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A century of *Azolla filiculoides* biocontrol: the economic value of *Stenopelmus rufinasus* to Great Britain

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Abstract

Background: The invasive aquatic fern *Azolla filiculoides* has been present in Great Britain (GB) since the end of the nineteenth century, while its specialist natural enemy, the weevil *Stenopelmus rufinasus* was first recorded nearly four decades later, in 1921. The purpose of this study was to estimate the economic value of management cost savings resulting from the presence of *S. rufinasus* as a biocontrol agent of *A. filiculoides* in GB, including the value of additional augmentative releases of the weevil made since the mid-2000s, compared with the expected costs of control in the absence of *S. rufinasus*.

Methods: Estimated economic costs (based on the length/area of affected waterbodies, their infestation rates, and the proportion targeted for management) were calculated for three scenarios in which *A. filiculoides* occurs in GB: (1) without weevils; (2) with naturalised weevil populations; and (3) with naturalised weevil populations plus augmentative weevil releases.

Results: In the absence of biocontrol, the expected average annual costs of *A. filiculoides* management were estimated to range from £8.4 to 16.9 million (US\$9.4 to 18.9 million) (£1 = US\$1.12). The impacts of naturalised *S. rufinasus* populations on *A. filiculoides* were expected to reduce management costs to £0.8 to 1.6 million (US\$0.9 to 1.8 million) per year. With additional augmentative releases of the weevil, *A. filiculoides* management costs were estimated to be lower still, ranging from £31.5 to 45.8 thousand (US\$35.3 to 51.3 thousand) per year, giving an estimated benefit to cost ratio of augmentative *S. rufinasus* releases of 43.7:1 to 88.4:1.

Conclusions: The unintentional introduction of the weevil *S. rufinasus* to GB is estimated to have resulted in millions of pounds of savings annually in management costs for *A. filiculoides*. Additional augmentative releases of the weevil provide further net cost savings, tackling *A. filiculoides* outbreaks and bolstering naturalised populations. The use of herbicides in the aquatic environment is likely greatly reduced due to *A. filiculoides* biocontrol. Although somewhat climate-limited at present in GB, climate change may result in even more effective biocontrol of *A. filiculoides* by *S. rufinasus* as has been observed in warmer regions such as South Africa, where the plant is no longer considered a threat since the introduction of the weevil.

Keywords: Biological control, Invasive non-native species (INNS), Management, Economic costs/benefits

Background

Azolla filiculoides Lamarck (Azollaceae), a small aquatic free-floating fern native to the Americas has been introduced to Europe, North and sub-Saharan Africa, China, Japan, New Zealand, Australia, the Caribbean and Hawaii (Lumpkin and Plucknett 1980). In Europe, *A. filiculoides*

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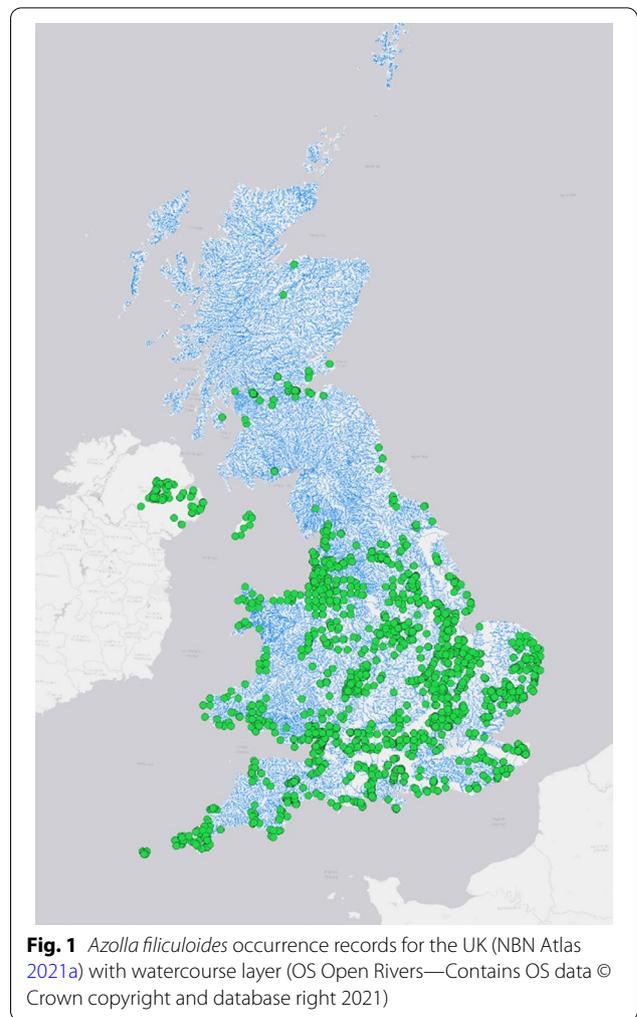
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is reported as an invasive alien species in numerous countries with its main occurrence in Atlantic-Mediterranean regions (Hussner 2012; Espinar et al. 2015; EPPO Global Database 2022). In Great Britain (GB) in 1883, *Azolla caroliniana* was reported from a pond in Middlesex, however it is now thought that *A. filiculoides* is the only *Azolla* species in the UK and as such there is a high likelihood that this was actually the first record of *A. filiculoides*, although herbarium specimens for confirmation are lacking (Odell 1883 in Reeder et al. 2018). Since its introduction, *A. filiculoides* has become naturalised and spread throughout lowland regions of southern and central GB in ponds, lakes, canals, ditches and other slow-moving fresh water (Preston and Croft 1997; Stace 2010), increasingly also infesting northerly sites in England and into Scotland (CABI data unpublished; NBN Atlas 2021a, b) (see Fig. 1). The main route for introduction was likely via the aquatic pond plant trade for ornamental use and in aquaria where *A. filiculoides* was previously sold or inadvertently carried on other water plants. The ornamental trade is considered a major pathway for the introduction of invasive alien plants globally (Hussner 2012; Kay and Hoyle 2001). However, *A. filiculoides* now spreads readily throughout water networks, is transferred by water birds and other animals and is carried on boats and equipment used in freshwater systems. *Azolla filiculoides* is listed under Schedule 9 to the Wildlife and Countryside Act (1981) making it an offence to plant or otherwise cause this species to grow in the wild in England and Wales, and was banned from sale in England in 2014 (legislation.gov.uk 2014, 2022).

Azolla filiculoides' preference for eutrophic water systems and its rapid growth rate allow it to outcompete indigenous vegetation. Under ideal conditions the fern can double in area in 4–5 days via rapid vegetative reproduction (Hill 1998; Lumpkin and Plucknett 1980). Dense mats form quickly across water bodies resulting in reduced light penetration into the water column (Janes et al. 1996), as is observed with other invasive floating water weeds such as *Salvinia molesta* (Motitsoe et al. 2020) and *Pistia stratiotes* (Coetzee et al. 2020). Thick mats of *A. filiculoides* in conjunction with decaying submerged root and leaf matter, create anaerobic conditions and reduced water quality (GB Non-Native Species Secretariat, 2015; Janes et al. 1996) with the potential to reduce dissolved oxygen by more than half (Gratwicke and Marshall 2001; Janes et al. 1996) and to lower pH levels (Pinero-Rodríguez et al. 2021). The presence of *A. filiculoides* at high density reduces water temperatures and prevents air-breathing organisms reaching the surface (GB Non-Native Species Secretariat 2015). In addition to outcompeting native plants, the presence of spreading *A. filiculoides* mats results in the disappearance of most



submerged plants, reduces macrophyte abundance, richness and biomass, causes changes in zooplankton composition, negative impacts on invertebrate communities and reduced survival and body condition of tadpoles (Janes et al. 1996; Gratwicke and Marshall 2001; Pinero-Rodríguez et al. 2021). The weed also detrimentally affects recreational use of water bodies, water transportation/navigation, impacts water flow and blocks irrigation pumps (Hill 1998).

