



Evaluating the role of predatory fish controlling the invasion of the Asian golden mussel *Limnoperna fortunei* in a subtropical river

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Funding information

Agencia Nacional de Investigación e Innovación, Grant/Award Number: ANII FCE_2_2016_1_126780 and PD_NAC_2015_1_108121; Comisión Sectorial de Investigación Científica, Grant/Award Number: CSIC I+D_2016_577-348; Postgraduate Academic Commission (CAP); UPM Pulp Mill Environmental Monitoring Program

Handling Editor: Robert Britton

Abstract

1. The invasive Asian golden mussel *Limnoperna fortunei* is continuously expanding through South America, altering aquatic ecosystem structure and functioning. While several native fish species predate on this mussel, these interactions, and their consequences for the food web, have not been studied in depth.
2. We combine a survey of the fish assemblage trophic structure using gut contents and stable isotope analysis with an in situ exclusion experiment in order to: (a) determine the main fish species preying on *L. fortunei*; (b) estimate the contribution of *L. fortunei* to the biomass of fish assemblage; and (c) evaluate the role of fish on the density and maximum shell length of *L. fortunei* in the lower Uruguay River (the Río de La Plata Basin).
3. We found that about one third of fish species in the assemblage (28 out of 81 species) consumed *L. fortunei*, which was an important food item (>10% of the dietary volume and >30% of frequency of occurrence) for 11 fish species. Stable isotope mixing models consistently suggested that >14% of the total biomass of the fish assemblage was derived directly from carbon derived from *L. fortunei* tissues. In addition, the exclusion experiment demonstrated that fish predation reduces the mussel density by c. 70% and the mussel maximum shell length by c. 40%.
4. *Synthesis and applications.* Our research suggests a top-down effect of fish on the invasive Asian golden mussel's abundance. This work highlights the need to preserve the native fish communities, particularly in South America, where many vulnerable migratory fish are of key relevance as *Limnoperna fortunei* consumers. In the light of these findings, actions such as implementing efficient fish passage technologies in the actual (and projected) dams of the Uruguay River basin and elsewhere become essential to avoid local extinctions of these natural invasion controls upstream of the dams.

KEYWORDS

biological invasion, boga *Megaleporinus obtusidens*, dams, fish exclusion, invasive mussel, origin of fish biomass, stable isotopes, top-down effect

1 | INTRODUCTION

Biological invasions are among the greatest global threats to biodiversity, causing local and global extinctions and altering food webs and ecosystem services (Dudgeon et al., 2006; Simberloff et al., 2013; Vitousek, D'Antonio, Loope, & Westbrooks, 1996). As invasive species increase in abundance and distribution, a continuous homogenization of global biodiversity is observed, with severe long-term consequences for ecosystem functioning (e.g. Cucherousset & Olden, 2011; Olden, Comte, & Giam, 2018; Sala et al., 2000). As invasions proceed, three different stages can usually be identified: introduction, establishment and integration into the system. During the final phase of integration many native species can be lost from the system and the community structure is commonly altered in permanent ways (Moyle & Light, 1996).

Aquatic ecosystems seem particularly sensitive to the introduction of exotic species that promote declines in native populations and biodiversity (e.g. Dudgeon et al., 2006), with about 25% of the world's most invasive species affecting aquatic systems (Lowe, Browne, Boudjelas, & De Poorter, 2000). In freshwater ecosystems, part of this high vulnerability can be explained by the high connectivity of drainage basins, which sometimes act as 'sinks' of materials, receiving a wide diversity of invasion propagules associated with human activities (e.g. navigation, aquaculture, recreation, etc.; Zedler & Kercher, 2004). Not surprisingly, some of the most globally renowned and extreme examples of biodiversity loss caused by invasive species come from freshwater ecosystems. One such example is the invasion by the Nile perch *Lates niloticus* in Lake Victoria, which caused the extinction of hundreds of endemic cichlids (particularly those from the genus *Haplochromis*; Craig, 1992; Marshall, 2018).

In particular, invaders with the capacity to modify both trophic interactions with other species and habitat structure are among the most negative for natural ecosystems (Crooks, 2002). An example of such invaders is freshwater mussels, such as the zebra mussel *Dreissena polymorpha*, a widespread invader in the northern hemisphere, and the golden mussel *Limnoperna fortunei*, which is currently invading large areas of Southeast Asia and South America (Boltovskoy & Correa, 2015; Karatayev, Boltovskoy, Padilla, & Burlakova, 2007; Moyle & Light, 1996). The Asian golden mussel *L. fortunei* is a native species from mainland China that was introduced in Río de La Plata Estuary in South America in the 1990s, when larval stages were probably transported in ballast water from commercial ships arriving from Southeast Asia (as suggested by Pastorino, Darrigran, Martin, & Lunaschi, 1993). Since then, rapid colonization and invasion have been reported, with both dispersal

of larval stages and translocation aided by human activities probably occurring, and by the year 2001, this species was highly abundant in the lower Uruguay River and its tributaries, becoming the dominant macrobenthic species in many areas (Brugnoli, Clemente, Boccardi, Borthagaray, & Scarabino, 2005; Clemente & Brugnoli, 2002; Langone, 2005; Muniz, Clemente, & Brugnoli, 2005). The present-day distribution range of this species in South America extends from Río de La Plata Estuary (Argentina) to the San Francisco River basin in Northeastern Brazil (Barbosa et al., 2016), but suitable environmental conditions are present in most of South and Central America as well as a large part of North America (Souza Campos et al., 2014; US Fish & Wildlife Service, 2014).

Limnoperna fortunei represents a fouling pest that clogs industrial and water supply infrastructures and causes large economic losses (Boltovskoy & Correa, 2015; Muniz et al., 2005). In addition, several alterations in the functioning of freshwater ecosystems have been observed as the golden mussel invades and dominates macrobenthic assemblages (Boltovskoy & Correa, 2015). For example, experimental evidence suggests that *L. fortunei* may modify planktonic communities, preying on specific groups of algae and zooplankton, and favouring fractions such as potentially toxic cyanobacteria, which form large colonies (Cataldo et al., 2012). Besides, cyanobacteria may further benefit from the modification in the N:P ratio that this mussel produces (Cataldo et al., 2012). Additionally, the accrual of benthic organic matter increases in *L. fortunei* colonies due to their faeces and pseudofaeces and the increased roughness of surfaces that reduces flow-scouring (Martin & Darrigran, 1994). This increased siltation seems to modify macroinvertebrate assemblages, favouring the abundance of many groups like annelids and nematodes (Duchini, Boltovskoy, & Sylvester, 2018). However, the effect of *L. fortunei* over macrobenthic communities remains largely unknown, although many authors have suggested potential risks for native mollusc biodiversity (Martin & Darrigran, 1994; Scarabino & Verde, 1995; Spaccesi & Rodrigues Capitulo, 2012).

