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Lower parasite pressure in invasive freshwater bivalves than in sympatric native Unionidae mussels in southern European lakes

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Abstract The Enemy Release Hypothesis (ERH) proposes that the success of bioinvasions is attributable to lower enemy pressure on invasive species compared to native ones, giving a competitive advantage for invaders. In line with the hypothesis, we previously observed in northern European bodies of fresh water that invasive bivalves were subject to lower parasite pressure than sympatric native mussels. Here, we investigated ERH in three southern European lakes, where the native mussels are rapidly declining and being replaced by non-native bivalves. In total, 679 bivalves (n of individuals per species per lake varying from 12 to 187) were collected during 2016–2018. Ten parasite taxa were found. The mean lake-specific number of parasite taxa in the native mussels (*Anodonta exulcerata*, *A. cygnea*, *A. anatina*

and *Unio elongatulus*) was 2.6 times that in the invasive bivalves (*Dreissena polymorpha*, *Corbicula fluminea* and *Sinanodonta woodiana*). Similarly, the mean lake-specific sum of prevalences of infection by different parasite taxa in the native mussels was 3.4 times that in the invasive bivalves. Notable was the complete lack of parasites in *C. fluminea*. Thus, the results supported the Enemy Release Hypothesis and were in accordance with previous results from northern Europe, suggesting, on average, a lower parasite pressure in invasive bivalves than in sympatric native mussels. As parasites are usually harmful, this may contribute to the observed successful invasion of non-native freshwater bivalves in Europe.

Keywords Bivalvia · Biological invasion · Enemy release hypothesis · Freshwater · Mussel · Parasite · Unionida

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Introduction

Biological invasions are one of the major causes of biodiversity loss, biotic homogenization and species endangerment (Olden et al. 2004; Lockwood et al. 2013). There are several hypotheses regarding the success and mechanisms of bioinvasions (Jeschke and Heger 2018), one of the prominent being the Enemy Release Hypothesis (ERH) (Elton 1958). The ERH suggests that the invaders are released from their natural enemies, e.g., predators, parasites or pathogens,

during the invasion process, which will lead to a low enemy pressure on invaders in the invaded area and give the invaders an advantage when competing with local, native species (Elton 1958; Heger and Jeschke 2014). Reduction in the invader's parasite and pathogen pressure in the invaded area when compared to the original area has been observed across a wide range of bioinvasions (e.g., Mitchell and Power 2003; Torchin et al. 2003; Blumenthal et al. 2009; Liu and Stiling 2006; Lowry et al. 2013) and host–parasite relationships can modify the invasion outcome, depending on several factors (Chalkowski et al. 2018).

There are three rationales behind the ERH related to parasites as enemies. First, parasites are harmful to host individuals and therefore may be able to regulate the host populations (e.g., Grenfell and Dobson 1995). Second, parasites are generally highly host-specific, i.e., can only infect certain species or even genotypes of hosts that exist in certain geographic areas or environments, and with which they have had a common co-evolutionary history (e.g., Price 1980). Third, the invaders often cannot bring their parasites with them, either because they were introduced as a larval stage, which is frequently parasite-free, or because of the lack of suitable intermediate hosts in the new environment if the parasite has a complex multi-host life cycle.

Unionid mussels are an important component of freshwater ecosystems because of their filter-feeding nature and potentially high biomass such that they can influence nutrient cycling and provide many essential ecosystem services (Strayer 2014; Vaughn 2018; Zieritz et al. 2022). However, the invasion of non-native bivalves is threatening native freshwater mussels (Unionida). Notably, *Corbicula fluminea* (Asia Clam) and *Sinanodonta woodiana* (Chinese pond mussel), both frequently outperforming native mussels, are rapidly expanding their range in Europe (Bespalaya et al. 2018; Karaouzas et al. 2020; Urbańska et al. 2021). Some studies have investigated the key characteristics associated with the success of invading freshwater bivalves (e.g., Donrovich et al. 2016; Labecka and Domagala 2018; Urbańska et al. 2018), although the role of enemy release as a contributor to their success has not received much attention. However, evidence for enemy release in freshwater bivalves was recently provided for northern European waterbodies (Taskinen et al. 2021), such

that in sympatric populations the invasive bivalves showed lower values of parasite pressure indices than the native freshwater mussels. In addition, according to the recent review by Karatayev et al. (2024), more natural enemies were found in *Dreissena* spp. in their native range in Europe than in invasive *Dreissena* spp. in North America.