Management of *A. filiculoides* using traditional approaches, namely manual/mechanical removal or chemical treatment has limited efficacy. The impacts of these techniques are short-lived with rapid clonal regrowth of any water fern not treated or removed resulting in a swift return to surface coverage, meaning these approaches must be repeated at significant cost. In addition, chemical control is often restricted in aquatic environments (Reeder et al. 2018), with a number of previously licenced herbicides no longer available. In GB,

although glyphosate can currently be used, this herbicide is non-selective and the requirement for repeat application increases costs (Reeder et al. 2018) and risks to the environment. Biological control (“biocontrol”) can be an effective and sustainable alternative if specific and damaging natural enemies can be identified and applied to a target weed. In North America two genus-specific insects found in association with *A. filiculoides* are the frond-feeding weevil *Stenopelmus rufinasus* (Gyllenhal) (Coleoptera: Curculionidae) and the flea beetle *Pseudolampsis guttata* (LeConte) (Coleoptera: Chrysomelidae) (Gassmann et al. 2006). Both insects are indigenous to southern USA; *S. rufinasus* is also found in western USA and has been collected on *A. filiculoides* in South America (Gassmann et al. 2006; Hill 1998).

In South Africa, *A. filiculoides* was introduced in 1948, infesting many water bodies and negatively affecting aquatic biodiversity and water utilization (Hill et al. 2008). In 1995, *S. rufinasus*, collected in Florida, USA were imported into South African quarantine for laboratory host-range testing. Here, *A. filiculoides* was demonstrated to be the significantly preferred host of *S. rufinasus* (Hill et al. 2008). Temperature is a key consideration for insect development and in South Africa, *A. filiculoides* has a temperate distribution across temperature ranges from -9 to 32 °C (Hill et al. 2008). In laboratory studies, McConnachie (2004) in Hill et al. (2008) found *S. rufinasus* to have an unusually wide thermal tolerance ranging from -12 °C to an upper limit of 36.5 °C, suggesting it would be able to establish in the majority of areas where the plant is present. The weevil was released in South Africa in 1997 where it successfully established at the majority of release sites and achieved complete control at 81% of those sites in an average time of $6.9 (\pm 4.3)$ months, and where *A. filiculoides* recolonized, the weevil spread successfully and controlled reinfestations within a year (McConnachie et al. 2004; Hill et al. 2008). In South Africa, five years after the weevil’s release *A. filiculoides* was reported to have been successfully controlled and no longer a threat to aquatic systems (McConnachie et al. 2004). The *A. filiculoides* population has been significantly reduced by *S. rufinasus* and no additional control methods are required (McConnachie et al. 2003).

In Europe, *S. rufinasus* is widespread, suspected to have been introduced from America as a stowaway on *A. filiculoides* (Janson, 1921). The weevil has been reported from several countries since the beginning of the twentieth century. First recorded in France in 1898 (Bedel, 1901 in Florencio et al. 2015) *S. rufinasus* is also reported to be present in Belgium, GB, Germany, the Netherlands, Ireland, Italy and Ukraine (Fauna Europaea; Florencio et al. 2015). In GB, the weevil was first recorded in Norfolk in

1921; in Spain on mats of *A. filiculoides* in 2003 (Dana and Viva 2006); collected in Portugal in 2011 (Carrapiço et al. 2011); and in Ireland from county Cork in 2007 (Kelly and Maguire 2009).

The long-term presence of *S. rufinasus* across much of the introduced distribution of its host plant, and the impacts the weevil is known to have on *A. filiculoides*, suggest that where both species are present, *S. rufinasus* will likely exert a significant degree of control on *A. filiculoides* populations. Indeed, in GB, where *S. rufinasus* is considered naturalised, populations have been observed effectively controlling *A. filiculoides*. Unfortunately, however, the level of control seen in GB is not equivalent to that in South Africa, likely due to the climatic constraints on *S. rufinasus* development rates, length of active season, dispersal ability and overwintering survival in GB, resulting in *A. filiculoides* outbreaks that are still numerous and significant. Therefore, augmentative releases of mass-reared *S. rufinasus* are carried out, in order to tackle *A. filiculoides* outbreaks as they occur (Reeder et al. 2018). The mass production of *S. rufinasus* takes place at the Centre for Agriculture and Bioscience International (CABI).

Ecological value of weed biocontrol

Evidence shows that *A. filiculoides* causes substantial deterioration of an ecosystem’s trophic web and that *S. rufinasus*, with its ability to clear large areas of *A. filiculoides*, could greatly benefit the invaded habitats into which it is introduced or disperses to from naturalised populations. Results from studies in South Africa into the impacts of two biocontrol agents used against the somewhat comparable floating aquatic weeds *Pistia stratiotes* (Coetzee et al. 2020) and *Salvinia molesta* (Motitsoe et al. 2020) demonstrate ecological benefits that *S. rufinasus* likely already provides in the UK through extensive biocontrol of *A. filiculoides*. In both studies, the introduction of the biocontrol agents (also highly damaging weevils) to invaded mesocosms resulted in improved water quality and increased aquatic biodiversity. The reduced biomass and surface coverage of these invasive aquatic weeds led to a significant increase in dissolved oxygen levels and saw a recovery of the benthic macroinvertebrates, resulting in a macroinvertebrate community comparable to the uninvaded state. Both studies found that biocontrol can drive aquatic ecosystem recovery within just one season. Although legacy effects of invasive aquatic macrophytes such as *A. filiculoides* can persist long after the target has been brought under effective control (Motitsoe et al. 2020), longer term recovery of biodiversity could approach that found pre-invasion given continued freedom from invasive macrophytes.

The indirect consequence of a reduction in the use of broad-spectrum herbicides for the control of *A. filiculoides* can be considered both an ecological, economic and human health benefit of biocontrol using *S. rufinasus*. Whilst the use of glyphosate on aquatic systems is restricted in the UK (Health and Safety Executive, 2022) and is increasingly considered inappropriate as a management tool on water bodies infested with *A. filiculoides* (e.g., Nottinghamshire Biodiversity Action Group 2020), biocontrol offers an alternative approach that allows land managers to move away from using such chemicals, which have the potential to kill non-target plant species and contaminate water.

Economic value of weed biocontrol

Several studies have assessed the economic value of biocontrol releases against floating aquatic invasive non-native weeds, using a range of approaches. For example, the total cost of a biocontrol programme for water hyacinth in Southern Benin was estimated at a present value of US\$2.09 million with the accumulated present value US\$260 million resulting in a benefit to cost ratio of 124:1 for direct economic benefits (under the conservative assumption the benefits stay constant over the next 20 years and also not accounting for indirect benefits or benefits to other countries) (De Groote et al. 2003). McConnachie et al. (2003) calculated the net present value (NPV) for *A. filiculoides* biocontrol in South Africa (from 1995 onwards) at US\$206 million with a benefit–cost ratio of 2.5:1 rapidly increasing to 15:1 by 2010. Recent research estimates the net present cost for biocontrol of *A. filiculoides* in South Africa at R 957,000 (=US\$64,000) with the cost for chemical application to give a similar level of control ranging from R30.6 to 206.7 million (US\$2 to 13 million) (depending on method used) (Maluleke et al. 2021). Across four invasive aquatic weed species (*P. stratiotes*, *S. molesta*, *A. filiculoides* and *Myriophyllum aquaticum*), the authors estimated the net present cost of biocontrol to be R7.8 million (US\$522,000) whereas the estimated cost of chemical control (to achieve the same level of control) varied from R149 million (US\$ 9.9 million) up to R1 billion (US\$ 67 million), giving a benefit to cost ratio from 90:1 up to 631:1.

The aforementioned studies were undertaken following a period of significant infestation by an invasive weed, with recorded impacts and management costs, followed by a classical biocontrol research programme, release of agents and substantial subsequent control of the target invasive weed. As such, in each case the authors were able to quantify costs relating to management of a wide-scale invasion using “traditional” methods of control (chemical, mechanical, manual) and/or estimates of impact-related costs given ongoing spread, along with

costs of conducting the classical biocontrol research and releases to provide control and reduce impacts. They were thus able to calculate the benefit to cost ratios of conducting the biocontrol research versus prior management using traditional means, and/or impact cost savings pre- and post-biocontrol.

