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INVASION NOTE

First record of the semi-aquatic invasive plant *Crassula helmsii* in the Iberian Peninsula and its link to potential dispersal drivers

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Abstract Aquatic neophytes are among the most harmful invasive species worldwide. Here we report the finding of the semi-aquatic invasive plant *Crassula helmsii*, naturalized in a freshwater reservoir that provides water to the large city of A Coruña, NW Spain. To better understand the extent and potential environmental correlates of *C. helmsii* invasion, we recorded the presence and frequency of *C. helmsii* in its emerged and floating mat forms at twelve sampling sites along the reservoir margins, and characterized the soil characteristics, plant community and environmental factors. *Crassula helmsii* is dispersed by fragmentation of the stems, potentially aided through shredding by local fauna such as the invasive crayfish *Procambarus clarkii*. We hypothesize that this could be a case of an invasional meltdown, when multiple invasive species facilitate one another and have synergistic effects on native ecosystems. The emerged form of *C. helmsii* was found in ten out of twelve sites with a mean cover value of 9.8 ± 10.4% (mean ± SD). We found no correlation between frequency of the emerged form of *C. helmsii* and abundance of *Procambarus clarkii*, but frequency of the emerged form of *C. helmsii* increased with higher soil nitrogen and vascular plant richness. We outline emergency actions for management of *C. helmsii* at this stage of the invasion, focusing on containment and avoiding spread to nearby water bodies.

Keywords Aquatic ecosystems · Crassulaceae · Freshwater reservoir · Invasional meltdown · *Procambarus clarkii* · Water quality

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Introduction

Invasive alien species are a major threat to global biodiversity. Aquatic neophytes are considered especially harmful as they can alter hydrological conditions, nutrient and light cycles, affect water quality and outcompete native species (Lazzaro et al. 2020). Some invasive aquatic species can trigger changes on the ecosystem that may facilitate other invasive species (Tasker et al. 2022), resulting in an invasional meltdown (Simberloff and Von Holle 1999).

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Here we report the occurrence of *Crassula helmsii* (Kirk) Cockayne (Australian swamp stonecrop, New Zealand pigmyweed) in a freshwater reservoir in NW Spain, to our knowledge the first confirmed record from the Iberian Peninsula. *Crassula helmsii*, native to New Zealand and Australia, has been reported as invasive in the British Isles, continental western Europe and the United States, invading freshwater systems like lakes, ponds and reservoirs (Dawson and Warman 1987; Van der Loop et al. 2019; Smith and Buckley 2020). In Spain, no occurrences have previously been reported, but *C. helmsii* is considered a species of concern (MITECO 2013) and was listed as having a "very high risk" of future invasion in a recent horizon scan for potential aquatic invaders (Cano-Barbacil et al. 2023).

Crassula helmsii is known to have negative impacts on aquatic ecosystems and species, water quality and hydrological problems associated to the accumulation of large mats on the water surface (EPPO 2007; Smith and Buckley 2020; Van der Loop et al. 2020). Once introduced, *C. helmsii* reproduces and spreads by stem fragmentation and clonal growth (Dawson and Warman 1987; Hussner 2009; Smith and Buckley 2020) or seed production (Denys et al. 2014, D`hondt et al. 2016). Local fauna may play an important role in fragmenting the stems of *C. helmsii*, thus aiding its dispersal (Crane et al. 2021). *Procambarus clarkii* Girard, the red swamp crayfish, is one animal species that shreds and promotes clonal dispersal of aquatic plants (Carreira et al. 2014; Thouvenot et al. 2017). *Procambarus clarkii* has been introduced to many areas of the world from its native range of the southeastern United States and causes several environmental issues including competition with and predation on local fauna, transmission of diseases, modification of the resident plant community and impoverishment of drinking water quality (Loureiro et al. 2015; McMahon et al. 2013; Oficialdegui et al. 2019; Gao et al. 2022; Souty-Grosset et al. 2016). Here we hypothesized that invasion of *C. helmsii* may be facilitated through fragmentation and dispersal by *P. clarkii* resulting in an invasional meltdown that may pose a risk to local biodiversity.

