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Rapid Communication

The expansion and establishment of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the freshwater ecosystems of Madeira Island (NE Atlantic)

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Abstract

This study reports the spread of the New Zealand mud snail *Potamopyrgus antipodarum* throughout freshwater ecosystems of Madeira Island, located in the NE Atlantic. *Potamopyrgus antipodarum* was first detected in 2017–2018 in two streams located in the north coast of the island. Since then, we have visually inspected the island's freshwater ecosystems and detected this gastropod in nine other streams. Previous evidence suggests that this species was introduced to Madeira since at least 2017, likely in the northern part. Our findings indicate that *P. antipodarum* is now well-established in the initial invaded locations and has since spread to the south region and upper streams of the island. Although it is difficult to conclusively determine the origin and vector of this introduction, it is plausible to assume that humans and fish may have contributed to its current distribution. Our records represent the first evidence of vast geographical distribution of *P. antipodarum* on Madeira Island. Madeira seems to be the first invaded oceanic island of Macaronesia and the westernmost European distribution range for this invasive species.

Key words: insular ecosystem, mollusc, alien species, exotic species, non-indigenous species, *Amnicola antipodarum*, *Potamopyrgus jenkinsi*

Introduction

The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) (Tateidae, formerly Hydrobiidae, Mollusca) is a prosobranch gastropod native to New Zealand freshwater ecosystems. This highly invasive species is established on all continents except Antarctica (Taybi et al. 2021; Geist et al. 2022). *Potamopyrgus antipodarum* was first introduced in Europe in 1859 (Ponder 1988), where it now ranks in the top hundred "worst alien species" and the third most invasive mollusc (Nentwig et al. 2018). Europe represents a non-native hotspot for this species. The New Zealand mud snail is registered in over half of the countries of this continent, including mainland Portugal (Cancela da Fonseca 1991; Patoka et al. 2017; Geist et al. 2022). The invasion success of the New Zealand mud snail is due to external factors, particularly those related to human activities. For instance, *P. antipodarum* is commonly transported in ballast water of ships or introduced via aquaculture and freshwater gamefish trade (Alonso and Castro-Díez 2008; Geist et al. 2022). Additionally, recreational fishing and fish stocking contribute to the spread of this species through "hitchhiking" gear and fish guts, respectively (Alonso and Castro-Díez 2008; Butkus and Rakauskas 2020; Vinson and Baker 2008). After reaching non-native areas, population densities tend to increase, particularly in disturbed habitats such as those with high eutrophication (Aarnio and Bonsdorff 1997; Spyra et al. 2015; Cieplok et al. 2023). Besides anthropogenic vectors, this mollusc can spread by floating in macrophytes or attaching to the beaks, feet or—less likely— inside the guts of waterbirds (Alonso and Castro-Díez 2008; Butkus et al. 2012; van Leeuwen et al. 2012). Furthermore, the species benefits from absent or reduced predation and parasitism within non-native areas – supporting the "enemy-release hypothesis" (Alonso and Castro-Díez 2012b; Gérard et al. 2017).

The invasiveness of *P. antipodarum* can be attributed to several intrinsic characteristics. Due to its small size (4–7 mm) and cryptic colour, this gastropod can be easily transported without being noticed (Patoka et al. 2017). The solid operculum protects from dehydration and digestion by some predators, simultaneously allowing it to adapt to various salinities and temperatures (Alonso and Castro-Díez 2012a; Romero-Blanco and Alonso 2019; Geist et al. 2022). These discrete and resistant morphological traits allow this snail to survive both transoceanic journeys and transport over short distances (Geist et al. 2022). This snail manifests behavioural avoidance strategies against predators and a detritivore-herbivorous diet based on various food resources (Geist et al. 2022). This high phenotypic plasticity ensures that *P. antipodarum* has a high survival and growth rate (Alonso and Castro-Díez 2008; Geist et al. 2022). The invasive morphotypes are mainly clones produced through parthenogenesis. The asexual continuous reproduction and rapid growth translate into high fecundity. Indeed, a single female can start a new population, raise multiple generations and a hundred juveniles yearly, and newborns reach sexual maturity in months (Richards 2002; Alonso and Castro-Díez 2008; Geist et al. 2022).