Several fish species in the inner Río de La Plata Estuary and Paraná River were reported as consumers of *L. fortunei* (Cataldo, 2015; García & Protogino, 2005; González-Bergonzoni, Teixeira de Mello, Vidal, D'Anatro, & Masdeu, 2010; Penchaszadeh et al., 2000). This leads to the speculation that fish may regulate mussel populations to a certain extent (Cataldo, 2015). However, the predator-prey interactions involving *L. fortunei* have not been studied using standardized methods that allow an accurate assessment of the particular role of different native fish species in the predation over the invasive species. Moreover, the effect that *L. fortunei* may have over the functioning of fish food webs remains largely unknown.

In this study we investigated the trophic interaction between the fish assemblage and *L. fortunei* populations in the lower Uruguay River, and the consequence of the invasion for local food webs. We analysed fish diets using gut content and stable isotope analyses at six sites spread along 300 km, and quantified the amount of fish biomass subsidized by mussels in three of these sites. In addition, we conducted an in situ fish exclusion experiment to analyse the role of fish in limiting mussel densities and maximum body sizes during the mussel recruitment period. We hypothesized that a large amount of the fish assemblage biomass is fuelled by *L. fortunei* biomass, and that fish can affect, at least to some extent, the *L. fortunei* abundance (and maximum shell length) in the lower section of the Uruguay River.

2 | MATERIALS AND METHODS

2.1 | Study area

The Uruguay River is the second most important tributary to the Río de La Plata Estuary (after Paraná River), with an approximate length of 1,800 km and a basin area of 365,000 km², flowing through the south of Brazil, Argentina and Uruguay in South America. The golden mussel has been reported as abundant and causing biofouling problems in industrial, water treatment and power plants of the lower Uruguay River at least since the year 2001 (Boltovskoy, Xu, & Nakano, 2015; Langone, 2005). In this study, we sampled six different sites located along the lower Uruguay River, distributed along a

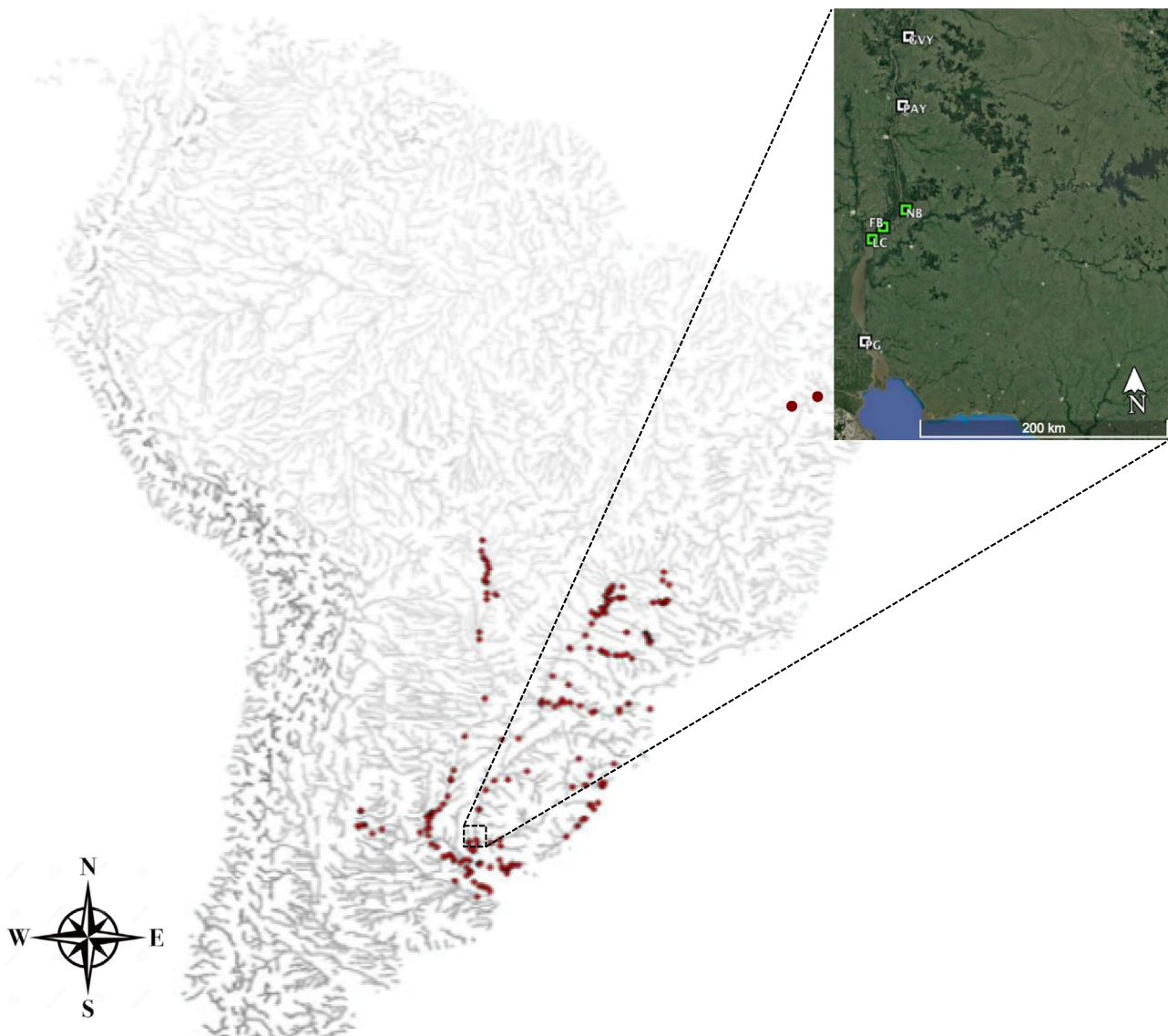


FIGURE 1 Distribution of *Limnoperna fortunei* in South America to the present (modified from Barbosa et al., 2016 and Souza Campos et al., 2014) and sampling area for our study. The six study sites in the lower Uruguay River are marked from upstream to downstream: Saladero Guaviyú (GVY), Paysandú (PAY), Nuevo Berlin (NB), Fray Bentos (FB), Las Cañas (LC) and Punta Gorda (PG). The three sites where stable isotopes were analysed are marked in green. At Las Cañas locality (LC), the in situ fish exclusion experiment was arrayed (see Figure 2 for details)

c. 300 km stretch of the river, within one of the oldest foci of invasion in the region (Figure 1).