In Europe, the decline of freshwater mussels is most alarming in the Mediterranean region (Benson et al. 2021; Lopes-Lima et al. 2021; Nogueira et al. 2021), a biodiversity hotspot region that is seriously threatened more generally (Cuttelod et al. 2009). Therefore, the aim of the present study was to extend the approach of Taskinen et al. (2021) to the Mediterranean region, to investigate the ERH in southern Europe by comparing the parasite loads of sympatric invasive and native bivalves. The target lakes were Lake Maggiore, Lake Varese and Lake Lugano in Italy, where the native mussel populations are declining rapidly (e.g., Riccardi et al. 2022). Importantly, sharp declines of native freshwater mussels in these lakes can be attributed to invasion by invasive bivalves. For instance, before the introduction of *Corbicula fluminea* (Kamburska et al. 2013a) and *Sinanodonta woodiana* (Kamburska et al. 2013b) the density of the native *Unio* population in Lake Maggiore remained stable even if subjected to periodic die-offs due to drought (Ravera et al. 2007), but after the establishment of *C. fluminea* it decreased by 75%. A similar trend was observed in Lake Varese and Lake Lugano after the invasion and establishment of *C. fluminea* and *S. woodiana* (N. Riccardi, personal communication). Many factors may be involved in the decline of native populations, including parasites, which may be favored by recent increases in temperatures (see Taskinen et al. 2022) and droughts, as the adverse effects of parasites are commonly intensified by environmental stress (e.g., Jokela et al. 2005). In this case, the impact of parasites could reduce the fitness of native mussels, already affected by climate change, in comparison to invasive species if invasive ones were less infected, as predicted by ERH. Therefore, we hypothesized in our study that the invasive bivalves experience, on average, lower parasite pressure than the native ones in these southern European lakes, as predicted by the ERH. To explore this hypothesis, we compared two parasite pressure indicators—parasite taxon richness and the sum of prevalences of all parasite taxa (Torchin et al. 2003;

Lafferty et al. 2010)—between the native and invasive bivalve populations living in sympatry in the three lakes.

Materials and methods

Sampling and laboratory work

The study was conducted in three Italian lakes, Lake Maggiore, Lake Varese and Lake Lugano, where both native and invasive freshwater bivalves live in the same sites and are potentially exposed to similar parasites. At each sampling location, we inspected an area of 50 m along the shoreline by 50 m offshore. The bivalves were collected by hand or by sieving the sediments through a 2×2 mm mesh size net within 0.5×0.5 m squares. All sites were surveyed by wading in shallow areas (<1 m) and by scuba diving at deeper depths (1–15 m). In Lake Maggiore, sampling was conducted in 2016, 2017 and 2018, and in Lake Varese and Lake Lugano in 2017. Material from Lake Varese (191 bivalves) and Lake Lugano (63 bivalves) originated from one

sampling occasion from one site. Those from Lake Maggiore (425 bivalves) were combined from 13 sampling occasions from eight sites around the lake (Breggia, Belgirate, Magadino, Baveno, Cannobio, Feriolo, Punta Granelli and Germignaga). The number of native and invasive species varied from one to four and from two to three per lake, respectively, and the number of individuals analysed per species per lake from 12 to 187 (Table 1).

Bivalves were transported alive to the laboratory in lake water, except for *Corbicula fluminea*, which were placed in ethanol immediately after collection. The tissues examined for parasites included mantle, gills, digestive gland and gonad, which are the typical sites of parasite infection in freshwater bivalves (Grizzle and Brunner 2009) and those that were examined by Taskinen et al. (2021) for northern Europe. Parasite examination was conducted under a stereo microscope, pressing the tissue, piece by piece, between two large, customized glass plates and inspecting microscopically using transmitted light (Taskinen et al. 1991). The ciliate results for *C. fluminea* were not included as the ethanol storage may interfere with their identification.