As *P. antipodarum* quickly reaches high densities and is highly competitive, native gastropods and other invertebrates tend to reduce in biomass, number, and taxa (e.g., Spyra et al. 2015; Collado et al. 2019; Riley et al. 2008 – but see Schreiber et al. 2002). In scenarios where this invasive species dominates the benthic biomass, its major grazing activity, preference for grazing green algae over diatoms and the relative increase in faeces leads to a change in the composition of producers, typically resulting in a decrease of available carbon and an increase in nitrogen fixation (Arango et al. 2009;

Moore et al. 2012). Subsequently, the modifications imposed by this snail at lower trophic levels endanger predators. With the native benthic community suppressed by populations of *P. antipodarum*, the diet of fishes shifts from nutritious to less digestible prey, jeopardising their fitness and survival (Rakauskas et al. 2016; Butkus and Rakauskas 2020; Vinson and Baker 2008; Cross et al. 2011). In summary, the introduction of the New Zealand mud snail can alter the structure and functioning of newly invaded ecosystems (Richards et al. 2001; Alonso and Castro-Díez 2012b; Moore et al. 2012; Spyra et al. 2015).

The effects caused by invasive morphotypes of *P. antipodarum* on freshwater ecosystems are broadly acknowledged (Geist et al. 2022). However, its introduction can be even more dangerous in the watercourses of island systems, which typically have a reduced but unique biodiversity. On Madeira Island, terrestrial biodiversity includes several endemic species, particularly molluscs and arthropods (Hughes 2003; Florencio et al. 2021). Streams occupy a large area of this island and are home to several endemic macroinvertebrates and a globally threatened fish: the European eel *Anguilla anguilla* (Linnaeus, 1758) (Marques 1994; Hughes 2003; Prada et al. 2005; Pike et al. 2020). Our study investigates the distribution of the highly invasive *P. antipodarum* in the streams of Madeira Island for the first time. Here, we highlight the potential risks of a progressive expansion and propose measures of control and eradication for the entire Macaronesian region. Finally, this account alerts us to the urgent need to monitor adjacent islands and archipelagos and to act immediately in the event of New Zealand mud snail detection.

Materials and methods

This study took place on Madeira, a Portuguese volcanic island located in the NE Atlantic Ocean (32°24′N, between 16°16′ and 17°16′W) about 700 km off the Moroccan coast (Figure 1A). Madeira is the biggest island (741 km^2) and one of two human-inhabited islands of the Madeira archipelago, which forms part of the Macaronesia region. Reaching 1861 m in altitude, this Island is characterized by a steep topography. The yearly mean precipitation in low-altitude regions typically ranges from 300 to 700 mm, while in high-altitude areas it can be as high as 2500 to 2800 mm (Couto et al. 2012). Rainfall and flood events are common on the Island (Baioni 2011). Freshwater ecosystems in Maderia Island comprise more than 200 streams (Marques 1994), including natural and man-made structures. Across this network of waterways, upstream regions tend to be more natural while downstream regions are generally more transformed due to more intense human activity near the coastline, particularly in the south (Baioni 2011; INE, IP/DREM 2021). We have surveyed streams across the Island in the north and south region, and included stretches at upper-, intermediate- and lower-regions.

A field survey was conducted in March and April 2023 to investigate the distribution of *Potamopyrgus antipodarum* across Madeira Island. This survey followed the first published evidence of the presence of this gastropod