2.2 | Fish species consuming *L. fortunei*

To determine the fish species feeding on *L. fortunei*, we analysed the gut content of fish species collected in two sampling campaigns, using standard 1.5 Nordic survey multi-mesh gillnets: (a) sampling of fish sites of Nuevo Berlin, Fray Bentos and Las Cañas in austral Spring (November) 2014 and austral Autumn (April) 2015; and (b) a fish sampling in all the six above-mentioned sites during austral Autumn of 2017 (May–early June). These two datasets were used to capture the spatial and temporal variability in fish diets and also to sample a greater number of fish species. Representative samples of the gut contents of each species were analysed, focusing on quantifying the consumption of *L. fortunei*. We estimated the frequency of occurrence (FO) and the relative gut volume (Vol) for each fish species, following standardized procedures (Hyslop, 1980), and estimated the index of relative importance in the diet, following Kawakami and Vazzoler (1980). Details on the fish sampling and gut content analysis are provided in González-Bergonzoni et al. (2019) and in Appendix S1.

2.3 | Fish biomass derived from *L. fortunei*

During the sampling campaign of late spring 2014 (November–December) and early autumn 2015 (beginning of April), samples of fish muscles and their potential preys were collected for the dual determination of stable isotopes of carbon (C) and nitrogen (N). Fish were collected using Standard Nordic 1.5 Survey nets and native invertebrates using a 1-mm mesh size hand net and by hand-picking large molluscs (see Appendix S1 for details). Bulk invertebrate samples collected for isotopic analysis included native crustaceans (*Hyalella* sp.), gastropods (*Heleobia*, *Potamolithus*, *Chilina* and *Pomacea* spp.), Ephemeroptera and Diptera: Chironomidae, which were the groups most frequently found in fish guts. Using isotopic data, the potential contribution of *L. fortunei* and native invertebrate sources to food webs was estimated by Bayesian mixing models, which use $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of food sources and consumers, together with their fractionation coefficients, to estimate the proportion of the biomass generated by each food item for each consumer species (Parnell, Inger, & Bearhop, 2010). The detailed procedure of the sampling and processing of tissue samples for stable isotope analysis is given in Appendix S1.

Based on gut content analysis, we selected a subset of species that mostly feed on a combination of *L. fortunei* and native

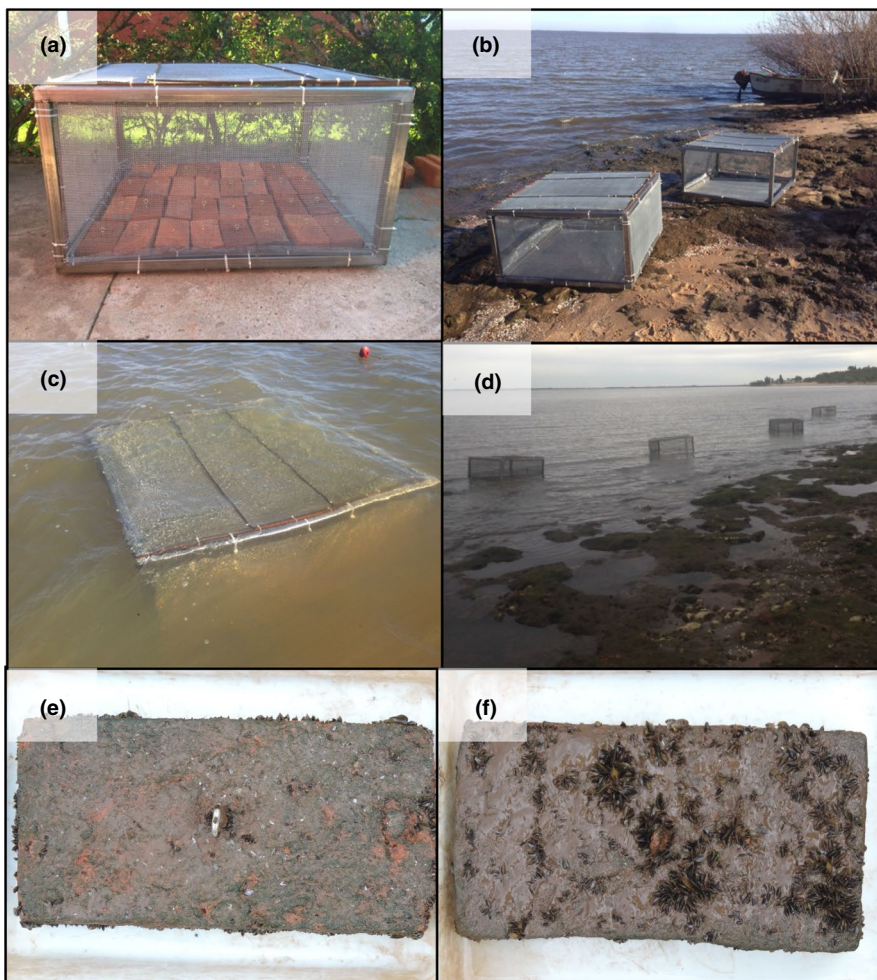


FIGURE 2 Fish exclusion experiment arrayed during 2016–2017 in the locality of Las Cañas. (a) Fish exclusion modules with the artificial substrates; (b) One fish exclusion module (left) and one fish access module (right), previous to the installation of artificial substrates and immersion in the river; (c) Exclusion module installed and anchored in the river bottom; (d) Four of the modules installed during one lowest river level scenario; (e) Superior view of an artificial substrate of a module with fish access after 181 days of colonization; (f) Superior view of an artificial substrate of a module with fish exclusion after 181 days of colonization