In GB, it is not clear for how long exactly *A. filiculoides* was naturalised in the absence of its specialist natural enemy, *S. rufinasus*, however it is likely to be for no more than ~40 years in the late 19th to early twentieth centuries and in the early stages of this period would have had to establish and spread from a small initial population (or populations). *A. filiculoides* was likely first discovered in 1883 and *S. rufinasus* discovered in a chance finding in 1921. *S. rufinasus* is very cryptic (much more so than mats of *A. filiculoides* covering water bodies) being both very small and not likely to be casually observed as it feeds on a floating aquatic species, so could well have been resident for longer than indicated by its first recorded sighting. Figures for *A. filiculoides* impacts and control costs for the period in which it lacked a specific natural enemy in GB are entirely lacking and cannot be used for comparative purposes. Beyond this timeframe, with the introduction of *S. rufinasus*, biocontrol of *A. filiculoides* was likely an increasingly important factor in limiting population size and density, mitigating the plant’s impacts and spread; population increase in *S. rufinasus* can be extremely rapid over the warmer months, even in temperate GB conditions. A classical biocontrol research programme was not, however, undertaken, so costs for this process also do not exist. As such, today the situation is one in which *A. filiculoides* is widespread, but only occasionally dominant on slow and stationary freshwater bodies (often temporarily). Although under-recorded (as evidenced by unpublished CABI field and shipping records of *S. rufinasus* presence/releases compared with limited records on NBN Atlas 2021b), naturalised populations of *S. rufinasus* are widespread across much of the range of *A. filiculoides* including into Wales and Scotland, providing significant levels of background control, typically unnoticed. Where *A. filiculoides* outbreaks do occur, augmentative biocontrol using mass-reared *S. rufinasus* can be implemented, in addition to the various traditional methods of control available. In order to estimate the value of *A. filiculoides* control provided by *S. rufinasus* (both naturalised populations and augmentative releases) in GB in comparison to control using traditional methods in the absence of *S. rufinasus*—given the lack of pre-biocontrol management cost data or costs for a classical biocontrol programme—a set of scenarios must be considered which represent expected management costs in the absence of biocontrol, with *A. filiculoides* widespread and dominant; with naturalised

and widespread *S. rufinasus* populations providing extensive control; and the current situation with naturalised *S. rufinasus* populations providing extensive control, but with augmentative releases of mass-reared weevils to tackle *A. filiculoides* outbreaks. This study attempts to quantify these costs.

Methods

Three scenarios were established in order to estimate the potential value of *A. filiculoides* biocontrol to GB:

Scenario 1—Azolla, no weevil

The first scenario is a theoretical one in which *A. filiculoides* arrived to GB in the nineteenth century and *S. rufinasus* was never introduced. *Azolla filiculoides* has a multitude of biological traits that make it an effective coloniser and dominant aquatic macrophyte in the absence of specialist natural enemies, as was the case in South Africa before the release of *S. rufinasus*. Amongst the most important of these traits are the following: extensive production of spores for sexual reproduction which are immune to significant climatic variability including sub-zero conditions, can survive in water or silt for prolonged periods, withstand long-term desiccation and are readily redistributed (Janes 1998b; Hill and Cilliers 1999); exhibits prolific vegetative reproduction with a doubling time of 5 days in ideal conditions, growth at temperatures as low as 5 °C and survival at sub-zero conditions (Janes 1998a); has a small form, is free-floating and easily transferred; exhibits various growth forms dependent on conditions and population density (Janes 1998a); and is able to fulfil a significant proportion of its nitrogen requirement via the nitrogen-fixing symbiotic cyanobacterium *Anabaena azollae* (Janes 1998b) (Fig. 2).

In the absence of specific natural enemies—namely *S. rufinasus* in the GB context—it could be expected that *A. filiculoides* would now be the dominant aquatic weed in GB, given its observed dominance in temperate South Africa pre-biocontrol, affecting most stationary and slow-moving lowland freshwater bodies, having spread relatively unchecked for well over a century (given the difficulty in preventing spread or eradicating populations using manual or chemical methods).

Impacts would be felt by stakeholders across all sectors dealing with stationary and slow-moving water systems, along with private individuals. Accumulation of extensive, dense *A. filiculoides* infestations would impact upon aquatic flora and fauna, with deoxygenation and fish deaths, invertebrate losses and reductions in submerged plant biodiversity. Drainage systems would be blocked, navigation inhibited, and angling heavily disrupted. Water quality would be reduced and livestock and human life would be at risk where thick, floating mats of

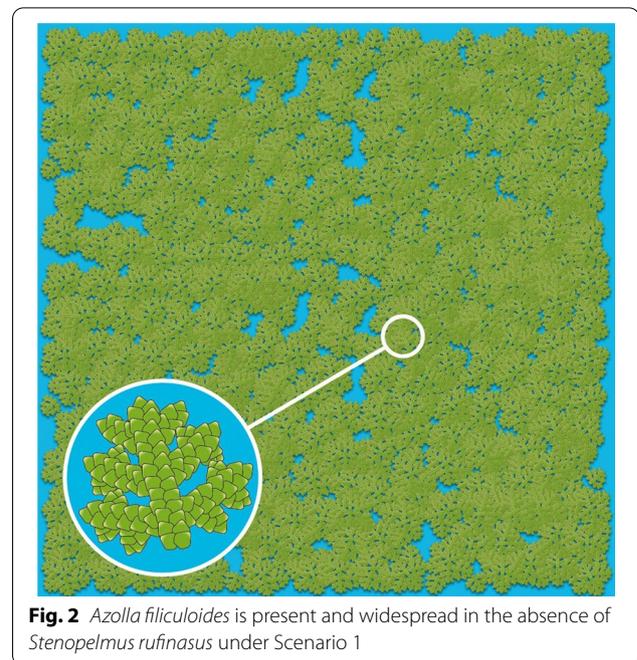


Fig. 2 *Azolla filiculoides* is present and widespread in the absence of *Stenopelmus rufinasus* under Scenario 1

A. filiculoides are mistaken for solid land. The impacts in GB could reasonably be expected to reflect those observed in heavily invaded regions lacking populations of specialist natural enemies, as in South Africa prior to the release of *S. rufinasus* and would be incurred over a large geographic range given the plant's adaptability, ease of spread and long period of residency.

The need for management would be constant from spring to autumn, with some reduction in *A. filiculoides* density likely during cold winters but rapid resurgence through vegetative growth and from spores as conditions improved. In the cost extrapolation, management scenarios conducted once and twice a season are described, using chemical, manual and mechanical approaches.

Scenario 2—Azolla, naturalised weevil

In this scenario, which was the situation prior to regular augmentative release of *S. rufinasus* conducted by CABI beginning in the mid-2000s, *S. rufinasus* has been present since at least 1921 when it was first detected in England and after a century of residency has a current distribution across most of the range of *A. filiculoides* in GB. Under this scenario, naturalised weevil populations reduce *A. filiculoides* dominance broadly, many infestations never reach high levels of coverage or density that result in the greatest impacts such as extensive blockages, deoxygenation and biodiversity loss and most populations are brought under full control without being actively managed. There is a reduced rate of *A. filiculoides* spread to surrounding water bodies, with most infestations

aesthetic, and required management interventions are greatly reduced. The *A. filiculoides* populations targeted for control using traditional methods are primarily large or dense outbreaks not yet located by the weevil; sites requiring management to meet targets (e.g., conservation targets or legislative requirements relating to Invasive Non-Native Species (INNS) presence or spread); drainage systems that can be blocked; designated sites, nature reserves and similar with high biodiversity value; organisations and individuals concerned by aesthetics and leisure impacts e.g., angling clubs, golf courses, canals, boating locations and private ponds; and public facing organisations subject to complaints and responsible for ensuring safety and limiting potential legal ramifications (and associated costs) e.g., canals. As *A. filiculoides* populations do not typically reach highly damaging levels, those with limited budgets, other higher priority INNS present, or without major concerns in terms of drainage, spread, biodiversity, legislation, leisure or aesthetics may not invest in *A. filiculoides* control even if affected, due to the lack of long-term efficacy of traditional approaches, namely manual or chemical application (Fig. 3).