Environmental factors are also known to be relevant for the establishment and cover of *C. helmsii*, including native plant species richness and cover (Dean et al. 2015; Van der Loop et al. 2023b) or soil and water conditions (Dawson and Warman 1987; Smith and Buckley 2020). Therefore, we quantified the frequency and cover of *C. helmsii*, abundance of *P. clarkii*, soil texture and nutrient levels, and composition and cover of the vascular plant community at twelve sampling sites in the Abegondo-Cecebre reservoir. These data were used to i) provide an initial description of the extent and severity of *C. helmsii* invasion; ii) assess potential for invasional meltdown between *C. helmsii* and *P. clarkii*; and iii) test the potential link between *C. helmsii* invasion and environmental variables, including soil condition and composition and diversity of the plant community.

Materials and methods

The reservoir of Abegondo-Cecebre covers an area of 365 ha in the confluence of the Mero and Barcés rivers in Abegondo, Galicia, NW Spain (Fig. 1). The reservoir and its surroundings are included in the Biosphere Reserve "Mariñas Coruñesas e Terras do Mandeo", a Special Area of Conservation (SAC) within the Natura 2000 network of EU protected areas.

To quantify the occurrence and abundance of the two invasive species *C. helmsii* and *P. clarkii*, we sampled at twelve sites located at approximately regular intervals along the reservoir shoreline (Fig. 1, Figure S1). At each site, we recorded the frequency of *C. helmsii* in three forms: emerged, submerged, and floating mats (Dawson and Warman 1987, Smith and Buckley 2020, supplementary materials and methods). Presence and cover of all vascular plant species was recorded in each site, and whenever needed, samples were collected to confirm field identification (supplementary materials and methods). The presence and cover of *C. helmsii* was recorded at each site using twenty 0.25 m^2 plots located at the beginning of each meter along a 20 m transect following the current water line. In order to sample a similar position across the study sites, we used the current waterline as the reference and placed the plots alternately on the wet and dry sides of the transect. In each plot, we estimated visual cover of *C. helmsii* to the nearest 5%. Species with very low cover were allocated a standard 2.5%, such as single plants of small annual species (supplementary materials and methods).

The presence and density of *P. clarkii* was assessed by direct capture of individuals. Captures