invertebrates to model the proportional contribution of these two dietary categories to their biomass. This selection was made to maximize the efficiency of these models, since the use of more than three potential sources increases the model uncertainty (Fry, 2013). We built one model for each of the selected species that feed on both *L. fortunei* and native invertebrates, based on mean and SD values of the isotopic signature of the native invertebrate and *L. fortunei* samples (covering all the size range). The mean fractionation values and their standard deviations used in the models were 3.3 ± 1.5 for N and 0.4 ± 0.1 for C, which were extracted from previously published data (Bunn, Leigh, & Jardine, 2013; Post, 2002). The stable isotope modelling was done using the SIAR package (Parnell, Inger, Bearhop, & Jackson, 2013) in R software (R Development Core Team, 2018).

2.4 | In situ fish exclusion experiment

An in situ fish exclusion experiment was carried out in Las Cañas, one of the three sites of the lower Uruguay River considered for dietary and abundance analyses. We created eight enclosures (size: 1.0 m long, 1.0 m wide \times 0.5 m high) protected with a metallic net (mesh size: 5.0 mm), and with an artificial substrate (composed of bricks of 0.0264 m² area each) covering the whole of the cage's floor (Figure 2a,b). Four of these enclosure modules had all sides covered with a metal net to prevent fish entrance ('closed modules'), and four enclosures had two lateral sides opened, allowing fish access to the modules ('open modules', Figure 2b). Each enclosure was firmly anchored at the bottom of the river at depths of 1.2 (minimum) to 1.7 m (maximum depth) on average over the sampling period (Figure 2c,d). The modules were installed at a distance from each other of 5–10 m, and treatment types ('closed modules' or 'open modules') were intercalated. The experiment started at the beginning of September, before the massive release of larvae by the invasive mussels, which occurs in spring, when the river water temperature exceeds 17°C (Brugnoli, Dabezies, Clemente, & Muniz, 2011; Darrigran, Damborenea, Penchaszadeh, & Taraborelli, 2003), and ran up to the beginning of March, c. 2 months after the massive settlement of mussel larvae. After 181 days of colonization, a massive settlement of *L. fortunei* was observed in the artificial substrate of each enclosure (Figure 2e,f). At this moment, we randomly selected and removed three samples of the substrates (i.e. three bricks) from each module. In the field, all the mussels that were present on the upper surface of the bricks (exposed surfaces) were removed and preserved in ethanol 95° for subsequent laboratory analysis. The individuals of *L. fortunei* were quantified and individual maximum shell lengths (per sample) were measured using a binocular stereomicroscope. The density (ind.m⁻²) and maximum sizes of mussels (as shell length in mm) were then compared between the closed and open modules, by means of a one-way mixed effects ANOVA test ($\alpha = 0.05$), considering the identity of the enclosure as a random effect. Density data were log₁₀ transformed prior to the analyses, in order to accomplish the assumptions of the model. All these analyses were run using the 'nlme' package in R software (R Development Core Team, 2018).

3 | RESULTS

3.1 | Fish species consuming *L. fortunei*

A total of 1,467 fish individuals belonging to 81 fish species collected along the study sites of the lower Uruguay River were dissected and 1,091 fish with non-empty guts were analysed to identify *L. fortunei* consumers. Golden mussel was present in the diets of 35% of overall fish species ($N = 28$ species) and in 23% of all individuals analysed, and it could be considered as an important food item (representing >10% of average gut volume and being present in >30% of the analysed individuals) for 11 species (Table 1).

3.2 | Fish biomass derived from *L. fortunei*

Based on the modelling selection criteria (i.e. species feeding on both native invertebrates and golden mussel), we selected eight of the 11 fish species that showed a high consumption of *L. fortunei* (*Megaleporinus obtusidens*, *Leporinus striatus*, *Pimelodus maculatus*, *Pimelodus absconditus*, *Iheringichthys labrosus*, *Crenicichla missioneira*, *Paraloricaria vetula* and *Loricariichthys anus*) to model the *L. fortunei* contribution to the fish biomass (Table 2). We built each model including all the individuals of each fish species as well as 43 native invertebrate samples (22 samples of molluscs, 9 of crustaceans and 12 of insect larvae) and 31 samples of *L. fortunei* (muscle tissue from 27 adults and 4 from adults' byssus).

The results obtained through the Bayesian mixing models agreed well with the gut content analysis, as the species consuming more *L. fortunei* were those deriving a higher proportion of their biomass from the mussel (Tables 1 and 2; Figure 3). Five species clearly originated most of their biomass (on average) from the assimilation of *L. fortunei*: *L. striatus* (66% of *L. fortunei* originated biomass), *M. obtusidens* (60%), *P. vetula* (59%), *C. missioneira* (57%) and *P. maculatus* (56%) (Table 2). In contrast, two species, *I. labrosus* and *L. anus*, were mostly fuelled by biomass derived from native invertebrates (*L. fortunei* derived biomass was 39% and 30% respectively). Finally, the biomass of *P. absconditus* was similarly fuelled by *L. fortunei* and native invertebrates (*L. fortunei* derived biomass of 51%; Table 2; Figure 3).

