REVIEW

Negative impacts of invasive predators used as biological control agents against the pest snail *Lissachatina fulica*: the snail *Euglandina 'rosea'* and the flatworm *Platydemus manokwari*

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Abstract Since 1955 snails of the *Euglandina rosea* species complex and *Platydemus manokwari* flatworms were widely introduced in attempted biological control of giant African snails (*Lissachatina fulica*) but have been implicated in the mass extinction of Pacific island snails. We review the histories of the 60 introductions and their impacts on *L. fulica* and native

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snails. Since 1993 there have been unofficial releases of *Euglandina* within island groups. Only three official *P. manokwari* releases took place, but new populations are being recorded at an increasing rate, probably because of accidental introduction. Claims that these predators controlled *L. fulica* cannot be substantiated; in some cases pest snail declines coincided with predator arrival but concomitant declines occurred elsewhere in the absence of the predator and the declines in some cases were only temporary. In the Hawaiian Islands, although there had been some

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earlier declines of native snails, the *Euglandina* impacts on native snails are clear with rapid decline of many endemic Hawaiian Achatinellinae following predator arrival. In the Society Islands, Partulidae tree snail populations remained stable until *Euglandina* introduction, when declines were extremely rapid with an exact correspondence between predator arrival and tree snail decline. *Platydemus manokwari* invasion coincides with native snail declines on some islands, notably the Ogasawara Islands of Japan, and its invasion of Florida has led to mass mortality of *Liguus* spp. tree snails. We conclude that *Euglandina* and *P. manokwari* are not effective biocontrol agents, but do have major negative effects on native snail faunas. These predatory snails and flatworms are generalist predators and as such are not suitable for biological control.

Keywords *Euglandina* · *Platydemus* · *Lissachatina* · Invasion · Biocontrol · Extinction

Introduction

Species extinction rates are currently higher than background levels, representing a sixth mass extinction event (Waters et al. 2014; Ceballos et al. 2015). The levels of extinction are not evenly spread across taxa with particularly high levels reported for land snails (Lydeard et al. 2004; Régnier et al. 2009, 2015a, b) estimated overall at 10% loss and an extraordinary 75% extinction of Polynesian island land snails (Régnier et al. 2015a). This high extinction rate is probably due in part to many snail species having very restricted geographical ranges, combined with low mobility, making them very sensitive to changes in land use, habitat quality and/or a range of non-native predators (Lydeard et al. 2004; Régnier et al. 2015b; Chiba and Cowie 2016; Cowie et al. 2017). This high extinction in land snails may be representative of invertebrates as a whole (Régnier et al. 2015a), but this is difficult to ascertain because of the lack of data for the vast majority of invertebrate species (Bouchet et al. 2002; Brodie et al. 2017). However, because mollusc shells persist for some time after the animal dies, it is possible to develop a better picture of historical distribution and extinction in terrestrial snails than in other invertebrate groups (Pearce 2008).

The majority of identified recent mollusc extinctions have been of gastropod land snails on tropical islands (Régnier et al. 2009). Although some modern species may have gone extinct naturally before facing human influence, many extinctions have been attributed to early habitat loss following the arrival of people (Florens and Griffiths 2000; Richling and Bouchet 2013), although such loss continues and its effects are exacerbated by more recent predation by introduced species (Cowie et al. 2017). Nonetheless, there have been no attempts to quantify either the range of plausible anthropogenic drivers of extinction, or the interactions and synergies among these drivers, on land snail declines in tropical and subtropical oceanic island systems. This is despite growing international recognition that our ability to partition species losses among multiple drivers is critical to advancing our understanding and mitigation

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of extinction processes (Sala et al. 2000). Among non-native predators adversely affecting land snails, *Euglandina* '*rosea*' (Spiraxidae) (now known to be a complex of species, of which at least two have been widely introduced: Meyer et al. 2017) has been considered most important (Lydeard et al. 2004; Régnier et al. 2009). Introduced deliberately by agriculture authorities since the 1950s (Cowie 1998a) as a biological control agent for the giant African snail *Lissachatina fulica* (Achatinidae), an estimated 134 land snail extinctions have been attributed to predation by it (Régnier et al. 2009). More recently, the New Guinea flatworm, *Platydemus manokwari* has emerged as an important threat to land snails; it is a particularly voracious predator (Sugiura 2010) that will even climb trees to prey on arboreal snails (Sugiura and Yamaura 2009). Following a 1981 release in the Philippines (Muniappan et al. 1986) as a biological control agent for *L. fulica*, *P. manokwari* has spread and continues to spread to Pacific island and continental sites (a greenhouse in France, mainland North America and south-east Asia; Justine et al. 2014, 2015) and has been heavily implicated in native land snail population declines and extinctions (Sugiura and Yamaura 2009; Chiba and Cowie 2016; Cowie et al. 2017). Due to their impacts on land snail populations both *Euglandina* '*rosea*' and *Platydemus manokwari* are listed in '100 of the World's Worst Invasive Species' (Lowe et al. 2000). We synthesized information regarding the distribution and status of the *Euglandina rosea* species complex and of *Platydemus manokwari*, and their impacts on *L. fulica* and native snails to evaluate the robustness of evidence for impacts on land snail persistence and thus provide a clearer picture of the threats these predators pose to the world's land snail faunas. Cowie et al. (2017) summarised the global situation, but this review is the first comprehensive compilation of information on the role of these particular predators in land snail extinctions.

In addition to *Euglandina* spp. and *Platydemus manokwari*, a number of other species have been deliberately introduced outside their native ranges as biological control agents, including the snails *Edentulina* spp., *Gonaxis kibweziensis* and *G. quadrilateralis* (e.g. Cowie 1997, 2000, 2001a). There are also numerous other non-native invertebrate species that prey on or parasitise land snails and that have been introduced outside their native ranges, most commonly accidentally through human activities. These include predatory snails such as *Gulella bicolor*, *Streptostele musaecola* and *Oxychilus alliarius* (Cowie 1997; Meyer and Cowie 2010; Curry et al. 2016, 2020), various flatworms, carabid beetles, ants, phorid and sarcophagid flies, nemertean ribbon-worms, and not inconsiderable numbers of helminth parasites (Barker 2004). For the most part, the impact of these non-native species on land snail communities has yet to be examined in any depth and is beyond the scope of this review.

Methods

This review covers areas where *Euglandina* spp. and *Platydemus manokwari* have been introduced deliberately as biological control agents (principally for control of *Lissachatina fulica*), and where they have been spread inadvertently to locations other than those where the biocontrol programs were implemented. For each of these predators, data on their historical distribution, impacts and present status are collated. These are summarised in the text below and in Table 1 for each geographic region, with specific details given for areas where introductions are known to have limited impacts (Western Indian Ocean), high impacts (Polynesia), are currently spreading (Florida) or are of historical interest (New Guinea). The only introduction of *Euglandina* species to the African mainland is not considered here, as the only information associated with this attempt to control introduced helicid snails is a scant record of the failed release with even the date being unrecorded (Barker and Efford 2004).

The systematics of the *Euglandina* species has not been fully reviewed from a modern, integrated molecular-morphological perspective. The *Euglandina* species used in biological control programmes, long considered the single species *E. rosea*, is now known to comprise two species but their specific identity is unresolved (Meyer et al. 2017). Accordingly, the two taxa in question, identified as 'Clade 1′ and 'Clade 2′ by Meyer et al. (2017) are here referred to as 'Species 1′ and 'Species 2′, respectively, when this is known. Species 1 is recognisable as possessing a dull pink shell, with a broad spire, coarse sculpture, parallel sided aperture and rounded base, whereas Species 2 possesses a shell brighter in colour, more slender, with finer sculpture and evenly tapering at the

Table 1 Summary of introduction dates and establishment success of *Lissachatina fulica*, *Euglandina* and *Platydemus manokwari*. Status—P = present, R = restricted, X = probably extinct,— = absent. For *Euglandina* species, the basis for identification are given as: D—DNA (in Meyer et al. 2017), S—shell, P—photograph

Area	*Lissachatina*	*Euglandina*			*Platydemus*	
	Date	Date	Status	Species	Date	Status
Comoros islands	1800 s	1970	R	?	–	–
Madagascar	By 1800	1962	R	1 P	–	–
Mascarene islands	1842	1960	P	1 P	–	–
Seychelles	1840	1960	R	1 and 2 S	–	–
India	1847	1962	X	?	–	–
Sri Lanka	1900	1950 s	X	?	–	–
Maldive islands	1957	–	–	–	1985	P
Andamans & Nicobar islands	1940 s	1968	X	?	–	–
Myanmar	1940 s	–	–	–	2020	R
Thailand	by 1937	1973	P	?	2010	P
Singapore	1917	–	–	–	2010	P
Malaysia	1911	1960 s	?	?	2010	P
Sumatra	–	–	–	–	2019	P
Borneo	–	–	–	–	2016	P
Hong Kong	1937	1960 s	X	?	2012	P
China (Guangzhou)	–	–	–	–	2018	P
Taiwan	1932	1967	P	?	2019	R
Philippines	1949	–	–	–	1981	P
Japan	1937	1958	P	?	1990 s	P
Australia	1977	–	–	–	1976	R
Palau	1938	1958	X	?	1986	R
Caroline islands	1938	1958	X	?	1992	P
Marianas islands	1943	1957	X	1 P	1977	P
New Guinea	1962	1950 s	X	?	Native	P
Solomon islands	By 2006	–	–	–	2014	?
Vanuatu	1967	1973	P	2 P	2002	?
New Caledonia	1972	1974	R	?	1990 s	P
Fiji (Viti Levu)	–	–	–	–	2014	R
Fiji (Rotuma)	–	–	–	–	2012	P
Wallis and Futuna	1987	1993	P	?	2007	?
Tonga	–	–	–	–	2002	?
Samoan islands	1977	1980	P	1 D	1996	P
Kiribati	–	by 2003	?	?	–	–
Society islands	1967	1974	P	1 and 2 S	2006	P
Austral islands	1984	1985	P	?	–	–
Tuamotu islands	?	?	P	?	–	–
Gambier islands	–	–	–	–	1997	?
Marquesas islands	1979	1992	P	1 S	2011	R
Hawaiian islands	1936	1955	P	1 and 2 D	1994	R
Jamaica	–	–	–	–	2018	?
Bahamas	–	1960 s	P	?	2018	?
Puerto Rico	After 1984	–	–	–	2014	P

Table 1 continued

Area	Lissachatina	Euglandina			Platydemus	
	Date	Date	Status	Species	Date	Status
US Virgin Islands	–	–	–	–	2020	P
Anguilla	–	–	–	–	2020	P
Bermuda	–	1958	P	?	–	–
Florida	1966, 2011	Native	Rare	1 and 2 D	2012	P
Texas	–	Native	Rare	others	2018	P
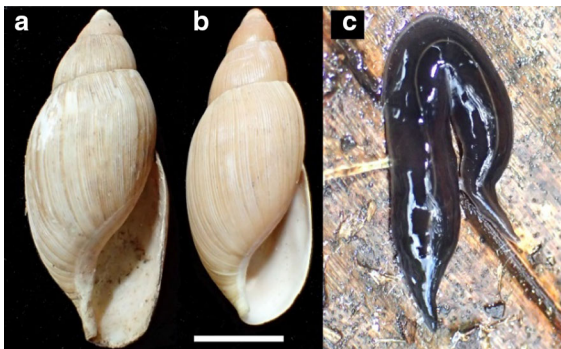
Fig. 1 Invasive predators covered in this review: **a** *Euglandina* 'Species 1′, **b** *Euglandina* 'Species 2′, **c** *Platydemus manokwari.* Scale bar 1 cm (**a**, **b**), 0.5 cm (**c**)

spire and base (Fig. 1). The shell differences are supported by differences in reproductive anatomy, Species 2 possessing an inflated genital atrium that is absent from Species 1 (figured by Meyer et al. 2017). If the specific identity of the species is unknown, and if it is unknown whether one or both of the species was introduced, we simply refer to the species as 'Euglandina'.

The giant African snail, *Lissachatina fulica* has been widely known as *Achatina fulica*. Bequaert (1950) placed the species in the subgenus *Lissachatina*, but on the basis of molecular phylogenetic studies of *L. fulica* and related species (Fontanilla et al. 2007, 2014; Fontanilla 2010), most authors have begun to use *Lissachatina* as a full genus with *Lissachatina fulica* included within it. A similar species, *Lissachatina immaculata*, has been introduced to western Indian Ocean islands. Although there is a need for the taxonomy and nomenclature of the Achatinidae to be formally reviewed, we follow recent usage as adopted by MollucsaBase (2019) in separating *Lissachatina* and *Achatina* and referring to the species as *Lissachatina fulica* and *Lissachatina immaculata*.

Species are considered to have become established if there are records of wild-reproducing populations or of persistence well beyond the generation times of the species (about 1 year for *Euglandina* and *Platydemus manokwari*; Chiu and Chou 1962; Kaneda et al. 1990). Reports of predators allegedly 'controlling' pest species are compiled; these consider control to be a reduction in the population of the target species. However, in our assessment, no introductions of *Euglandina* or *P. manokwari* achieved levels of prey reduction that would constitute 'control', and post-release evaluations were almost all anecdotal or qualitative rather than quantitative. Similarly, no data exist on changes in levels of damage caused by the pests targeted by biocontrol programmes.

Localities are grouped geographically rather than politically and are listed roughly west to east, beginning in the Indian Ocean (Fig. 2, Table 1).