Table 1 Parasite taxon richness (N taxa) and sum of prevalences of infection (Prev. sum) in native and invasive bivalve species in the three study lakes, together with the number of studied bivalve individuals (N studied)

	Bivalve species	N studied	N taxa (orig.)	N taxa (std.)	Prev. sum
<i>Lake Maggiore</i>					
Native	<i>Anodonta anatina</i>	37	6	4.62	130
	<i>Anodonta cygnea</i>	35	4	3.64	174
	<i>Anodonta exulcerata</i>	21	5	4.44	229
	<i>Unio elongatulus</i>	187	7	4.66	197
	Native mean ± s.e			4.3 ± 0.2	482 ± 21
Invasive	<i>Corbicula fluminea</i>	30	0	0	0
	<i>Dreissena polymorpha</i>	53	4	2.39	47
	<i>Sinanodonta woodiana</i>	62	4	3.37	177
	Invasive mean ± s.e			1.9 ± 1.0	75 ± 53
<i>Lake Varese</i>					
Native	<i>Unio elongatulus</i>	48	6	5.39	285
Invasive	<i>Dreissena polymorpha</i>	18	2	1.63	27
	<i>Corbicula fluminea</i>	99	0	0	0
	<i>Sinanodonta woodiana</i>	26	3	2.36	138
	Invasive mean ± s.e			1.3 ± 0.7	55 ± 42
<i>Lake Lugano</i>					
Native	<i>Anodonta cygnea</i>	12	3	3.00	125
Invasive	<i>Dreissena polymorpha</i>	32	1	0.32	13
	<i>Corbicula fluminea</i>	19	0	0	0
	Invasive mean ± s.e			0.5 ± 0.5	7 ± 7

For the parasite taxon richness, both the original values (orig.) and those standardized (std.) to the sample size of 12 by bootstrapping are given

Statistical analyses

We used population-specific parasite taxon richness (number of parasite taxa) and sum of prevalences (sum of the prevalence—proportion of the population infected with a particular taxon—of all parasite taxa for each host species, can be more than 100%) as the response variables as they have generally been used as the measures of parasite pressure in studies exploring enemy release (Torchin et al. 2003; Lafferty et al. 2010; Taskinen et al. 2021). Population in this study is defined as all individuals of the same species in the sampling site (lake) and is the unit for which the parasite taxon richness and the sum of prevalences were calculated and used in the analyses.

The estimate of the parasite taxon richness depends on the sample size but the sample size for each bivalve species varied (Table 1). Hence, bootstrapping was carried out to scale the results to be comparable to each other and standardize the sampling effort before further statistical analyses. In this study, the smallest acceptable sample size was set to 12, which was the number of *Anodonta cygnea* collected from Lake Lugano (Table 1). In the bootstrapping process, 2000 resamples (with replacement) of 12 individuals were drawn from all other population-specific samples of bivalves and the averages of the 2000 results were used instead of the original values when comparing the parasite taxon richness between invasive and native bivalve species.

In total, the data consist of eight invasive bivalve populations and six local, native populations across the three waterbodies. The species- and lake-specific parasite taxon richness (standardized) and sum of prevalence with rank-transformation were used as the response variables in Two-way ANOVA in R statistical computing software (version 4.2.2), where ‘invasion status’ (invasive/native) and ‘lake’ (study site) were used as fixed factors.

Lake-specific information on infection prevalences of all parasite species without standardization is provided as supplementary material (Tables S1, S2 and S3). To have a detailed view of each waterbody and each parasite taxon, we performed site-specific Chi-square (χ^2) tests in IBM SPSS Statistic (version S28.0.1.1) on the parasite presence–absence data of all parasite taxa in each lake between each pair of invasive and native species (Tables S1, S2 and S3). Yate’s continuity correction was applied if the number

of cells with expected count less than five was greater than one (Sokal and Rohlf 1981) and p -values < 0.05 were considered statistically significant.

Results

Among the four native bivalve host species (*Anodonta anatina*, *A. cygnea*, *A. exulcerata* and *Unio elongatulus*) and three invasive species (*Sinanodonta woodiana*, *Dreissena polymorpha*, *Corbicula fluminea*) that were collected from the three study lakes, 10 parasite taxa were observed (Table 1, Table 2). At the regional scale, over the three study lakes, the total number of parasite taxa found from each bivalve species was from four to seven in the native hosts and from zero to five among the invasive bivalves, as the invasive *C. fluminea* did not have any parasites (Table 1).