3.3 | In situ fish exclusion experiment

A significant difference in the density of *L. fortunei* between the closed and open modules was observed ($F = 17.36$, $p = .006$, $df = 6$), with $18,712 \pm 9,295$ ind.m⁻² ($M \pm SD$) being the density for the closed modules, and $5,809 \pm 2,178$ ind.m⁻² ($M \pm SD$) the density for the open modules (Figure 4). As for the *L. fortunei* maximum size, there was also a significant difference between the open and closed modules ($F = 30.98$, $p = .001$, $df = 6$). Specifically, it was found that 6 months after mussel larvae settlement, the mean maximum size (as shell length) for the closed modules was 12.1 ± 2.1 mm ($M \pm SD$), while the

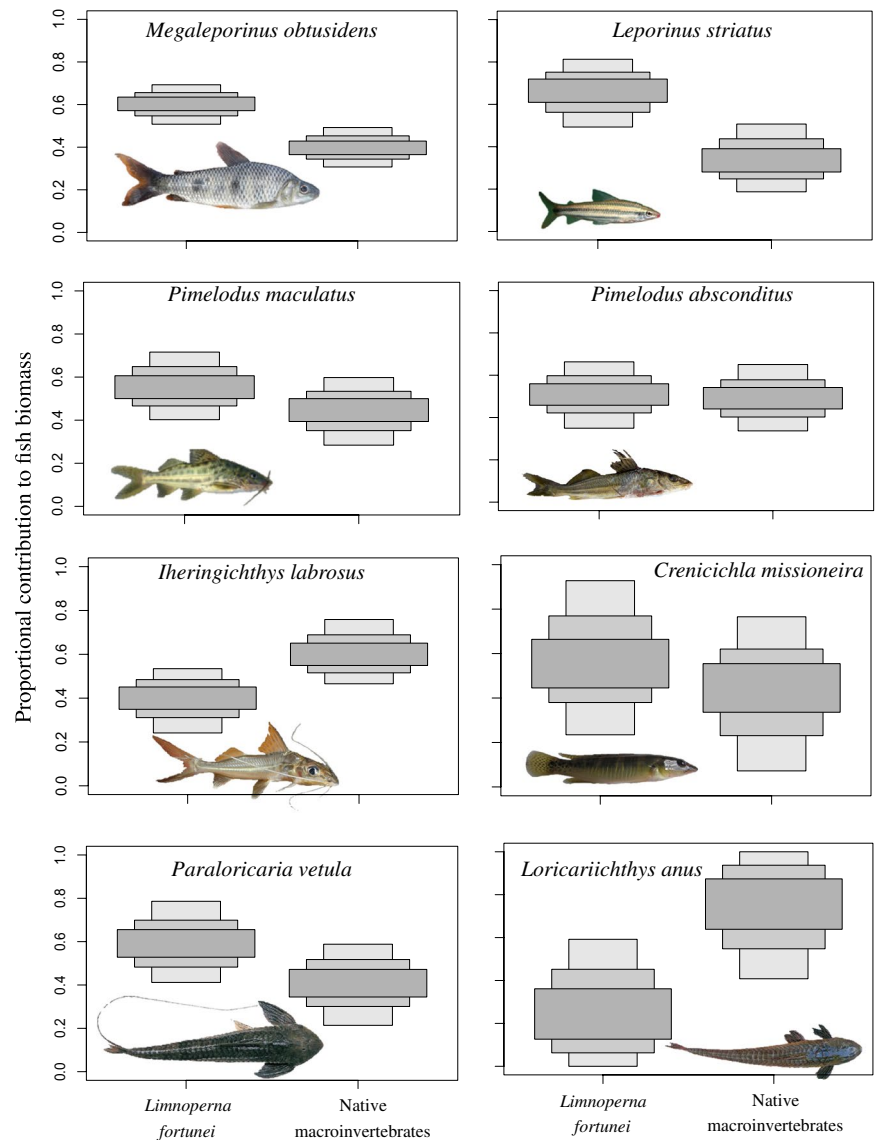
TABLE 1 Fish species consuming *Limnoperna fortunei* along six sites of the lower Uruguay River. Species are sorted by the relevance of *L. fortunei* as a dietary item in gut content analysis (according to the index of relative importance, IRI), grouping all sites and seasons sampled. Relative volume in diet and frequency of occurrence (FO) are also shown

