Biol Invasions
https://doi.org/10.1007/s10530-024-03334-1

INVASION NOTE

Massive decline of invasive apple snail populations after blue crab invasion in the Ebro River, Spain

Vanessa Céspedes · Rubén Bernardo-Madrid · Félix Picazo · Montserrat Vilà · Cristóbal Rubio · María García · Ismael Sanz · Belinda Gallardo

Received: 17 April 2023 / Accepted: 30 April 2024

Abstract The negative interaction between multiple invasive species, when an invasive predator benefits from a previously introduced and abundant prey, poses unanticipated challenges for the joint management of invaders. To illustrate this question, we describe the surge and collapse of the invasive apple snail *Pomacea maculata* population before and after the arrival of the invasive blue crab, *Callinectes sapidus*, in the Ebro River (NE Spain). These two invaders have coincided for the first time beyond their respective native and prior invasive ranges, and thus lack any previous shared eco-evolutionary history facilitating coexistence. We leverage data from a 9-year apple snail removal programme (2014–2022) conducted by authorities to evaluate the effectiveness of the management programme and describe the apple snail temporal dynamics in the Ebro River. Since its arrival in 2013, the apple snail population increased exponentially along the river and adjacent rice-fields despite labour-intensive eradication efforts. Unexpectedly, riverine populations of the apple snail declined by 90% in 2018 relative to the prior year without apparent association with previous management efforts. Simultaneously, the blue crab was first recorded in the Ebro River in 2018, and its distribution rapidly overlapped the whole area invaded by apple snails. We suggest that over-predation by the blue crab is the main cause of the decline observed in the apple snail, and discuss the implications of this new invader-invader interaction for management. This study underscores the unforeseen consequences of subsequent waves of invasion, and the importance of supporting management with a deeper understanding of ecological interactions among invasive predator and prey species.

Keywords *Callinectes sapidus* · Ebro River · Over-predation · Invader–invader interaction · *Pomacea maculata*

V. Céspedes · F. Picazo · B. Gallardo (✉)
Instituto Pirenaico de Ecología (IPE), CSIC, Avda, Montañana, 1005, 50059 Zaragoza, Spain
e-mail: Belinda@ipe.csic.es

V. Céspedes · R. Bernardo-Madrid · M. Vilà
Estación Biológica de Doñana (EBD), CSIC, C/Américo Vespucio 26, 41092 Seville, Spain

R. Bernardo-Madrid · M. Vilà
Department of Plant Biology and Ecology, University of Sevilla, 41012 Seville, Spain

F. Picazo
Department of Ecology/Research Unit Modeling Nature (MNat), Facultad de Ciencias, Universidad de Granada, Campus Fuentenueva S/N, 18071 Granada, Spain

C. Rubio · M. García · I. Sanz
Paleoymas, C/Retama, 17, La Cartuja Baja, 50720 Zaragoza, Spain

Published online: 21 May 2024

Introduction

The proliferation of invasive species in aquatic ecosystems is a global concern, yet in many cases invasive species are documented as simply co-ocurring, with limited insight into their complex interactions and the cumulative repercussions for native species and ecosystems (Johnson et al. 2009; Gallardo and Aldridge 2015; Guareschi et al. 2021). Invasive species may exhibit facilitative interactions, promoting establishment, spread and impacts—a process known as "invasional meltdown" (Simberloff 1995). Invasional meltdown involves environmental changes that facilitate establishment of subsequent invaders and/or provision of essential food sources. One of the most well-known examples in aquatic ecosystems is the zebra mussel, which not only shapes its environment but also provides food and habitat for multiple Ponto Caspian invasive species of plants, fish and gammarids (Bij de Vaate et al. 2002; Gallardo and Aldridge 2015). In this case, a shared evolutionary history might facilitate coexistence, overcoming hurdles such as predation or resource competition. An equally plausible, yet less studied interaction, is over-predation, observed when two species (prey and predator) are introduced into a new ecosystem. In this situation, the predator benefits from the highly abundant invasive prey, leading to an increase in the predator population that may eventually eradicate the invasive prey and cause further cascading effects on the native community. We may expect over-predation to be more common among invasive species that have never interacted before and therefore lack mechanisms of coexistence.

