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Monographs on invasive plants in Europe N° 2: *Eichhornia crassipes* (Mart.) Solms

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ABSTRACT

Eichhornia crassipes is notorious as the world's worst aquatic weed, and here we present all aspects of its biology, ecology and invasion behaviour within the framework of the new series of *Botany Letters* on *Monographs on invasive plants in Europe*. Native to the Amazon in South America, the plant has been spread around the world since the late 1800s through the ornamental plant trade due to its attractive lilac flowers, and is established on every continent except Antarctica. Its distribution is limited in Europe to the warmer southern regions by cold winter temperatures, but it has extensive ecological and socio-economic impacts where it invades. Its reproductive behaviour, characterised by rapid vegetative spread and high seed production, as well as its wide physiological tolerance, allows it to proliferate rapidly and persist in a wide range of environments. It has recently been regulated by the EU, under Regulation No. 1143/2014, which states that *E. crassipes* shall not be brought into the territory of the Union, kept, bred or transported to, from or within the Union. However, in the absence of effective control measures, such as herbicidal and biological control, it will continue to be a significant threat to European waterways, particularly in eutrophic waters, and under future climate change scenarios.

1. Taxonomy

1.1. Names and classification

Scientific name: *Eichhornia crassipes* (Mart.) Solms

Synonyms: *Pontederia crassipes* Mart. (Basionym), *Eichhornia cordifolia* Gand., *Eichhornia crassicaulis* Schltdl., *Eichhornia speciosa* Kunth, *Heteranthera formosa* Miq., *Piaropus crassipes* (Mart.) Raf., *Pontederia crassicaulis* Schlecht., *Pontederia crassipes* Roem. & Schult

Taxonomic position: Monocotyledons, Order: Commelinales, Family: Pontederiaceae

Common names: aguapé, baronesa (Brazil), jacinto-aquatico (Portugal), bisnidh, zanim, zoqqueym et.tani Baqaqa, camalote (Mexico) habba, halassandi/halassant (Egypt), buchón (Colombia), bora (Venezuela), jacinthe d'eau (France), gulbakauli (Pakistan), jacinto de agua o camalote, lechuguilla, lirio acuatico (Spain), lila de agua (Dominican Republic), tokozelka (former Czechoslovakia), top-chawa (Thailand), violeta de agua (Chile), wampee (former U.S.S.R.), Wasserhyazinthe (Germany), susümbülü (Turkey), tarulla (Colombia), vanhyacint (Denmark), water hyacinth (U.K.), waterhyacinth (U.S.A.) yakinton hamaim (Israel), jacinthe d'eau (Côte d'Ivoire), wasserhyazinthe (Namibia), wota haisin (Papua New Guinea), curse of Bengal (India), namasupuni (Malawi), putu putu (Zambia)

EPPO code: EICCR

1.2. Morphological description

1.2.1. Species description

Eichhornia crassipes is a free-floating aquatic macrophyte, which reproduces both vegetatively through daughter plant (ramet) production and sexually via seeds (Penfound and Earle 1948) (Figures 1 and 2). It has 6–10 shiny green leaves arranged in basal rosettes, borne on bulbous or elongate petioles, depending on crowding conditions: in dense stands, the petioles are elongate, up to 1 m tall, but in sparse infestations or at the edge of infestations, the petioles are bulbous and short (<30 cm) (Center and Spencer 1981). The rhizome and feathery roots are submerged, and respond to changes in nutrient availability, where longer, denser roots are associated with limited phosphorus (P) availability (Xie and Yu 2003).

The attractive flowers are pale blue to mauve and borne on inflorescences, and produce many long-lived seeds, remaining viable in seedbanks for up to 20 years (Gopal 1987). The flowers display the genetic

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Figure 1. *Eichhornia crassipes*. Drawn by W. Roux, first published in Henderson and Cilliers (2002).

polymorphism of tristyly where all flowers of an individual plant possess one of three distinct corresponding style and stamen length phenotypes (Eckenwalder and Barrett 1986). In its native range, the short-style forms are dominant, while in the introduced range, the intermediate-style form is prevalent, and the long-styled form less common (Barrett 1977; Barrett and Forno 1982).

1.2.2. Distinguishing features

Eichhornia crassipes is the only floating species in the genus. In its native range, *E. crassipes* co-occurs with the morphologically similar *Eichhornia azurea* (Sw.) Kunth but differs in that it is free-floating, while *E. azurea* is rooted. There are no other *Eichhornia* species outside South America, apart from *E. natans* (P.Beauv.) Solms which is native to tropical Africa, and readily distinguished from *E. crassipes* by its rooted habit, and leaves that occur on the water's surface.

1.2.3. Variations at the infraspecific level

No varieties or subspecies are currently recognised within the species.

2. Distribution and status

2.1. Native range

Eichhornia crassipes is indigenous to tropical South America, first described from Brazil in 1823 by C.F.P. Martius. Its centre of origin is Amazonia, Brazil, with anthropogenic spread to areas such as Argentina, Venezuela and central South America and the Caribbean islands (Barrett and Forno 1982; Edwards and Musil 1975; Penfound and Earle 1948).

South America: Argentina, Brazil, Chile, Columbia, Costa Rica, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela.

2.2. Introduced range

Eichhornia crassipes occurs on every continent except Antarctica, and in more than 50 countries, as the result of anthropogenic spread. Its distribution is largely restricted by cold winter temperatures to between 40°N and S, while it occurs abundantly in tropical freshwater bodies around the world (Figure 3). Below is a list of invaded countries per global region:

Asia: Bangladesh, Cambodia, China, Brunei Darussalam, India, Indonesia, Israel, Lebanon, Japan, Jordan, Laos, Malaysia, Maldives, Myanmar, Philippines, Singapore, South Korea, Sri Lanka, Syria, Taiwan, Thailand, Turkey, Vietnam.

North America: Mexico, U.S.A. *Eichhornia crassipes* has also been reported in ephemeral summer and autumn populations on the border of southern Canada (Ontario Province, tributaries to the southern side of Lake St. Clair and the Detroit River) (Adebayo et al. 2011). It is assumed that the finding of water hyacinth in these locations is due to repeated re-invasion from

Figure 2. A flowering *Eichhornia crassipes* plant, illustrating the beautiful lavender-blue flowers, largely responsible for its anthropogenic spread around the world. Photograph: J. Coetzee.

anthropogenic release by humans, rather than propagation by seed.