Fish species	Sample size	IRI (relative volume, FO)	Fish species	Sample size	IRI (relative volume, FO)
<i>Brochiloricaria chauliodon</i>	2	100 (1; 1)	<i>Charax stenopterus</i>	1	Not found
<i>Leporinus striatus</i>	9	97 (0.9; 0.8)	<i>Characidium tenue</i>	2	Not found
<i>Crenicichla missioneira</i>	4	87 (0.9; 0.8)	<i>Crenicichla vittata</i>	3	Not found
<i>Megaleporinus obtusidens</i>	51	49.6 (0.5; 0.5)	<i>Cyphocharax voga</i>	1	Not found
<i>Loricariichthys anus</i>	4	21.7 (0.3; 0.3)	<i>Characidium zebra</i>	1	Not found
<i>Rhinodoras dorbignyi</i>	6	14.6 (0.2; 0.7)	<i>Gymnotus sp.</i>	2	Not found
<i>Odontesthes humensis</i>	8	13.7 (0.3; 0.4)	<i>Hypostomus aspilogaster</i>	2	Not found
<i>Pimelodus absconditus</i>	16	12.7 (0.2; 1)	<i>Hoplosternum littorale</i>	7	Not found
<i>Apareiodon affinis</i>	29	12.4 (0.2; 0.4)	<i>Hypostomus luteomaculatus</i>	1	Not found
<i>Paraloricaria vetula</i>	31	6.5 (0.1; 0.6)	<i>Hypostomus uruguayensis</i>	1	Not found
<i>Pimelodus maculatus</i>	25	5.3 (0.1; 0.6)	<i>Loricariichthys edentatus</i>	6	Not found
<i>Iheringichthys labrosus</i>	94	3 (0.04; 0.7)	<i>Lycengraulis grossidens</i>	46	Not found
<i>Pimelodella gracilis</i>	56	2.4 (0.03; 0.5)	<i>Luciopimelodus pati</i>	12	Not found
<i>Pseudobonocephalus sp.</i>	3	2.3 (0.1; 0.3)	<i>Odontesthes argentinensis</i>	2	Not found
<i>Rhaphiodon vulpinus</i>	5	1.4 (0.1; 0.2)	<i>Otocinclus flexilis</i>	1	Not found
<i>Parapimelodus valenciennes</i>	41	1.2 (0.02; 0.2)	<i>Oligosarcus jenynsii</i>	10	Not found
<i>Galeocharax humeralis</i>	24	1 (0.1; 0.1)	<i>Oligosarcus oligolepis</i>	6	Not found
<i>Hypostomus commersoni</i>	7	0.8 (0.02; 0.3)	<i>Odontostilbe pequirá</i>	5	Not found
<i>Pimelodus albicans</i>	15	0.7 (0.03; 0.2)	<i>Odontesthes perugiae</i>	6	Not found
<i>Schizodon nasutus</i>	8	0.6 (0.01; 0.4)	<i>Pimelodella australis</i>	2	Not found
<i>Ricola macrops</i>	45	0.2 (0.02; 0.1)	<i>Pachyurus bonariensis</i>	58	Not found
<i>Astyanax lacustris</i>	30	0.1 (0.005; 0.1)	<i>Potamotrygon brachyura</i>	1	Not found
<i>Eigenmannia sp.</i>	11	0.1 (0.004; 0.5)	<i>Pseudocorynopoma doriae</i>	1	Not found
<i>Pimelodella australis</i>	2	0.1 (0.002; 0.5)	<i>Pellona flavipinnis</i>	14	Not found
<i>Auchenipterus nuchalis</i>	11	0.00001 (0.0001; 0.1)	<i>Pygocentrus nattereri</i>	4	Not found
<i>Loricariichthys melanocheilus</i>	54	0.0006 (0.0004; 0.1)	<i>Platanichthys platana</i>	1	Not found
<i>Pterodoras granulosus</i>	2	0.04 (0.0004; 0.5)	<i>Pseudosteophilus sp.</i>	2	Not found
<i>Prochilodus lineatus</i>	13	0.02 (0.001; 0.1)	<i>Potamorhinus squamorlevis</i>	1	Not found
<i>Ageneiosus inermis</i>	7	Not found	<i>Roeboides affinis</i>	4	Not found
<i>Ageneiosus militaris</i>	25	Not found	<i>Roeboides microlepis</i>	1	Not found
<i>Auchenipterus osteomystax</i>	14	Not found	<i>Rineloricaria parva</i>	1	Not found
<i>Acestrorhynchus pantaneiro</i>	15	Not found	<i>Rhamdia quelen</i>	2	Not found
<i>Astyanax aff. fasciatus</i>	74	Not found	<i>Rineloricaria sp.</i>	2	Not found
<i>Brycon orbygnianus</i>	7	Not found	<i>Schizodon borelli</i>	1	Not found
<i>Bryconamericus stramineus</i>	24	Not found	<i>Salminus brasiliensis</i>	12	Not found
<i>Cynopotamus argenteus</i>	37	Not found	<i>Steindachneria brevipinna</i>	2	Not found
<i>Catathyrion lorentzii</i>	1	Not found	<i>Sorubim lima</i>	1	Not found
<i>Cyphocharax platanus</i>	29	Not found	<i>Serrasalmus maculatus</i>	12	Not found
<i>Characidium rachovii</i>	1	Not found	<i>Trachyloperus albicrux</i>	3	Not found
<i>Crenicichla scottii</i>	1	Not found			
<i>Cyphocharax spilotos</i>	6	Not found	Total	1,091	7.4 (0.1; 0.2)

TABLE 2 Proportion of biomass generated from *Limnoperna fortunei* in a subset of *L. fortunei* predators, according to stable isotope Bayesian mixing models. Consumption (GCA, shown in Table 2) and assimilation (SIA mixing models results) of *L. fortunei* correlate positively (Pearson's correlation test $p = .03$, $r^2 = .72$)

Fish species	Sample size	<i>L. fortunei</i> mean (lower–Higher 95% CI)	Native invertebrates mean (lower–Higher 95% CI)
<i>Leporinus striatus</i>	9	65.7 (49.1–89.5)	34.2 (18.4–50.8)
<i>Megaleporinus obtusidens</i>	51	60.1 (50.7–69.2)	39.8 (30.7–49.2)
<i>Paraloricaria vetula</i>	31	59.5 (40.8–78.4)	40.5 (21.5–59.1)
<i>Crenicichla missioneira</i>	4	56.7 (23.7–92.9)	43.2 (7.0–76.5)
<i>Pimelodus maculatus</i>	25	55.7 (40.2–71.6)	44.2 (28.3–59.7)
<i>Pimelodus absconditus</i>	16	50.6 (34.7–66.1)	49.3 (33.9–65.2)
<i>Iheringichthys labrosus</i>	94	38.1 (23.3–52.4)	61.8 (47.6–76.6)
<i>Loricariichthys anus</i>	4	29.7 (0.0–59.3)	70.7 (40.6–100.0)

FIGURE 3 Results of SIAR Bayesian mixing models for the estimation of *L. fortunei* and native invertebrate contribution to biomass (95%, 75% and 50% credibility intervals, in increasing colour tone respectively), for eight fish species that feed on both native invertebrates and *Limnoperna fortunei* (see Table 1). *L. fortunei* is the main generator of biomass in *Megaleporinus obtusidens* and *Leporinus striatus* (Anostomidae, Characidae); *Pimelodus maculatus* (Siluriformes, Pimelodidae); *Crenicichla missioneira* (Perciformes, Cichlidae); and *Paraloricaria vetula* (Siluriformes, Loricariidae), while native invertebrate mostly fuelled *Loricariichthys anus* and *Iheringichthys labrosus*



mean maximum size for the open modules was 7.4 ± 1.9 mm ($M \pm SD$) (Figure 4). Finally, it is worth mentioning that during this experiment, qualitative visual assessments at the experimental site allowed us to

confirm the presence of the *L. fortunei* predators (like *M. obtusidens*, *P. maculatus*, *I. labrosus* and *C. missioneira*) in the surroundings of the open modules.