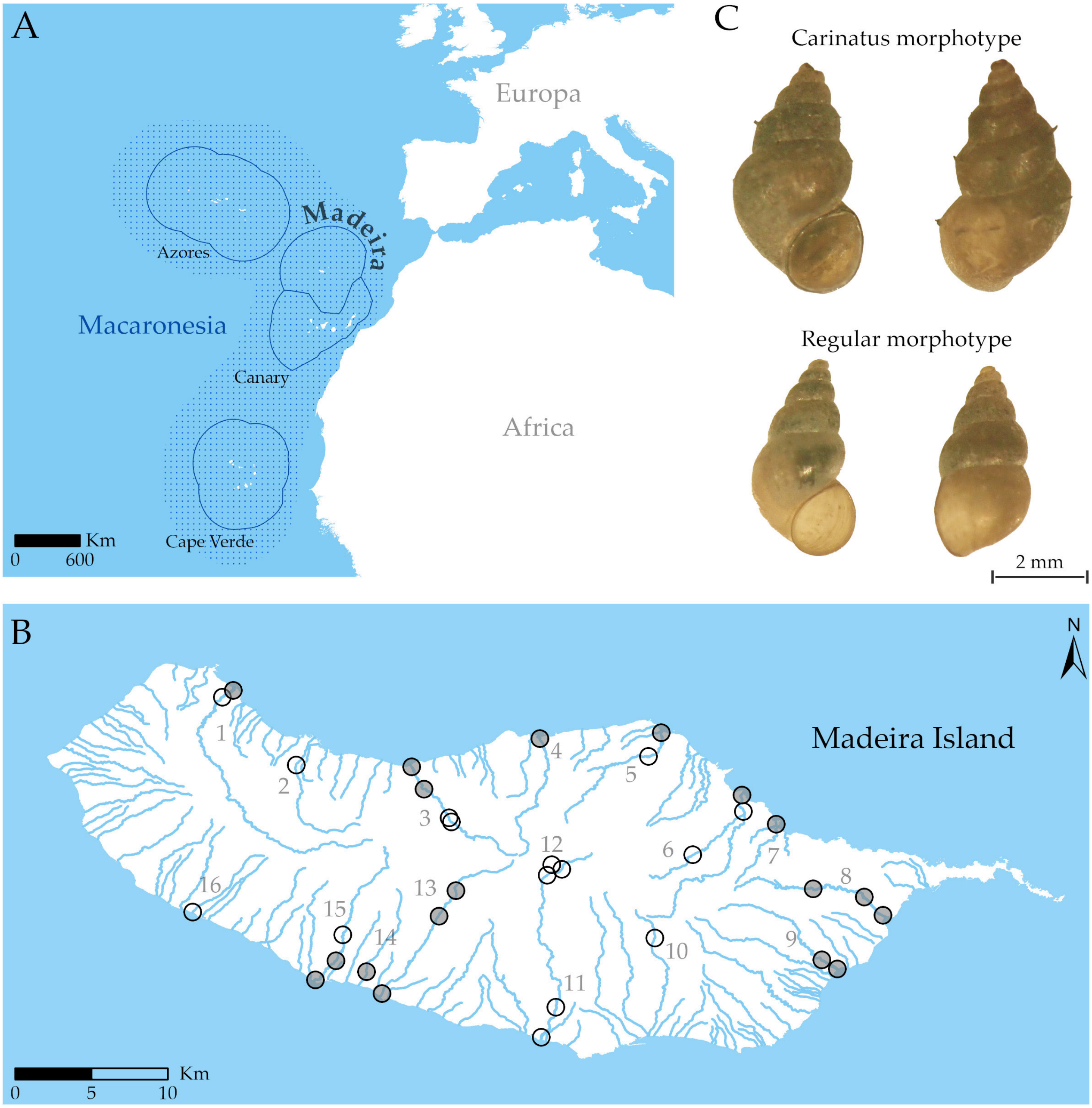

Figure 1. Study contextualisation: A – study region position in Europe and Macaronesia; B – Madeira Island with sampling sites and records of *Potamopyrgus antipodarum* in 2023 represented with full circles for detected and empty circles for non-detected specimens; and C – representative of the two morphotypes – ventral and dorsal section – of the New Zealand mud snail *P. antipodarum* collected in Madeira Island.