Central America: Guatemala, Honduras, Nicaragua, Panama.

Caribbean: Bahamas, Cuba, Dominican Republic, Haiti, Jamaica, Puerto Rico.

Oceania: American Samoa, Australia, Cook Islands, Fiji, French Polynesia, Guam, Marshall Islands, Federated States of Micronesia, Nauru, New Caledonia, New Zealand, Northern Mariana Islands, Palau, Papua New Guinea, Samoa, Solomon Islands, United States minor outlying islands, Vanuatu.

Africa: Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Congo, Côte d'Ivoire, Democratic Republic of Congo, Egypt, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Guinea Bissau, Kenya, Liberia, Madagascar, Malawi, Mali, Mauritania, Mauritius, Mozambique, Niger, Nigeria, Reunion, Rwanda, Senegal, Sierra Leone, South Africa, Sudan, Swaziland, Tanzania, Togo, Uganda, Zambia and Zimbabwe.

Europe: Established populations in Portugal, Spain, Italy and France (Q-Bank Invasive Plants 2017) (Figure 4). In the Paúl do Boquilobo Biosphere Reserve in Central Portugal, it forms dense floating mats over extensive areas of wetlands and is considered the most obvious threat to the ecosystem. It is a permanent but controlled invasive aquatic weed in the irrigation canals, rice fields and riverine habitats of the Sado and Soraia River Basins, near Lisbon and the Atlantic Ocean, but is limited in the estuaries of these systems because it does not tolerate high salinity (Ruiz Téllez et al. 2008). The plant is also recorded as a casual invasive in Asturias, Huelva, Málaga, Cáceres, Taragona, Castellón, Alicante (Ruiz
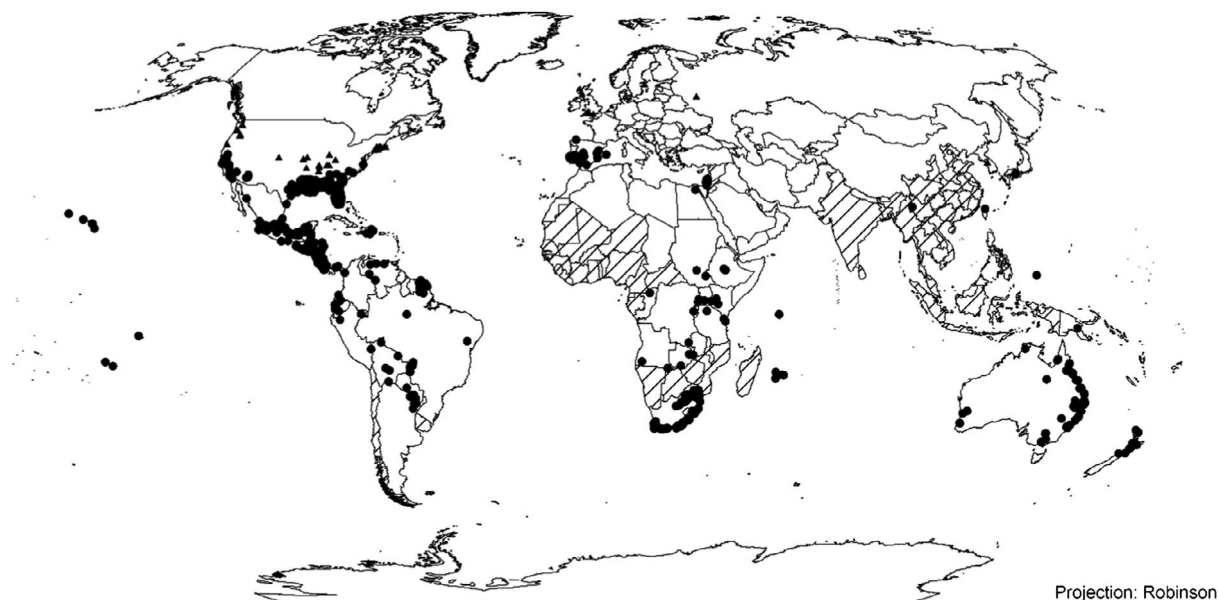
Figure 3. Global distribution of *Eichhornia crassipes*, including established and casual populations. Where information has been provided by country, these administrative areas have been shaded. Where more precise distribution data is available this is indicated as dots, with established population indicated as circles, and ephemeral populations as triangles. Source: Kriticos and Brunel 2016 (with permission).
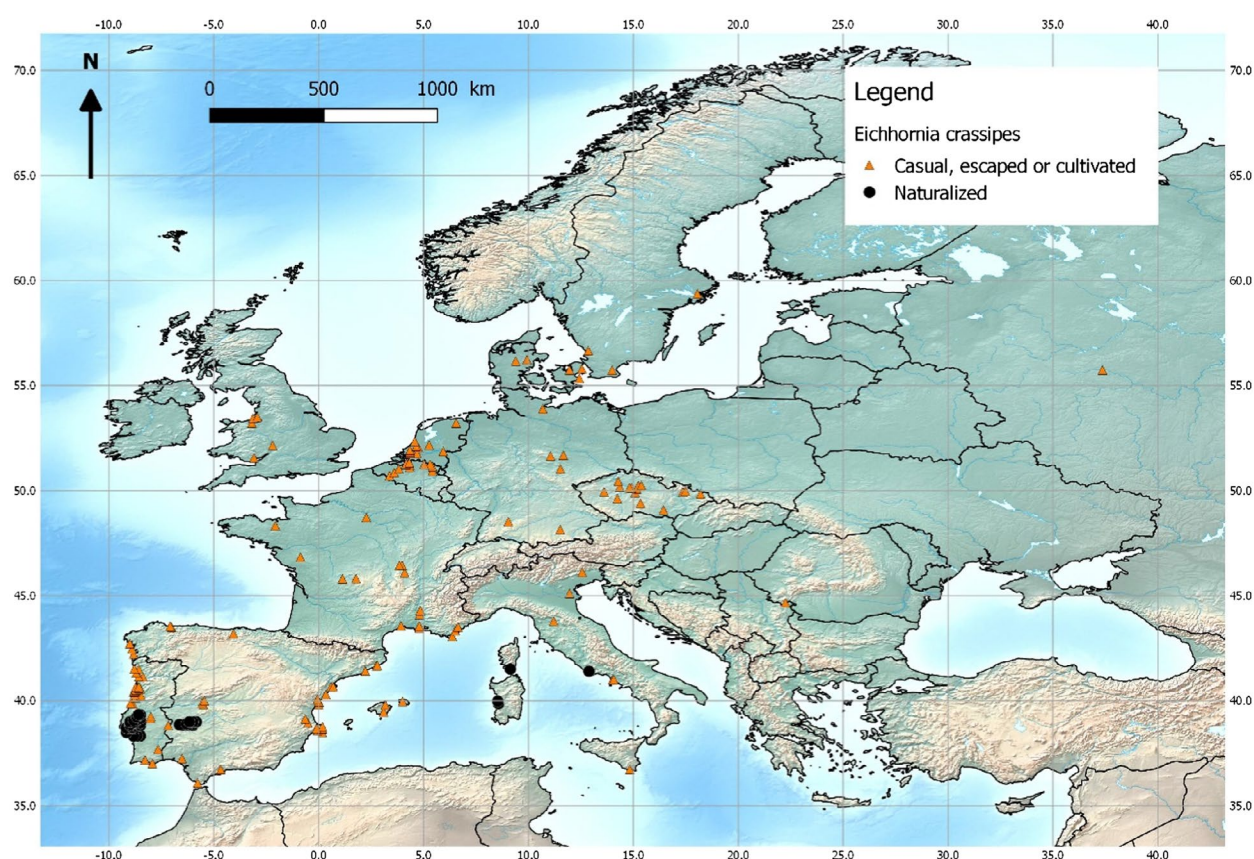