Here, we describe a novel interaction between two of the worst aquatic invaders globally, the apple snail *Pomacea maculata* Perry, 1810 and the blue crab, *Callinectes sapidus* Rathbun, 1896. Notably, these invaders lack a shared evolutionary history because they originate from distinct parts of the Americas, and their invasive distributions are so far not known to overlap. The apple snail is originally from South America (Argentina, Bolivia, Paraguay, Uruguay and Brazil) and has been spread intentionally and accidentally to Southeast Asia, USA and Europe (Hayes et al. 2008). It probably arrived in Spain, in the Ebro Delta, through an unintentional release from the aquarium trade, from unknown origin (López et al. 2010; Joshi and Parera 2017). The herbivorous apple snail was detected for the first time in 2013 in the Ebro River, an area with high biodiversity and agricultural value (Mañosa et al. 2001). The apple snail caused substantial alarm given its well-documented high reproduction rates and detrimental impacts on rice cultivation (Joshi et al. 2017). Species of the genus *Pomacea* exhibit early sexual maturation, with females able to reach maturity and commence spawning at 3–6 months of age (Estoy et al. 2002), and in the case of *P. maculata* yielding a substantial number of offspring (~ 1500 eggs per clutch) once a week for three summer months (Barnes et al. 2008). Initial control measures in the area targeted rice fields, ranging from completely drying down the fields on one side of the Ebro Delta, to changes in rice planting practices and the application of pesticides (Gallego et al. 2020).

The blue crab, native to the east coast of the Americas from Nova Scotia in Canada to northern Argentina (Nehring 2011), exhibits a remarkable ability to thrive in a diverse range of marine, estuarine and coastal freshwater habitats. This adaptability is due to a broad environmental tolerance in terms of temperature and salinity, coupled with a high trophic flexibility (Nehring 2011). The blue crab is an important predator that has caused substantial impacts on the structure and function of benthic food webs and fisheries (Nehring 2011; Clavero et al. 2022). While it has been present in the Mediterranean since the early twentieth century, its expansion has accelerated since 2010 (Mancinelli et al. 2021), with an outbreak in the Ebro River in 2018 (Clavero et al. 2022). Because of their distinct habitat preferences—freshwater for apple snails and marine or brackish water for blue crabs—the two species have never been reported to co-occur before their colonization of the Ebro River.

This study leverages data from a 9-year apple snail intensive removal programme (2014–2022) to: (1) evaluate the effectiveness of the management programme, and (2) describe the temporal dynamics of the species before and after the arrival of the blue crab in the study area. This information has significant implications for managing aquatic ecosystems affected by multiple waves of invaders.

Material and methods

Removal of apple snails and eggs in the Ebro River

In 2013, the apple snail was recorded for the first time in the main channel of the Ebro River, presumably spreading from colonies previously established in irrigation channels in the Delta (López et al. 2010). To counter the invasion, the Ebro River Water Authority (*Confederación Hidrografica del Ebro*, CHE), initiated an annual removal campaign in 2014 targeting apple snails from a 12.5 km segment of the river channel (Fig. 1). The target area was situated between the localities of Tortosa and Amposta (upper limit of study area at Long 0.4957, Lat 40.9199; lower limit at Long 0.5043, Lat 40.7991; Fig. 1). Operating during the breeding season from June to November, the removal protocol systematically focused on both adult specimens and egg clutches. This proactive intervention aimed to control the spread of the apple snail along the river corridor and mitigate potential ecological impacts in the region.

On a weekly basis, a thorough survey of the study area was conducted by a team of four experienced technicians. The distinctive bright pink egg clutches, deposited by apple snails above water, were meticulously removed during a dedicated day-long effort, totalling 8-h of survey. Adult specimens were targeted at night when they are more active and easier to detect, for a 6-h survey (Gallego et al. 2020). The diurnal removal effort amounted to 32 person-hours each week, with an additional 24 person-hours allocated to nocturnal removal. The duration of removal efforts varied from seven to 28 weeks per year, depending on population size and administrative permits (Table 1). For instance, effort was low (7–8 weeks) in 2014–2015 because of the incipient size of the population, and also in 2020 because of COVID-19 restrictions, while effort was high in 2022 (28 weeks), prompted by exceptionally elevated temperatures that extended the breeding season. The information used in this study encompasses the total number of egg clutches and adults removed per week, over the 9-year study period. Data were transformed to catch per unit effort (CPUE) for analysis, representing the total number of snails removed divided by the sampling effort (person-hours) each year. We differentiated between the two life stages because the efficiency of management efforts, as well as the impacts of the newly arrived predator, may differ between adults (low detectability, high predation pressure by the blue crab) and egg clutches (high detectability, no predation). Given the consistency in personnel, collection methods and timing of removal efforts, we assumed that removal data reflect real variation in the species density over time.