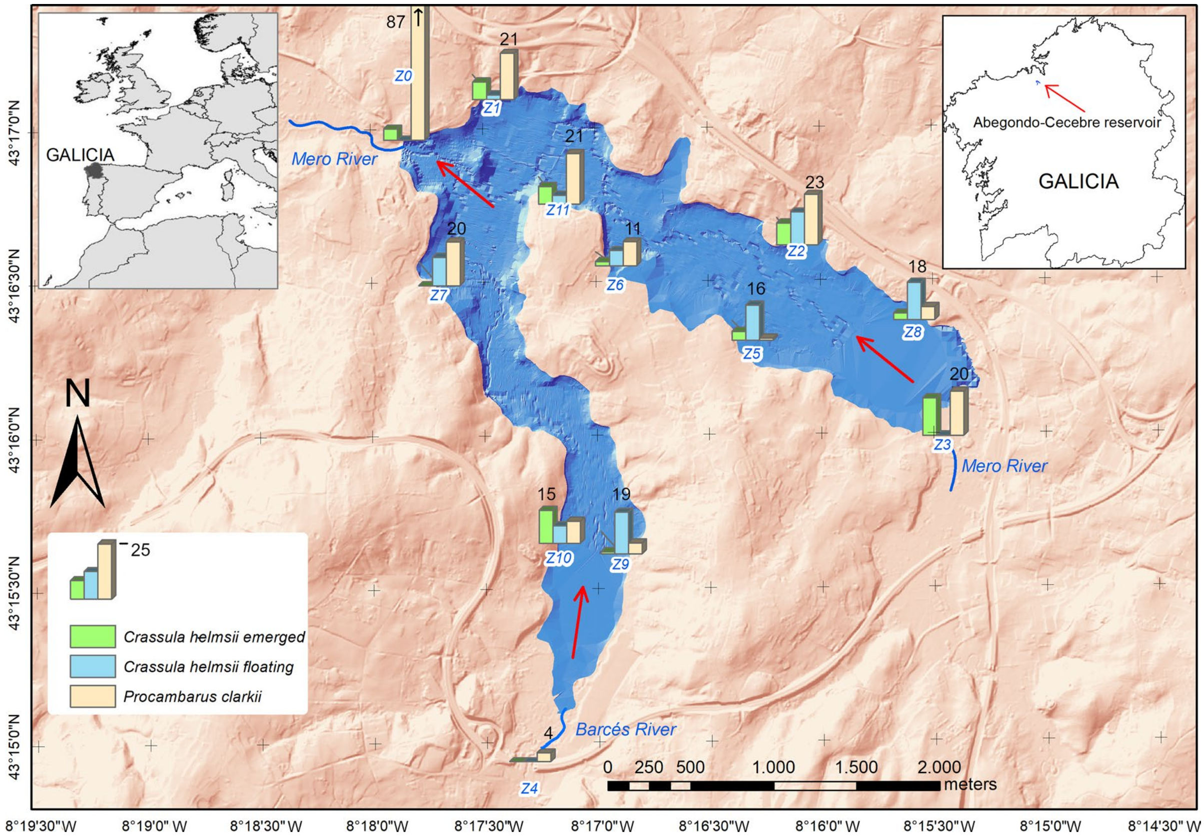

Fig. 1 Location of twelve sampling sites on the margin of the Abegondo-Cecebre reservoir in northern Galicia (upper-right box, arrow), NW Iberian Peninsula (upper-left box), Spain. At each site, three columns represent the value of emerged and floating mat forms of *Crassula helmsii* and the number of *Procambarus clarkii* adults captured. Values for *C. helmsii* are the number of plots with presence for each form (emerged or floating mat) out of twenty. A reference value of 25 is indicated in the legend and applies to the three parameters. The highest value in each site is also given in numbers. All values are shown in Table S4. Red arrows in the reservoir depict the direction of the water flow

were performed using underwater traps from May to June 2023. Number of adults captured were counted and summed for a final abundance data at each sampling site (supplementary materials and methods). To evaluate the potential link between the forms of *C. helmsii* (emerged, submerged, floating), and abundance of *P. clarkii*, we calculated Spearman rank correlations (Rho, supplementary materials and methods).

To test the relationship between environmental factors and the occurrence and cover of emerged *C. helmsii*, each sampling site was characterized according to a number of environmental variables (Table S1). A mixed sample of the topsoil of the emerged zone was collected at each sampling site. Soil texture was calculated as percentage of coarse (particles $>$ 2 mm diameter), sand (2 – 0.05 mm) and fine fraction ($<$ 0.05 mm). Acidity (pH) and soil organic matter (OM) were calculated for each sample. Total carbon (C), nitrogen (N) and phosphorus (P) were also measured in the soil fine fraction (supplementary materials and methods and Table S1). We applied a generalized linear model (GLM) with a Poisson distribution and logarithmic link function with emerged *C. helmsii* cover as the dependent variable to select the best explanatory model from the set of environmental variables based on Akaike's information criterion adjusted for small sample sizes (AICc). The statistical significance of the selected variables was tested by Wald χ^2 statistic (supplementary materials and methods).

Results

Floating mats of *Crassula helmsii* were first observed and identified in the Abegondo-Cecebre reservoir in March 2023. We then confirmed the occurrence of established plants at several sites along the margins of the reservoir (Figs. 1, 2B). Plant samples were collected, and herbarium sheets will be deposited in the public herbarium SANT at Santiago de Compostela University facilities.