Figure 4. Distribution map of *Eichhornia crassipes* in Europe. The map is given according to GBIF.org (2017) with corrections based on our expertise on the species. Kaplan et al. (2016) was used for distributon in Czech Republic; for France, we used the système d'information « Flore, Fonge, Végétation et Habitats » de la Fédération des Conservatoires botaniques nationaux (2016); Brundu et al. (2012, 2013), Lastrucci and Foggi (2006), Masin and Scortegagna (2012) and Stinca, D'Auria, and Motti (2012) were used for Italy; and Ruiz Téllez et al. (2008, 2016) and Peña Bretón and de la Cruz (2014) for Portugal and Spain. Black dots denote established populations, and orange triangles denote casual, escaped or cultivated populations. It is unlikely that all casual and cultivated records appear on this map, but, where present, they provide useful information showing where the species has escaped from cultivation or could potentially do so (propagule pressure). This information could be used along with the modelled potential distribution of *Eichhornia crassipes* under current climate conditions (Figure 5). Map prepared by Guillaume Fried.

Téllez et al. 2008) and Valencia (Peña Bretón and de la Cruz 2014) in Spain. In 2005, it was reported to cover 75 km (approximately 200 ha) of the Guadiana River in the South Western Iberian Peninsula (Ruiz Téllez et al. 2008), which has since increased in extent to the Spain-Portugal border (Ruiz Téllez et al. 2016). There are also recent records of its invasion in Italy in Sardinia and Lazio (Brundu et al. 2012), while in other parts of the country (Campania, Tuscany, Sicily, Veneto), it is considered as a casual alien (Brundu et al. 2013) (Figure 4). In France, the species is only naturalised in Corsica and has not spread (Tison and de Foucault 2014). In France mainland, the species has been increasingly recorded as escaped in the wild, in the west, the south-west, the Mediterranean region, and more rarely elsewhere (e.g. Georges and Pax 2002), but populations cannot tolerate continental winters (Fried 2017). In addition, it is recorded as a casual in several European countries with temperate climates, e.g. Belgium (Verloove 2006) Germany (Buttler, Thieme, and Mitarbeiter 2017), the Netherlands, the U.K. (Q-Bank Invasive Plants 2017) and the Czech Republic (Kaplan et al. 2016; Pyšek et al. 2012).It is also listed as present in Hungary and Romania (DAISIE 2008). The species was recorded in Moscow (Russia) but did not thrive. The species is also known to occur in thermally abnormal waters in Russia and Germany, e.g. the River Erft (Hussner and Lösch 2005), where it would normally be excluded due to cold winter temperatures.

2.3. History of introduction and spread

The main mode of spread of water hyacinth is anthropogenic, via horticultural and aquarium trades due to the appeal of its beautiful flowers, and attractive smooth, green foliage and ease of cultivation. It continues to be introduced and spread through this pathway. The first authentic record of *E. crassipes* outside South America was from a trade fair in New Orleans in 1884 (Penfound and Earle 1948). Visitors to the cotton exposition were given plants as souvenirs by Japanese delegates, and many of these plants found their way into the waters of Louisiana, Texas, and Florida (Klorer 1909). A particularly troublesome invasion was on the St Johns River in Florida in 1895, when gale force winds blew the plant 160 km up and down the river, creating expansive floating mats up to 40 km long. Thereafter, *E. crassipes* plants spread around the U.S.A., remaining most problematic in the southern States as well as California. By the end of the nineteenth century, the plant was recorded in Egypt, India, Australia and Java (Gopal 1987). Its distribution is limited to latitudes of 40°N and S, with most invasions sites in the tropics, but it also occurs in warm temperate regions of the world (Gopal 1987). *Eichhornia crassipes* was first recorded in Australia in 1894, and by 1900, it was well established throughout Queensland and New South Wales (Wright and Purcell 1995). Introductions

into China occurred during the early 1900s, and it is now widely distributed in sixteen provinces in southern China largely as a result of increased eutrophication of Chinese water bodies (Jianqing et al. 2001). Even though *E. crassipes* was first introduced to the African continent in Egypt between 1879 and 1892, and in South Africa in 1910 (Edwards and Musil 1975), many invasions in Africa were first noticed only in the 1980s, and it continues to invade many waterways of Africa, despite regional bans on its transport, and the implementation of numerous control efforts (Navarro and Phiri 2000).