Within each lake, the average n-standardized parasite taxon richness per bivalve species was lower in the invasive bivalves than in the native bivalves. Two-way ANOVA for ranked, standardized parasite taxon richness data indicated a statistically significant difference in the parasite taxon richness between sympatric native and invasive bivalves (effect of the factor ‘invasion status’ $F_{1,8} = 14.42$, $p = 0.005$). On average, the number of parasite taxa of the native species was 2.6 times as high as that of the invasive bivalves in the same site (Table 1). The effect of lake ($F_{2,8} = 2.52$, $p = 0.142$) and the interaction between lake and invasion status ($F_{2,8} = 1.172$, $p = 0.358$) were not significant, indicating that the parasite taxon richness did not differ among lakes and that the effect of invasion status also did not differ among lakes. Similarly, the second indicator of parasite pressure, sum of prevalences of infection, differed significantly between native and invasive species (Two-way ANOVA with ranked data, factor ‘invasion status’, $F_{1,8} = 8.32$, $p = 0.020$), indicating that the sum of prevalences of infection in native species was significantly higher—on average 3.4 times as high as that of the invasive bivalves (Table 1). The effects of lake ($F_{2,8} = 1.672$, $p = 0.247$) and the interaction between lake and invasion status ($F_{2,8} = 0.53$, $p = 0.606$) were not significant, indicating that the summed prevalences of infection and the effect of invasion status did not differ significantly between lakes.

In addition, the site-specific paired comparisons between each invasive and native bivalve revealed that

Table 2 Occurrence (X=occurred;—=did not occur) of the 10 observed parasite taxa in each native (*Anodonta anatina*, *A. cygnea*, *A. exulcerata* and *Unio elongatulus*) and invasive (*Sinanodonta woodiana*, *Dreissena polymorpha* and *Corbicula fluminea*) bivalve species, all three waterbodies (Lake Maggiore, Lake Varese, Lake Lugano) combined

Bivalve	N wb	N bivalves	Trematoda sporo-cysts			Ac	Cl	UN	Con	M1	M2	M3	Total
			Rc	Bp	Pm								
Native													
<i>Anodonta anatina</i>	1	37	X	–	–	X	–	–	X	X	X	X	6
<i>Anodonta cygnea</i>	2	47	–	–	–	X	–	–	–	X	X	X	4
<i>Anodonta exulcelrata</i>	1	21	X	–	–	–	–	–	X	X	X	X	5
<i>Unio elongatulus</i>	2	282	X	–	–	X	X	–	X	X	X	X	7
N of host species			3	0	0	3	1	0	3	4	4	4	
Invasive													
<i>Sinanodonta woodiana</i>	2	88	X	–	–	–	X	–	–	X	X	X	5
<i>Dreissena polymorpha</i>	3	103	–	X	X	–	–	X	X	–	–	–	4
<i>Corbicula fluminea</i>	3	129	–	–	–	–	–	–	–	–	–	–	0
N of host species			1	1	1	0	1	1	1	1	1	1	
Total N of hosts			4	1	1	3	2	1	4	5	5	5	

Numbers of waterbodies per bivalve species, the total number of individuals studied and the total number of observed parasite taxa per bivalve species are given in columns N wb, N bivalves and Total, respectively

Number of host species observed per parasite taxon are given separately for the native and the invasive bivalves. In addition, the total number of host species for each parasite taxon (combining the invasive and native bivalves)—a measure of host specificity of the parasite—is given in the row Total N of hosts

Trematoda sporocysts of tissue-dwelling, larval, castrating trematodes; Rc=*Rhipidocotyle campanula*, Bp=*Bucephalus polymorphus*, Pm=*Phyllodistomum macrocotyle*

Ac=*Aspidogaster conchicola* (adult trematode), Cl=*Chaetogaster limnaei* (Oligochaeta), UN=Unknown larval nematode in gonad, Con=*Conchophthirus* sp. (Ciliata)