Results

Indian Ocean Islands

Comoro Islands

Lissachatina fulica was established in the Comoros in the nineteenth century (Mead 1961) or earlier (Bequaert 1950). In 1965 biological control was attempted with introduction of *Euglandina* on Mayotte and on Grande Comore in 1970 (Ranaivosoa 1971). *Euglandina* populations have become established (Barker and Efford 2004) but further information is lacking.
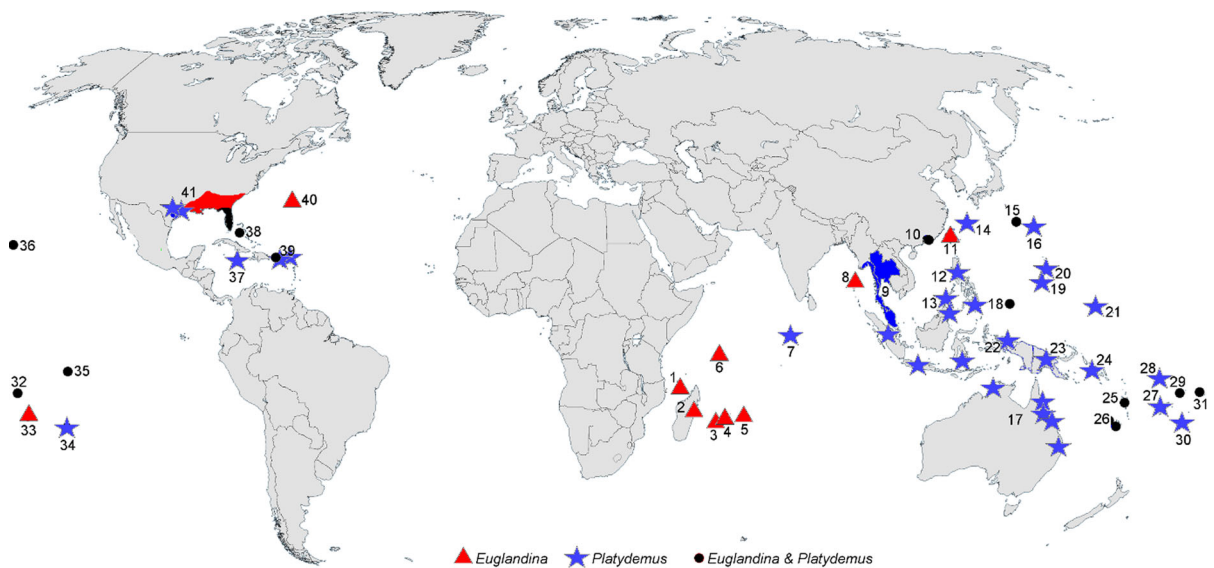
Fig. 2 Established distribution of species of the *Euglandina rosea* complex and *Platydemus manokwari*. Localities (in the order treated in text): 1—Comoros, 2—Madagascar, 3-5—Mascarenes (3—Réunion, 4—Mauritius, 5—Rodrigues), 6—Seychelles, 7—Maldives, 8—Anadman & Nicobars, 9—Thailand, Malaysia & Singapore, 10—Hong Kong & Guangzhou, 11—Taiwan, 12-13—Philippines (12—Manila, 13—Bugsuk), 14-16—Japan (14—Ryukus, 15—Ogasawaras, 16—Daitos), 17—Australia, 18—Palau, 19-20—Carolines (19—Pohpei, 20—Kosrae), 21—Marianas, 22—Irian Jaya (Manokwari), 23—Papua New Guinea (Kainantu), 24—Solomons, 25—Vanuatu, 26—New Caledonia, 27–28—Fiji (27—Viti Levu, 28—Rotuma), 29—Wallis & Futuna, 30—Tonga, 31—Samoa, 32—Societies, 33—Australs, 34—Gambiers, 35—Marquesas, 36—Hawaii, 37—Jamaica, 38—Bahamas, 39—Puerto Rico, 40—Bermuda, 41—U.S.A

Madagascar

Lissachatina fulica was established on the island before 1800 (Bequaert 1950) and biological control was attempted in 1962 with *Euglandina* introduced from Mauritius by the Institut de Recherches Agronomiques à Madagascar (Appert et al. 1969). Initially imported stocks did well, with 50 snails being reared and released at Toamasina in 1966 and 158 at Antalaha in 1967 (summarised by Jenkins 1987). There are no subsequent reports from Antalaha but further releases occurred at Toamasina: 738 in 1967 and 1970 (Appert et al. 1969; Ranaivosoa 1971; Jenkins 1987). *Euglandina* were found regularly at Toamasina in 1971 and the introductions were considered successful (Jenkins 1987); however, no further studies were carried out. Their continued presence was confirmed in 1996 at An'ala (A. Andriamamonjy pers. comm.) and in 2009 and 2012 with small numbers found in gardens in Toamasina (Griffiths pers. obs.). A shell was found at Toliara on the west of island in 2020 (Cordenos 2020).

Mascarene Islands

Lissachatina fulica and *L. immaculata* were introduced to Mauritius by 1824 and 1847 respectively, and to Réunion by 1821, with some suggestion that one or more of these may have been deliberate releases (Germain 1921; Mead 1961). Accidental introduction occurred on Rodrigues at an unknown date before the 1960s (Griffiths and Florens 2006). Both species are now found throughout the islands. While both occur in heavily transformed habitats (agricultural and residential), *A. immaculata* is more commonly found in native forest remnants than is *L. fulica* (Griffiths and Florens 2006).

Euglandina was introduced as a biological control agent for *Lissachatina fulica* and *L. immaculata*, to Mauritius in about 1960, Rodrigues in 1961 and Réunion in 1966 (Etienne 1973). They have spread throughout the former two islands but by 1991 had not invaded the highest parts of Mauritius (Piton de la Petite Rivière Noire, 828 m), although in 2007 it did occur at Mare Longue at 610 m (Florens and Baider 2007). On Réunion the highest observations were

made at 850 m in 1991. This elevation limitation is thought to be due to climate with temperatures in sites above 1000 m being too low (occasionally below 10 °C) for *Euglandina* establishment (Gerlach 1994). In 1991, population densities were low in most areas of Réunion, with only one site (Le Tremblet in the southeast) reaching 2500 per hectare (Gerlach 1994), although abundant shells in some localities suggested that there had been recent population declines. The highest population density on Mauritius was 1000 per hectare at Senneville, which also had the largest *L. fulica* population (5000 per hectare; Gerlach 1994). The impacts of the predators on native snails cannot be clearly disentangled from declines caused by other predators and habitat degradation. Although *Euglandina* preys on native snails preferentially in this environment (Griffiths et al. 1993), there has been a long coexistence, which may reflect the western Indian Ocean land snails having evolved alongside native predatory molluscs (Gerlach 1994). Mascarene snails face many stressors: predation by species such as rats, tenrecs and toads (Baxter-Gilbert et al. 2020), habitat destruction (Florens 2013) and habitat modification by alien plants (Florens and Baider 2007; Florens et al. 2017).

Seychelles

Lissachatina fulica and *L. immaculata* were introduced, apparently accidentally, in the nineteenth century (first records from 1839 and 1895 respectively; Gerlach 2006). Surveys in 1988–2012 (Gerlach, pers. obs.) indicated that *L. immaculata* was restricted to lowlands (< 250 m) on nine islands whereas *L. fulica* had spread up to 500 m elevation on at least 17 islands. The latter species remains at high density locally (up to 20,000 per hectare) in lowland and agricultural areas but is generally rare (densities below 1000 per hectare) at higher elevation, including in all forest habitats, except around rock outcrops with a dense herbaceous vegetation (similar to lowland habitats). Local extinctions of *L. fulica* and *L. immaculata* have occurred on some small islands (Cousin and Cousine), where old shells are abundant and extensive searches have failed to locate any survivors over the past 2 decades (Gerlach, pers. obs.), despite the lack of any evidence of predators. These local extinctions may have been the result of climate

stresses and stochastic population fluctuations (Samways et al. 2010).

Euglandina was deliberately introduced to St. Anne island in 1960 by the Department of Agriculture, followed by Mahé in 1974 (summarised by Mead 1979). On St. Anne a *Euglandina* shell was reputedly found in the 1970s, but the presence of an extant population could not be confirmed in 1987 (Gerlach 1994). In 1988 its presence near Victoria on Mahé was confirmed. Further surveys in 1989 and 1990 recorded it from three sites, with a total of 12 live animals. There were also unconfirmed reports from two other sites (Gerlach 1994). The confirmed range was restricted to an area of 20 hectares around Victoria. In 1991 numbers were reported to have decreased at one site (Gerlach 1994). In 2011 this range was resurveyed and only a single old shell was located at Trois Frères (Gerlach pers. obs.). The spread of *Euglandina* appears to be restricted, perhaps because of being surrounded by areas of degraded habitat supporting very low abundances of potential prey species preventing range expansion (Gerlach 1994), although the possible continued presence of the species raises the risk of its transfer to more suitable areas. *Lissachatina fulica* and *L. immaculata* remain abundant, including in areas occupied by *Euglandina* (Gerlach 2001). Two *Euglandina* species were identified in 1991 from shells on Mahé, with 'Species 1' comprising 86% of shells and 'Species 2' 14% (n = 14).

Maldives

Lissachatina fulica was established on the Maldives by 1957 when it was present on Addu atoll (Mead 1961). *Euglandina* have not been introduced but *Platydemus manokwari* was deliberately introduced to six islands, including Favahmulah (Fua Mulaku) and the atolls of Addu and Male in 1985 (Muniappan 1987) (also see Eldredge and Smith 1994, 1995). On Favahmulah *P. manokwari* spread up to a radius of 180 m within approximately! year and was claimed to have controlled the *L. fulica* population, even though Muniappan (1987) acknowledged that snail declines had occurred on islands where flatworms appeared not to have become established. The flatworm was photographed on Rasdhoo Atoll in 2017 (A. Pichler pers. comm.), possibly following accidental transport

between the islands; *L. fulica* was highly abundant on Rasdhoo at the time.

Andaman and Nicobar islands

Lissachatina fulica has been present in the Andaman and Nicobar islands since the 1940s (Shah 1992). Introductions of *Euglandina* took place in 1968 (Mead 1979); there are no recent reports of its status (Ali 2010).

South Asia

India

Lissachatina fulica has been present in India since 1847 (Mead 1961). It spread from India into Bangladesh, Nepal and Bhutan, possibly in the 1930–40s (Raut 1999; Budha and Naggs 2008). Introductions of *Euglandina* took place in India in 1962 and 1973 (Mead 1979). There are no reports of its persistence.

Sri Lanka

Lissachatina fulica has been present in Sri Lanka since 1900 (Mead 1961). It was reported to be well established throughout the island, but populations were reported to have declined as early as 1910 (summarised by Mead 1961). *Euglandina* were introduced in the 1950s (Mead 1979). Although there are some reports that *Euglandina* did become established in Sri Lanka (Rao et al. 1971; Sankaran 1974; Barker and Efford 2004) there have been no unequivocal records since its introduction (Naggs and Raheem 2005).

East Asia

Myanmar

Mead (1961) reported that *Lissachatina fulica* had become established in Myanmar either spreading from India, or having been introduced from Malaysia during World War II (subsequently confirmed by molecular data—Fontanilla et al. 2014). *Platydemus manokwari* was first recorded in Yangon in 2020 (Chuu 2020).
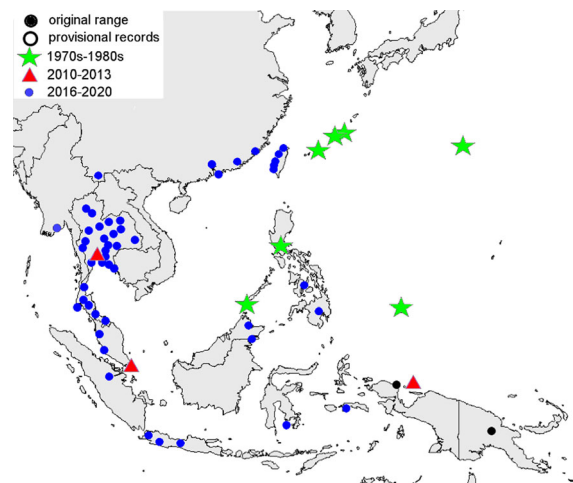

Fig. 3 Known distribution of *Platydemus manokwari* in Asia

Thailand

Lissachatina fulica has been present in Thailand since 1937 (Mead 1961). *Euglandina* was deliberately introduced in 1973–1977 as a biological control agent for *L. fulica* (Mead 1979). Barker and Efford (2004) reported established populations of *Euglandina* but impacts on the target pest or non-target species are not known. *Platydemus manokwari* has been observed in Thailand from 2010 (Justine et al. 2015) and has spread extensively (Chaisiri et al. 2019, summarised in Fig. 3).

Malaysia

Lissachatina fulica has been recorded in Sabah (Schilthuizen and Rutjes 2001) and is widespread throughout the state (Phung et al. 2017). *Euglandina* was introduced to Sabah as a biological control agent for *L. fulica* in the early 1960s (Griffiths et al. 1993) but its present status there is not known. *Platydemus manokwari* has spread extensively throughout peninsular Malaysia since 2018 (Chaisiri et al. 2019, summarised in Fig. 3). Photographs from the islands of Borneo and Sumatra suggest that the species is now established throughout Malaysia (Fig. 3).

Singapore

Lissachatina fulica arrived in Singapore in 1917 (Mead 1961). *Euglandina* has not been introduced

but *Platydemus manokwari* has been present since 2010 (Justine et al. 2015).