Scenario 3—Azolla, naturalised weevil and augmentative releases

The third scenario represents the current situation in which CABI has conducted regular augmentative releases of *S. rufinusus* since the mid-2000s (scaling up production c. 2010). Every summer since the mid-2000s, CABI has mass-reared *S. rufinusus* and shipped the weevils to

locations across GB [2011–2020 average of $43,000 \pm 6700$ (SE) weevils to 27.7 ± 3 (SE) sites each year]. Under this scenario, the weevil population across the country has been augmented through targeted releases of large numbers of weevils at widely distributed sites at which *A. filiculoides* outbreaks have occurred. Augmented weevil populations at an outbreak site increase the likelihood of population presence/persistence in the locality, boosting weevil numbers and likely overwintering survival, meaning sites where the weevil has been released and nearby tend to have reduced *A. filiculoides* outbreaks in subsequent years. CABI has seen evidence of this with weevil order cancellations in outbreak areas where significant releases have been made in recent seasons, suggesting weevils may have spread, bolstering populations and contributing to *A. filiculoides* reduction in surrounding locations. Anecdotal reports have suggested an apparent ongoing national decrease in *A. filiculoides* populations since mass rearing and augmentative releases of *S. rufinusus* began, however this is difficult to confirm, with higher awareness of weevil application leading to enquiries from additional individuals and organisations each year and the size, number and density of *A. filiculoides* infestations variable year on year and difficult to monitor at the national scale (Fig. 4).

In this scenario outbreaks are expected to be less common still than in scenario two, less dense, shorter-lived and controlled longer-term by *S. rufinusus* (compared to traditional management approaches). Investment in mass

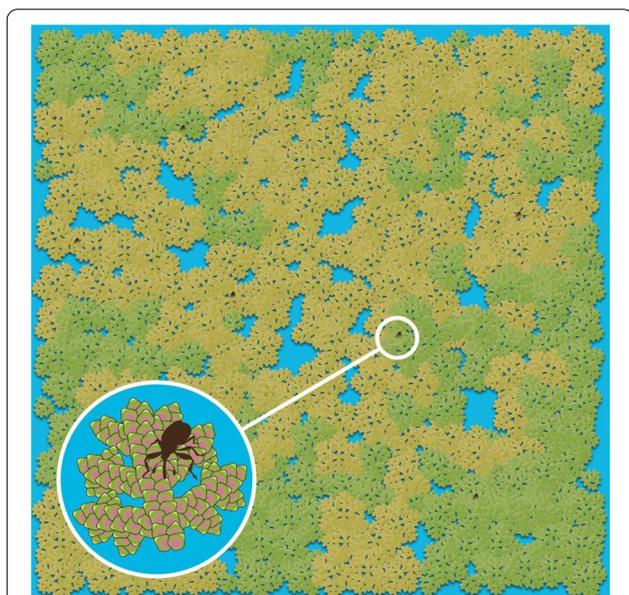


Fig. 3 *Azolla filiculoides* is present but subject to extensive attack by naturalised *Stenopelmus rufinusus* populations under Scenario 2

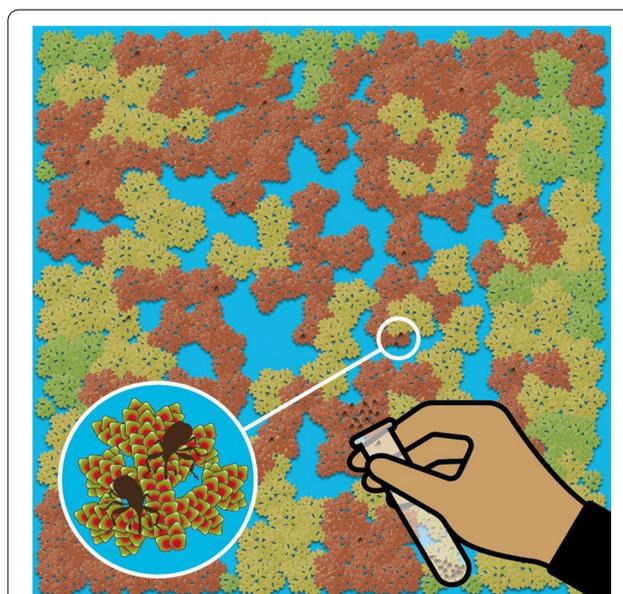


Fig. 4 *Azolla filiculoides* is present but subject to extensive attack by naturalised *Stenopelmus rufinusus* populations and augmentative weevil releases at outbreak sites under Scenario 3

reared *S. rufinasus* for local application also significantly reduces the overall national expenditure required for widespread *A. filiculoides* control. *A. filiculoides* is commonly referred to as transient in this scenario, simply because it is often briefly present before being brought under full control by *S. rufinasus*, typically without the observer being aware of the weevil.

Releases are targeted to sites that naturalised weevils may not locate for a period of time, for example in cooler active periods when flight is less likely or when the site is small, isolated or distant from naturalised weevil populations.

Those treating *A. filiculoides* will typically do so due to certain driving factors, such as site biodiversity value or conservation targets (e.g., nature reserves and natural ponds); aesthetic and recreation impacts (e.g., angling clubs, golf clubs, boating lakes, public access lakes and canals, private ponds—typically those with available funds); or regulatory or legislative requirements (e.g., canals and public safety).

Augmentative releases of *S. rufinasus* are used for a significant proportion of outbreaks. Use of traditional control methods is often limited to organisations or individuals yet to be aware of biocontrol as an approach (with this number decreasing over time) and those that require rapid clearance of *A. filiculoides* outbreaks and cannot afford to wait for the action of the weevil (typically 8–12 weeks for extensive control of a significant outbreak in the summer months at a suitable application rate). This can include sites such as canals, where public safety requirements demand that *A. filiculoides* is managed rapidly, for example using weed removal boats.

Management cost calculations

For each scenario, estimates of *A. filiculoides* infestation rate, proportion of infestations targeted for control and the cost of control per unit length/area were made for various freshwater systems, namely: rivers and streams; canals and canal feeders (the latter a canal serving to conduct water to a larger canal); drainage channels; lakes and ponds; and ditches. By multiplying the total length/area of water systems by the proportion of each system infested, proportion of infestations targeted for treatment and treatment cost per unit length/area it was possible to estimate the economic cost of *A. filiculoides* management under each scenario. In the third scenario these “traditional” approaches were estimated to account for 50% of the area treated, with the remaining 50% managed using biocontrol with a value equivalent to the mean annual expenditure on augmentative releases of *S. rufinasus* provided by CABI (2011–2020) at current prices exclusive of Value Added Tax (VAT), split proportionately between England and Wales versus Scotland in line with estimated

area of *A. filiculoides* treated and conducted once yearly. Costs are given in GBP where £1 = US\$1.12.

The “traditional” methods of control used in each of the first two scenarios and accounting for 50% of the area treated in the third scenario were expected to include a mix of herbicide spraying from the bank (or boat for wider waterbodies) and mechanical removal using weed boats, along with more manual approaches such as booming and netting. As such a representative cost per unit area was used. These were £500 per km (rivers and streams; canals and feeders; drainage channels—some spraying from bank/boat, some use of booms and manual removal, some weed boat removal, navigable); £350 per km (ditches—relatively narrow, some manual removal, bank-side spraying, often agricultural); £1500 per km² (lakes and ponds—some use of booms and manual removal, boats frequently required for spray/removal, potential access and navigation challenges, sensitive and amenity sites may limit spraying). Treatment cost estimates per unit distance or area were based on consultations with experts at the Canal & River Trust and the Environment Agency and those used are somewhat conservative.

The total lengths/areas of each water body type used in the calculations for GB are detailed in Table 1.