by Vidaña Glauser (2020) and our own occasional detection since June 2018. The survey was conducted in 33 sites in 16 streams (Figure 1B) through substrate inspection of stones located in the shallow water along the banks. Streams and reaches were selected to assess the species' establishment success and the spread between and along the waterlines. Sampling was conducted in thirteen streams previously surveyed by us, Vidaña Glauser (2020), and in a previous study on freshwater macroinvertebrates in Madeira Island (Raposeiro et al. 2022), as well as in three new streams. Among those that had already been sampled, we considered four streams with previous confirmation of

Table 1. Evidence of the occurrence of the New Zealand Mud Snail *Potamopyrgus antipodarum,* in Madeira Island over time and represented as follows: "●" for detected, "○" for non-detected specimens, and " " for no evidence (i.e., not sampled). The years of sampling (from left to right) are as follows: 2015 (Raposeiro et al. 2022), 2017–2018 (Vidaña Glauser 2020), 2018 (opportunistic substrate inspection), and 2023 (field survey).

Region	ID	Stream	2015	2017–2018	2018	2023
North	1	Janela	○	○		●
	2	Seixal				○
	3	Grande / São Vicente	○	●		●
	4	Porco				●
	5	São Jorge	○	○	●	●
	6	Faial	○	●	●	●
	7	Maçapez			●	●
South	8	Machico	○			●
	9	Santa Cruz	○			●
	10	João Gomes / Cales				○
	11	Socorridos / Curral das Freiras	○	○		○
	12	Gomeira	○			○
	13	Ribeira Brava	○			●
	14	Tábua		○		●
	15	Ponta do Sol	○			●
	16	Fonte do Bugio / Calheta	○			○

the species' occurrence and nine streams without such confirmation. In streams with past data, we inspected locations where *P. antipodarum* was and was not detected, and sampled different sites along eight of the streams. We sampled either exact or approximate locations previously sampled (coordinates were not always accessible). All collected specimens were stored in 96% ethanol and later analysed and photographed using a binocular microscope with an integrated digital camera (Leica S9D + FlexaCam C3; Figure 1C).

Results

Specimens were first collected in 3 northern streams: São Jorge, Faial, and Maçapez (Table 1). Later in 2023, *P. antipodarum* was confirmed in 18 sites of eleven streams of Madeira Island (Figure 1B, Supplementary material Table S1). Mud snails were detected in both streams where previously detected and with no prior information (Table 1). Across the Island, we have detected specimens in the north since 2018 and in the south in 2023. Within streams, specimens were detected near the coast in 2018 and captured in upper streams in 2023 at a maximum altitude of 409 m and 9.41 km from the sea. We found specimens in 83.3% of the sites sampled near the coast and in 40.0% of sites sampled in upper regions. The specimens collected presented two morphotypes: carinatus and regular (Figure 1C). The specimens were deposited at the regional natural history museum *Museu de História Natural do Funchal* under voucher number MMF50002, 50003, 50005–50024 (see Table S1).

Discussion

This study shows that *Potamopyrgus antipodarum* has successfully established in Madeira and was introduced on this island at least six years ago. While the first sightings were reported in streams of the northern part, our recent sampling confirmed the occurrence of this invasive gastropod in streams in the south and upper reaches. This suggests that the New Zealand mud snail has spread to other locations across the island. Furthermore, the species has likely become well-established, as we have repeatedly found specimens at the initial identification sites. Finally, the high incidence of this snail highlights the need to closely monitor sites with *P. antipodarum* and investigate their impact on native species and ecosystem functioning.

Combined with previous studies, our results help identify the likely period when *P. antipodarum* was first introduced. Apart from the study by Vidaña Glauser conducted between 2017 and 2018, no previous research on freshwater macroinvertebrates detected the New Zealand mud snail. This includes the studies conducted in 1991–1992 by Hughes et al. (1998), and in 2015 by Raposeiro et al. (2021, 2022). Therefore, *P. antipodarum* was most probably introduced directly or indirectly to the north of the island between 2015 and 2017. Eventually, the species was introduced more than once as the collected snails presented two morphotypes (Butkus et al. 2012). However, it is necessary to analyse the morphotypes in more detail and the lineages of specimens in this region to identify the number of introductory events (Butkus et al. 2012; Geist et al. 2022). Furthermore, genetic analyses will contribute to identifying the origin of the specimens.