Indonesia

Lissachatina fulica was established on islands in Indonesia as early as 1903 (Riau Archipelago; Bequaert 1950). It had spread to East Kalimantan and Sumatra by 1921 and Java in 1925 (Bequaert 1950; Mead 1961). It has only recently been recorded from Borneo, in 2016 (Fig. 3). Irian Jaya is part of Indonesia and contains part of the probable native range of *Platydemus manokwari*; this is covered in the New Guinea section below (under Melanesia). Other Indonesia records of *P. manokwari* include Ambon in 2013 (Wongkar 2013), Kabaena island (Sulawesi) in 2015 (Maples 2015) and Java 2019 (Afriandi 2019).

China and Taiwan

Lissachatina fulica was deliberately introduced to Taiwan in 1932–1933 and reached Hong Kong in 1937 (Mead 1961). *Euglandina* was deliberately introduced to Hong Kong and Taiwan in the 1960s (Chiu and Chou 1962; Simmonds and Hughes 1963), apparently successfully establishing only on Taiwan. *Platydemus manokwari* was first recorded in China on Hong Kong island in 2012 (Tam 2019) and the mainland (Guangzhou) in 2018 (Hu et al. 2019). It was recorded in south-west Taiwan in 2014 (Chang 2014) and was found throughout the east of the island in 2019 (Fig. 3).

Philippines

Lissachatina fulica has been present since 1949 (Mead 1961), or possibly 1931 (Muniappan et al. 1986). Although *Euglandina* has not been introduced, *Platydemus manokwari* was deliberately released (150 individuals) on Bugsuk in 1981–1982 (Muniappan et al. 1986) in the first deliberate release of this species as a biological control agent. Initial results were said to be poor, with few flatworms found. Experimental placement of snails in the areas where flatworms had survived were claimed to have resulted in increases in snail mortality over a 2-month period (increasing from 0.53 to 4.13% of the population). After 1 year, counting all snails (live and empty shells) found that in areas without flatworms 84% of *L. fulica* were alive

compared to 26% in an area with flatworms. This simple correlation was used to conclude that introduction of flatworms could control the snails. By September 1983, 19 months after the last release of flatworms, they were abundant, and 6 months later snail populations were reported to be reduced (Muniappan et al. 1986), although this was not quantified and no follow-up surveys were undertaken to determine if these effects, if any, were long-lasting. Nor was decline for other reasons considered as an alternative explanation for observed decreases.

Platydemus manokwari had spread to urban Manila by 1985, apparently through accidental introductions. It was still present in 2019 and *L. fulica* remained abundant in the Manila region (Constantino-Santos et al. 2014), refuting the claim by Waterhouse and Norris (1987) that it had controlled the *L. fulica* population. There are subsequent records from Mindanao and Cebu in 2020 (Muico 2020).

Japan

Lissachatina fulica has been present in the Ogasawara (formerly Bonin) Islands since 1937 (Mead 1961). It established high population densities on these islands, recorded at 1,000,000 per hectare on Chichijima in 1985 (Takeuchi et al. 1991) and even more abundant on Hahajima (Ohbayashi and Takeuchi 2007). It is now found throughout the Ogasawaras and has spread to the Amami, Okinawa, Miyako and Yaeyama Islands and the Japanese mainland in Kagoshima (Matayoshi et al. 1987).

Euglandina were introduced to the Ogasawara Islands (Chichijima) (references to Okinawa, e.g. Simmonds and Hughes 1963, appear to be in error) in 1958–1961 as a biological control agent for *Lissachatina fulica* (Simmonds and Hughes 1963). *Platydemus manokwari* was reported to have been released on the Japanese mainland at Yokohama in 1984 (Waterhouse and Norris 1987), whereas in fact this was based on their import for laboratory culture in 1985 (Kaneda et al. 1990), the flatworms never being released. Wild populations of *P. manokwari* were present in the Ryukyu islands (including Okinawa, Kumejima, Miyakojima, Irabujima, Ikejima, Henzajima) in 1990 (Takeuchi et al. 1991; Kawakatsu et al. 1993), the Ogasawaras (Chichijima) in the 1960s (Kawakatsu et al. 1999) and the Daito islands in 2004 (Matsui et al. 2010).

In the Ogasawara islands *Lissachatina fulica* populations declined after 1985 (Takeuchi et al. 1991). On Chichijima they remained at 8% of peak levels, whereas on Hahajima partial recovery was apparent by 1998 (reaching 38% of peak levels by 2001) (Ohbayashi and Takeuchi 2007). *Euglandina* has been on Chichijima since 1965 but remained relatively restricted and scarce (Takeuchi et al. 1991). It has not been reported from other islands of the group. As with *L. fulica*, populations declined between 1985 and 1995 (Ohbayashi and Takeuchi 2007). The differences between Chichijima and Hahajima may be a result of the presence of *P. manokwari* on Chichijima, but not on Hahajima.

Native snails in the Ogasawara Islands have exhibited population declines. On Chichijima *Mandarina mandarina* was in decline by the early 1990s with range contraction apparent by 1995, reportedly because of localised predation by *Euglandina* (Ohbayashi et al. 2005). *Platydemus manokwari* was first recorded in the northwest and central areas of Chichijima in the early 1990s (Ohbayashi et al. 2007). The rapid contraction of the ranges of five species of *Mandarina* endemic to the island, including *M. mandarina* and *M. chichijimana* from 1995, corresponds to the spread of *P. manokwari* (Fig. 4); by 2003
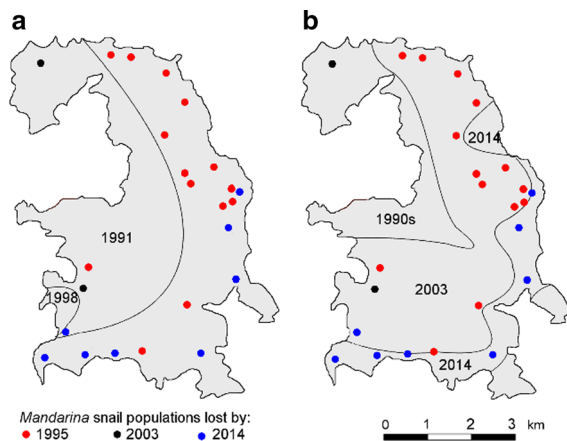
these snails only survived in the eastern and southern coastal areas where *P. manokwari* was absent or had only recently invaded; and by 2014 only *M. chichijimana* remained, confined to two small peninsulas in the south-east of the island (Ohbayashi et al. 2007; Chiba and Cowie 2016). Declines on Hahajima were recorded in *M. polita* but were less pronounced (Ohbayashi et al. 2007). These declines on Hahajima, where neither *Euglandina* nor *P. manokwari* have been recorded, have been attributed to predation by other flatworm species (*Bipalium* sp., *Platydemus* sp. and *Australopacifica* sp.) (Kawakatsu et al. 1999; Okochi et al. 2004). *Platydemus manokwari* has also been suggested to have reduced populations of other flatworms and the nemertine worm *Geonemertes pelaensis* on Chichijima (Ohbayashi et al. 2005, 2007). Of Chichijima's 25 native snail species, 16 are believed to be extinct because of *P. manokwari* predation, with only three species coexisting with the flatworm (Chiba and Cowie 2016).

Australia

Lissachatina fulica has been recorded in Australia as an occasional customs interception. There has been only one temporarily established population, in Gordonvale, north Queensland. This was discovered in April 1977 but was eradicated by using pesticides and by hand picking (Colman 1977, 1978; Winsor 1990).

Platydemus manokwari has been recorded from Queensland (1976) and the Northern Territory (2002) (Winsor 1990; Justine et al. 2014). There have been accidental movements of *P. manokwari* by people (e.g. in north Queensland, from Bluewater to Weipa, Cape York; Waterhouse and Norris 1987) and these probably account for the additional records of the species in Bowden and Brisbane in Queensland. It is restricted to urban gardens and has not spread into drier natural habitats, except at Lake Eacham, Atherton Tablelands, where gardens abut rainforest. This invasive population seems constrained by surrounding dry farmland (Winsor pers. obs.).

In the relatively dry conditions of much of Australia dispersal is slow even in urban environments; it took 1 year to move between suitable garden habitats separated by 20–30 m of lawn (Winsor 1990). In this strongly seasonal environment numbers show fluctuations corresponding to rainfall, with peaks in February–March towards the end of the monsoon season.

Fig. 4 *Mandarina* snail declines compared to predator ranges on Chichijima, Bonin Islands. Points—extinct *Mandarina* populations with date when only shells recorded; lines on map—maximum ranges of predators at different times. **a** *Euglandina* range (showing decline from 1998 to 1991, none recorded live in 2001; data from Ohbayashi and Takeuchi 2007); **b** *Platydemus manokwari* range (expansion from the 1990s range, in 2014 the south-east peninsulas remained unoccupied; data from Ohbayashi et al. 2005, 2007; Chiba and Cowie 2016)

Micronesia

Palau

Lissachatina fulica has been present in Palau since 1938 (Mead 1961; Eldredge 1988; Tillier et al. 1993). It was present on the islands of Babeldaob, Koror and Peleliu at least by 1946 (Eldredge 1988) and additional islands by 1950 (Mead 1961). Rundell (2010) recorded it on Babeldaob and Koror in 2003–2007. However, Mead (1979) reported that it was absent from "many of the isolated islands of Palau" and recent surveys have found it to be localised (Rundell 2005). *Euglandina* was released as a biological control agent for *L. fulica* in 1958, although the release location was not reported (Schreiner 1989). It appears not to have become established (Waterhouse and Norris 1987); it was not found in 2003–2007 during surveys by Rundell (2005, 2010). *Platydemus manok-wari* was reputed to have been introduced accidentally to Palau in 1986 (Schreiner 1989) and was present in 1991 when it was found on Koror, and in 1992 on Ulong and Babeldoab (Eldredge and Smith 1994, 1995). It was recorded again on Koror in 2020 (Malsol 2020). There is presently no information on the effects of *Euglandina* and *Platydemus* on either *L. fulica* or native fauna.

Caroline Islands (Federated States of Micronesia)

Lissachatina fulica was established on Pohnpei by 1938 and subsequently spread to other islands of the Pohnpei and Chuuk groups (Mead 1961; Eldredge 1988; Tillier et al. 1993). Observations on Pohnpei in 2011 indicated *L. fulica* was abundant in all habitats, from gardens to forest, including cloud forest (B. Holland pers. comm.). *Euglandina* was introduced to Pohnpei in 1960 as a biological control agent for *L. fulica* (Department of State 1961; Schreiner 1989; Merlin and Raynor 2005), and in 1992 was reportedly found throughout the island (Merlin and Raynor 2005), although this has not been substantiated and they have not been observed since (B. Holland pers. comm.). Eldredge (1988) reported that *L. fulica*, although found on Yap, had been eradicated, and that it was not present on Kosrae. Neither *L. fulica* nor *Euglandina* were recorded during surveys on Kosrae by Rundell and Czekanski-Moir (2015).

Platydemus manokwari was present in Pohnpei by 1992 (Eldredge and Smith 1994, 1995). Merlin and Raynor (2005) reported that it was introduced in the 1950s but there appears to be no evidence for this. It may be the cause of the extinction of the large ground-living *Partula guamensis*, which was formerly highly abundant (based on the numbers of shells in museum collections dating from the 1950s) (Pelep and Hadfield 2011), and of most populations of the arboreal *P. emersoni*, isolated individuals of which still persisted in 2011 (B. Holland pers. comm.). However, the causal link has not been established. *Platydemus manokwari* has been recorded on Pohnpei from sea level to the summit of Mt Nahnalaud (782 m), which it had reached by 1992 (A. Kerr pers. comm.), although it was not found there in 2011 (B. Holland pers. comm.).

Mariana Islands

Lissachatina fulica is thought to have been introduced to the Northern Mariana Islands of Rota, Saipan and Tinian in 1936–1938 (Mead 1961; Eldredge 1988; Nafus and Schreiner 1989). Mead (1961) reported it being taken to Pagan in 1939 to raise for medicinal purposes, as well as for food, and that the island was "the most northern of the infested islands in the Mariana chain". He also reported that it had been taken to Aguiguan shortly before World War II, and that by 1949 it was well established there. It was first found on Guam in 1943 or 1945 (Mead 1961; Eldredge 1988).

The first attempt at biological control of *Lissachatina fulica* was by the Insect Control Committee for Micronesia in 1950, with *Gonaxis kibweziensis* being released on Aguiguan and later on Saipan, Tinian and Rota (Mead 1979). This species was introduced to Guam in 1954, as was *G. quadrilateralis* in 1967 (Waterhouse and Norris 1987; Nafus and Schreiner 1989). *Euglandina* was released as a biological control agent for *L. fulica* on Guam in 1957, but not on the other islands, although it was subsequently recorded on Saipan along with one or more of the *Gonaxis* species (Nafus and Schreiner 1989) and on Agrihan (Kurozumi 1994). Bourquin (2002) recorded *Euglandina* from Aguiguan and Guguan, but its current status on these islands is not known as we are not aware of any more recent surveys or reports. Initially, introduction of these three species

to Guam was considered somewhat successful; *Euglandina* was abundant throughout the island in 1977 (B. Smith pers. comm.).Yet although the *L. fulica* populations declined, the species remained a problem (Nafus and Schreiner 1989), and although *Euglandina* was sufficiently abundant to be the source of snails for introduction to Samoa in 1984 (Eldredge 1988), by 1992 it could no longer be found (Hopper and Smith 1992). The extirpation of *Euglandina* and apparently also of the Guam *Gonaxis* spp. populations, as well as the decline in *L. fulica* populations, have been attributed to predation by *Platydemus manokwari* (Nafus and Schreiner 1989; Kerr 2013). However, *G. kibweziensis* disappeared on Aguiguan before the introduction of *P. manokwari* (Mead 1961). *Euglandina* was recorded on Agrihan in 1992 only (Kurozumi 1994) and its subsequent status is not known. On Saipan in 2002 *Euglandina* was recorded only as shells, based on collections cited by Bourquin (2002).