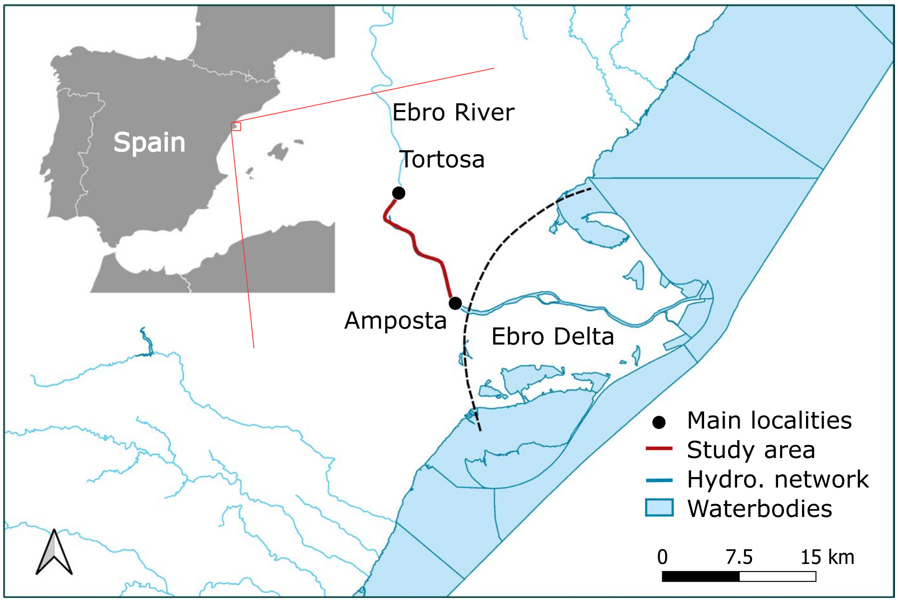

Fig. 1 Location of the study area in the Ebro River. The removal of apple snails was conducted in the main river channel between the localities of Tortosa and Amposta. The dashed line approximately separates the main channel of the Ebro River from its Delta

Table 1 Total number of apple snails removed from the main channel of the Ebro River (NE Spain) between 2014 and 2022

Year	Adult snails (total)	Egg clutches (total)	Removal effort (person-hours)	Adult snails (CPUE)	Egg clutches (CPUE)	Blue crabs (CPUE)
2014	2196	688	256/192	3.58	8.58	0
2015	1026	850	224/168	5.06	4.58	0
2016	7553	6922	576/432	16.02	13.11	0
2017	25,251	9821	704/528	18.60	35.87	0
2018	2339	697	640/480	1.45	3.65	0.71
2019	2045	461	736/552	0.84	2.78	1.01
2020*	163	111	224/168	0.66	0.73	0.48
2021	230	841	576/432	2.19	0.45	1.17
2022	273	546	896/672	0.81	0.30	0.74

Removal effort in person-hours of daytime surveys (for egg clutches) / night-time surveys (for adult snails), respectively. Blue crab CPUE represents sightings of the species during the apple snail night-time removal, so the CPUE is the same.

*Effort was limited in 2020 because of COVID19 restrictions

The blue crab in the Ebro River

The blue crab was first observed in 2012 in the Ebro Delta (Castejón and Guerao 2013). Following a lag phase of 5 years, its populations increased exponentially, leading to its wide distribution across the Ebro Delta and surrounding coast (Clavero et al. 2022). Despite its mostly marine nature, in August 2018, blue crabs were noted in the main channel of the Ebro River. Subsequently, these crabs have consistently been detected in areas were apple snail removal occurs (Fig. 1), although specific abundance information remains unreported. Notably, blue crabs have been recorded feeding on adult apple snails (Fig. 2a). Unfortunately, there exists no dedicated programme monitoring the expansion and abundance of blue crabs in the Ebro River (but see Clavero et al. 2022 for a description of population trends and impacts in the Delta and adjacent coast).