While the circumstances and vector(s) responsible for the appearance of *P. antipodarum* in Madeira Island cannot be concluded from the present data, there are several plausible introductory pathways. One possible pathway explaining the introduction of this snail could be recreational fishing. Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) is a fish known to transport this snail (Vinson and Baker 2008; Alexandre da Silva et al. 2019). It was introduced to Madeira Island for fishing purposes (Freitas and Canning-Clode 2008; official information by the regional entity *Instituto das Florestas e de Conservação da Natureza*). This possibly pathway coincides with the initial detection of *P. antipodarum* in the north (Janela, São Vicente, and São Jorge), where rainbow trout was first introduced. On the other hand, trout stocking began in the 1960s, long before the first recorded appearance of *P. antipodarum*. Another recognised pathway for transoceanic transport of species is through boats and ships, via biofouling or ballast water (Alonso and Castro-Díez 2008; Patoka et al. 2017; Geist et al. 2022). Madeira Island has long provided essential refuelling and rest stop for ships between Europe, America, and Africa, which has led to the introduction of new species (Castro et al. 2020; Ramalhosa et al. 2021). Nevertheless, the chances that the first specimens appeared through shipping are slim, as the main harbours and shipping traffic are concentrated in the south of the island. Thus, alternative pathways could have been through hitchhiking on fishing gear, ornamental plants used for pet aquaculture, or marine litter (Alonso and Castro-Díez 2008; Patoka et al. 2017; Cardoso and Caldeira 2021; Geist et al. 2022). Future studies should evaluate the correlation between the abundance or biomass of this invasive species and potential introductory vectors (e.g., distance to the nearest harbour). Also, conducting questionnaires to aquarium shops and users should tackle the contribution of the aquarium trade to this species' introduction.

The recurring detection of *P. antipodarum* in the same locations in recent years suggests that these are established populations. These findings are well aligned with previous research showing that this species quickly adapts to non-native regions (Geist et al. 2022), but further studies will be needed to evaluate population densities and corroborate establishment success.

Aligned with previous studies showing that the species thrive in highly altered habitats (Spyra et al. 2015; Cieplok et al. 2023), the snail was mainly found on the coast at low elevations of the island where the human density and anthropogenic pressure mainly concentrate (Baioni 2011; INE, IP/DREM 2021). In Madeira Island, the streams tend to be more degraded at lower reaches, with riparian galleries deforested or composed of alien plants, and with water rich in nitrogen and poor in oxygen (Luis et al. 2015). In addition, the artificial feeding of the common non-native waterfowl muscovy ducks *Cairina moschata* (Linnaeus, 1758) and their faeces' accumulation contributes to eutrophication (Xavier et al. 2007; Johnson and Hawk 2009). It is also expected that the density of this snail will remain higher near the coastline, given the downstream drift and a lower water flow (Geist et al. 2022). Still, as this gastropod has a plastic behavior and only recently reached some sites, more populations are expected to appear and establish in other areas. In this context, the increasing number of locations where we found *P. antipodarum* suggest that the species has spread to other locations and along streams. Based on previous research, we suppose that this species has passively moved between watercourses, transported by migrating birds, freshwater fish, and humans – e.g., in fishing and canyoning gear (Alonso and Castro-Díez 2008; Geist et al. 2022).