Eichhornia crassipes was thought to have been introduced into Europe in the 1930s into Portugal, where it has since spread over the central-west of the country through irrigation canals. More recent investigations into the literature, however, have revealed records of *E. crassipes* introduction into the U.K. from Trinidad between 1823 and 1825, and it has been cited as cultivated at Kew Gardens in 1851 (Hooker 1851 in Brundu et al. 2013). It also appears that the plant was cultivated at various Botanical Gardens throughout Europe in the early 1800s, such as the Paris Botanic Garden from 1829 (Desfontaines 1829 in Brundu et al. 2013), and in the Vienna and Amsterdam Botanic Gardens (Endlicher 1842; Miquel and Groenewegen 1857, in Brundu et al. 2013), while instructions on how to cultivate it were published in Spain in 1859 (Colmeiro 1859 in Brundu et al. 2013), and in Italy in 1924 (Vagliasindi and Masera 1924 in Brundu et al. 2013). Brundu et al. (2013) have subsequently deduced that *E. crassipes* was in fact quite a common garden plant in Europe in the early 1800s, calling into question Penfound and Earle's (1948) claim that the first authentic record in its adventive range was in 1884 in the U.S.A. However, establishment of permanent populations of the plant in Europe is more recent and has been limited to the warmer Mediterranean regions of the Iberian Peninsula, Italy and Corsica.

3. Ecology

3.1. Response to abiotic factors

3.1.1. Climate

The distribution of *E. crassipes* is largely pantropical, with optimal growth occurring between 28°C and 30°C, while cold winter temperatures and frost events limit its spread (Owens and Madsen 1995). *Eichhornia crassipes* ceases to grow when water temperatures drop below 10°C (Gopal 1987), and during these times of stress, stored carbohydrates from the stem base are used as energy reserves (Owens and Madsen 1995). *Eichhornia crassipes* can withstand near-freezing temperatures for a limited period of time but exhibits a steady decline in regrowth potential under these conditions (Owens and Madsen 1995). However, during spring, regrowth of *E. crassipes* can occur from the crown of the plant, quickly resulting in new infestations under warmer

climate conditions. Although prolonged cold weather may kill plants, the seeds remain viable (Ueki and Oki 1979) and allow regeneration when favourable conditions return. For these reasons, *E. crassipes* invasive range is restricted to the warmer Mediterranean regions in Europe, in Portugal, Spain, Italy and Corsica (France). However, according to future climate change projections (Figure 5), the greatest potential for future range expansion lies in Europe. Countries at the greatest risk include Albania, Algeria, Bosnia and Herzegovina, Croatia, France (including Corsica), Greece, Israel, Italy (including Sardinia, Sicilia), Jordan, Montenegro, Portugal (including Azores and Madeira), Slovenia, Spain (including Baleares and Canary Islands), Turkey and Tunisia (Kriticos and Brunel 2016) (Figure 5).

3.1.2. Waterbody types in native/invaded areas

Eichhornia crassipes invades still and slow-moving water bodies, resulting in thick extensive mats. It can tolerate pH levels between 4 and 10, but its proliferation prefers neutral pHs. These ranges do not limit its proliferation in most natural waters (Haller and Sutton 1973). It also thrives in fresh to brackish waters (up to 4 ppt) but is limited by very high salinity in coastal estuaries where concentrations between 6 and 8 ppt are lethal (de Casabianca and Laugier 1995; Muramoto, Aoyama, and Oki 1991), although there are reports that the plant may adapt its tolerance to higher salinities (de Casabianca and Laugier 1995).

By far the most significant factor affecting *E. crassipes* growth and proliferation is nutrient availability. *Eichhornia crassipes* growth is directly correlated with nutrient concentrations (Gopal 1987) – as nitrogen (N) and phosphorus (P) increase in concentration, so too does *E. crassipes* biomass accumulation (Gossett and Norris 1971; Reddy, Agami, and Tucker 1989, 1990). (See '4.2.1 Response to nutrient availability' for more detail.)

3.2. Response to biotic factors

Eichhornia crassipes typically invades open waters, and because it is free-floating, it is not limited by depth of the water body. For this reason, it is able to outcompete littoral vegetation, forming dense uniform mats. Succession may follow by plants that use the floating mats of water hyacinth as a substrate. For example, in Lake Victoria, the succession of macrophytes increased dramatically after invasion by water hyacinth. After
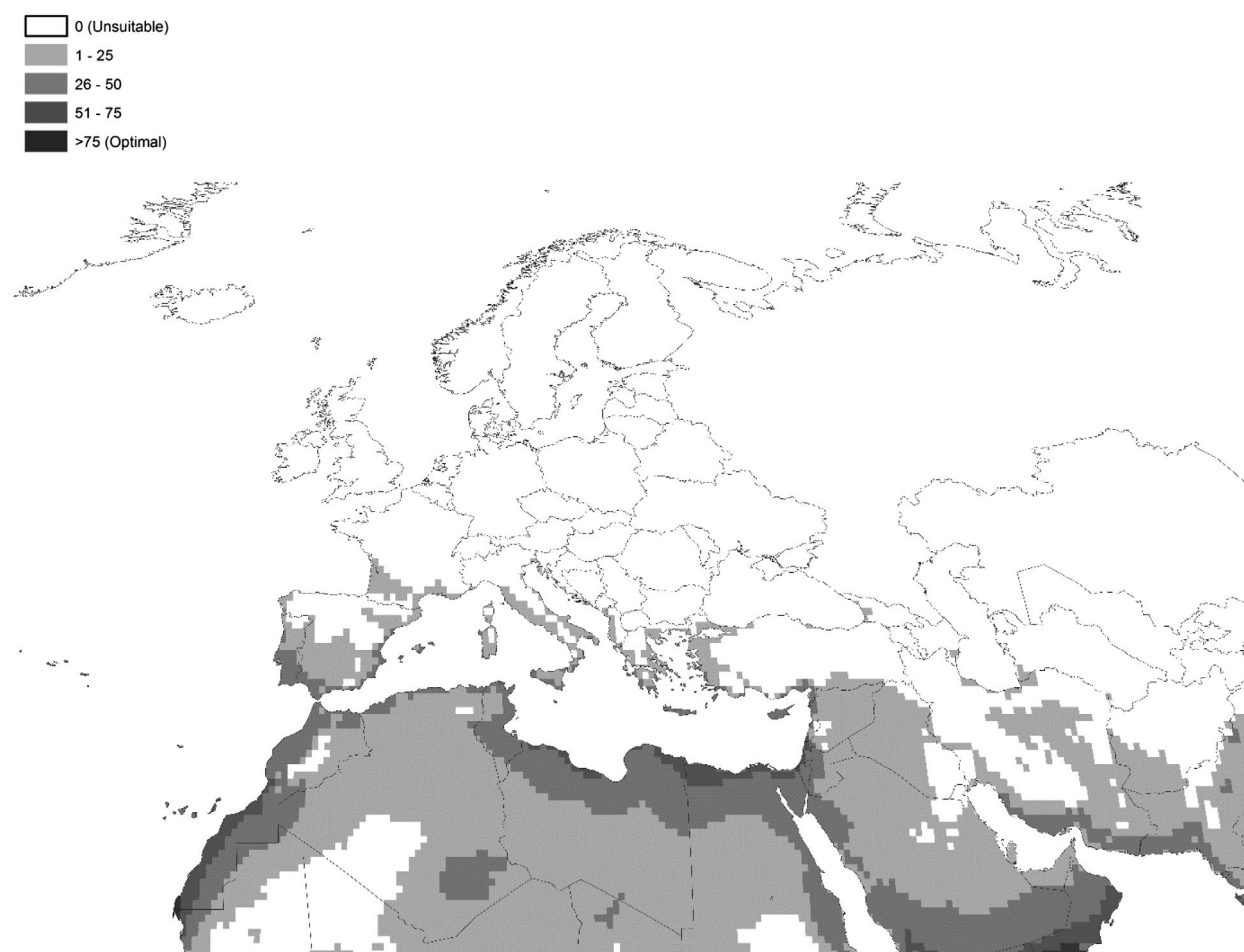