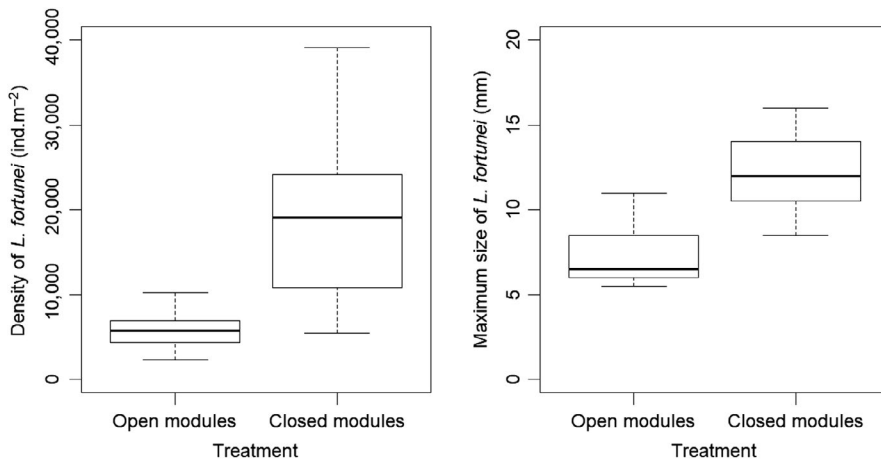


FIGURE 4 Changes in density (left panel) and body size (right panel) of *Limnoperna fortunei* caused by predatory fish, after a 181-day exclusion experiment conducted in Las Cañas, lower Uruguay River. Differences in mean density and maximum body size are highly significant (mixed effects ANOVA $p < .01$)

4 | DISCUSSION

In what follows, we will discuss the main implications of our findings, focusing on evaluating the role of fish as potential mitigators of this invasion and the main fish species preying on the golden mussel. First, we quantify the fish species that predate on *L. fortunei* in the lower Uruguay River and demonstrate how this invasion modifies food web pathways. Second, we discuss the available evidence for mussel density control by native fish in the region, and the need to preserve these species to mitigate the negative effects of the invasion.

4.1 | Fish species consuming *L. fortunei*

More than one-third of the native fish species in the assemblage of the lower Uruguay River predated on *L. fortunei*. Most of these species had been previously reported as *L. fortunei* consumers in different areas of the Río de La Plata Basin, such as the Paraná River channel and reservoirs, and the inner Río de La Plata Estuary (Boltovskoy et al., 2015; Cataldo, 2015; Catanhêde, Hahn, Gubiani, & Fugi, 2007; Penchaszadeh et al., 2000). These studies were conducted in different watersheds, and thus bear different fish assemblages. However, there is a strong consistency in the fish families and genera that are able to feed on the invasive mussel: among the more effective are the Anostomidae with strong teeth, such as *Megaleporinus* and *Leporinus* genus, and the Loricariidae with strong dentition, like *Paraloricaria* and *Brochiloricaria* genus (García & Montalto, 2006; García & Protogino, 2005; Penchaszadeh et al., 2000). Also, *L. fortunei* is consumed by some pimelodid catfishes, such as the *Pimelodus* species, which frequently ingest mussel prey without the need to crush them (García & Montalto, 2006; García & Protogino, 2005). The report of the cichlid *C. missioneira* as a consumer of *L. fortunei* is novel, although at least two other species of the same genus were also reported as mussel consumers (e.g. Casciotta et al., 2013; Lopes, 2010; Montalto, Oliveros, Ezcurra de Drago, & Demonte, 1999). In the case of the small-sized *Crenicichla* species (maximum size of about 25 cm), its large

and protractile mouth and strong pharyngeal teeth might be the key that allows them to feed and crush smaller mussels. In addition, our dietary analysis indicates that even herbivorous fish, such as *Apareiodon affinis*, frequently consume mussel byssus when grazing on epilithic periphyton with their spatulate brush-like teeth. Moreover, planktivorous fish with modified gill rakes to filter plankton, such as *Parapimelodus valenciennes*, frequently consume *L. fortunei* larvae. Thus, there is a combination of species with contrasting traits that are continuously preying on the mussel in different ways and habitats, controlling its expansion, at least in exposed substrates. In newly invaded sites, the presence of such fish species seems essential to exert some control on *L. fortunei* populations.

As a footnote to this section, we suggest readers check the number of individuals analysed as reported in our results for the species preying or not on the mussel. We have also included some rare species with low numbers, and for those, further evidence could be desirable.

4.2 | Fish biomass derived from *L. fortunei*

The golden mussel was found to be a key dietary item for the fish assemblage, fuelling more than 30% of the biomass in eight dominant fish species, which altogether accounted for 26% of the total assemblage biomass (fish assemblage structure reported in González-Bergonzoni, D'Anatro, Stebniki, & Teixeira de Mello, 2015). When the amount of biomass derived from *L. fortunei* in these eight species is summed, at least 14% of the overall fish biomass in the sampled area originated from *L. fortunei*. Even though this proportion of total fish biomass fuelled by *L. fortunei* seems impressive, we emphasize that this estimation is highly conservative as it only considers eight of the direct consumers of *L. fortunei* and neglects the biomass further transported in the food web up to the top piscivorous predators. Thus, we show that the invasion of *L. fortunei* promotes large-scale dietary shifts, affects whole fish assemblages and modifies the natural flow of carbon across the food webs. Similar prominent changes in the energetic

resources fuelling food webs have been observed for certain fish species after the invasion of the zebra mussel in North America (e.g. Locke, Bulté, Marcogliese, & Forbes, 2014). In fact, the invasion of the zebra mussel in the northern hemisphere and the more recent invasion of *L. fortunei* have been treated as parallels promoting similar effects (Karatajev et al., 2007). However, the much higher fish density and diversity in the freshwaters of the warmer Neotropical region, in comparison to northern temperate systems (e.g. Meerhoff et al., 2012), might imply higher predation pressure on invasive mussels than in the northern hemisphere, increasing the chances that some species rapidly adapt to the use of a new food resource. Finally, along with changes in the carbon pathways, the input and flow of other materials, such as contaminants, have probably been altered since the invasion of the Asian golden mussel, as is the case of the invasion by the zebra mussel in the northern hemisphere (e.g. Orlova, Golubkov, Kalinina, & Ignatieva, 2004).