Crassula helmsii was found in its emerged form at ten of the twelve sites, with a mean frequency (number of 0.25 m^2 plots with presence of the species out of a total of 20 per sampling site) of 6.1 ± 5.7 (mean ± SD) plots, ranging between 0 and 17 plots, and cover ranging from 0 to 35.6% (mean 9.8% ± 10.4%, Table S2). Floating mats of *C. helmsii* were recorded at nine sites, but no correlation was found between frequencies of emerged and floating mat forms (correlation coefficient Rho −0.251; $p = 0.432$). We recorded maximum cover values of floating mats of 71.9% (mean 19.8% ± 21.9%). In contrast, the submerged form was only observed at one site (Table S2 and supplementary Results).

The cumulative number of *P. clarkii* adults per study site ranged from 1 to 87 with a mean value of 19.25. A high variation was observed among sampling periods, with higher numbers in late June (Table S3). We found no significant relationships between *P. clarkii* abundance and emerged (correlation coefficient Rho 0.465; $p = 0.128$) or floating *C. helmsii* cover (-0.424; $p = 0.170$).

Site conditions varied in their width, slope and vegetation condition (Table S4). The three mineral soil fractions were roughly balanced (coarse: mean 29.7%; sand: 27.4%; fine: 42.7%). Soils had a mean organic matter fraction of 5.6% (SD 2.52%; range 1.0%–9.6%), with low values for total N (mean 0.11 ± 0.084%, range 0.01—0.28%) and C (mean 1.31 ± 1.00%, range 0.14—3.19%). Soil P was found in a mean concentration of 33.1 mg per g in the fine fraction (SD 14.56) (Table S4). Herbaceous plant cover at each site ranged from 5 to 100% (mean 33.6%, SD 32.78%). We recorded a mean of 10.8 plant species per site, SD 4.17 and ranging from three to 18 per site, from a total of 48 plant species. Two other exotic species were recorded: *Cyperus eragrostis* Lam. and *Conyza* sp. (Table S5).

Emerged *C. helmsii* cover increased with a combination of higher soil total nitrogen and plant species richness (supplementary Results, Table S7,

Fig. 2 A View of the reservoir transition zone with limited vegetation and dead tree cover. **B**. Photo of *C. helmsii*. **C**. An example 0.25 m^2 plot with sparse *C. helmsii* in its emerged form, and other species including *Pseudognaphalium luteoalbum* (Pl), *Hypericum humifusum* (Hh) and *Lotus hispidus* (Lh). **D**. *C. helmsii* (Ch) plants in the vicinity of a *Procambarus clarkii* burrow (Bu)

Figure S3). Other combinations of environmental variables did not have any effect on emerged *C. helmsii* (supplementary Results).

Discussion

This record of *C. helmsii* in the Abegondo-Cecebre reservoir is the first confirmed from the Iberian Peninsula. According to the literature review and available databases, including gbif (www.gbif.org) and anthos (www.anthos.es), there are no published records of the species from the Iberian Peninsula. Two localities have been reported in the citizen science website iNaturalist (www.inaturalist.org) in central Portugal and central South Spain, but these need to be confirmed.

The new invasion is a serious issue with potential implications for biodiversity and water quality. We found that sites ranged from heavily invaded to uninvaded compared to other areas (e.g. Van der Loop et al. 2023b), suggesting that this is a recent introduction. However, an alternative explanation to the low cover values recorded could be that the habitat is not suitable for increased dominance of the invader. This could be due to the depth and size of the reservoir, but previous studies have shown that although *C. helmsii* generally invades smaller lakes and ponds with shallow waters, it can also adapt to water bodies of greater depth (Diaz 2012).

Emerged *C. helmsii* cover was not related with *P. clarkii* abundance. Since *C. helmsii* can grow new plants from fragments as short as 20 mm (Coughlan et al. 2022), there is potential for its spread to be facilitated through shredding by crayfish (Dean et al. 2015). *Procambarus clarkii* is known to aid in clonal dispersal of aquatic species such as *Ludwigia grandiflora* (Michx.) Greuter & Burdet, another invasive aquatic species from South America (Thouvenot et al. 2017). Although crayfish consume large quantities of *L. grandiflora*, they promote its dispersal and colonization of new areas through fragmentation of rooting stems, which is a common clonal strategy in hydrophytes (Santamaria 2002). This relationship was not observed in our study, either because this facilitation effect does not occur between these two invasive species, or due to small sample sizes or inadequate study scale. Further investigation could include manipulation experiments of the species to address this potential invasional meltdown.