While our apple snail removal campaign was not originally designed for blue crab monitoring, our team was the first to detect its presence in the main channel of the Ebro River upstream from the Delta. We therefore possess unique data on blue crab sightings, consistently recorded during nocturnal activities when the crabs are actively hunting, and therefore more detectable. We calculated the catch per unit effort (CPUE) as the total number of blue crab sightings per person-hour of nocturnal snail removal effort. Although data interpretation necessitates caution, we believe it provides important insights regarding the exponential increase of the blue crab in the Ebro River.

Statistical analyses

We used repeated measures analysis of variance based on Kruskal–Wallis tests followed by post-hoc HSD Tukey Tests to investigate whether apple snail abundances differed significantly between consecutive years. The TukeyHSD command of R automatically adjusts the p values for multiple comparisons to ensure that the family-wise error rate is controlled across all pairwise comparisons. The selection of a non-parametric test was based on the data not meeting the normality and homoscedasticity assumptions of parametric tests. We expected a significant reduction in the abundance of the adult apple snails because of predation by the blue crab after August 2018. This would in turn result in a delayed decrease in egg clutches 3 to 6 months later, which corresponds to the age of first copulation and spawning in the genus *Pomacea*, specifically *P. canaliculata* (Estoy et al. 2002).

Results

Throughout the period from 2014 to 2022, a comprehensive removal effort resulted in the elimination of 20,937 adult apple snails and 41,076 egg clutches from the Ebro River. Between 2014 and 2017, the

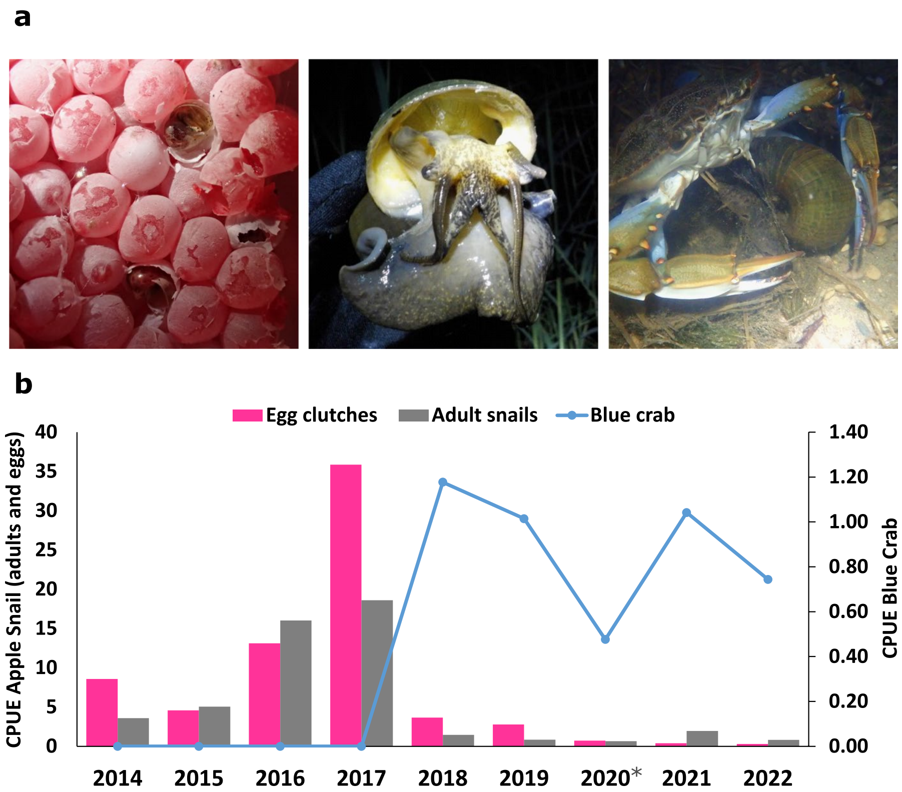

Fig. 2 Trends in the removal of apple snails from the Ebro River before and after the colonization by the blue crab. **a** Photographs of the pink egg clutches, an adult apple snail, and a blue crab in the act of feeding on an adult snail (photos: Ismael Sanz-Paleoymas). **b** Catch per unit effort (CPUE) of egg clutches and adult snails between 2014 and 2022 (left axis). Statistical differences across subsequent years can be consulted in Table 2. Blue crab CPUE represents sightings of the species during the apple snail night-time surveys (right axis).* Sampling effort was limited in 2020 because of COVID19 restrictions

CPUE of adult snails increased substantially, escalating by 141% in 2015, 317% in 2016, and 116% in 2017, with each percentage calculated relative to the preceding year (Fig. 2a, Table 1). The CPUE of adults and egg clutches was highest in 2017 (Fig. 2b, see results from pairwise HSD Tukey Test in Table 2).