4.3 | Role of fish as control of *L. fortunei* populations

As hypothesized in this study, and previously discussed by others (e.g. Cataldo, 2015; Sylvester, Boltovskoy, & Cataldo, 2007), our investigation supports that fish species that are better adapted to the consumption of hard prey represent an important top-down control of mussel populations. In line with this, our exclusion experiment shows a marked difference in mussel density between open and closed modules, supporting the role of fish as mitigators of this invasion. The average density of *L. fortunei* in the surfaces of the modules exposed to predation registered in this work (i.e. $5,809 \pm 2,177 \text{ ind.m}^{-2}$) was similar to the natural abundances reported in other studies from the Paraná River. For example, Boltovskoy and Cataldo (1999) analysed the settlement of *L. fortunei* in PVC monitors in the Paraná de las Palmas River, and after 182 days of colonization, they recorded a density of $3,924 \text{ ind.m}^{-2}$. Similarly, Duchini et al. (2018), also using PVC monitors, found a mean density of $7,344 \text{ ind.m}^{-2}$ at the end of a colonization period of 12 months in the lower Paraná River. Here, we found experimental evidence showing that, at least on exposed substrates, fish are able to control the *L. fortunei* growth rate, since they eliminated c. 70% of mussel cover. This is consistent with an 18-month experimental study in the Paraná River basin, which used substrates suspended in the water column to evaluate the effect of *L. fortunei* predators (including fish) on *L. fortunei* density; this study demonstrated that natural predators could eliminate up to 79% of *L. fortunei* natural density (Sylvester et al., 2007).

The complete removal of this invasive mussel species currently seems unlikely due to the widespread nature of the invasion, which is in continuous dispersal, and the fact that the mussel can maintain elevated populations in areas that act as refuges from predation (i.e. beneath hard substrates, among dense plants mats, among others; Cataldo, 2015). However, it is important to highlight that our results support that predatory fish of *L. fortunei* in

the lower Uruguay River play a relevant predation role on mussel populations and, therefore, that predators could mitigate some of the consequences of the golden mussel invasion for the riverine ecosystem.

4.3.1 | Application of findings

Although the potential application of fish for the biocontrol of exotic mussels seems complex from a technical point of view, our results propose a set of potential species to be explored as potential biocontrol agents, at least in specific scenarios and in combination with the application of other control agents. Furthermore, this research highlights the need to preserve these species to partially mitigate the advance of the invasion by golden mussel in already invaded systems, such as the Uruguay River basin. Moreover, in some highly invaded systems from which these native fish species that consume *L. fortunei* have been removed (e.g. as a consequence of habitat fragmentation by dams) the re-introduction of some migratory *L. fortunei* predators (such as *M. obtusidens*) may help to mitigate some of the more severe ecological impacts of this invasion. Such could be the case of the Río Negro River in Uruguay, where *L. fortunei* is currently altering the ecosystem (Brugnoli et al., 2011), and its main predator *M. obtusidens* has disappeared from the middle and upper sections of the river since the construction of hydroelectric dams (Loureiro, Zarucki, González-Bergonzoni, Vidal, & Fabiano, 2013). A few experiments focusing on the use of *M. obtusidens* as a biocontrolling agent have been tested in the region with promising results, although these works have not been conducted in natural systems (De-Melo-Rosa, Da-Costa-Gaspar, Silva, & Santos-Pompeu, 2019). Besides its role as a predator of *L. fortunei*, *M. obtusidens* is the second most important fish in Uruguay River fisheries (Vidal, D'Anatro, Stebniki, González-Bergonzoni, & Teixeira-de Mello, 2016). Thus, it could be feasible that the *L. fortunei* invasion may also be affecting the growth, survival and movement of this fishery stock. In this respect, we highlight that in the last 10 years, catches of *M. obtusidens* by artisanal fisheries in the lower Uruguay River have increased (Vidal et al., 2016), similar to that was observed in the Parana River (Boltovskoy & Correa, 2015). Although many climatic and anthropogenic factors could be driving this trend, and firm conclusions in this regard cannot be made without further evidence, the invasion of *L. fortunei* may also be playing a role in the changes observed for this fishery.

Limnoperna fortunei is an invasive species that produces ecological and economic losses spreading across the Americas, so studies generating information to be used to mitigate their effects are continuously increasing (Boltovskoy, Correa, Bordet, Leites, & Cataldo, 2013; Boltovskoy et al., 2015; Souza Campos et al., 2014). The management practices are, so far, based on the prevention of new introductions via controls of ballast waters, using anti-fouling paint products and applying mechanical removal in infrastructures. However, no mitigation efforts are being applied on natural ecosystems yet (at least in the lower Uruguay River). In this work, we quantified the importance of native South American fish—with closely related species (e.g. the

same genus) distributed all over the continent—as potential natural control agents of the invasive golden mussel, and showed some of the food web changes that occurred as a consequence of the invasion. The results obtained in this work could be useful to predict food web changes and species that may easily adapt to the consumption of *L. fortunei* in some newly invaded areas. This is a starting point for further research refining the potential use of fish for biocontrol, for which we must first quantify the species-specific mussel removal experimentally. However, given that the introduction or re-introduction of biocontrolling agents can have highly problematic results (e.g. Thomas & Willis, 1998), the preservation of native fish communities may be a complementary strategy to mitigate (at least partially) some of the ecological consequences of this invasion.

ACKNOWLEDGEMENTS

We gratefully thank Maite Burwood, Clementina Calvo and Tatiana Vernasa for helping in sampling campaigns and Dr. Christine Lucas for manuscript grammar editing, and Gonzalo Hernandez-Fripp for drawing the graphical abstract. This research project was funded by the National Agency for Innovation and Research (ANII) project ANII FCE_2_2016_1_126780 and scholarship ANII PD_NAC_2015_1_108121 and partly by the Scientific Research Sectorial Commission (Uruguay) project CSIC I+D_2016_577-348. I.S. received financial support from the Postgraduate Academic Commission (CAP) scholarship programme. I.G.-B., D.E.N., A.D., N.V. and F.T.d.M. received financial support by ANII. Monitoring sampling campaigns (2005–2014) were financed by the UPM Pulp Mill Environmental Monitoring Program; we thank Gervasio Gonzalez for logistics and data accessibility.


AUTHORS' CONTRIBUTIONS

I.G.-B., D.E.N. and F.T.d.M. participated in the conception and design of the study. All authors carried out the fieldwork; I.G.-B., I.S., N.V., L.B., S.S. and D.E.N. carried out the laboratory work; I.G.-B. and I.S. analysed the data and drafted the manuscript with the help of all authors. All the authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4qrfj6q6g> (González-Bergonzoni et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: González-Bergonzoni I, Silva I, Teixeira de Mello F, et al. Evaluating the role of predatory fish controlling the invasion of the Asian golden mussel *Limnoperna fortunei* in a subtropical river. *J Appl Ecol*. 2020;57:717–728. <https://doi.org/10.1111/1365-2664.13573>