Platydemus manokwari was supposedly an accidental introduction to Guam in 1977 or 1978 (Eldredge 1988; Nafus and Schreiner 1989; Hopper and Smith 1992). It may, however, have been present as early as 1969; in that year a number of flatworms near the George Washington High School were identified as a *Platydemus* species by L.G. Eldredge (R.H. Randall pers. comm.). This may indicate that the introduction occurred in the late 1960s but that the population and geographical range did not constitute an invasion until later. *Platydemus manokwari* was present in 'large numbers' in 1978 and had spread throughout the island by 1980 (Eldredge 1988; Eldredge and Smith 1994, 1995) (Fig. 5). Its release on Saipan in 1981 was deliberate, whereas colonisation of Tinian (1984), Rota (1988), Anatahan (1991) and Aguiguan (1991) may have been accidental (Eldredge 1988; Eldredge and Smith 1994, 1995; Kawakatsu and Ogren 1994; Bauman 1996; Smith 2013).

Lissachatina fulica populations were studied on Aguiguan as part of the '*Gonaxis* Program' of biological control. Kondo (1952) estimated the population to be 1,122,500, with a decline to 37,600 two years later (Davis 1954) and by 1961 it appeared to be extinct on the island; none could be found alive in 1984 (Eldredge 1988). This decline was taken to be indicative of control by *G. kibweziensis* (see Davis 1954), but this is not conclusive as some mass mortality events had been reported from the Marianas
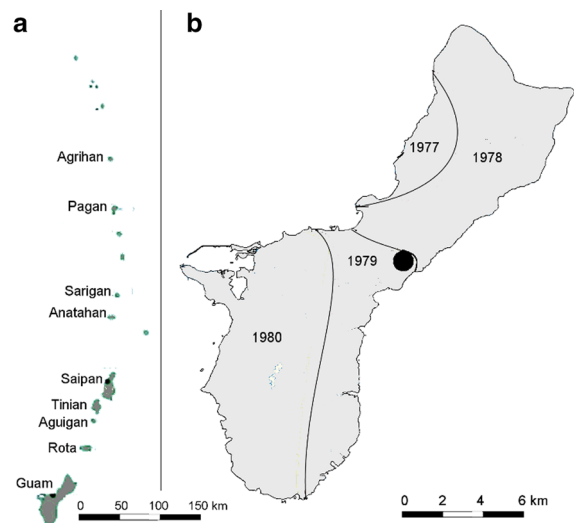

Fig. 5 Changes in *Platydemus manokwari* ranges in the Marianas islands. **a** Marianas islands showing the islands mentioned in the text; **b** *P. manokwari* range on Guam showing the spread across the island (1977–80 distributions after Muniappan 1990), black dot—1969 record

in 1950, before the introduction of predators (Lange 1950; Kondo 1952) and on other islands without the predators (Mead 1961). Similarly, in 1981 no *L. fulica* could be found on Pagan, and in 1984–1985 none was found on Tinian. On Saipan and Guam *L. fulica* was reputedly controlled by the flatworms, with claims that 95% of the snails had been eliminated on Saipan (Muniappan 1983) and reduction "to the status of a minor pest" on Guam (Waterhouse and Norris 1987) with a population reduction reputedly again reaching 95% in some areas (Muniappan 1983). No possible alternative causes of decline were considered.

Declines in the native partulid snails on Guam were reported by Hopper and Smith (1992) and Saipan by Smith and Hopper (1994). An estimated 68% of the 39 native snail species of Rota were extinct or declining by 1996 (Bauman 1996). On Aguiguan *Partula gibba* and *P. langfordi* were present in 1992 but the presence of many relatively fresh empty shells at several sites suggested that mortality had occurred within the previous year; by 2006 only old shells could be found (Smith 1995, 2013). The rapid decline of *Partula* spp. coincides with the invasion by *Platydemus manokwari*. It is not known when declines started on Tinian; by the time the island was surveyed in 2008 (Smith 2013) all *Partula* were extinct, and *Lissachatina fulica* was represented only by abundant old shells.

Similarly, *P. manokwari* is probably responsible for the partulid declines on Rota after 1969, although local partulid populations have survived on Saipan in very small numbers despite the presence of the flatworms. On islands without introduced predators, partulids have declined where cattle and goats have damaged the habitat (Sarigan and Pagan) (Hadfield 2015).

Kiribati

Although *Lissachatina fulica* was reported to have arrived in Kiribati it failed to become established (South Pacific Commission 1979) and was reported as "not present" by Waterhouse and Norris (1987). Waterhouse and Norris (1987) did not list *Euglandina rosea* in Kiribati in their table of predators introduced to control *L. fulica* but said in their text that it had been "successfully transferred" to Kiribati. Cowie (2000, 2001a), based on that statement, listed it as present in Kiribati. However, there is no information regarding which island(s) the record came from, whether the introduction was deliberate and its present status; the record may be in error.

Melanesia

New Guinea

Lissachatina fulica was established in the Bismarck Archipelago in the early 1940s and had declined from an early population peak by 1951 (Mead 1961). It did not reach the mainland of Papua New Guinea until 1976–1977 (Mead 1979; Tillier et al. 1993). *Euglandina* was introduced to Papua New Guinea in the 1950s as a biological control agent for *L. fulica* (Mead 1979; Waterhouse and Norris 1987), Irian Jaya in 1959 (Waterhouse and Norris 1987) and New Britain at an unknown date (Parkinson et al. 1987). In 1962 it was apparently abundant in the west of New Guinea at Manokwari (de Beauchamp 1962).

Platydemus manokwari was first described from the Agricultural Research Station at Manokwari, Irian Jaya in 1963 (de Beauchamp 1963). In Papua New Guinea it has been recorded from Pindaude Station on Mt. Wilhelm in 1969 at an elevation of 3625 m (de Beauchamp 1972) and Kainantu (1558 m) in 1973 (Winsor 1990). These localities appear to be part of its natural range (Justine et al. 2015), although this is uncertain at present. Manokwari is at 193 m above sea

level and under lowland tropical forest and plantations, whereas the Mt. Wilhelm and Kainantu habitats are described as sub-alpine forest, grasslands, bogs and fens, with a closed canopy forest dominated by *Amaracarpus* and *Pittosporum* (summarised by Winsor 1990). The Mt. Wilhelm record is an immature specimen of '*P. joliveti*', which Winsor (1990) considered synonymous with *P. manokwari* but which may be a cryptic species (Winsor pers. obs.). Accepting this, the highest elevation record is therefore Kainantu. Daily mean temperatures from the nearest site to Kainantu with available temperature records (Goroka) are 15–23 °C (Allen 1989), suggesting that conditions in the natural range may be similar to those experienced by many of the introduced populations. There is also a recent (2013) photographic record from Palau Biak in the Schouten Islands near Manokwari (Langner 2018a); this may also represent a native population.

Under the assumption that all these populations are representative of the native range of *P. manokwari*, the question then is: what has been the impact on introduced *Lissachatina fulica*? However, the current situation regarding *L. fulica* on the island of New Guinea is not clear. It is reported to be common near Manokwari and flatworms resembling *P. manokwari* have been found at the same site (R. Tapilatu pers. comm.), but no data on numbers are available. We have found no additional information.

Solomon Islands

Lissachatina fulica was reported from the Solomons on the basis of a brief newspaper article published in 1999 without additional details (Cowie 2000). However, since 2006 it has been firmly established and is spreading in the vicinity of Honiara, eastwards along the north coast of Guadalcanal, probably having been transported on earth-moving or logging equipment (Stronge 2016). It was first reported at Ranadi, Honiara, in 2006 (BSI 2016) and is a major pest (Stronge 2016; Kiddle et al. 2017).

Platydemus manokwari has been recorded from Guadalcanal since 2014 (Justine et al. 2015). Biosecurity Solomon Islands (BSI) has been actively promoting *P. manokwari* as a biological control agent for *L. fulica*, with habitat manipulation and crop husbandry attempts to enhance predatory efficacy, and has also engaged in spreading it to new areas (BSI

2016; B. MacFarland pers. comm.). These activities are occurring despite the possible adverse effects on the native fauna.

Vanuatu

Lissachatina fulica has been widely established on the islands of Vanuatu since 1967 (Tillier et al. 1993; Gargominy et al. 2011). *Euglandina* was deliberately introduced in 1973–1974 and 1982–1983 as a biological control agent for *L. fulica* (Barker and Efford 2004; Gargominy et al. 2011) and is present on Santo, Aore and Ambrym (Bowden 2000) and Efate (Barker pers. obs. 2012). *Platydemus manokwari* was present by 2002 (FAO-SAPA 2002), apparently on more than one island. Previously recorded partulids had disappeared from Santo by 2006, although other snail species persist (Fontaine et al. 2011).

New Caledonia

Lissachatina fulica was first recorded on the main island (Grand Terre) in 1972, reputedly after an accidental introduction with garden plants from Tahiti (Tillier and Clarke 1983; Gargominy et al. 1996). Through natural invasiveness and deliberate in-country translocations, it rapidly became very abundant throughout mainland New Caledonia, satellite islands, and the Loyalty Islands, first occupying gardens, fallow areas, and degraded natural habitats, but in natural habitats being essentially confined to the edges of native forests. Although still common in gardens, *L. fulica* did not exhibit in the 2000–2010s the enormous densities it achieved in the 1970–1980s (Bouchet pers. obs., 1978–2019). In an attempt to control the new invasion, on the recommendation of the Commission du Pacifique Sud, *Euglandina* was introduced by the Services Ruraux in 1974–1978 to several locations in the north (Ouégoa, Koumac), east (Ponérihouen) and south (Nouméa, Plum) of the island (Tillier and Clarke 1983). By 1992 the Nouméa population was restricted to a small number of gardens in the Magenta area and thought to be constrained by areas of unsuitable habitat (Gerlach 1994); there was no trace of this population, and of the Plum, Ponérihouen and Koumac populations in the 2010s. The Ouégoa population flourished initially, especially on the left bank of the Diahot River, but had become extinct in the late 1990s (Bouchet local interviews 2018). However, snails

from that population were translocated—apparently accidentally—to Tomo, near Boulouparis, where the species persisted in 2018 but was confined to possibly a single garden (Bouchet pers. obs.). In the mid-1980s, *Euglandina* was introduced from mainland New Caledonia to the Loyalty island of Maré where it became invasive (Brescia et al. 2008). Although it has now become uncommon (Bouchet pers. obs. 2019), *Euglandina* has heavily impacted the local populations of the native *Placostylus* snails, once abundant and widespread throughout the island but now confined to a single site at Dranin (Brescia et al. 2008; Bouchet local interviews 2019).

In 2014–2015 *Platydemus manokwari* was recorded from Mont-Dore, Nouméa, Dumbéa, Paita, La Foa, Poya, Koné and Hienghène, as well as in 2015 from the Loyalty Islands of Lifou and Maré (Justine et al. 2015) (Fig. 6). It is thought that the species was introduced to New Caledonia after the 1990s (Justine et al. 2015); the earliest record seems to be a photograph from near Nouméa in 2007 (Langner 2018b). Field work by P. Bouchet and colleagues in 2018–2019 showed *P. manokwari* to be commonly infesting *L. fulica* populations in degraded lowland habitats, including patches of native dry forests, throughout mainland New Caledonia and Maré, but none was seen in native rainforests, although native land planarians do occur in such undisturbed habitats.

Fiji (see Polynesia for Rotuma information)

Lissachatina fulica has been detected by biosecurity authorities on cargo but has not become established
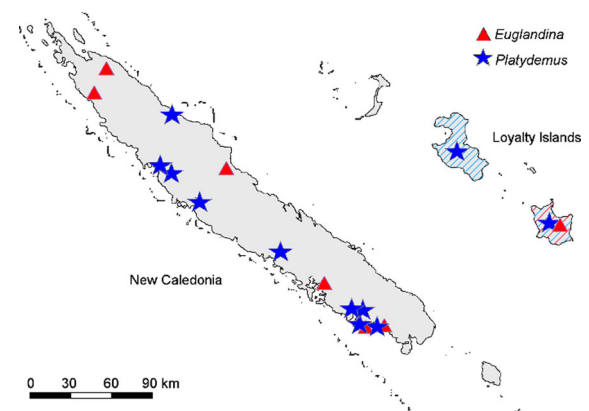

Fig. 6 Distribution of *Euglandina* and *Platydemus manokwari* in New Caledonia

beyond transiting vessels or impounded cargo (Brodie and Barker 2011). *Platydemus manokwari* was found for the first time in Suva on Viti Levu around 2013 (Brodie pers. obs.) but there are no confirmed records for other islands except Rotuma. Surveys of the Nakauvadra and Nakorotubu ranges in 2008 and 2009 (Morrison and Nawadra 2009; Morrison et al. 2009), a 2012 survey of the island of Cicia in the Lau Group (Brodie et al. 2013) and more recent intensive surveys on the Natewa Peninsula of the island of Vanua Levu did not detect *P. manokwari* (Barker and Narosamalua 2018). The impact of *P. manokwari* on the Fijian land snail fauna is presently unknown. In reviews of Fijian Placostylinae (Bothriembryontidae) and Partulidae (Barker et al. 2016; Brodie et al. 2016), *P. manokwari* is highlighted as an emerging threat to Fijian endemic land snail species.