Figure 5. Modelled potential distribution of *Eichhornia crassipes* under current climate conditions in European and Mediterranean countries. It is assumed that *Eichhornia crassipes* will always be restricted to waterways within this climatically suitable envelope. Source: Kriticos and Brunel 2016 (with permission).

smothering other free-floating macrophytes like *Pistia stratiotes* L. (Araceae), native emergent macrophytes such as *Ipomoea aquatica* Forsk. and *Enydra fluctuans* Lour. invade the floating mat during early stages of succession. Thereafter, the rooted emergent hippo grass, *Vossia cuspidate* (Roxb.) Griff. (Poaceae), invades the floating mats at a later stage of succession, taking advantage of the anchorage and nutrients provided by the floating mats (Gichuki et al. 2012). This results in sediment accumulation, creating large floating sudds, at which point, *E. crassipes* biomass starts to decrease as it is shaded out. The floating islands of hippo grass subsequently decline, as the plants cannot extract nutrients from the water. Any surviving *E. crassipes* plants that survive beneath the mat may then float out into the open water, initiating new mats and starting the cycle all over again (Gichuki et al. 2012).

The ability of *E. crassipes* to multiply rapidly vegetatively confers significant competitive advantage over other aquatic macrophytes. It displays two phenologies – a short bulbous adventitious growth form that is prevalent at the leading edge of invasions, and a tall elongated growth form that dominates established mats. During invasion, as the density increases, the plants start vertical growth (elongation of petioles) together with an increase in leaf surface area (Center and Spencer 1981). The great morphological plasticity of the plant coupled with its wide ecological amplitude, which allows a high growth rate over a long period, also provide water hyacinth a competitive advantage over other free-floating macrophytes (Gopal and Goel 1993). For example, studies have demonstrated the superior competitive nature of *E. crassipes* when grown in culture with *Pistia stratiotes* L. (Agami and Reddy 1990; Center et al. 2005; Coetzee et al. 2005; Tag El Seed 1978). *Eichhornia crassipes* shades and stresses *P. stratiotes* plants through its high productivity and morphological plasticity (Agami and Reddy 1990).

3.3. Habitats and syntaxonomy

Eichhornia crassipes evolved in large, slow-flowing lowland rivers, such as the Amazon River, and the extensive marshes and lagoons of the Pantanal region in western Brazil, which were subject to regular hydrological cycles over long periods of time, where water levels fluctuate dramatically because of seasonal changes in rainfall. It has thus evolved to exploit such permanent and predictable water bodies. The Amazon River rises and falls about 10 m annually, as far as 2000 km upstream from its mouth. Under these conditions, rooted plants perish under submerged conditions, while free-floating species such as *E. crassipes* flourish.

In its native range, it usually occurs at relatively low densities, but becomes a problem where the hydrological regime of a water body has been altered by human activities, where the level of nutrients in the water has been increased, or where flushing of the plant and

natural enemies occurs and the plant populations recovers faster than that of the natural enemies. Eventually the balance is restored as the populations of the natural enemies increase to reduce the plant populations (Julien, Griffiths, and Wright 1999), although there are some populations that require the use of other control methods under extreme human-mediated disturbance (Thomaz and Bini 1999).

In its invaded range, it invades still and slow-moving water bodies, forming thick impenetrable mats. It occurs in a wide range of aquatic habitats including estuarine habitats such as the Sacramento-San Joaquin River (Anderson 1990) and Mississippi Deltas (Penfound and Earle 1948) in the U.S.A., and the Nile Delta in Egypt (Navarro and Phiri 2000); lakes such as lakes Naivasha, Tanganyika, and Victoria in East Africa (Navarro and Phiri 2000); urban areas such as canals throughout Florida (Schmitz et al. 1991), water courses throughout the world, such as the Yangtze River in China (Gu 1991), the Hawkesbury River in Australia (Osmond and Petroeschevsky 2013), the Vaal River in South Africa (Cilliers 1991) and the Sepik River in Papua New Guinea (Orapa and Julien 2001); as well as numerous types of wetlands.