Cover of floating and emerged *C. helmsii* were not correlated, suggesting that other factors such as dominant winds or hydrological dynamics may define the movement and accumulation of the floating mats (red arrows in Fig. 1). Previous studies have shown that the submerged form of *C. helmsii* is linked to water level fluctuations that expose deeper substrate for a period of time (Diaz 2012). This form was only observed in one site, further indicating a recent introduction as seasonal fluctuations are common in the reservoir water levels. This evidence suggests that *C. helmsii* could be in the process of colonizing the reservoir and has not yet reached an equilibrium.

Emerged *C. helmsii* cover was positively related to native plant species richness, whereas other variables such as total plant cover or tree cover had no relationship with the invader. This contradicts the general assumption that high cover of native vegetation can counteract the invasion process (Dean et al. 2015), and the diversity-invasibility hypothesis that claims a higher resistance to invasion linked to species diversity of the resident community (Levine and D'Antonio 1999). The vascular plants recorded in the sampling sites showed a mixed community with hygrophilous and opportunistic species, which may not be suitable to counteract the spread of the invader (Van der Loop et al. 2023b). Soil nitrogen had the strongest predictive value on *C. helmsii* cover, especially when combined with native species richness, suggesting that a nutrient rich soil environment may be best suited both for native species and the new invader *C. helmsii*. This also contradicts previous studies that consider the probability of *C. helmsii* invasion as indifferent to nutrient availability (Van der Loop et al. 2019).

Implications for management

Eradication of *C. helmsii* is unlikely once the species is established. Therefore, control and mitigation or containment plans should be established to counteract future impacts. Management approaches trialed to control *C. helmsii* have used physical, chemical and biological control. The use of non-specific herbicides has proven mostly unsuccessful in areas with an established population (Brunet 2002), although aerial plant cover can be reduced by up to 80% after its application (Anon 2004). Regarding biological control, the mite *Aculus crassulae* has been shown to reduce *C. helmsii* height and development of lateral shoots, although this agent is still under development (Varia et al. 2022).

Combined measures of physical control using geotextile with a mesh size of 0.1 mm or less, avoiding eutrophication, and revegetation of bare soils to promote competition seem to be the most promising management approach to avoid full colonization of the reservoir. Reducing nutrient availability may promote an environment that favors native species (Van der Loop et al. 2023a), but our results show that soil N coupled with native species richness was the best predictive model of *C. helmsii* cover (Figure S3). Restoring natural vegetation of reservoir margins could be an effective management action to mitigate against *C. helmsii* invasion, since a diverse native plant community promotes competition and balances nutrient levels (Bakker and Wilson 2004; Ewald 2014; CEH 2002; Van der Loop 2020, 2023b), although this was not supported by our data (see above). In addition, avoiding water acidification linked to eutrophication will constrain the expansion of *C. helmsii* (Dean 2015; Smith and Buckley 2020). Finally, reducing the use of the invaded area by people, and promoting good practices such as boot disinfection, may aid in avoiding colonization of new water bodies in the region.

Conclusion

Crassula helmsii, an invasive semi-aquatic species of concern in western Europe, occurs in high frequencies but low to medium cover in the freshwater reservoir of Abegondo-Cecebre in NW Spain, to our knowledge the first confirmed record from the Iberian Peninsula. The singularity of reservoirs as potential hotspots for invasive species and the high ecological, economic and social impacts of invasional meltdowns in these habitats urge increased vigilance to prevent the introduction and spread of new exotic species. Thus, a rapid response in the containment of *C. helmsii* in the reservoir, and the vigilance of its expansion to nearby water bodies, will lower future management costs. Future research should focus on the species dispersal ability, and continuous monitoring must be performed to address the potential expansion of *C. helmsii* at the reservoir and elsewhere.

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Authors contributions All authors collected field data, J.F. and M.J.S. wrote the first draft, and all authors contributed to the final version.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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