Polynesia

Rotuma (Fiji)

Lissachatina fulica has not been reported by residents or recorded from Rotuma during four snail surveys since 1996 (Brodie et al. 2014). *Platydemus manokwari* was present by 2012 when it was seen at three sites on the west of the island (Brodie et al. 2013, 2014). During surveys in 2012 local adult people stated that the flatworm had been present at these locations for as long as they could remember. The status of Fiji's four species of endemic partulids (including one species, *Partula leefei*, endemic to Rotuma) was reviewed by Brodie et al. (2016). Only empty shells of *P. leefei* were found during the 2012 survey, despite the species having been reported as numerous in 1938 (Gerlach 2016). *Platydemus manokwari* was considered to be a major threat, if not the major cause of *Partula leeefi* decline (Brodie et al. 2014). Subsequent sightings in late 2015 of two living but juvenile *P. leefei* specimens on low vegetation surrounded by ground cover infested with *Platydemus manokwari* (Brodie pers. obs.) confirmed persistence but indicated the critically endangered status of *P. leefei*.

Wallis and Futuna

Lissachatina fulica is established on the islands (Tillier et al. 1993). It was first recorded in 1987 on Wallis (Tillier et al. 1993) when it remained restricted to within a 1 km radius around Vaitupa. It is now found throughout Wallis and in disturbed areas of Futuna, and is present on Alofi (Richling 2010). *Euglandina* was released on Futuna in 1993 in an unofficial attempt to control *L. fulica* despite a ban on its release there (Gargominy 1996) and had colonised Alofi by 2008 (Richling 2010). On Wallis it spread throughout the island but now appears to be extinct (Richling 2010). It may persist on Futuna as fresh shells were found in 2008. Live animals were found on Alofi in 2008 (Richling 2010; Meyer pers. obs.).

Platydemus manokwari was first recorded on Wallis and Futuna in 2007 (Richling pers. obs.), but so far no impacts have been reported. The spread of *Euglandina* coincided with the decline of *Partula obesa* (*P. subgonochila* is a junior synonym; Gerlach 2016) by 2008 on both Futuna and Alofi in areas invaded by *Euglandina* (Richling pers. obs.). Small relict populations survived on both islands, especially on Alofi in 2014 in native coastal forest and mid-elevation rainforest between sea-level and about 400 m elevation (Meyer pers. obs.). Similarly, *Trochomorpha ludersi* only survived as small populations (Richling pers. obs.).

Tonga

As *Lissachatina fulica* has not become established in Tonga there have been no deliberate introductions of *Euglandina* there. However, *Platydemus manokwari* was reported to be present by 2002 (FAO-SAPA 2002). Partulids have declined in Tonga, including the probable extinction of *Eua globosa*, but the declines predate the first records of *P. manokwari* and can be attributed to habitat loss (Ó Foighil 2012).

Samoan Islands

Lissachatina fulica was introduced to Tutuila, the main island of American Samoa, in 1977 (Eldredge 1988). Eldredge (1988) also reported it in the Manua Islands (Ofu, Olosega, Tau) of American Samoa without specifying which island, but considered it eradicated. However, in 1992 and 1998 it was recorded on Tau, although not on Ofu or Olosega (Cowie 1998b, 2001c) and in 2001 it was again not found on Olosega (Cowie et al. 2002), nor on Aunuu, a small islet off the eastern end of Tutuila (Cowie and

Rundell 2002). It was first introduced to independent Samoa (formerly Western Samoa) in the 1990s: to Upolu in 1990 (Cowie 1998b, 2000) and Savaii in 1996 (Brook 2012a).

In 1980 *Euglandina* was introduced to American Samoa (to Tutuila) as a biological control agent for *L. fulica* (see Eldredge 1988); by 1992 it had also been introduced to Tau (Cowie 1998b), although in surveys on Ofu in 1998 (Cowie 2001c) and Olosega in 2001 (Cowie et al. 2002) it still appeared to be absent from these islands. It seems not to have been introduced to independent Samoa (Cowie and Robinson 2003; Brook 2012a).

Platydemus manokwari was introduced to Savaii by the Samoan Ministry of Agriculture and Fisheries in 1996–1998 and 2001 as a biological control agent for *L. fulica* (see Brook 2012b) and was present on Upolu by 1998 (Purea et al. 1998). However, it was not found in the uplands of Savaii in 2012 (Brook 2012b). In 2006 it was found on Tutuila and Tau (based on material collected by Mark Schmaedick, American Samoa Community College).

In independent Samoa partulid declines (or possible declines) had occurred on Savaii and Upolu by 1994 (Cowie and Robinson 2003), predating the introduction of *Euglandina* or *P. manokwari*, and may be attributed to habitat degradation. In American Samoa, *Samoana abbreviata* had declined by 1975 (Cowie 2001c), before the introduction of *Euglandina*. The later declines of *Eua zebrina* and *S. conica* (see Cowie 2001c) may have resulted from predation, while the decline of *S. thurstoni* on Ofu (Cowie 2001c) and its extreme rarity on Olosega (Cowie et al. 2002), in the absence of *Euglandina*, are harder to explain, although habitat modification at least on Ofu may be implicated.

Society islands

Lissachatina fulica escaped from a snail farm on Tahiti in 1967 and spread to Moorea, Huahine, Raiatea and Tahaa by 1973 and to Bora Bora by 1982 (Pointier and Blanc 1984). The date of its arrival on Maupiti is not known, the first record being of old shells found in 2017 (Gerlach 2017). Use of *Euglandina* as a biological control argent was recommended by the South Pacific Commission and it was introduced to Tahiti in 1974 (Pointier and Blanc 1984) and to Moorea in 1977 (Tillier and Clarke 1983), and subsequently spread to the other islands: Raiatea (by 1986), Tahaa (by 1994),

Bora Bora and Huahine (by 1991) and Maupiti (before 2017) (Gerlach 2017) (Fig. 7). Spread within the islands was estimated at 1.2 km per year on Moorea (Tillier and Clarke 1983). It had expanded throughout the south of Tahiti-Nui within 10 years and throughout the lowlands in 13 years. The Taravao Plateau on the Tahiti-Iti peninsula was a *Euglandina* introduction point in 1974 but the south-east of the peninsula (Te Pari) was not invaded until 2001 (Coote 2007) (Fig. 7). *Euglandina* has not established significant populations at higher elevations, being absent above 1400 m and not forming permanent populations above 1200 m; on Mt. Marau, Tahiti, invasions in the 960–1257 m range have been temporary (Coote pers. obs.). Dead shells of adults and hatchlings can be found in this zone, suggesting that adults periodically invade from the valleys but that long-term survival is currently impossible. Similarly, the disappearance of several species of partulids from Mt. Toomaru on Raiatea (1017 m) is probably due to temporary invasion by *Euglandina* although none has been recorded there (Gerlach 2016). On the nearby Teme-hani plateaux (750–821 m) *Euglandina* incursions do occur (as indicated by the presence of shells), but there are no permanent populations (Gerlach pers. obs.).

In 1991 *Euglandina* population densities were high on Raiatea, varying from 4000 per hectare in the centre of Faaroa valley, to 2000 in the north-west of the valley, and 3000 in the Miti Miti Aute river valley and 1000 at Vaiapu (Gerlach 1994). By 2004 *Euglandina* population declines were apparent and they were rare in all valleys. Subsequently (2007) population out-breaks occurred in some valleys on Tahiti, with particularly large outbreaks in Haapaponi, Faarapa and Matatia. Other nearby valleys were not affected (Maruapo, Papehue), and only one outbreak occurred later in Tiapa. These high population densities rapidly subsided, except in Te Faaiti and Fautaua where *Euglandina* remains relatively common (Coote pers. obs.). In 2015 live *Euglandina* were found in 47% of 92 accessible valleys on Tahiti and 31% of 26 on Moorea. (Coote pers. obs.).

Euglandina now appears to be extinct on Tahaa, Huahine, Bora Bora, Maupiti and the lowlands of Raiatea as only old shells were found in those areas in 2017 (Gerlach 2017). Both *Euglandina* species were introduced to the islands; in 1991 60% were 'Species 2′ on Raiatea (n = 112) and both were still present there in 2017 (Gerlach 2017). On Tahiti in Fautaua
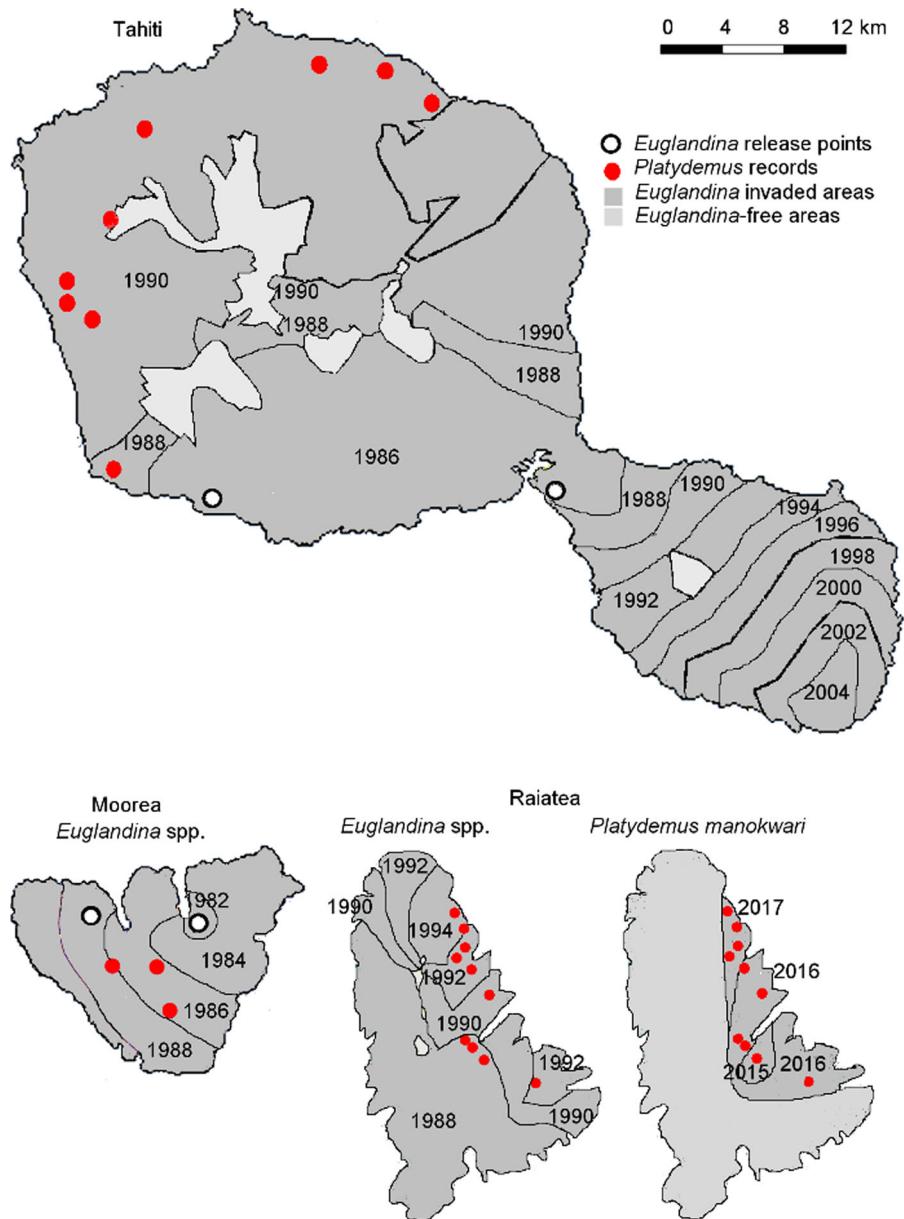
Fig. 7 Distribution of *Euglandina* spp. and *Platydemus manokwari* in the Society islands of Tahiti, Moorea and Raiatea. Areas occupied by *Euglandina* spp. shown in 2-year intervals (modified from Aberdeen 2013), areas occupied by *P. manokwari* on Raiatea shown in yearly intervals (based on surveys in 2016–2017)

valley 18% (n = 11) were 'Species 1′ in 2018. Only two individuals were examined from Moorea, one of each species.

Platydemus manokwari was first observed on Tahiti in 2006 in Tiapa valley in the west of the island. It was later found in the south-west (Tereia valley 2012), the north-east (Faarapa valley 2013) and at higher elevations (above 900 m—Mt. Aorai 2013) (Coote and

Meyer pers. obs.). It has now been recorded in all valleys searched (Papehue, Faaa, Fautaua, Orofara, Haapoponi and Maruapo) (Justine et al. 2015). The highest record is from Mt. Aorai at 1000 m (Justine et al. 2015). It was present on Moorea by 2009 (Lovenburg 2009), Huahine and Raiatea by 2016, Bora Bora and Maupiti by 2017 (Gerlach 2017). Its populations reached extremely high densities in the

early stages of invasion on Raiatea; up to 0.83 m^{-2} in the main invaded area (Faaroa valley) and 3 m^{-2} in newly colonised areas (Hamoa valley). Twelve months later densities in the latter had fallen to 0.75 m^{-2} (Coote pers. obs.).

Lissachatina fulica population declines appeared to coincide with the introduction of *Euglandina* on Tahiti but on Huahine, Raiatea and Tahaa declines predated the introduction of *Euglandina* (Tillier and Clarke 1983), and thus cannot be attributed to predation by that species. By 2017 fresh shells or live *L. fulica* could only be found on Tahiti, Moorea, and in agricultural areas of Huahine and Raiatea, with only old shells on Tahaa, Bora Bora and Maupiti.