The situation reverted following the arrival of the blue crab in 2018, when the CPUE of adult apple snails collected plummeted by 92% relative to 2017 (Tables 1 and 2, Fig. 2b). This negative trend persisted in 2019 (−42% relative to 2018), and 2020 (−21% relative to 2019), marking the period of minimum abundance of the snails (Fig. 2b, Table 1). While there was a resurgence in the CPUE of adult snails in 2021, the numbers remained very low (Table 1). There were significant differences in the CPUE of adult snails (Kruskal–Wallis Test, $Chi^2 = 84.64$, $df = 1$, $P < 0.001$) and egg clutches (Kruskal–Wallis Test, $Chi^2 = 90.23$, $df = 1$, $P < 0.001$) before and after the first sighting of the blue crab in August 2018.

A single blue crab individual was first detected in the last week of July 2018 and the following week, 30 individuals were encountered over the 2.5 km study area. In total, between 2018 and 2022, the team registered 1929 blue crab sightings during their snail removal activities. Temporal trends show an exponential increase of the blue crab in 2018, with numbers decreasing slightly the following years (Fig. 2b). The drop in blue crab numbers in 2020 is attributed to the limited removal effort (168 person-hours in 2020 due to COVID-19 restrictions, as opposed to 552 person-hours in 2019) as well as the timing of the campaign (June–July) before the peak of blue crabs that is often registered in August–September. Blue crabs were often observed hunting or in the process of eating adult apple snails.

Discussion

Despite management efforts between 2014 and 2017, our analysis of the removal campaign showed annual increases in apple snail abundance in the Ebro River of 100–300%. This rapid population growth aligns with observations in other countries (e.g. Burks et al. 2017), as well as for the congeneric *P. canaliculata* (e.g. Estoy et al. 2002). Besides the high reproduction rates of the different species of apple snail already

Table 2 Results from Kruskal Wallis tests with post hoc HSD Tukey tests of differences across years in the number of adults and/or egg clutches removed weekly

Formula	Test	Chi-sq
Adult snails ~ before/after blue crab	Kruskal Wallis test	$\chi^2 = 84.64$ df = 1 p value < 0.001
Egg clutches ~ before/after blue crab		$\chi^2 = 90.23$ df = 1 p value < 0.001

Formula	Test	Years	Difference	p value (adj)
Adult snails~year	HSD Tukey test	2014–2015	35.42	0.99
		2015–2016	**263.12**	**< 0.001**
		2016–2017	61.85	0.80
		2017–2018	**411.56**	**< 0.001**
		2018–2019	14.80	0.99
		2019–2020	4.18	1.00
		2020–2021	36.70	0.99
		2021–2022	33.06	0.99
Egg clutches ~ year	HSD Tukey test	2014–2015	127.92	0.99
		2015–2016	273.03	0.42
		2016–2017	**728.16**	**< 0.001**
		2017–2018	**1030.82**	**< 0.001**
		2018–2019	28.03	0.99
		2019–2020	65.62	0.99
		2020–2021	8.91	1.00
		2021–2022	4.62	1.00

p values automatically adjusted for multiple comparisons. Significant differences are indicated in bold

mentioned before (Estoy et al. 2002; Barnes et al. 2008), the surge in population growth can be attributed to several factors. First, apple snails probably benefited from the ample availability of food sources in the Ebro River, including rice plants and submerged macrophytes such as *Ceratophyllum demersum*, *Potamogeton densus* and *Ranunculus* spp. (Burlakova et al. 2009).

Second, the apple snail lacks natural enemies in the Ebro River able to prey intensively on its poisonous eggs or to overcome the thick shell of adults. Only the glossy ibis has been reported to start feeding on apple snails in the rice fields adjacent to the Ebro Delta (not in the Ebro River), but only 6 years after the introduction of the apple snail (Bertolero and Navarro 2018). Its predatory pressure was considered insufficient to have an impact on apple snail numbers.

Finally, there is also the possibility that the removal programme led to stage-specific overcompensation, resulting in rapid population increases, a phenomenon observed in the invasive European green crab (*Carcinus maenas*) in North America (Grosholz et al. 2021). This is known as the "hydra effect", where the removal of one life stage of the invasive species (typically adults), reduces the control of juveniles thereby facilitating the population explosion (Grosholz et al. 2021).