In Europe, water hyacinth has invaded a range of habitats, including the Pateira de Fermentelos, one of the largest natural freshwater lagoons in the Iberian Peninsula of Portugal (Laranjeira and Nadais 2008), the Guadiana and Júcar River Basins in Spain (Ruiz Téllez et al. 2008), and the river Mare'e Foghe, as well as the Pontine Marshes in Lazio, Italy (Brundu et al. 2012).

In all of these habitats, it can tolerate extremes of water-level fluctuation and seasonal variations in flow velocity, and extremes of nutrient availability, pH, temperature and heavy metals (Gopal 1987), but does not tolerate brackish and saline water (Muramoto, Aoyama, and Oki 1991) so is limited in estuarine habitats close to the ocean.

3.4. Ecological interactions

3.4.1. Herbivory

Due to the successful biological control programmes against *E. crassipes* in many parts of the world, herbivory in both the native and invaded ranges has been well researched (Cordo 1999; Perkins 1974). Initial surveys for phytophagous natural enemies were limited to the Amazon Basin, as this is considered the centre of origin of *E. crassipes*, with the highest diversity of co-evolved herbivores. Perkins (1974) identified 43 herbivorous insects associated with water hyacinth in the Amazon, of which 19 were identified as inflicting sufficient damage, and potentially host-specific to be considered biological control agents. Perkins divided the type of damage into four categories: (1) defoliators and external leaf feeders, such as grasshoppers (e.g. *Cornops* spp. (Scuder 1875), Orthoptera: Acrididae), caterpillars (Lepidoptera), and

the most well-known weevils, *Neochetina eichhorniae* and *N. bruchi* (Coleoptera: Curculionidae), which are the most widely used biological control agents throughout the tropics and subtropical areas of the world; (2) petiole borers, considered the most destructive herbivores as the result of subsequent waterlogging, such as the moth larvae (e.g. *Niphograpta albiguttalis*, and *Xubida infusellus* (both Lepidoptera: Crambidae), and *Bellura densa* (Walker 1865) (Lepidoptera: Noctuidae), as well as boring by the *Neochetina* spp. (Hustache 1926) larvae; (3) leaf tunnellers, with a single representative, the mite, *Orthogalumna terebrantis* (Sarcoptiformes: Galumnidae), specific to the Pontederiaceae; and (4) scavenger species, which enhance the attack by other species, but are not specific to water hyacinth. The most well-represented members are scarab beetles in the genera *Dyscinetus* (Harold 1869), *Chalepides* (Casey 1915) and *Cyclocephala* (Dejean 1821) (Coleoptera: Scarabaeidae), which feed inside the petioles or the crown, or at the base of the petioles, resulting in rotting of the plant material.

Because of the long history of exploration for natural enemies in South America, the discovery of additional species was thought unlikely; however, 30 years later, surveys conducted in 1999 and 2000 by the USDA (U.S.A. and Argentina), CABI (U.K.) and ARC-PPRI (South Africa) near Iquitos, Peru, at the confluence of the Marañon and Ucayali rivers (04°19′29″S 73°18′11″W), found a greater abundance and diversity of natural enemies on water hyacinth there than anywhere else on the continent, including most of the arthropods previously known to be associated with water hyacinth, and a range of new fungal isolates (Cordo 1999; Evans and Reeder 2001). These herbivores inflict a range of additional types of damage to *E. crassipes*, including flower feeding (e.g. *Brachinus* sp. (Weber 1801) (Coleoptera: Carabidae)), oviposition damage (e.g. *Megamelus scutellaris* (Hemiptera: Delphacidae)) and sap-sucking (e.g. *Eccritotarsus catarinensis* (Hemiptera: Miridae)).

Sufficient damage from herbivores can reduce biomass and vegetative reproduction, limiting population growth, under low-nutrient conditions and tropical to subtropical climates. However, results from biological control programmes around the world have shown that eutrophication of water bodies and cold winter temperatures limit the impact caused by herbivory (Akers, Bergmann, and Pitcairn 2017; Coetzee and Hill 2012; Hill and Olckers 2001).

In addition to arthropod herbivory, water fowl and livestock inflict sporadic damage to *E. crassipes*. Hippopotamus (*Hippopotamus amphibius* (Linnaeus 1758)) are also known to graze on the plant in infestations in Africa, and in 1910, a bill was almost passed in Louisiana, U.S.A., to introduce hippopotamus from Africa to eat *E. crassipes* and, at the same time, provide meat for the growing population (Miller 2013). Manatees (*Trichechus manatus* (Linnaeus 1758)) also include

E. crassipes in their diet, where it is invasive in Florida, and *E. crassipes* has even been proposed as a diet supplement to increase this endangered species' population numbers (https://www.conservationmagazine.org/2014/03/water-hyacinth-in-kings-bay/).

3.4.2. Plant pathogens

Various studies have been carried out around the world to isolate, identify and measure the pathogenicity of the fungi associated with *E. crassipes* in its native range, as well as in several infested areas of the world (Aneja, Srinvas, and Manpreet 1993; Bateman 2001; Charudattan 1996, 2001; Dagno 2006, 2011; El-Morsy 2004; Evans and Reeder 2001; Freeman, Charudattan, and Conway 1981; Kusewa 2002; Ray and Hill 2012; Ray, Sushilkumar, and Pandey 2008; Shabana, Charudattan, and Elwakil 1995a, 1995b; Tegene et al. 2012). Of the 60 fungi reported around the world, ten have been found to be highly virulent and known to generate diseases on *E. crassipes*. These fungi are: *Acremonium zonatum* (Sawada) W.Gams, *Alternaria alternata* (Fr.) Keissler, *Alternaria eichhorniae* Nag Raj & Ponnappa, *Bipolaris* spp., *Cercospora piaropi* Tharp. (=*Cercospora rodmanii* Conway), *Fusarium chlamydosporum* Wollenw & Reinking, *Helminthosporium* spp., *Myrothecium roridum* Tode ex Fr., *Rhizoctonia solani* Kühn and *Uredo eichhorniae* Gonz.-Frag. & Cif. (Charudattan 1996; Shabanna 2005). In Africa, priority was given to developing *A. eichhorniae*, *A. zonatum*, *C. piaropi*, *R. solani*, *A. alternata* and *M. roridum* as mycoherbicides for the control of water hyacinth (Bateman 2001).