There is no evidence of *Partula* declines in the Society Islands until the arrival of *Euglandina* and immediately following the invasion of their ranges by the predator; although no quantitative population studies were done before 1962. The studies in the 1960s and 1970s recorded populations densities of 3500–12,600 adults per hectare on Moorea (Murray et al. 1993) and 763–13,200 per hectare on Tahiti (Murray and Johnson in Gerlach 2016). By 1987 only local lowland populations survived on Tahiti (Murray et al. 1988). Higher elevation populations still persisted, as did some small relict lower elevation populations of *P. hyalina* and *P. clara* (Coote et al. 1999). Moorean *Partula* were in decline within 5 years of *Euglandina* introduction and all populations were lost by 1987 (Murray et al. 1998), with the exception of relict populations of *P. taeniata* and a record of a single individual in the *P. suturalis* clade (Haponski et al. 2019). Raiatean *Partula* were extinct within 12 years of *Euglandina* arrival except for one high-elevation species (*P. meyeri*), which survived above the range of permanent *Euglandina* populations (Gerlach 2016). With this close correspondence of predator arrival and tree snail decline the extinction of 30 Society island Partulidae species can be attributed to predation by *Euglandina*. A similar pattern of decline occurred in three *Trochomorpha* species (relatively fresh shells of *T. cressida* are still found only on Mt Marau, Tahiti) (Gerlach 2016). Further evidence in support of *Euglandina* predation being the primary cause of partulid extinctions is that the few species that coexist with the predators have unusually high reproductive rates for the family (Bick et al. 2016).

Smaller snail species have also declined recently; resurveying the same sites on Raiatea in 1992 and 2017 recorded a 7% drop in abundance of leaf-litter inhabiting snails in Hamoa and Faaroa valleys (Gerlach 2017). This may be attributed to changes in predator populations, principally the invasion by *P. manokwari*, although other changes in the intervening years have not been recorded. During the invasions by the predators, comparisons of sites already invaded with adjacent sites that were still predator-free showed that during the *Euglandina* invasion there were concurrent declines in several taxa, principally Subulinidae, *Ovachlamys fulgens* (an invasive species first recorded in the islands in 1991; Gerlach pers. obs.) and *Partula* species (Gerlach 1994). With *P. manokwari* invasion, decreases were apparent in ground-dwelling *Georissa* spp., with no notable change in arboreal species of Achatinellidae (Gerlach pers. obs.).

Austral Islands

Lissachatina fulica has been present on Tubuai since 1984 but has not been recorded on any other of the Austral Islands (Fontaine and Gargominy 2002, 2004; Gargominy and Fontaine 2003, 2014) until 2012 when it was observed spreading over Rimatara (Tahiata 2015; Tiarii 2015). *Euglandina* was introduced to Tubuai in 1985 as a biological control agent for *L. fulica* (Gargominy and Fontaine 2003, 2014). By 2003 *Partula hyalina* had become restricted to the western side of the island, but remains widespread on the islands lacking *Euglandina*, i.e. Rimatara, Rurutu and Raivavae (Gargominy and Fontaine 2014), supporting the conclusion that *Euglandina* is primarily responsible for the declines on Tubuai. *Euglandina* has also not been recorded on Rapa (Fontaine and Gargominy 2002). There are no records of *Platydemus manokwari* from the Austral Islands.

Gambier Islands

Lissachatina fulica was recently introduced to Mangareva (2017 or 2018) and by July 2019 had become an "invasion" (Anon 2019). *Platydemus manokwari* has been recorded in the Gambiers since 1997 (Winsor 1999); its current status is not known. The snail fauna has suffered greatly from habitat loss with only two of the 36 endemic species surviving (e.g. Richling and Bouchet 2013). There are still no records of

Euglandina or *Platydemus manokwari* from the nearby Tuamotu Islands, whereas *L. fulica* is present on Mururoa, Hao and Apataki (Pointier and Blanc 1984; Cowie 2000).

Marquesas Islands

The presence of *Lissachatina fulica* was first confirmed in the Marquesas in 1979 on Hiva Oa, and then on Nuku Hiva in 1983 (Pointier and Blanc 1985). It is now also a notable garden pest on Fatu Hiva (Gargominy et al. 2016).

Euglandina was introduced as a biological control agent for *L. fulica* to Nuku Hiva and Hiva Oa in 1992 (Meyer 2000a, b). It was apparently still absent from Fatu Hiva, Tahuata, Ua Huka and Ua Pou in 1995 but had been introduced to Fatu Hiva in 1998 (Meyer 2000a). *Platydemus manokwari* was abundant on Ua Huka (La Réserve et Le Parc de Vaikivi) at 800 m in 2011 (B. Holland pers. comm.). How and when it arrived on the islands is not known.

Partulid declines attributed to *Euglandina* predation were rapid on Nuku Hiva, and only a single species (*Samoana gonochila*) restricted to one known colony remained by 1995 (Coote 2011); the colony was still extant in 2004 (Lee et al. 2014). Declines of Partulidae were also apparent on Hiva Oa by 1995 when they had disappeared from the area in the west of the island invaded by *Euglandina*. During expeditions in 1996 and 2000, partulids were confirmed as surviving on Hiva Oa but restricted to higher elevations, although some of these sites had been invaded by *Euglandina*. However, *Euglandina* did not occur above 1050 m (Meyer 2000a). Individuals of *Samoana decussatula* were observed in 2005 and 2007 in the presence of *Euglandina* and in 2011 continued to survive between 600 and 1045 m (Gargominy et al. 2016). On Fatu Hiva populations of *Samoana minuta* persisted along the trail to the "col Ouia" and in the valleys below, at 580–600 m and on the ridges up to 950 m (Meyer 2000a), but in 2003 none could be found on the trail leading to the col de Teavapuhia where *Euglandina* was present (Meyer 2003). The timing of the decline and the survival of the snails in areas not invaded by *Euglandina* indicates that this predator was the primary cause of the declines. However, even in the absence of *Euglandina*, declines have also occurred on Tahuata, Ua Huka and Ua Pou (after 1995). On these islands partulids had

been abundant in lowlands in 1995 but on Ua Huka they were rare by 2005 and on Ua Pou valley populations could not be located (except in Hokatu valley) (Meyer 2000b). Partulids are now absent from most of Tahuata. The cause of these declines is unknown. However, given that *Platydemus manokwari* had invaded Ua Huka by 2011, it could have been overlooked on other islands even prior to this.

Hawaii

Lissachatina fulica was first recorded in the Hawaiian Islands in 1936 (Pemberton 1938), on Oahu. It was on Maui by 1944, and on Kauai and the island of Hawaii itself by 1958, and Molokai by 1963 (Mead 1961; Davis and Butler 1964). It has since been recorded from all six of the largest islands, including Lanai (Cowie 1997) (Fig. 8). By the 1950s, local populations of *L. fulica* had become so dense (estimates suggested snail densities of 600,000–800,000 per hectare in wet lowland areas of Oahu) that it was considered a significant agricultural pest and a public nuisance (Kekauoha 1966; Mead 1961, 1979; Cowie 2001b). After the use of chemicals and other methods were deemed economically unfeasible, the Hawaiian Department of Agriculture (then Board of Agriculture and Forestry) began a biocontrol programme using predatory snails and beetles (Davis and Butler 1964) (also see discussion in Cowie 2001b).

Between 1948 and 1963, 30 invertebrate predators of snails (19 snail species and 11 beetles) were imported into the Hawaiian Islands (Davis and Butler 1964). Following studies in quarantine, 11 snails and
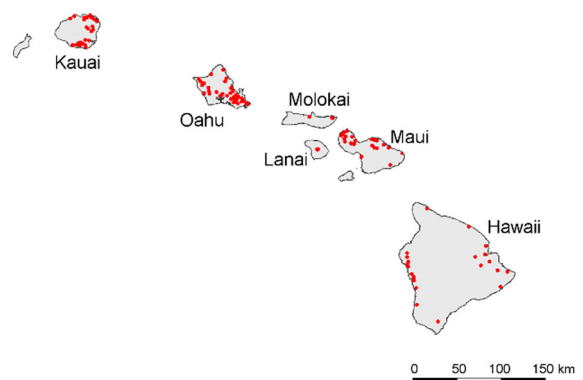

Fig. 8 Map of the Hawaiian Islands showing the locations of sites where *Euglandina* spp. populations have been recorded since 2004

10 beetles were released, with four snails (*Euglandina* spp., *Gonaxis kibweziensis*, *Gonaxis quadrilateralis* and *Gulella wahlbergi*) and the beetle *Teffus zanzibaricus* being recovered in surveys following release, indicating that at least five of the non-native predatory species had established populations (Davis and Butler 1964). However, Meyer et al. (2017) demonstrated that releases of *Euglandina* 'rosea' by this biocontrol effort actually comprised a species complex of at least two *Euglandina* species. Surveys during 2004–2014 recovered both *Euglandina* species (Meyer et al. 2017).

Intentional introduction of *Euglandina* was not confined to one island. The Hawaii Board of Agriculture and Forestry released them on Oahu in 1955; 365 were released at Hauula, 156 near the Kailua-Waimanalo boundary and 95 in the Makiki district of Honolulu (Davis and Butler 1964). Within 3 years 12,000 were collected from these areas and distributed to establish populations throughout Oahu and on other Hawaiian Islands (Kauai, Maui and Hawaii) and elsewhere (Davis and Butler 1964). Populations were also established on Molokai, and it was reported on Lanai by Cowie et al. (2008), with an established population recorded in 2018 (Yeung et al. pers. obs.). On Oahu *Euglandina* spread into the Honouliuli-Palikea sector of the Waianae Mountains (Van der Schalie 1969) but had not spread further by 1972 (Davis 1972). Declines in *L. fulica* populations in areas occupied by *Euglandina* were reported to be associated with the dramatic population increases of *Euglandina* at this time, and Davis and Butler (1964) and Nishida and Napompeth (1975) inferred high predation rates on *L. fulica* from the absence of small shells in surveys of several localities on Oahu. However, there is little direct evidence of predation to support the claims and these studies, and others, failed to consider seasonality, other predators or indeed other factors such as disease, parasites or genetic effects akin to inbreeding depression (Christensen 1984; Cowie 2001b). Additionally, there were suggestions that *Gonaxis quadrilateralis* temporarily eliminated *Euglandina* in the Tantalus Drive area (Davis and Butler 1964; Davis 1972), making it unlikely that *Euglandina* played any role in the declines of *L. fulica* in that area. Like many biocontrol efforts, these lacked the kind of controls needed to evaluate causation, and declines could simply be attributed to delayed, spontaneous declines (i.e.

'boom-and-bust' cycles) in population sizes that are often seen after such an invasion (Simberloff and Gibbons 2004; Strayer et al. 2017).

The current distributions of *Lissachatina fulica* and the *Euglandina* species (Fig. 8) highlight the catastrophic failure of the biocontrol programme in Hawaii. *Lissachatina fulica* is currently found almost exclusively at lower elevations (i.e. < 500 m). Conversely, *Euglandina* occupies a large elevational range and can be found near the highest elevations on Oahu and Kauai where many of the remaining extant native land snails persist (Hadfield and Mountain 1981; Hadfield et al. 1993; Meyer 2006; Meyer and Cowie 2011). Additionally, there is evidence that *Euglandina* continues to expand its range, both within and among islands (Cowie et al. 2008). Examining elevational distributions of *Euglandina* on Maui and Hawaii, the highest islands, an elevation threshold for *Euglandina* can be identified at approximately 1000 m (Meyer pers. obs.). This means that, given the maximum elevations of the islands, most, if not all, native snails on Lanai (∼ 1000 m) and Oahu (∼ 1200 m), most on Molokai (∼ 1500 m) and Kauai (∼ 1600 m), and many on Maui (∼ 3000 m) and Hawaii (∼ 4200 m) are vulnerable to *Euglandina* predation. However, population densities of this predator seem to be lower on high elevation ridges, providing small refuges where native species might persist (Meyer and Cowie 2011).

Platydemus manokwari was first observed on Oahu in 1992 (Eldredge and Smith 1994, 1995). It has only been observed in the south-east of the island but in 2018 it was found on Kauai (Loarie 2019), in 2019 on Molokai and Maui (Hayes pers. obs.) and on Hawaii (Keen 2019).

Caribbean and west Atlantic

Lissachatina fulica has been established in the Caribbean region since 1984 when it was recorded on Guadeloupe (Frankiel 1989). From published reports, Raut and Barker (2002) and Ciomperlik et al. (2013) listed the species also on Anguilla, Antigua, Barbados, Dominica, Marie-Galante, Martinique, Puerto Rico, St. Lucia, St. Martin and Trinidad. Since 2013, *L. fulica* has been known from Curaçao (Hovestadt and van Leeuwen 2017) and from Cuba since 2014 (Vázquez et al. 2017).

However, it was other species of snails introduced to Bermuda that were targeted by a biocontrol programme. These were two Mediterranean species, primarily *Otala lactea*, imported for food in 1928, and *Rumina decollata*, introduced accidentally with plants in the late 1870s (Bennett and Hughes 1959; Simmonds and Hughes 1963; Bieler and Slapcinsky 2000). Based on the supposedly successful but ultimately ill-conceived, unsuccessful and catastrophic attempts to control *L. fulica* with predatory snails in Hawaii, the Commonwealth Institute of Biological Control deliberately released *Euglandina* (and other predatory species) in Bermuda in 1958 and 1960 to control *O. lactea* and *R. decollata*, which by then were considered agricultural pests (Simmonds and Hughes 1963). *Euglandina* has since spread throughout much of the larger islands of Bermuda (Bieler and Slapcinsky 2000). Although control of *O. lactea* was reported in 1962 by the Bermuda Department of Agriculture, ultimately control of neither species was achieved (Bieler and Slapcinsky 2000). However, *Euglandina* may have been responsible for the decline of endemic species, notably species of the endemic genus *Poecilozonites*, which began in the 1960s (Bieler and Slapcinsky 2000). By 2004 the two non-fossil *Poecilozonites* species were thought to be on the verge of extinction and individuals were brought into captivity to establish a captive rearing programme, which has become highly successful to the extent that large numbers of *P. bermudensis* have already been released back into the wild on the offshore Nonsuch Island, a reserve free of *Euglandina* (Outerbridge et al. 2019).