A distinction was made between *A. filiculoides* infestation rates for water bodies in England and Wales versus Scotland. Scottish waters are expected to be significantly less affected by *A. filiculoides* due to various abiotic and biotic factors including northerly latitudes limiting ideal growth periods for *A. filiculoides*, high altitude water bodies being less climatically suitable for *A. filiculoides* growth and biogeochemistry, and photoreactive processes typical to Scottish peatland lochs potentially limiting suitability (Turner et al. 2016; Pickard et al. 2017). The suspected lower suitability of Scottish waters for *A. filiculoides* proliferation is reflected both in the distribution records for *A. filiculoides* (NBN Atlas 2021a) and the significantly lower volume of orders received by CABI for weevils to manage outbreaks. With climate change, however, the suitability of Scottish freshwaters for colonisation by *A. filiculoides* may well increase (Whitehead et al. 2009; Kernan, 2015).

As such, infestation rates of various water body types in Scotland were set at 20% of the infestation rate used for England and Wales for cost calculations. In England and Wales, higher *A. filiculoides* infestation rates (and associated weevil impacts) may be expected in south and central regions where the plant is longest established, but for calculations average rates across the country are provided (Table 2).

It was assumed that different types of water body would attract different levels of management, driven by a variety

Table 1 Lengths/areas for each water body type in GB used for *A. filiculoides* management cost calculations

Freshwater system	England and Wales	Scotland	References
Rivers and streams (km)	172,123 ^a	125,000	(Riley et al. 2018; Critchlow-Watton et al. 2014; Scotland's Environment Web 2019)
Canals and feeders (km)	2717	220	(Canal & River Trust 2020; Critchlow-Watton et al. 2014; Scotland's Environment Web 2019)
Drainage channels (km)	22,000 ^b	14	(Association of Drainage Authorities 2017, 2018, 2022a, b)
Ditches (km)	391,934	208,066	(Riley et al. 2018; Brown et al. 2006) ^c
Lakes and ponds (standing waters) (km ²)	902	1296	(Hughes et al. 2004) ^d

Potential for some overlap of water bodies e.g. ditches (primarily agricultural) and drainage channels; drainage channels and rivers/canals etc. Figures intended to be indicative

^a Extrapolated from stream lengths cited at 73.4% of total running water network in England and Wales to 100% to include rivers

^b Approximate across several sources

^c 600,000 across GB divided proportionately by area for England, Wales and Scotland

^d Area by country estimated as proportion of total area of standing waters for GB. Proportions based on number of lakes recorded per country out of total number for GB as proxy

of factors such as legislation, public pressure, recreation or amenity value, budget availability of responsible authority, biodiversity value, infrastructure impact e.g., blockages to drainage. As such, estimates for rates of control in different water bodies were made and are detailed for each scenario, along with assumptions, in Table 3.

The calculation used to estimate the cost of *A. filiculoides* control under each scenario was:

$$AC = \sum W_b \times I_r \times C_p \times C_c \times C_f [+A_c]$$

where AC is the annual cost of *A. filiculoides* control to GB, W_b is water body length or area, I_r is infestation rate, C_p is proportion of infestations targeted for control, C_c is cost of control per unit length/area of given water body type, C_f is frequency of control (annual or biannual), A_c is cost of augmentative weevil releases (scenario 3 only). Costs for each water body type are summed to give total annual cost under each scenario with a range representing annual or biannual management. Infestation rates and management required are expected to fluctuate by year influenced by climatic conditions, previous management, and nutrient status with the annual cost estimates representing an average year scenario and the annual versus biannual management range capturing the potential variation in management requirement year on year. Rapid growth rates of surviving plants and germination of overwintering spores are expected to allow consistent recovery of *A. filiculoides* populations, requiring ongoing control year on year.

Results

The total annual costs of *A. filiculoides* management under the three scenarios described are detailed in Table 4.

The average annual cost of management of *A. filiculoides* under the first scenario in which *S. rufinus* is not present in GB, the plant is widespread and dominant (less so in Scotland), and control relies on traditional methods is estimated at approximately £8.4 to £16.9 million for GB (US\$9.4 to 18.9 million), with the range describing annual versus biannual management. With a widely naturalised population of *S. rufinus* providing broad control of *A. filiculoides*, but outbreaks frequent and targeted using traditional methods as in scenario two, the annual cost of management is estimated at £0.8 to £1.6 million (US\$0.9 to 1.8 million). This was the situation prior to mass rearing and release of *S. rufinus* by CABI. Under the current scenario in which naturalised *S. rufinus* populations are supplemented by mass releases of weevils each summer targeting *A. filiculoides* outbreaks, bringing these under control, limiting *A. filiculoides* spread and bolstering naturalised weevil populations, the cost of management (augmentative biocontrol plus traditional) is estimated at £31.5 to £45.8 thousand (US\$35.3 to 51.3 thousand).

As described, *Stenopelmus rufinus* was introduced to GB unintentionally and as such there was never investment in a classical biocontrol research and release programme. It is not possible, therefore, to assign a benefit to cost ratio to this approach in relation to impacts and/or management costs expected without biocontrol, as has been done in South Africa in relation to *A. filiculoides* and in a number of countries for classical biocontrol releases against various targets (e.g., McConnachie et al. 2003; van Wilgen et al. 2004; Culliney 2005). The savings resulting from the unintentional large-scale biocontrol of *A. filiculoides* by naturalised *S. rufinus* populations compared to the estimated traditional management costs

Table 2 *Azolla filiculoides* infestation rates for each water body type used in cost calculations

Scenario	Region	Azolla infestation rate (%)					Assumptions
		Rivers and streams (%)	Canals and feeders (%)	Drainage channels (%)	Lakes and ponds (%)	Ditches (%)	
Scenario 1—Azolla, no weevils	England & Wales	5.00	80.00	60.00	50.00	40.00	Slow sections of streams and rivers at some risk, but <i>A. filiculoides</i> washed through system. Canals and feeders interconnected, slow moving and heavily infested. Drainage channels potentially higher flow especially in flooding periods. Medium-large sheltered lakes and ponds frequently visited by water birds heavily infested, but isolated and smaller ponds potentially <i>A. filiculoides</i> free. Ditches primarily associated with agriculture, poor interconnectivity across regions limiting <i>A. filiculoides</i> spread, less suited for water birds, but high nutrient
	Scotland	1.00	16.00	12.00	10.00	8.00	
Scenario 2—Azolla, naturalised weevils	England & Wales	1.00	16.00	12.00	10.00	8.00	
	Scotland	0.20	3.20	2.40	2.00	1.60	
Scenario 3—Azolla, naturalised and augmented weevils	England & Wales	0.05	0.80	0.60	0.50	0.40	
	Scotland	0.01	0.16	0.12	0.10	0.08	

incurred under a widespread high-level invasion of *A. filiculoides* across GB can be estimated, however, and range from £7.7 to £15.3 million (US\$8.6 to 17.1 million) per year.

By comparing the management cost savings brought about by conducting annual augmentative releases of *S. rufinasus* which has an established cost with the estimated management costs incurred under scenario two, with a naturalised weevil population, but no augmentative releases, it is possible to estimate the benefit to cost ratio of conducting these releases. The average annual cost of augmentative releases (2011–2020) is £17,146 ± £2633 (SE) (US\$19,203 ± 2949), and the

estimated savings in terms of total management cost reductions resulting from these augmentative releases range from £748,953 to £1,515,055 (US\$838,827 to 1,696,862) per year, giving a benefit to cost ratio range of 43.7:1 to 88.4:1.

