more sensitive to physical habitat alteration resulting from *C. fluminea* colonization than those based on taxonomic variables. These results indicate the importance of considering the taxonomic and functional structure of aquatic macroinvertebrates in the biomonitoring of neotropical hydropower reservoirs. The results also help us understand the influence of invasive species as ecosystem engineers on the structure and functioning of these aquatic ecosystems. Thus, we strongly recommend that environmental monitoring and hydropower companies that focus on invasive species assessments use functional indices, that are more sensitive to the changes caused by their function as ecosystem engineers.

CRedit authorship contribution statement

Marden S. Linares: Conceptualization, Methodology, Writing – original draft. **Pedro H.M. Amaral:** Methodology, Writing – review & editing. **Marcos Callisto:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109115>.

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