Simmonds and Hughes (1963) reported that 500 *Euglandina* were easily collected in a few days for shipment from Bermuda to various places including the Bahamas for release against pest snails; whether they ever were shipped to the Bahamas is not known, nor is it known whether, if they had been released, they became established. Nonetheless, this report may be the basis for *Euglandina rosea* being listed (with no details) in numerous non peer-reviewed reports and websites, including the Bahamas National Invasive Species Strategy 2013 (Moultrie 2013), as occurring in the Bahamas.

Platydemus manokwari is now present in Puerto Rico (Justine et al. 2015), including Vieques island (Parr 2019) and there is photographic evidence of its presence in the Bahamas in 2018 (Frade 2018),

Anguilla (Adriaens 2020) and the US Virgin Islands in 2020 (Angeli 2020). No impacts have yet been reported.

USA

Lissachatina fulica was first introduced to Florida in 1966, with the infestation finally eradicated in 1975 following an expenditure of over 67,000 person-hours of effort and $700,000 (Poucher 1975). However, a newly established population was discovered in 2011 and the snails rapidly spread to several locations in south-eastern Florida (Ciomperlik et al. 2013; Iwanowicz et al. 2015). A major eradication programme was implemented, led by the U.S. Department of Agriculture and the Florida Department of Agriculture and Consumer Services (Roda et al. 2016), and the snails are close to being eradicated.

The *Euglandina rosea* species complex is naturally distributed throughout Florida and parts of neighbouring states (Meyer et al. 2017) (Fig. 9), and Florida was the original source of the *Euglandina* employed in biological control programmes initiated by the Hawaiian Board of Agriculture and Forestry (see above). Native *Euglandina* population densities are low (Hubricht 1985), although local population densities in Florida may rise to 8500 per hectare (Davis et al. 2004). This may be because of the low abundance of snails generally in the state's largely acidic waterlogged soil (e.g. pH 3.6–8.4 in Okeechobee County—Lewis et al. 2003). In addition to the native range in the south-eastern USA, *Euglandina* was introduced to California in 1960 in an attempt to control *Cornu aspersum* but did not become established (summarised by Cowie 2001b, Barker and Efford 2004). There was also a population, suspected to have been accidentally introduced, in Nashville, Tennessee, with live individuals recorded from 2006 to 2013, but that is now thought to have died out (Irwin et al. 2016).

Platydemus manokwari was first found in Florida in 2012 (Justine et al. 2015). It is widespread in south Florida with an isolated population in the west (Fig. 9). The rapid geographic expansion of records suggests that it had become established and dispersed before it was first identified. By 2015 a significant increase in mortality of *Liguus* tree snails, much of it directly attributed to flatworm predation, was observed in some areas invaded by *P. manokwari* (e.g. Castellow Hammock Complex Preserve) (Collins
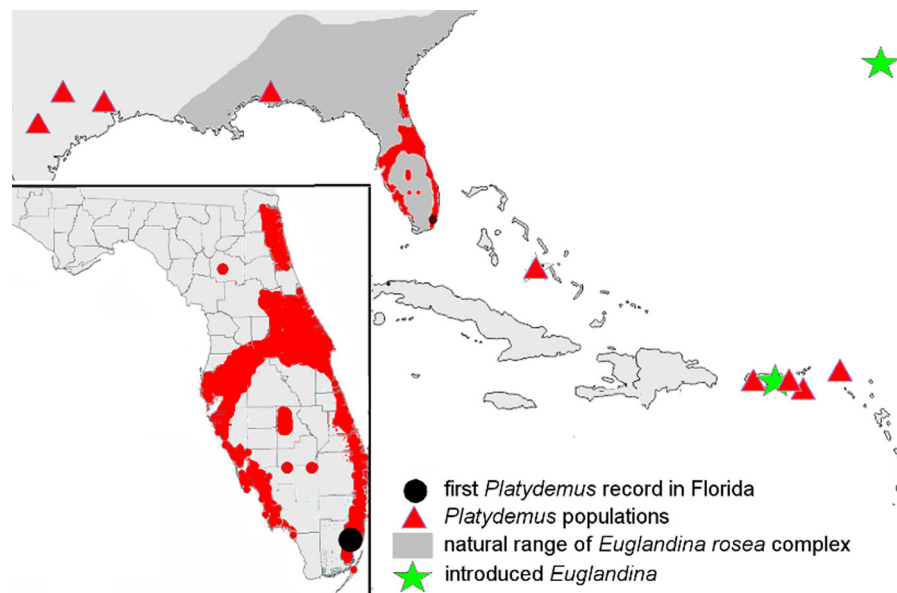
Fig. 9 Distribution of *Euglandina* spp. and *Platydemus manokwari* in the Caribbean region, showing the natural and introduced distribution of *Euglandina* and the spread of *P, manokwari* in Florida (inset), Florida data from EDDMapS (2020)

and Warren 2017). *Platydemus manokwari* was identified in Texas in 2018 and has now been recorded near Austin, San Antonio and Houston (Kempf 2019; Robin 2020; Texas Invasive Species Institute 2019).

Discussion

The introductions of *Euglandina,* and latterly *Platydemus manokwari*, have been some of the most extensive and long-running attempted biological control programmes. *Euglandina* has been introduced to 27 island groups and continental countries (India, Thailand, Malaysia) over 38 years (1955–1993). *Platydemus manokwari* is known to have been introduced deliberately to three island groups (Philippines, Maldives and Samoa) and has spread to a total of 28 island groups and mainland Myanmar, Thailand, Malaysia, China and the USA.

Deliberate introductions of *Euglandina* took place despite warnings of likely non-target impacts, from malacologists from the beginning of the control programme (Mead 1955, 1956a), and later releases also disregarded advice from malacologists, as discussed by Cowie (2001b). Despite the *Euglandina* releases being recognised as ecologically catastrophic within 14 years of the start of the programme (van der

Schalie 1969) and widespread demonstrations of the problems (Hadfield and Mountain 1981; Pointier and Blanc 1982; Clarke et al. 1984), documented official releases continued until 1993 (Wallis and Futuna) (Gargominy et al. 1996). Official releases of *P. manokwari* have been much more restricted, to the Philippines and Maldives during 1981–1985 (Muniappan 1990) and to Samoa in 1996–2001 (Brook 2012a, b). As with *Euglandina*, concerns over the risks in using this species were raised long before agriculture departments ceased the introductions (Kaneda et al. 1990).

The spread of *Euglandina* species is thought to be entirely due to deliberate introduction, mostly official introductions by government agencies, but also unofficial transport by private individuals within countries. No official introductions have been recorded since 1993, although some transport within island groups has occurred since then. Introduction of *P. manokwari* may originally have been accidental; its probable movement from New Guinea to Australia in the 1970s and from there to Guam by 1978 predated the suggestion that it could be used as a biocontrol agent. Most introductions of *P. manokwari* appear to have been accidental, probably through the transport of plant material. Once deliberate releases occurred, multiple populations became potential introduction

sources and the rate of documentation of new invasions is increasing (from two introductions in the 1970s to 17 since 2010), although this may in part be the result of increased publicity. As *P. manokwari* has only been identified as a species of concern since 1992 (Hopper and Smith 1992) and the focus of attention recently, it is likely to have been under-recorded and may have a much wider distribution than is currently known. Detection of *P. manokwari* may be relatively more difficult than of *Euglandina* as it does not leave behind shells when it dies.

In attempts at biological control, predators have been released when pest populations are problematically high. Inevitably this means that if the pest species have any form of cyclical or 'boom and bust' (Strayer et al. 2017) population dynamics, the predators will have been released at or near the peak in the pest population. As a result, unless rigorously demonstrated otherwise, reports that predators have controlled pests may be coincidental rather than causative. In the case of *Lissachatina fulica*, *Euglandina* was reported to have caused population declines in Hawaii (Davis and Butler 1964). However, there have been declines in *L. fulica* in the absence of *Euglandina* on several islands in the Marianas and French Polynesia. On Moorea *L. fulica* populations collapsed in 1978, just after the introduction of *Euglandina*, but this was not due to the introduction of the predator as it occurred even in areas that had not been invaded by *Euglandina* (Clarke et al. 1984). Similarly, declines also occurred on Huahine, which lacked *Euglandina* at the time (Pointier and Blanc 1985). Due to the abundance of empty shells and scarcity of living snails, Kondo (1952) thought that *L. fulica* "had passed its peak of expansions" in the Marianas between 1949 and 1952. Similar collapses in *L. fulica* populations in the absence of *Euglandina* occurred on Rota, Saipan, Tinian, Aguiguan and Pagan (Kondo 1952), and also occurred in the Ogasawara Islands and parts of Palau (Takeuchi et al. 1991). Clearly, introduced *L. fulica* populations decline in the absence of *Euglandina*, suggesting that other causative factors, currently unknown (but see below regarding possible effects of infections), were involved (Pointier and Blanc 1982, 1984; Clarke et al. 1984; Civeyrel and Simberloff 1996; Cowie 1992, 2001b).

The biocontrol programme's purported success at controlling *Lissachatina fulica* populations in Hawaii have not been supported experimentally (Christensen 1984; see Cowie 1992, 2001b for detailed descriptions of the evidence). While populations of *L. fulica* did decline following biocontrol efforts, studies in Hawaii (1) never addressed the role of other potentially causative factors, including disease, parasitism, or natural population fluctuations associated with invasion processes, (2) did not include adequate control sites without predators and (3) at times, failed to incorporate the role of reproductive seasonality into patterns recorded. These problems have been discussed by Kekauoha (1966), Nishida and Napompeth (1975), Christensen (1984), Civeyrel and Simberloff (1996), Cowie (2001b) and Simberloff and Gibbons (2004). Furthermore, even when any experimental work was undertaken before release, it was often just to assess whether *Euglandina* would prey on the target species. That it will do so is insufficient to demonstrate that it can have a population level effect, which would depend on the abundance of the predator, its consumption rate, and the abundance and reproductive productivity of the target species, i.e. their respective life-histories (Cowie 2001b). Often, possible impacts on non-target species were completely ignored.

Even if *Euglandina* and *Platydemus manokwari* played a role in some population declines of *Lissachatina fulica*, this may not result in long-term control as populations may recover from the effects of initial predator population growth. There is no evidence of effective long-term control of *L. fulica* by either *Euglandina* or *Platydemus manokwari*. For the latter, data are more scarce; the only attempt to record an effect was in the Maldives where declines reportedly occurred in 67% of areas where flatworms had been established (4 out of 6 sites) compared to 11% (2 of 9 sites) without flatworms (Muniappan 1987). Recent data from the release sites in the Maldives are lacking, but *L. fulica* persists in the archipelago alongside *P. manokwari* (A. Pichler pers. comm.). The fact that declines did also occur in the absence of flatworms may question the significance of any control effect. Declines were also claimed in Manila in the Philippines and on Guam. If *P. manokwari* did affect *L. fulica* populations in Manila this was only temporary as the snails were more recently considered abundant there (Constantino-Santos et al. 2014). Information from Guam is only anecdotal and with numerous other invasive species on the island, the impact of this introduction is difficult to ascertain. The presence of substantial *L. fulica*

populations throughout Pohnpei in the presence of *P. manokwari* (B. Holland pers. comm.) further indicates that the flatworm may not exercise effective control of these snails.

Population declines of *Lissachatina fulica* in the absence of introduced predators have been attributed to a disease in which the bacterium *Aeromonas hydrophila* is associated with 'leucodermic lesions' (Mead 1956b, 1961, 1979; Gerlach 1994, 2001). The pathology of infection is not understood and as *A. hydrophila* is a ubiquitous bacterium it may not be the causative agent, or may be associated with a wider disease syndrome. For example, Civeyrel and Simberloff (1996) suggested that an epizootic event may be triggered by stress caused by other pathogens, such as the rat lungworm, *Angiostrongylus cantonensis*. The effect of the visible signs of infection, the pale lesions in the skin, is also not known, although in a study of *Euglandina* some evidence was found that lesions on the sensory tentacles impair feeding and that there is some associated damage to the hepatopancreas (Gerlach 1994). Mead (1961) presented evidence for the association between increased disease incidence in *L. fulica* and population decline, but invasion by *Euglandina* disrupted the study by adding an additional potential cause for the observed declines. In introduced *Euglandina* populations incidence of symptoms in 1991–1992 ranged between 14% (n = 14) in Mauritius and 35% (n = 63) on Raiatea (excluding small samples; Gerlach 1994). At the same time incidence in *L. fulica* reached a maximum of 51% (n = 85) in the Seychelles islands (Gerlach 1994).

Although there are few data indicating that *Euglandina* species had any impact on *Lissachatina fulica* populations, strong evidence indicates that they were a major contributor to the decline/loss of many endemic Hawaiian land snail species, particularly Hawaiian tree snails in the genera *Achatinella* and *Partulina* (Hadfield and Mountain 1981; Hadfield and Miller 1989; Hadfield et al. 1993) and partulid tree snails across many islands in the Pacific Ocean (Tillier and Clarke 1983; Clarke et al. 1984).