The expansion of *P. antipodarum* throughout Madeira is a significant cause for concern, particularly given the high level of endemic species and areas with pristine conditions in this island, such as the Laurel Forest – a world heritage site (UNESCO 1999). Increasing evidence shows that the presence of the New Zealand mud snail leads to a reduction in the population or even disappearance of native macroinvertebrates (Alonso and Castro-Díez 2012b). This includes families native to Madeira, such as the common Ephemeroptera *Baetis* spp. (Kerans et al. 2005; Spyra et al. 2015). The loss of such species is known to reduce water quality (Cross et al. 2011; Sandvik et al. 2022). A reduction of native macroinvertebrates could also cause predators to suffer population decline, due to a reduction of prey availability. In the case of native fish, the replacement of native prey by this introduced snail has been seen to compromise food intake (Vinson and Baker 2008; Cross et al. 2011; Butkus and Rakauskas 2020). Madeira's only freshwater native fish, the European eel (*Anguilla anguilla),* has not been studied in the context of mud snail invasion and the food web. However, prior studies do note the risk of this snail introducing non-indigenous parasites that can also infect the European eel (e.g., Morley et al. 2008; Gérard et al. 2017; Alonso et al. 2023). It remains to be seen whether and how this invasion in Madeira will impact the critically endangered European eel (see, for example, Rakauskas et al. 2016; Butkus and Rakauskas 2020). Considering that a reduction in food intake can compromise the survival, sexual maturation, and reproductive migration of the European eel (van Ginneken et al. 2005; Pelster 2015; Bourillon et al. 2022), this invasion should be considered a high-risk threat to the species. Further research should be made a conservation priority. Lastly, the introduction of the New Zealand mud snail could lead to a trophic cascade effect impacting the entire ecosystem. This effect is a particular risk given the reduced number of top predators in the streams of Madeira (e.g., only two freshwater fish species). To manage all these vulnerabilities and threats, it is crucial to monitor the populations of *P. antipodarum* closely and investigate factors relevant to their impact. These factors include species abundance, abiotic environmental conditions, niche overlap, and time since introduction (Alonso and Castro-Díez 2012b; Geist et al. 2022). By doing so, we can better understand the impact of this snail on Madeira's freshwater ecosystems and develop effective management strategies to minimize their impact on native species and maintain water quality.

Our study highlights the occurrence and discusses the potential consequences of the invasive gastropod *P. antipodarum* in Madeira Island. We emphasize the urgent need to survey other Macaronesian islands, which are equally sensitive and are economically and biogeographically connected to Madeira. Early detection of non-indigenous species within these insular ecosystems is crucial and can be done through substrate inspection – a simple, non-expensive tool. Genetic tools such as environmental DNA (eDNA) are more informative but also more expensive (Clusa et al. 2016). To prevent and manage future introductions of the species, it is essential to model its ecological conditions and act before its arrival (Lustig et al. 2017; Alexandre da Silva et al. 2019). Monitoring studies will assist in controlling the species' establishment and expansion by determining population fluctuations and defining periods of control, such as seasons and the time of introduction (Gérard et al. 2018; Geist et al. 2022). In addition to research, it is essential to raise public awareness about the risk of indirectly promoting *P. antipodarum*. Key vector risks include boats, canyoning and fishing gear, aquarium products, and feeding ducks (Clusa et al. 2018). As such, education initiatives jointly developed by regional entities and scientists should provide information in harbours and to target groups such as canyoning companies and fishermen associations. This information should include procedures to prevent the introduction of this invasive snail – e.g., material decontamination with quaternary ammonium compounds (QAC) or air exposure (Oplinger and Wagner 2011; Alonso and Castro-Díez 2012a). Additionally, local authorities and relevant stakeholders should monitor recreational activities and implement efficient cleaning and restoration strategies for freshwater ecosystems. Finally, a future management plan of the New Zealand mud snail in Madeira archipelago (and in Macaronesia, as relevant) should involve concerted efforts of various entities and follow recommendations, adapted to insular ecosystems, such as those proposed by the International Union for Conservation of Nature in 2018 (IUCN 2018).

Authors contribution

Research conceptualisation: IO, JCC. Sample design and methodology: IO, FK. Investigation and data collection: IO, PR, FK and JCC. Data analysis and interpretation: IO, PR. Funding provision: JCC. Writing: IO (original draft), PR, FK and JCC (review and edit).

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Ethics and permits

IO, PR and JCC have a permit from the regional entity to collect freshwater macroinvertebrates (01/IFCN/2023 - FAU MAD).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Records of New Zealand Mud Snail *Potamopyrgus antipodarum* in Madeira Island.

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