The positive population growth exhibited by the apple snail underwent a dramatic reversal in 2018, with a decline of over 90% from the previous year. The decline in egg clutches occurred several months afterwards. This temporal sequence suggests that the decline in apple snail populations was not primarily attributable to reproductive constraints, such as a reduction in egg production, but rather to a decline in the adult population.

We suggest that the collapse of the apple snail population is probably associated with over-predation by the blue crab, which rapidly colonized the main channel of the Ebro River in 2018, ultimately sharing the same habitat with the apple snail. In other zones of the Ebro River invaded by the blue crab, similar massive and rapid declines have been observed in other prey crab and fish species (Clavero et al. 2022), as well as in invasive molluscs like the Asian clam and the zebra mussel (Ventura et al. 2018; Wasson et al. 2020). These impacts can reasonably be attributed to the blue crab's versatile diet, encompassing a broad array of vertebrate and invertebrate prey (Mancinelli et al. 2017; Prado et al. 2022). Locally, the blue crab has been observed breaking the shells of adult apple snails with its strong claws and consuming them (Fig. 2a). Indeed, during the removal campaigns, the team observed blue crabs attracted by the apple snails they were removing, and during experimental tests we found intensive predation rates (unpublished data). To the best of our knowledge, there were no other significant environmental, biological or management changes that could explain the massive decline exhibited by the apple snail after 2018. The interest of the Ebro River case study lies in the behavioural flexibility displayed by the blue crab that has rapidly adjusted to exploit a novel and abundant prey, the apple snail. This flexibility contrasts with native predators in the Ebro River, with the sole exception of the glossy ibis, as they predominantly remain incapable of feeding on the apple snail.

The biological control exerted by the blue crab on the apple snail may be viewed as a positive outcome. However, the associated rise in blue crab populations may intensify the predatory pressure on other native species. This is evident in the swift and severe declines observed in native fish and crab species in the adjacent Delta and coastal region (Clavero et al. 2022). This is a process of hyper-predation, where the increase in the invasive predator fuelled by the abundant invasive prey adds pressure on native species, eventually leading to their local extinction (Courchamp et al. 2000). This possibility, underscores the need for a comprehensive understanding of ecological interactions and potential cascading effects when managing invasive species.

Management implications

The time series between 2014 and 2017 suggests that efforts to eradicate the apple snail within the study area have, to a large extent, fallen short (Gallego et al. 2020). The manual removal of apple snails was highly time and resource consuming but it provided critical information to understand the population structure and temporal trends of the species in the study area, which is the sole invaded location in Europe. Nevertheless, there is a need for a more detailed examination in diverse habitat types within the Ebro River and adjacent environments, such as canals, ditches, and rice fields.

The interaction between the apple snail and blue crab in the Ebro River poses three management challenges. First, any attempt to control blue crabs runs the risk of triggering an outbreak in apple snail populations. Second, if the apple snail removal programme continues, achieving its control in the river might escalate the predatory pressure of the blue crabs on native prey (Zavaleta et al. 2001). Third, the current management options for the blue crab, based on overfishing, carry the risk of establishing a local economy dependent on an invasive species. This last point is further elaborated below.

Overfishing and commercialization of the blue crab are currently the only management options to control populations, not only in Spain but also in various other invaded areas (Nehring 2011; Clavero et al. 2022). However, the managing of long-established commercially valuable invasive species can be controversial; this was the case of the red crayfish (*Procambarus clarkii*) in Europe (Oficialdegui et al. 2020). Unlike the red crayfish, the blue crab is a relatively recent invader in the Ebro River and, while it has economic benefits, local economies are not heavily reliant on crab fishing as a source of income. Consequently, further research is needed to better understand and quantify the population growth, feeding habits and dynamics of both the apple snail and blue crab, supporting informed decisions. The long-term conservation goals for the Ebro River should involve establishing a dynamic and resilient ecosystem, capable of withstanding the impacts of invasive species while fostering the recovery of native biodiversity (Guareschi et al. 2021; Britton et al. 2023). By understanding the synergies or conflicts that may arise among invaders coming from different origins, we can refine our management strategies and fortify the river ecosystem against the multifaceted challenges posed by invasive species under changing environmental scenarios.