Discussion

The costs described for the management of *A. filiculoides* in GB under the three scenarios are intended to be indicative, giving an estimate of potential expenditure required in the absence of biocontrol and the magnitude of savings resulting from biocontrol, both 'classical' (though unintended) and with additional augmentative

Table 3 Proportion of *A. filiculoides* targeted for control in each water body type used in cost calculations

Scenario	Region	Proportion of Azolla targeted for control					Assumptions	
		Rivers and streams (%)	Canals and feeders (%)	Drainage channels (%)	Lakes and ponds (%)	Ditches (%)		
Scenario 1—Azolla, no weevils	England & Wales	10.0	90.0	50.0	70.0	5.0	Highest rates of management in major public access and recreation focused systems e.g., canals, angling and boating ponds and lakes. Canals with particular requirement to ensure public safety and manage invasive species. Drainage channels with some risks of blockage and responsibility to prevent spread. Ditches mainly agricultural and low priority except e.g., on nature reserves. River management only in slow sections and side channels where public have access and raise concerns	
	Scotland	10.0	90.0	50.0	70.0	5.0		
Scenario 2—Azolla, naturalised weevils	England & Wales	5.0	70.0	20.0	40.0	2.0		
	Scotland	5.0	70.0	20.0	40.0	2.0		
Scenario 3—Azolla, naturalised and augmented weevils	England & Wales	3.0	50.0	15.0	30.0	1.5		Infestations less intense in all systems, but public pressure still significant particularly for canals and amenity lakes and ponds. Aesthetics important and substantial <i>A. filiculoides</i> outbreaks targeted. Drainage channels at reduced risk of major infestation and blockages. Infestations typically more transient and less damaging, regularly brought under control before management applied. Ditches of lesser concern and most river or stream infestations temporary and requiring limited intervention
	Scotland	3.0	50.0	15.0	30.0	1.5		
Scenario 3—Azolla, naturalised and augmented weevils	England & Wales	3.0	50.0	15.0	30.0	1.5	Most infestations observed are new outbreaks that <i>A. filiculoides</i> weevil has yet to locate. Infestations rarely reach large scale and density except in waters high in nutrients. Most sites actively managed are for aesthetics, leisure and safety under public pressure (e.g., canals, some public lakes and ponds), regulatory demands, or due to high sensitivity such as designated sites, reserves and private ponds. Significant outbreaks on some drainage channels targeted to prevent blockages and limit spread of INNS. Significant proportion of reported outbreaks are brought under control by naturalised weevil populations before augmentative release (or traditional management) is carried out	
	Scotland	3.0	50.0	15.0	30.0	1.5		

Table 4 Estimated management costs for *A. filiculoides* under three described scenarios (in GBP £)

Scenario	Region	Mean annual cost of <i>Stenopelmus rufinasus</i> releases	Annual cost of traditional control—once yearly management	Annual cost of traditional control—twice yearly management	Total annual cost of control—once yearly management	Total annual cost of control—twice yearly management
Scenario 1—Azolla, no weevils	England & Wales	N/A	7,925,743	15,851,485	7,925,743	15,851,485
	Scotland	N/A	506,103	1,012,205	506,103	1,012,205
Scenario 2—Azolla, naturalised weevils	England & Wales	N/A	732,812	1,465,623	732,812	1,465,623
	Scotland	N/A	47,600	95,199	47,600	95,199
Scenario 3—Azolla, naturalised and augmented weevils	England & Wales	16,109.22 ^a	13,443 ^a	26,886 ^a	29,552	42,995
	Scotland	1038.78 ^a	867 ^a	1734 ^a	1906	2772

^a Of total area of *A. filiculoides* treated, 50% apportioned to *S. rufinasus* releases and 50% to traditional control methods. *S. rufinasus* applied only once per site per year. Value of *S. rufinasus* releases in England and Wales vs Scotland allocated at same proportions of total cost as traditional control costs for Scenario 3 (94% vs 6%). Mean annual value of augmentative *S. rufinasus* releases (2011–2020) at current prices is £17,146 ± £2633 (SE) (exclusive of VAT) (CABI unpublished)

releases. For the third scenario, which represents the current situation in GB it is possible to be confident in the magnitude of cost estimates, based both on expenditure on augmentative releases of *S. rufinasus*, for which CABI holds records, and for typical expenditure on traditional, non-biocontrol methods following consultation with various stakeholders.

The findings of this study indicate that the potential costs of managing *A. filiculoides* in the absence of biocontrol could be very significant, with expenditure on repeated management across the range of a long-established and dominant macrophyte estimated at £8.4 to £16.9 million (US\$9.4 to 18.9 million) per year, based on conservative costs per unit distance/area treated and up to two treatments per year only, although more could realistically be necessary. In addition to the management costs associated with controlling widespread and dense *A. filiculoides* there would be major biodiversity impacts from the infestations themselves and the likely extensive application of herbicides across freshwater systems. This scale of infestation and population density would also result in significant impact-related costs to industry and recreation, which are not captured in this economic assessment, but could be sizeable given the costs reported for South Africa before biocontrol releases against *A. filiculoides* (McConnachie et al. 2003). The management cost savings resulting from the unintended widescale naturalisation of *S. rufinasus* on *A. filiculoides* are estimated to range from £7.7 to £15.3 million (US\$8.6 to 17.1 million) per year, a reduction in expenditure of approximately 90%. This significantly increased level of control will reduce *A. filiculoides* impacts (and associated costs) and negative ecological impacts directly associated with dense infestations and from extensive herbicide treatment. The costs of management in this scenario of £0.8 to £1.6 million (US\$0.9 to 1.8 million) per annum

are somewhat comparable in magnitude to figures provided by Williams et al. (2010) who estimated the cost of waterway management of several invasive weeds including *A. filiculoides* to be £3 million per species per annum. At the time of the assessment augmentative releases of *S. rufinasus* were only beginning to be taken up by industry stakeholders and up to this point weevil provision had been comparatively small-scale, making it somewhat analogous to scenario two, rather than scenario three with its longer-term widescale mass releases of weevils (using weevil mass production data for 2011–2020).

The reduction in overall management costs for *A. filiculoides* in GB in scenario three indicates that although the naturalised weevil populations have a major impact on *A. filiculoides*, the release of *S. rufinasus* is both worthwhile and highly cost-effective, with the savings provided far greater than the cost of the weevils applied. Estimated costs are reduced from £0.8 to £1.6 million (US\$0.9 to 1.8 million) to £31.5 to £45.8 thousand (US\$35.3 to 51.3 thousand) and reliance on traditional methods including repeated herbicide application is reduced further still. Reduction in *A. filiculoides* infestation rates and density of populations can also be expected to encourage recovery of native biodiversity, with mats of the plant smaller, less common and rarely reaching high densities and significant thickness for prolonged periods. A demonstration of the short and longer-term economic benefits of *A. filiculoides* management using *S. rufinasus* is provided in a recent case study, in which the weevil was released to manage *A. filiculoides* on several waterways in the Midlands under the Canal & River Invasive Species Eradication Project (CRISEP 2021–2025) (Hughes Unpublished). The *A. filiculoides* infestation covered sections of several waterways at various levels of density over a linear length of 12 km. Weevils to the value of £2100 were

released in 2021 and after 8 weeks 58% of sites showed either complete or near complete control of *A. filiculoides*. In 2022 all locations were monitored and the *A. filiculoides* remained under widespread control with only a small number of top up releases of weevils made at specific locations. A comparative analysis of costs expected under a mechanical removal management regime for this extent of *A. filiculoides* was made and would require four weeks of removal by boat at a total cost of £12,600. This would likely need to be carried out up to three times annually and repeated year on year in the absence of *S. rufinasus* at a total cost of £37,800 per year. This estimate would also depend on competitive contractor rates for an organisation undertaking extensive land and water management and does not account for challenging access requirements or disposal of plant material which can significantly increase costs (Hughes Unpublished).

The benefit to cost ratios of augmentative releases of *S. rufinasus* may increase in time, as naturalised populations are boosted by regular releases of the weevil onto *A. filiculoides* outbreaks and more people become aware of augmentative biocontrol application as a method of control, potentially reducing the number of sites at which *A. filiculoides* is poorly controlled or left untreated and acting as a propagule source yet to be located by naturalised weevil populations. With climate change and warming conditions, it may also be that, in time, augmentative releases will be surplus to requirements. With warmer conditions, *S. rufinasus* could complete more generations in GB, over a longer active season and with greater dispersal capacity. Mild winters could also enhance overwintering survival. Control of *A. filiculoides* may be more complete, as is observed in South Africa where ongoing weevil releases are not necessary. Richerson and Grigarick (1967) estimated that *S. rufinasus* would complete four to six generations per year in part of its native range of California and Hill (1998) estimated up to ten overlapping generations per year would be feasible in parts of South Africa. For comparison, in typical GB conditions (1980–2016) London accumulates approximately 1280 growing degree days above 10 °C annually, with Edinburgh accumulating 600 (Weather Spark 2022); using the values calculated by McConnachie (2004) (in Hill et al. 2008) of a requirement for 256.4 days above a threshold of 9.18 °C it could be expected that roughly five generations could be completed in London, with approximately 2.4 in Edinburgh.