3.4.3. Pollination

Although the major form of reproduction in *E. crassipes* is vegetative propagation, it still retains the potential for sexual reproduction in many regions of the world (Barrett 1980). The flowers of *E. crassipes* are tristylous, but unlike some other tristylous species, there is no incompatibility between the different forms (Barrett 1977). Flowers in both the native and introduced ranges are characterised by the predominance of a single style form, a condition atypical for heterostylous species. In most of the introduced range of *E. crassipes*, the midstyled form predominates, with long-styled forms occurring less frequently, while the short-styled form is restricted to the native range. The three floral forms of *E. crassipes* are highly self-compatible, and within style forms there is little difference in seed production between self and arthropod pollinations. In a study in the native range, the major insect visitor to flowers of *E. crassipes* was the bee, *Ancyloscelis gigas* (Friese 1904), while in the introduced range, the honeybee, *Apis melifera* (Linnaeus 1758), is the dominant pollinator (Barrett 1980). An inflorescence with 20 flowers can produce over 3000 seeds, and up to four inflorescences can be produced by a single rosette during a 21-day period (Barrett 1980).

3.4.4. Dispersal

Water flow is the main mode of natural dispersal of *E. crassipes* within a waterbody. Daughter plants break off from the parent plant and are moved downstream, while seeds are considered hydrochorous, dispersed by rain wash, downstream flow and floods (Albano Pérez, Ruiz Téllez, and Sánchez Guzmán 2011). In addition, wind moves the plants around systems, too, creating large mats in the direction of the prevailing winds. Birds and mammals may disperse plants within and between water bodies; for example, hippopotamus are known to move plants large distances over land (Figure 6). In addition, seeds may be transported over longer distances by birds and mammals when caught up in mud.

However, the main vector of dispersal is humans, through accidental or intentional spread. Recreational boaters and fishermen may inadvertently transport the plant in trailers or boat hulls between water bodies, while subsistence fishermen and recreational anglers are known to move plants around to increase habitat for fish fry (Hill 2003). However, it is the high ornamental value of the plant that has led, and still does lead, to its intentional introduction to water features around the world. Despite bans on its sale, it is still available directly from outlet stores or internet suppliers (Figure 7) (Martin and Coetzee 2011; Padilla and Williams 2004).

4. Biology

4.1. Phenology

The growth form of *E. crassipes* plants is sympodial, and individual rosettes produce clones/ramets whose stolons decay or break once they have developed roots,

separating them from the mother plant. These daughter plants form extensive floating mats supporting canopies that, in mature stands, extend a metre or more above the water surface (Center and Spencer 1981). These populations increase rapidly through the spread of these plants, being able to double their numbers under suitable conditions in one to two weeks (Edwards and Musil 1975), dependent on water nutrient content and temperature. In the Guadiana River in Spain, the doubling time varied between 10 and 60 days (Ruiz Téllez et al. 2008). Gopal (1987) reviewed doubling times and showed them to vary from 5.9 to 28.1 days for weight, and from 3.7 to 57.8 days for numbers of plants as measured in the open (outside ponds) or in the field. At very high densities, self-thinning (density declines and biomass increases) regulates density (Center and Spencer 1981; Madsen 1993). Knowing the growth rate of plants in an area to be controlled and the condition that encourage growth is important for some control techniques (Julien 2008).

Eichhornia crassipes is also capable of sexual reproduction through the production of flowers and seeds. When flowering on a spike is complete, the flower stalk bends so that the inflorescence drops into the water, where the fruits split and seeds are carried away by flow, and eventually settle in the substrate. The seeds are capable of germinating immediately but may remain dormant for many years (Gopal 1987). Germination is encouraged by aerobic conditions and alternating temperatures; large populations of seedlings may become established on exposed mud at the edges of water bodies when water levels fall. Seedlings are rooted in mud initially, and after a short period of growth under water, they pop to the surface and float (Wright and Purcell

Figure 6. Hippopotamus appear out above an infestation of *Eichhornia crassipes* on the Mkhadzi River, in the Kruger National Park, South Africa. Hippopotamus are known to disperse plants within and between waterbodies. Photograph: J. Coetzee.

Figure 7. *Eichhornia crassipes* plants for sale at a garden centre south of London, U.K., in May 2017. Photograph: Benjamin Price.

1995), becoming free-floating as a result of wave action or rising water levels. Seeds are the source of new infestations or re-invasions (Pieterse 1978), as are vegetative propagules. In the Iberian Peninsula, flowering occurs from June to October, and fruiting lasts until November (GIC 2006).

4.2. Physiology

4.2.1. Response to nutrient availability

Studies have shown that in nutrient-rich sites, water hyacinth biomass can increase eightfold compared with sites that are nutrient-poor (Reddy, Agami, and Tucker 1990), while increasing concentrations of nitrogen and phosphorus result in increases in ramet production, shoot/root ratio and plant height (Reddy, Agami, and Tucker 1989, 1990). Importantly, water phosphorus content significantly affects growth and nutrient storage by water hyacinth. All measures of water hyacinth growth increase with increasing phosphorus, but the rate of increase is not proportional (Reddy, Agami, and Tucker 1990). Although *E. crassipes* can grow in nutrient-poor (oligotrophic) waters, such as the Upper Shire

River in Malawi, the plants do not grow well and are seldom problematic (Hill et al. 1999). On the other hand, eutrophication of Hartebeespoort Dam in South Africa resulted in a massive *E. crassipes* infestation during the 1970s and 1980s, which was subsequently reduced through chemical control alone (Ashton et al. 1979).