Acknowledgements We thank two anonymous reviewers for their throughout comments on a previous version of the manuscript. This research was funded by the Spanish Ministry of Science and Innovation (PCI2018-092939, PCI2018-092986, MCI/AEI/FEDER, UE) participating in the project InvasiBES through the 2017–2018 Belmont Forum and BIODIVERSA joint call for research proposals, under the BiodivScen ERANet COFUND programme. BG was supported by a research fellowship funded by the Spanish Programme of R+D+I (RyC2018-025160-I). RBM was supported by MICINN through the European Regional Development Fund (SUMHAL, LIFEWATCH-2019-09-CSIC-13, POPE 2014–2020) and the research fellowship Margarita Salas funded by the European Union—NextGeneration EU) through the Spanish Ministry of Universities. We thank the Ebro River Water Authority and Regional Government of Catalonia for their data support provided.

Author contributions CR, MG and IS conducted field work and contributed to the study design. RBM and BG conducted the statistical analyses. VC prepared material and wrote the first version of the manuscript. BG and MV updated the initial manuscript. All authors read and approved the final manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was funded by the Spanish Ministry of Science and Innovation (PCI2018-092939, PCI2018-092986, MCI/AEI/FEDER, UE) participating in the project InvasiBES through the 2017–2018 Belmont Forum and BIODIVERSA joint call for research proposals, under the BiodivScen ERANet COFUND programme. BG was supported by a research fellowship funded by the Spanish Programme of R+D+I (RyC2018-025160-I). RBM was supported by MICINN through the European Regional Development Fund (SUMHAL, LIFEWATCH-2019-09-CSIC-13, POPE 2014–2020) and the research fellowship Margarita Salas funded by the European Union—NextGeneration EU) through the Spanish Ministry of Universities. We thank the Ebro River Water Authority and Regional Government of Catalonia for their data support provided.

Data availability Data used to conduct this analysis are openly available through the Ebro River Water Authority, *Confederación Hidrográfica del Ebro* (https://www.chebro.es/en-GB/inicio).

Declarations

Conflict of interest CR, MG and IS conducted the sampling programme described in this research through a contract commissioned by the Ebro River Water Authorities.

References

Barnes MA, Fordham RK, Burks RL, Hand JJ (2008) Fecundity of the exotic apple snail, *Pomacea insularum*. J N Am Benthol Soc 27:738–745. https://doi.org/10.1899/08-013.1

Bertolero A, Navarro J (2018) A native bird as a predator for the invasive apple snail, a novel rice field invader in Europe. Aquat Conserv Mar Freshwat Ecosyst 28:1099–1104. https://doi.org/10.1002/aqc.2917

Bij de Vaate A, Jazdzewski K, Ketelaars H et al (2002) Geographical patterns in range expansion of macroinvertebrate Ponto–Caspian species in Europe. Can J Fish Aquat Sci 59:1159–1174. https://doi.org/10.1139/f02-098

Britton JR, Lynch AJ, Bardal H et al (2023) Preventing and controlling non-native species invasions to bend the curve of global freshwater biodiversity loss. Environ Rev 31:310–326. https://doi.org/10.1139/er-2022-0103

Burks RL, Bernatis J, Byers JE et al (2017) Identity, reproductive potential, distribution, ecology and management of invasive *Pomacea maculata* in the southern United States. In: Joshi RC, Cowie RH, Sebastian LS (eds) Biology and management of invasive apple snails. Philippine Rice Research Institute, Philippine, pp 293–333

Burlakova LE, Karatayev AY, Padilla DK et al (2009) Wetland restoration and invasive species: apple snail (*Pomacea insularum*) feeding on native and invasive aquatic plants. Restor Ecol 17:433–440. https://doi.org/10.1111/j.1526-100X.2008.00429.x

Castejón D, Guerao G (2013) A new record of the American blue crab, *Callinectes sapidus* Rathbun, 1896 (Decapoda: Brachyura: Portunidae), from the Mediterranean coast of the Iberian Peninsula. BioInvasions Rec 2:141–143. https://doi.org/10.3391/bir.2013.2.2.08

Clavero M, Franch N, Bernardo-Madrid R et al (2022) Severe, rapid and widespread impacts of an Atlantic blue crab invasion. Mar Pollut Bull 176:113479. https://doi.org/10.1016/j.marpolbul.2022.113479

Courchamp F, Langlais M, Sugihara G (2000) Rabbits killing birds: modelling the hyperpredation process. J Anim Ecol 69:154–164. https://doi.org/10.1046/j.1365-2656.2000.00383.x