Not assessed in this study are the potential direct impact (e.g., recreation, drainage, flooding) and biodiversity related costs of *A. filiculoides* and the potential savings brought by traditional management, 'classical' biocontrol and additional augmentative

biocontrol releases. These figures would increase costs and potential cost savings brought by the various management approaches further still.

Conclusions

In the absence of the specialist weevil *S. rufinasus*, *A. filiculoides* could be expected to be the dominant aquatic macrophyte in GB, requiring extensive, costly management and likely widespread use of herbicides in the aquatic environment. For the last century, *S. rufinasus* has been naturalised in GB, providing widespread and typically unseen background control of *A. filiculoides*, bringing potential economic savings worth millions of pounds each year. Further augmentation of *S. rufinasus* populations using mass reared weevils to tackle *A. filiculoides* outbreaks provides further net cost savings and biodiversity benefits. *Stenopelmus rufinasus* is likely climate-limited in GB, allowing *A. filiculoides* to persist at a level that justifies ongoing management, however, with climate change the level of control delivered by this weevil may approach that observed in parts of South Africa, where *A. filiculoides* is considered to be under full control.

Acknowledgements

The authors thank Jonathan Newman, Environment Agency for helpful discussions relating to the biology and ecological impacts of *A. filiculoides* and *S. rufinasus*, and Charles Hughes, Canal & River Trust for valuable feedback on control costs and for sharing a pertinent case study of *Azolla* biocontrol.

Author contributions

CP proposed the premise for the study, which was developed by all authors. CP led the economic analysis, with contributions from all authors. All authors contributed to the writing of the manuscript. All authors read and approved the final manuscript.

Funding

This work was financially supported by the UK Department for Environment Food and Rural Affairs (Defra) Reference 32570. CABI is an international intergovernmental organisation, and we gratefully acknowledge the core financial support from our member countries (and lead agencies) including the United Kingdom (Foreign, Commonwealth & Development Office), China (Chinese Ministry of Agriculture and Rural Affairs), Australia (Australian Centre for International Agricultural Research), Canada (Agriculture and Agri-Food Canada), Netherlands (Directorate-General for International Cooperation), and Switzerland (Swiss Agency for Development and Cooperation). See <https://www.cabi.org/about-cabi/who-we-work-with/key-donors/> for full details.

Availability of data and materials

Data used for calculations will be available at <https://ckan.cabi.org/data/>.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 16 May 2022 Accepted: 19 October 2022
Published online: 14 November 2022

References

- Association of Drainage Authorities. An introduction to internal drainage boards. p. 8. 2017. https://www.ada.org.uk/wp-content/uploads/2017/12/IDBs_An_Introduction_A5_2017_web.pdf. Accessed 1 Nov 2022.
- Association of Drainage Authorities. The Work of Internal Drainage Boards (IDBs). 2018. <https://www.ada.org.uk/wp-content/uploads/2020/12/ADA-Infographic-IDBs-in-Futures.jpg>. Accessed 3 Jan 2022.
- Association of Drainage Authorities. Drainage districts in Wales and Scotland. 2022a. <https://www.ada.org.uk/our-members/wales-and-scotland/>. Accessed 1 May 2022a.
- Association of Drainage Authorities. Internal drainage boards. 2022b. https://www.ada.org.uk/member_type/idbs/. Accessed 1 May 2022b.
- Brown CD, Turner N, Hollis J, Bellamy P, Biggs J, Williams P, Arnold D, Pepper T, Maund S. Morphological and physico-chemical properties of British aquatic habitats potentially exposed to pesticides. *Agr Ecosyst Environ*. 2006;113(1–4):307–19. <https://doi.org/10.1016/j.jagee.2005.10.015>.
- Canal & River Trust. Annual report & accounts 2019/20; 2020. p. 85.
- Carrapiço F, Santos R, Serrano A. First occurrence of *Stenopelmus rufinus* Gyllenhal, 1835 (Coleoptera: Eirrhinidae) in Portugal. *Coleopt Bull*. 2011;65(4):436–7.
- Coetzee JA, Langa SDF, Motitsoe SN, Hill MP. Biological control of water lettuce, *Pistia stratiotes* L., facilitates macroinvertebrate biodiversity recovery: a mesocosm study. *Hydrobiologia*. 2020;847(18):3917–29. <https://doi.org/10.1007/s10750-020-04369-w>.
- Critchlow-Watton N, Dobbie KE, Bell R, Campbell SDG, Hinze D, Motion A, Robertson K, Russell M, Simpson J, Thomson D, Towers W. Scotland's state of the environment report, 2014. p. 249. 2014. <https://www.environment.gov.scot/media/1170/state-of-environment-report-2014.pdf>. Accessed 1 Nov 2022.
- Culliney TW. Benefits of classical biological control for managing invasive plants. *Crit Rev Plant Sci*. 2005;24(2):131–50. <https://doi.org/10.1080/07352680590961649>.
- Dana ED, Viva S. *Stenopelmus rufinus* Gyllenhal 1836 (Coleoptera: Eirrhinidae) naturalized in Spain. *Coleopt Bull*. 2006;60(1):41–2. <https://doi.org/10.1649/881.1>.
- De Groote H, Ajuonu O, Attignon S, Djessou R, Neuenschwander P. Economic impact of biological control of water hyacinth in Southern Benin. *Ecol Econ*. 2003;45(1):105–17. [https://doi.org/10.1016/S0921-8009\(03\)00006-5](https://doi.org/10.1016/S0921-8009(03)00006-5).
- EPPO Global Database. *Azolla filiculoides* (AZOFI). 2022. <https://gd.eppo.int/taxon/AZOFI/distribution>. Accessed 11 May 2022.
- Espinara JL, Díaz-Delgado R, Bravo MA, Vilà M. Linking *Azolla filiculoides* invasion to increased winter temperatures in the Doñana marshland (SW Spain). *Aquat Invasions*. 2015. <https://doi.org/10.3391/ai.2015.10.1.02>.
- Fauna Europaea. *Stenopelmus rufinus* Gyllenhal, 1835. https://fauna-eu.org/cdm_dataportal/taxon/efe60c19-c4ec-4f82-8a85-8c5cb809c9c3. Accessed 11 May 2022.
- Florencio M, Fernández-Zamudio R, Bilton DT, Díaz-Paniagua C. The exotic weevil *Stenopelmus rufinus* Gyllenhal, 1835 (Coleoptera: Curculionid) across a 'host-free' pond network. *Limnetica*. 2015;34(1):79–84.
- Gassmann A, Cock MJW, Shaw R, Evans HC. The potential for biological control of invasive alien aquatic weeds in Europe: a review. *Hydrobiologia*. 2006;570:217–22. <https://doi.org/10.1007/s10750-006-0182-4>.
- GB Non-Native Species Secretariat. Water Fern: *Azolla filiculoides*. 2015. <https://www.nonnativespecies.org/non-native-species/information-portal/view/451>. Accessed 11 May 2022.
- Gratwicke B, Marshall BE. The impact of *Azolla filiculoides* Lam. on animal biodiversity in streams in Zimbabwe. *Afr J Ecol*. 2001;39:216–8.
- Health and Safety Executive. Plant protection products with authorisation for use in Great Britain and Northern Ireland. 2022. <https://secure.pesticides.gov.uk/pestreg/ProdSearch.asp>. Accessed 8 May 2022.
- Hill MP. Life history and laboratory host range of *Stenopelmus rufinus*, a natural enemy for *Azolla filiculoides* in South Africa. *Biocontrol*. 1998. <https://doi.org/10.1023/A:1009903704275>.
- Hill MP, Cilliers CJ. *Azolla filiculoides* Lamarck (Pteridophyta: Azollaceae), its status in South Africa and control. *Hydrobiologia*. 1999;415:203–6. <https://doi.org/10.1023/A:1003869230591>.
- Hill MP, McConnachie J, Byrne MJ. *Azolla filiculoides* Lamarck (Pteridophyta: Azollaceae) control in South Africa: a 10-year review. *Proceedings of the XII International Symposium on Biological Control of Weeds, La Grande Motte, France, 22–27 April, 2007*. 2008;558–560. <https://doi.org/10.1079/9781845935061.0558>.
- Hughes C. Canal & river invasive species eradication project (CRISEP 2021–2025): *Azolla* management case study. Unpublished.
- Hughes M, Hornby DD, Bennion H, Kernan M, Hilton J, Phillips G, Thomas R. The development of a GIS-based inventory of standing waters in Great Britain together with a risk-based prioritisation protocol. *Water Air Soil Pollut Focus*. 2004;4(2/3):73–84. <https://doi.org/10.1023/B:WAFO.0000028346.27904.83>.
- Hussner A. Alien aquatic plant species in European countries. *Weed Res*. 2012;52(4):297–306. <https://doi.org/10.1111/j.1365-3180.2012.00926.x>.
- Janes R. Growth and survival of *Azolla filiculoides* in Britain. I. Vegetative reproduction. *New Phytologist*. 1998a;138:367–75.
- Janes R. Growth and survival of *Azolla filiculoides* in Britain. II. Sexual reproduction. *New Phytologist*. 1998b;138(2):377–84. <https://doi.org/10.1046/j.1469-8137.1998.00113.x>.
- Janes RA, Eaton JW, Hardwick K. The effects of floating mats of *Azolla filiculoides* Lam. and *Lemna minuta* Kunth on the growth of submerged macrophytes. *Hydrobiologia*. 1996;340:23–6. <https://doi.org/10.1007/BF00012729>.
- Janson OE. *Stenopelmus rufinus* Gyll., an addition to the list of British Coleoptera. *Entomol Mon Mag*. 1921;57:225–6.
- Kay SH, Hoyle ST. Mail order, the internet, and invasive aquatic weeds. *J Aquat Plant Manage*. 2001;39:88–914.
- Kelly J, Maguire CM. *Azolla filiculoides* invasive species action plan. 2009. p. 14.
- Kernan M. Climate change and the impact of invasive species on aquatic ecosystems. *Aquat Ecosyst Health Manage*. 2015;18(3):321–33. <https://doi.org/10.1080/14634988.2015.1027636>.
- legislation.gov.uk. The wildlife and countryside act 1981 (prohibition on sale etc. of invasive non-native plants) (England) order 2014. 2014. <https://www.legislation.gov.uk/uksi/2014/538?view=plain>. Accessed 8 May 2022.
- legislation.gov.uk. Wildlife and countryside act 1981. 2022. <https://www.legislation.gov.uk/ukpga/1981/69/schedule/9>. Accessed 8 May 2022.
- Lumpkin TA, Plucknett DL. *Azolla*: botany, physiology, and use as a green manure. *Econ Bot*. 1980;34(2):111–53.
- Maluleke M, Fraser GCG, Hill MP. Economic evaluation of chemical and biological control of four aquatic weeds in South Africa. *Biocontrol Sci Tech*. 2021;31(9):896–911. <https://doi.org/10.1080/09583157.2021.1900783>.
- McConnachie AJ, De Wit MP, Hill MP, Byrne MJ. Economic evaluation of the successful biological control of *Azolla filiculoides* in South Africa. *Biol Control*. 2003;28(1):25–32. [https://doi.org/10.1016/S1049-9644\(03\)00056-2](https://doi.org/10.1016/S1049-9644(03)00056-2).
- McConnachie AJ, Hill MP, Byrne MJ. Field assessment of a frond-feeding weevil, a successful biological control agent of red waterfern, *Azolla filiculoides*, in southern Africa. *Biol Control*. 2004;29(3):326–31. <https://doi.org/10.1016/j.biocontrol.2003.08.010>.
- Motitsoe SN, Coetzee JA, Hill JM, Hill MP. Biological control of *Salvinia molesta* (D.S. Mitchell) drives aquatic ecosystem recovery. *Diversity*. 2020;12(5):204. <https://doi.org/10.3390/d12050204>.
- NBN Atlas. *Azolla filiculoides*: water fern. 2021a. <https://species.nbnatlas.org/species/NBNSYS0000002090>. Accessed 1 May 2022.
- NBN Atlas. *Stenopelmus rufinus*: *Azolla* Weevil. 2021b. <https://species.nbnatlas.org/species/NBNSYS00000025285>. Accessed 1 May 2022.
- Nottinghamshire Biodiversity Action Group. Water fern control: canal & river trust. 2020. <https://nottsbug.org.uk/projects/invasive-non-native-species/water-fern-control-canal-river-trust/>. Accessed 8 May 2022.
- Odell TW. Hardwicke's science-gossip: an illustrated medium of interchange and gossip for students and lovers of nature, vol. 19. Madison: The University of Wisconsin; 1883. p. 279.
- Pickard AE, Heal KV, McLeod AR, Dinsmore KJ. Temporal changes in photoreactivity of dissolved organic carbon and implications for aquatic carbon fluxes from peatlands. *Biogeosciences*. 2017;14(7):1793–809. <https://doi.org/10.5194/bg-14-1793-2017>.
- Pinero-Rodríguez MJ, Fernández-Zamudio R, Arribas R, Gomez-Mestre I, Díaz-Paniagua C. The invasive aquatic fern *Azolla filiculoides* negatively impacts water quality, aquatic vegetation and amphibian larvae in Mediterranean environments. *Biol Invasions*. 2021;23(3):755–69.