M1=larval/egg stages of watermites in the mantle, M2=larval/egg stages of watermites in the gills, M3=adult watermites

most parasite taxa had significantly higher infection prevalence in the native than in invasive host species (Supplementary Tables S1, S2 and S3). Clearly, the majority of the significant paired prevalence differences were in favour of the native mussel. Of the 68 statistically significant parasite-taxon-specific within-lake paired comparisons in the three study lakes, 55 (79% of the associations) were such that the native counterpart had a significantly higher prevalence of infection than the invasive bivalve (Supplementary material). When the *Dreissena*-specific trematodes *Bucephalus polymorphus* and *Phyllodistomum macrocotyle* were excluded, there were 61 statistically significant pairwise differences of which 54 (89%) showed higher prevalence in the native mussel (Supplementary material). The infrequent cases of statistically higher prevalence of infection in the invasive partner were associated with *Sinanodonta woodiana*. The invader *S. woodiana* in Lake Maggiore showed a

higher prevalence of eggs and larvae of watermites in the mantle than any native mussel. In addition, a similar pattern was found in eggs and larvae of watermites in the gills of *S. woodiana* as compared to *Anodonta anatina* and *Unio elongatulus*, as well as a higher prevalence of the trematode *Rhipidocotyle campanula* in *S. woodiana* than in *A. anatina* and *A. exulcerata* in Lake Maggiore (Supplementary Table S2). The invader *Dreissena polymorpha* also was in some cases significantly more frequently infected by the trematodes *B. polymorphus* and *P. macrocotyle*, but these trematodes are *Dreissena*-specific and do not infect the native unionids.

Discussion

The assumptions underlying the Enemy Release Hypothesis (ERH) are that: (1) parasite load in the

invasive species is lower in their invaded range than in their original range, and (2) in the invaded range, invasive species have lower parasite loads than native species. In this study on southern European lakes, we focused on the second assumption. For both indicators of parasite pressure, i.e., parasite taxon richness and the sum of prevalences of parasite infections, the overall average value in the native species was at least double that in the invaders. In addition, the vast majority of the within-lake and within-host-species parasite comparisons showed a significantly higher prevalence of infection in the native species than in the invasive species. The results are in accordance with the corollary of the EHR and previous observations from northern European water bodies (Taskinen et al. 2021) that the native species frequently experience higher parasite pressure than the sympatric invasive bivalves.

An important prerequisite of the ERH is that parasites are harmful and costly to the host. We did not study this, but several previous studies have documented the negative effects of parasitism in mollusks. Watermites ingest mucus and tissue of their molluscan hosts (Fisher et al. 2000) and higher mite and trematode parasite abundances are associated with reduced reproductive output and physiological condition of the hosts (Gangloff et al. 2008). *Chaetogaster limnaei* produces gill damage and increases the respiration rate of its hosts (Liquin et al. 2021). *Aspidogaster conchicola* feeds on hemocytes, hemolymph and epithelium of the host (Gentner 1971; Bakker and Davids 1973; Huehner et al. 1989). Several studies have focused on trematodes in bivalve gonads. For example, bucephalids (*Rhipidocotyle* spp.) and gorgoderids (*Phyllodistomum* spp., *Cercaria duplicata*) can cause partial or complete sterility, parasite-induced mortality, and negative impact on the growth of mussels (Davids and Kraak 1993; Taskinen and Valtonen 1995; Taskinen et al. 1997; Jokela et al. 2005; Müller et al. 2015) and have negative impact on reproductive output at the population level (Brian et al. 2021). Since many parasites are host-specific and adapted to their local host population (Price 1980; Saarinen and Taskinen 2005), parasite pressure of invaders in their new environment can be expected to remain low.

Studying sympatric native unionids and invasive bivalves is crucial for understanding the possible shared parasitism (Brian and Aldridge 2019). *Sinanodonta woodiana* was introduced to Europe as

glochidia with the fish trade (Watters 1997; Konečný et al. 2018), and no parasites have been reported yet from the parasitic glochidia stage of *S. woodiana*. Thus, all the parasites found in *S. woodiana* are originally European parasites of native unionids in Europe, which means that many of the parasites of native European unionids could infect the invasive unionid *S. woodiana*. In turn, this means that parasite spillback is possible, i.e., intensification of parasitism in native freshwater mussels caused by the multiplication of local parasites (Kelly et al. 2009) in the invader, *S. woodiana*. Parasite spillback caused by *Dreissena polymorpha* in the invaded Lake Naroch in Belarus was observed by Mastitsky and Veres (2010): the native parasites tended to have higher abundance in the presence of *D. polymorpha* than prior to its invasion. However, as *S. woodiana* presumably did not bring its own parasites during the invasion of Europe as glochidium larvae (Konečný et al. 2018) the novel weapon scenario in the case of *S. woodiana*—invader bringing pathogens that infect the natives (e.g., Vilcinskis 2015)—is less probable.