Estoy GF, Yusa Y, Wada T et al (2002) Size and age at first copulation and spawning of the apple snail, *Pomacea canaliculata* (Gastropoda: Ampullariidae). Appl Entomol Zool 37:199–205. https://doi.org/10.1303/aez.2002.199

Gallardo B, Aldridge DC (2015) Is Great Britain heading for a Ponto–Caspian invasional meltdown? J Appl Ecol 52:41–49. https://doi.org/10.1111/1365-2664.12348

Gallego EP, Millán CR, Halcón RMÁ et al (2020) El caracol manzana en el curso bajo del río Ebro. Gestión de una plaga. Nat Aragonesa Rev De La Soc De Amigos Del Museo Paleontol De La Univ De Zaragoza 22:49–56

Grosholz E, Ashton G, Bradley M et al (2021) Stage-specific overcompensation, the hydra effect, and the failure to eradicate an invasive predator. Proc Natl Acad Sci 118:e2003955118. https://doi.org/10.1073/pnas.2003955118

Guareschi S, Laini A, England J et al (2021) Multiple co-occurrent alien invaders constrain aquatic biodiversity in rivers. Ecol Appl 31:e02385. https://doi.org/10.1002/eap.2385

Hayes KA, Joshi RC, Thiengo SC, Cowie RH (2008) Out of South America: multiple origins of non-native apple snails in Asia. Divers Distrib 14:701–712. https://doi.org/10.1111/j.1472-4642.2008.00483.x

Johnson PTJ, Olden JD, Solomon CT, Vander Zanden MJ (2009) Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system. Oecologia 159:161–170. https://doi.org/10.1007/s00442-008-1176-x

Joshi RC, Parera XV (2017) The rice apple snail in Spain: a review. Int Pest Control 59:106

Joshi RC, Cowie RH, Sebastian LS (2017) Biology and management of invasive apple snails. Rice Research Institute, Philippine

López MA, Altaba CR, Andree KB, López V (2010) First invasion of the apple snail *Pomacea insularum* in Europe. Tentacle 18:26–28

Mancinelli G, Guerra MT, Alujević K et al (2017) Trophic flexibility of the Atlantic blue crab *Callinectes sapidus* in invaded coastal systems of the Apulia region (SE Italy): a stable isotope analysis. Estuar Coast Shelf Sci 198:421–431. https://doi.org/10.1016/j.ecss.2017.03.013

Mancinelli G, Bardelli R, Zenetos A (2021) A global occurrence database of the Atlantic blue crab *Callinectes sapidus*. Sci Data 8:111. https://doi.org/10.1038/s41597-021-00888-w

Mañosa S, Mateo R, Guitart R (2001) A review of the effects of agricultural and industrial contamination on the Ebro delta biota and wildlife. Environ Monit Assess 71:187–205. https://doi.org/10.1023/A:1017545932219

Nehring S (2011) Invasion history and success of the American blue crab *Callinectes sapidus* in European and adjacent waters. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place-alien marine crustaceans: distribution biology and impacts. Springer, Cham, pp 607–624

Oficialdegui FJ, Delibes-Mateos M, Green AJ et al (2020) Rigid laws and invasive species management. Conserv Biol 34:1047–1050. https://doi.org/10.1111/cobi.13481

Prado P, Ibáñez C, Chen L, Caiola N (2022) Feeding habits and short-term mobility patterns of blue crab, *Callinectes sapidus,* across invaded habitats of the Ebro Delta subjected to contrasting salinity. Estuaries Coasts 45:839–855. https://doi.org/10.1007/s12237-021-01004-2

Simberloff D (1995) Why do introduced species appear to devastate Islands more than mainland areas? Pac Sci 49:87–97

Ventura MP, Salgado SQ, de Arenas JHN et al (2018) Predation of the blue crab *Callinectes sapidus* Rathbun, 1896 on freshwater bivalves (Unionidae & Corbiculidae) in eastern Iberian Peninsula. Folia Conchyliol 47:3–9

Wasson K, Fabian RA, Fork S et al (2020) Multiple factors contribute to the spatially variable and dramatic decline of an invasive snail in an estuary where it was long-established and phenomenally abundant. Biol Invasions 22:1181–1202. https://doi.org/10.1007/s10530-019-02172-w

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16:454–459. https://doi.org/10.1016/S0169-5347(01)02194-2