- Preston C, Croft J. Aquatic plants in Britain and Ireland. Colchester: Harley Books; 1997.
- Reeder RH, Bacon ETG, Caiden MJ, Bullock RJ, González-Moreno P. Effect of population density of the *Azolla weevil* (*Stenopelmus rufinasus*) on the surface cover of the water fern (*Azolla filiculoides*) in the UK. *Biocontrol*. 2018;63(2):185–92. <https://doi.org/10.1007/s10526-017-9861-5>.
- Richerson PJ, Grigarick AA. The life history of *Stenopelmus rufinasus* (Coleoptera : Curculionidae). *Ann Entomol Soc Am*. 1967. <https://doi.org/10.1093/aesa/60.2.351>.
- Riley WD, Potter ECE, Biggs J, Collins AL, Jarvie HP, et al. Small water bodies in Great Britain and Ireland: ecosystem function, human-generated degradation, and options for restorative action. *Sci Total Environ*. 2018;645:1598–616. <https://doi.org/10.1016/j.scitotenv.2018.07.243>.
- Scotland's Environment Web. Scotland's freshwater. 2019. Scotland's Environment. <https://www.environment.gov.scot/our-environment/water/scotland-s-freshwater/>. Accessed 29 April 2022.
- Stace C. New flora of the British Isles. Cambridge: Cambridge University Press; 2010.
- Turner TE, Billett MF, Baird AJ, Chapman PJ, Dinsmore KJ, Holden J. Regional variation in the biogeochemical and physical characteristics of natural peatland pools. *Sci Total Environ*. 2016;545–546:84–94. <https://doi.org/10.1016/j.scitotenv.2015.12.101>.
- van Wilgen BW, de Wit MP, Anderson HJ, Maitre DCL, Kotze IM, Ndala S, Brown B, Rapholo MB. Costs and benefits of biological control of invasive alien plants: case studies from South Africa. *S Afr J Sci*. 2004;100(1):113–22.
- Weather Spark. Compare the December Weather in London and Edinburgh. <https://weatherspark.com/compare/m/12/45062~38026/Comparison-of-the-Average-Weather-in-London-and-Edinburgh-in-December>. Accessed 11 May 2022.
- Whitehead PG, Wilby RL, Battarbee RW, Kernan M, Wade AJ. A review of the potential impacts of climate change on surface water quality. *Hydrol Sci J*. 2009;54(1):101–23. <https://doi.org/10.1623/hysj.54.1.101>.
- Williams F, Eschen R, Harris A, Djeddour D, Pratt C, Shaw RS, Varia S, Lamontagne-Godwin J, Thomas SE, Murphy ST. The economic cost of invasive non-native species on Great Britain. Northampton: Edward Elgar Publishing; 2010. p. 199.

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