While controlled experiments with treatments that exclude *Euglandina* have never been conducted, long-term demographic studies on the endangered and slow-reproducing Hawaiian tree snails demonstrate that mortality rates increased when *Euglandina* was present, and that slight increases in mortality can drive the local extinction of *Achatinella* and *Partulina*

populations/species (Hadfield et al. 1993). Although not designed as experimental tests of *Euglandina* predation, the creation of exclosures to protect remnant tree snail populations in Hawaii (Rohrer et al. 2016), or for reintroduction in the Society islands (Coote et al. 2004), provides additional support for the role of *Euglandina* in tree snail declines. These exclosures have prevented declines in populations of tree snails through exclusion of predators (primarily *Euglandina* and rats). The Hawaiian exclosures do not enable the impacts of different predator species to be distinguished but in the case of *Partula* reintroductions on Moorea, failure of the barrier allowed *Euglandina* to invade the exclosure, leading to complete elimination of the *Partula* population (Coote et al. 2004).

The influence of *Euglandina* predation on other native Hawaiian land snail species (Fig. 10) has not been well characterized, but its widespread distribution, use of diverse ground and arboreal habitats, and generalist feeding behaviours indicate that most of the remaining Hawaiian land snails are susceptible to this predator (Meyer and Cowie 2010, 2011). More than 750 species of endemic Hawaiian land snails have been recognized across the Hawaiian Islands (Cowie

Fig. 10 *Euglandina* sp. in a *Pisonia umbellifera* tree approximately 2 m off the ground, where it was hunting among the last known population of *Auricullela perpusilla* in the same tree (photo: K. Hayes)

et al. 1995). However, Solem (1990) estimated that 65–75% of this fauna was already extinct and Lydeard et al. (2004) suggested that the figure could be as high as 90%. More detailed estimates based on surveys over the last decade, and including newly discovered cryptic species, indicate that the remaining fauna numbers approximately 290 species, with estimates of extinctions within families ranging from 30 to 97% excluding families with fewer than ten species (Régnier et al. 2015b; Yeung and Hayes 2018; Hayes and Yeung unpublished). While widespread habitat modifications, shell collecting and other invasive species (e.g. ants, rats and lizards) also play (or played) a role in the decline of the Hawaiian land snail fauna (Hadfield 1986; Hadfield et al. 1993; Chiaverano and Holland 2014; Meyer and Shiels 2009; Régnier et al. 2009, 2015b) their roles relative to predation by *Euglandina* and by the widespread unintentionally introduced predatory snail *Oxychilus alliarius* (see Meyer and Cowie 2010; Curry et al. 2016, 2019) are difficult to evaluate.

In the Society Islands the decline of partulid tree snails following *Euglandina* release was monitored on Moorea (and Tahiti to a lesser extent) from the first declines in 1982 (5 years after *Euglandina* release) to their apparent extinction in 1988 (Clarke et al. 1984; Murray et al. 1988). Here there is an exact correspondence between the presence of the predator and partulid population decline. In American Samoa, although declines in partulids were demonstrable in 1992 (Miller 1993; Miller et al. 1993), there was evidence that they had started long before and were accelerated by the presence of *Euglandina* (Cowie and Cook 2001).

The declines of native snails following the introduction of *Euglandina* and *P. manokwari* have been most pronounced on Pacific islands and have affected tree-snails most conspicuously. The lack of any clear evidence of these predators causing population declines on Indian Ocean islands has been attributed to those snail faunas having some degree of resilience because of their coevolution with native snail predators (Gerlach 1994, 1999). Having evolved with predators, these snails have some defensive behaviours and high reproductive rates. In contrast many Pacific Ocean snails lack such defences and have very low reproductive rates. This may be most extreme in the Partulidae and Achatinellinae. For example, *Partula taeniata* reach maturity at a little less than a year

and produce 16–18 young per year (Cowie 1992; Gerlach 2017) and *Achatinella mustelina* mature at 3–5 years and produce an average of 7.4 young per year (Hadfield et al. 1993). This makes these taxa extremely vulnerable to predation; even infrequent predation or a short-lived invasion by a predator may be devastating as the population will recover only very slowly, if at all under ongoing predation. Evaluating the impacts of predators for potential biological control needs to take into account life-history characteristics of non-target prey. The relevant data for most snails are lacking; most of the data for *Partula* and *Achatinella* are derived from conservation breeding efforts or following the extirpation of wild populations.

On islands invaded by *Euglandina* and *P. manokwari*, some tree snail populations survive at high elevations. This is in accord with the suggestion that *Euglandina* would not invade the highest parts of many islands, being limited to areas with temperatures that never drop below 10 °C (Gerlach 1994), roughly around 1000–1200 m on most of the islands concerned. This has partly been borne out, in that permanent *Euglandina* populations have not become established in areas above this elevation. Whether there is any difference in thermal requirements and corresponding elevation ceilings for the two *Euglandina* species is not known. As the climate warms, these elevation ceilings may shift upwards (cf. Kim et al. 2019).

Experimental data indicate that *Platydemus manokwari* will only survive in areas with temperatures in the range 10–32 °C (Kaneda et al. 1992; Sugiura 2009; Gerlach 2019). The presence of the species in northern Florida does, however, demonstrate that survival is possible in areas that fluctuate outside this range seasonally. How tolerant they are to such seasonality will determine the northern limit of this invasive population. The other continental invaded region, south-east Asia, has a considerable area that is climatically suitable. The primary limit on tropical and subtropical island invasion is probably moisture, with only the very highest points of a few islands lying outside the temperature range. Currently the highest record for an introduced population is Mt. Aorai, Tahiti at 1000 m (Justine et al. 2015), although the highest confirmed native record is 1558 m at Kainantu, New Guinea. The fact that all new records of this species since 1985 result from undocumented

introductions demonstrates that it is being transported accidentally between islands and island groups. This makes it probable that new introductions will be frequent, and the rate of dispersal may increase as the number of potential source populations increases. It may yet reach higher elevations in its invaded range.

The rate of range expansion of *Platydemus manokwari* has been recorded at between 30 m per year (Winsor 1990) and 180 m per year (Muniappan 1987) via direct recording in different habitats. Mapping distribution changes gives much higher rates of dispersal; maps estimating range expansion give rates of 2–3 km per year on Guam (Muniappan 1990) and on Raiatea in the Society islands (Fig. 7). The speed of range expansion in Florida is considerably higher—up to 190 km per year inferred from recorded distribution points in EDDMapS (2020)—and suggests that many populations there are being established through secondary (probably accidental) introductions as *P. manokwari* can readily be transported in soil on boots and construction machines or on plant material (Okochi et al. 2004).

Other invasive flatworms may also pose a threat to native snail populations. Some species, such as

Caenoplana coerulea and *Parakontika ventrolineata* will attack live snails but are not specialist molluscivores (Winsor et al. 2004; Breugelmans et al. 2012). Other predatory terrestrial flatworms (*Bipalium vagum*, *Gigantea gouvernoni* and *Diversibipalium* spp.) and ribbon worms (*Geonemertes pelaensis*) feed on snails (Gerlach 1998; Jones and Sterrer 2005; Can 2018) and have been implicated in the decline of Bermuda's endemic land snails (Outerbridge et al. 2019). *Endeavouria septemlineata* will attack live snails (Mead 1979) despite its relatively small size but appears to prey mainly on dead animals (Boll et al. 2015) and was not thought by Hadfield (1986) to be a serious threat to Hawaii's Achatinellinae. In experiments, Okochi et al. (2004) showed that *Platydemus manokwari* consumed snails readily but that *Bipalium kewense* did not prey on snails at all, while other flatworms (different species of *Bipalium* and *Platydemus* and a species of *Australopacifica*) ate the snails in some instances. Thus, of the few flatworm species that have been studied ecologically, *Platydemus manokwari* may be unusual in being predominantly a predator of living molluscs.

Apart from the considerable threats that they pose to native and endemic biodiversity of molluscs on

tropical and subtropical islands where they have been introduced, the invasions of *Lissachatina fulica*, *Euglandina* species and *Platydemus manokwari* have human health implications as all three act as intermediate hosts of the nematode *Angiostrongylus cantonensis*, the rat lungworm (e.g. Asato et al. 2004; Kim et al. 2014). This nematode is the main cause of human eosinophilic meningitis (Cowie 2017; McBride et al. 2017). In a study of an outbreak of neuroangiostrongyliasis in Okinawa, Japan, in 2000, 10% of *L. fulica* and 14% of *P. manokwari* were infected (Asato 2004), making these two of the most significant reservoirs of infection in the islands. In Hawaii 21% of *Euglandina* and 11% of *L. fulica* were infected by *A. cantonensis* (Kim et al. 2014).

The spread of *Lissachatina fulica* throughout the islands of the tropics and subtropics has been taken as a stratigraphical marker of what has been called the 'Anthropocene' (Hausdorf 2018). In addition, its introduction also highlights the complexity of biological invasions (e.g. Green et al. 2011) as well as the risks of ill-conceived biological control efforts. Because of the impacts of *Euglandina* on endemic snails, malacologists universally agree that the introduction of *Euglandina* represents one of the most ill-fated biocontrol programmes ever implemented (Holland et al. 2008). Proponents of modern biocontrol contend that these are historical failures (Messing 2007) and that contemporary efforts are much safer. It is well recognized that generalist predators and parasites offer the greatest risk of non-target impacts, and as such are excluded from consideration in the majority of contemporary biocontrol programmes. Cowie (2001b) made the point well that predatory snails are never safe candidates for biocontrol agents, because they are generalist feeders. Modern biological control has well-established protocols to minimise environmental risks, by combining selection of only the most specialist (host-specific) parasitoids and parasites as candidate control agents with rigorous host-range testing prior to any field release, although this is not always followed (Holland et al. 2008). Despite this, generalist predators and parasites continue to be employed in biological control programmes targeting pest snails, often initiated by local communities impacted by invasive pests such as *L. fulica* but also frequently sanctioned and sponsored by ill-informed government authorities

(reviewed by Howarth 1991; Follett and Duan 2000, see also Jourdan et al. 2019).

In our reassessment of the literature pertaining to *Lissachatina fulica* biological control programmes that used *Euglandina* species and *P. manokwari* as control agents, it is clear that these do not meet the modern international standards for biosecurity and biocontrol practice (e.g. IPPC 2006). The pre-release host specificity testing and post-release assessments by authorities initiating those programmes have been woefully inadequate. It is easy to dismiss these gross deficiencies as being products of an inexact biocontrol science operating at that time (e.g. *L. fulica* biocontrol was first initiated in the 1950s). However, the legacy of these biocontrol programmes lives on. There has been poor learning from past dire non-target impacts of generalist predators in that *Euglandina* and *P. manokwari* continue to be introduced to new areas purposefully for *L. fulica* control (Coote pers. obs.). These problems are heightened by the fact that *L. fulica* continues to spread throughout the tropical and subtropical world (both passively and via deliberate introductions) and hence demands pest control solutions. *Platydemus manokwari* is easily dispersed via trade and commerce and because of its generalist feeding on land snails is a pest in its own right. These problems are well appreciated by the scientific community, but there are huge outreach challenges in discouraging further spread of predatory snails and flatworms as biocontrol solutions to pest snails. The literature on biological control is primarily focussed on control of insects and plants and little attention has been given to the risks involved with attempts to control snails. This creates a risk that additional predators and parasites may be released without adequate background research (e.g. see concern over the use of nematodes as biological control agents to control snails; Christensen 2019).

Diverse kinds of data provide varying levels of robustness regarding the evidence of decline in land snails (Supplementary Information). In large part, however, the information on the level of pest control by *Euglandina* and *P. manokwari* in biological control programmes and the effects of these predators on non-target native land snails is anecdotal or correlative as there were no adequate studies at the time of release. Evaluation of the impacts on other species has also been qualitative in many cases (e.g. Marquesas, Carolines), or with low levels of quantification (e.g.

Marianas, Samoa, Hawaii), usually after the declines had occurred. More reliable quantitative data on rates of decline have been gathered in the Ogasawara and Society islands (Clarke et al. 1984; Gerlach 1994, 2001; Coote et al. 1999; Coote and Loève 2003; Ohbayashi et al. 2007; Chiba and Cowie 2016). With these few exceptions there has been only limited scientific enquiry supported by robust experimental designs, appropriate sampling methodologies, and statistical analyses. In general, few studies have attempted to establish a causal link between decline and predation specifically by *Euglandina* or *P. manokwari*, either based on statistical comparisons of declines in sites with differing levels of predator numbers or predation intensity. What is more, for the most part studies have not adequately considered the range of possible extinction drivers, and their interactions with *Euglandina* and *P. manokwari*, on land snail decline operating at specific sites. Nonetheless, as outlined above, there are strong indications that neither *Euglandina* nor *P. manokwari* has been effective in regulating *L. fulica*, but instead that they have had adverse consequences for many land snail species and communities.

Conclusions

The lack of evidence that *Euglandina* and *Platydemus manokwari* provide effective control of *Lissachatina fulica*, and the strong indications that they have negative consequences for native snail faunas, mean that these species should not be used in pest management. All the present authors, and the majority of malacologists familiar with the impacts of these predators and to whom we have spoken, agree that 1) preventing further spread of *Euglandina*, *Platydemus manokwari* and other invasive predators is an imperative for preserving the world's terrestrial mollusc fauna, and 2) as there is no evidence for their benefit as biological control agents, their continued use in biocontrol efforts should cease.

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