In Europe, *Corbicula fluminea* has been expanding its range rapidly, even spreading to the southern edges of the Arctic (Bespalaya et al. 2018), and continues to expand, e.g., to Greece (Karaouzas et al. 2020). Similarly, *Sinanodonta woodiana* successfully invaded most European countries, where it outperforms native European freshwater mussels (Urbanska et al. 2021). Many factors have been suggested as contributing to the success of invasive bivalves, including fouling of native mussels, induction of cross-resistance in host fish of native mussels, long breeding season, high fecundity, wide spectrum of suitable fish hosts, as well as free-living parasitic larvae (e.g., Yanovych 2015; Donrovich et al. 2016; Dzierzynska-Białonczyk et al. 2018; Labecka and Domagała 2018; Urbanska et al. 2018). Current results and those of Taskinen et al. (2021) indicate that parasitism may play a crucial role in the invasions of freshwater bivalves, if the harmful parasites disproportionately infect the local, native mussels.

Dreissena polymorpha was infected by the trematodes *B. polymorphus* and *P. macrocotyle*, which are specific to this invasive bivalve (Taskinen et al. 1991; Petkeviciute et al. 2014). These findings of *D. polymorpha* infections show that at least these enemies were not “left behind” but were carried along with the invader during the invasion process. Since

D. polymorpha mostly colonized Europe via waterways—along the canal network connecting Caspian and European watersheds—the invasion with its own parasites was easier than, for example, for *Sinano-donta woodiana*. These *D. polymorpha*-specific parasites have not been able to infect native mussels in Europe (Taskinen et al. 2021; the present study). On the other hand, evidence for enemy release is offered by the Asian clam *Corbicula fluminea*. While *C. fluminea* seems to be completely parasite-free in Europe (Taskinen et al. 2021; present study), it has been reported to harbor endosymbionts in its native range, for instance, *Phyllodistomum mingensis* (Tang 1985), several species of aspidogastroid trematodes (Tang 1992) and *Echinostoma* trematodes (Chung et al. 2001), and it can also serve as a host of the larval stage of mayflies and chironomids (Bespalaya et al. 2022). Therefore, to explore the central prediction of the ERH, release from enemies, it would be important to compare the possible reduction of parasite pressure on *D. polymorpha*, *C. fluminea* and *S. woodiana* during their invasion process by comparing parasitism of these species in their original and invaded ranges. In addition, the harm caused by parasites to their bivalve hosts in general has only been studied for some of the parasite taxa, and even less often quantified, and can vary remarkably among parasites and bivalve–parasite combinations (Brian and Aldridge 2019; Brian et al. 2021). Therefore, the effects of parasites and endosymbionts on freshwater bivalves at the host individual and population levels should be thoroughly investigated to assess the potential impact of each parasite taxon, and its role in parasite-mediated competition among bivalves, and eventually the specific role of parasites in invasions of freshwater bivalves.

The present results reveal a diverse parasite fauna of freshwater bivalves in these lakes in southern Europe and, on average, lower parasite pressure in the invasive than the native bivalves. Since parasitism is costly to the host, such unbalanced parasite pressure could favor invasive species and further exacerbate the observed decline of native freshwater mussels (Nogueira et al. 2021; Riccardi et al. 2022) and aid the observed establishment and dominance of the invasive bivalves (Kamburska et al. 2013a, b) in this threatened biodiversity hotspot (Cuttelod et al. 2009).

The ERH studies that we have conducted were consistent with Colautti et al. (2004) comparing the effect of native enemies on species in the same

community. Such an approach together with seeking the answers to what other factors may be crucial for invasion success is essential for determining the real impact of parasites on sympatric populations. It would help expand our understanding of the complex processes that probably underlie biological invasions and improve our ability to manage natural ecosystems.

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Author contributions All authors contributed to the study conception and design. Sampling was performed by Nicoletta Riccardi, material preparation and data collection were performed by all authors. Data analysis was performed by Binglin Deng. The first draft of the manuscript was written by Binglin Deng and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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