Eichhornia crassipes growth responds positively up to an N concentration of 5.5 mg/l and P concentration of 1.06 mg/l, but biomass accumulation does not significantly increase above these levels (Reddy, Agami, and Tucker 1989, 1990). However, N storage in the plant increases up to a maximum at 50.5 mg/l (Reddy, Agami, and Tucker 1989), while P storage in the plant increases indefinitely as the concentration of P in the water increases (Reddy, Agami, and Tucker 1990). Yet, net N storage within the plant is at a maximum when water P concentration reaches 2.56 mg/l (Reddy, Agami, and Tucker 1990), and net P storage is at a maximum when water N concentration is 5.5 mg/l (Reddy, Agami, and Tucker 1989). These N and P concentrations fit into the hypertrophic category of trophic terminology according to the Organization for Economic Co-operation and Development (Vollenweider and Kerekes 1982), reinforcing the fear that water bodies with excessive nutrient loading are at risk to *E. crassipes* invasion. In short, the availability of N in the culture medium affects the uptake of both N and P in the plant, as does the availability of P, suggesting that the N: P ratio in the water affects the N and P use efficiency by the plants. Haller and Sutton (1973) found that if the phosphorus concentration falls below 0.1 mg/l, active growth of water hyacinth is halted, but concentrations above this allow for growth as well as the uptake of nutrients in excess of the plant's requirements.

4.2.2. Response to flooding and drought

Eichhornia crassipes evolved traits to survive in its native habitat where desiccation and flooding are regular occurrences. It has tolerance to desiccation once water has receded, leaving the plants exposed on mud, and because it is free-floating and mobile, it is capable of surviving and flourishing on variable water levels. Germination occurs when substrates are exposed as water recedes and also as dry substrates are moistened when water levels rise. Seeds also survive in wet mud and are long-lived (Center and Spencer 1981), and flowers can be produced within 10–15 weeks after germination (Barrett 1980).

Therefore, in systems prone to flooding and drought, unscheduled, sporadic removals of *E. crassipes* result in resurgence from dormant seed banks and subsequent proliferation (Hill and Olckers 2001). The inflow of nutrient-rich water following flooding events is also key in stimulating *E. crassipes* production, as evidenced on the Paraná River floodplain in its native range (Neiff, Neiff, and Casco 2001). Recently, during times of drought in the Sacramento Delta, U.S.A., lower water flows and an influx of nutrients from agriculture and

treated municipal sewage that was not flushed out of the system have resulted in the proliferation of *E. crassipes* (Anderson 2014; Khanna et al. 2012).

4.3. Reproductive biology

Eichhornia crassipes' showy flowers are pale blue or violet, with a central yellow patch, and are borne on spikes. Flowers display the genetic polymorphism of tristyly in which all flowers of an individual plant possess one of three distinct corresponding style and stamen length phenotypes (Eckenwalder and Barrett 1986). Tristylous plants are usually self-incompatible, where very few seeds are produced as a result of self-pollination and pollination by plants of the same morph. However, *E. crassipes* defies this trend, because high levels of seed fertility are achieved in single morph colonies. The intermediate-style form of *E. crassipes* is prevalent in its introduced range, whereas the long-styled form occurs less frequently. The short-style forms predominate in restricted areas of its native range in South America but have not been recorded in its introduced range probably because of its relationship with a local pollinator, the long-tongued bee, *Ancyloscelis gigas* (Apidae) (Barrett 1977; Barrett and Forno 1982). *Apis mellifera* is documented as a pollinator in Argentina with potential economic importance to beekeepers, especially in coastal regions in the late summer and autumn when flowering terrestrial plants may be low in abundance (Fagúndez, Reinoso, and Aceñolaza 2016). In Europe, it is also pollinated by *Apis mellifera* (Ruiz Téllez et al. 2008).

When flowering on a spike is complete, the flower stalk produces narrow fruits, made up of three-celled capsules, 1–1.5 cm long. The number of mature fruits per flower spike is variable, and the number of seeds per capsule is also variable, 3–452. Seeds are oval and 1–1.5 mm long with longitudinal striations (Gopal 1987). A single *E. crassipes* inflorescence with 20 flowers can produce up to 3000 seeds, which are released in capsules that can accumulate in the floating mat or sink into the sediment below (Cronk and Fennessy 2001). Estimates of the number of seeds per square metre of vegetation range from 400 to 3400, depending on the sampling site and time of year (Cronk and Fennessy 2001; Pieterse and Murphy 1993). Seed banks are reportedly long-lived, remaining viable up to 20 years in sediments (Gopal 1987; Matthews 1967), and dormancy can be broken by wetting, drying and re-wetting (Baskin, Baskin, and Chester 2003). Seed bank persistence is therefore a significant factor influencing its eradication (Cacho et al. 2006) and long-term control. Despite these reproductive traits, which give *E. crassipes* an enormous potential for seed production, the majority of individuals in natural populations are probably produced by clonal growth (Barrett 1980). Sexual reproduction is most likely restricted in its introduced range by a scarcity of suitable pollinators, which limits fecundity, and unsuitable ecological conditions for seed germination and establishment (Barrett 1980).

Seed biology and germination conditions have been studied by Albano Pérez, Ruiz Téllez et al. (2011) and it is influenced by the physicochemical composition of the water. This study investigated seed bank dynamics in South Africa, which has had a long history of invasion with those in Spain where the weed has been present for a far shorted period of time. Soil seed density varied between 0 and 2534 seeds/m² but did not differ significantly between the type of waterbody (impoundment vs. river) or the history of control carried out at a site. Average germination was 54.17% and maximum germination around 3 days. The results from this study indicated that a combination of factors such as water fluctuation, eutrophication and seed decomposition might have had a great influence on dispersal and persistence of seeds.

5. Impacts

5.1. Uses and positive impacts

One hectare of *E. crassipes* may contain more than two million individual plants with a total wet weight of over 300 tonnes (Center and Spencer 1981), and it is this sheer biomass of plant material that has provoked research into its utilisation (Julien, Griffiths, and Wright 1999). Proposed uses for the weed include biogas production (Harley 1990), waste-water treatment, water-quality management, animal fodder, fertiliser, and the manufacture of paper and furniture (Julien, Griffiths, and Wright 1999). However, these industries all require investments and technological skills that would impose problems in developing countries where *E. crassipes* is often found, and there are risks of re-infestations from many of these uses (Albano Pérez et al. 2015). Nonetheless, there are numerous examples of utilisation in the developing countries of Africa and south east Asia, from cottage industries to internationally funded programmes aimed at minimising its impact on local communities. As an example, a German organisation promotes manufacturing furniture from *E. crassipes* in Thailand for sale in Germany (https://www.waterhyacinth.de/). *Eichhornia crassipes* is also widely available as an ornamental plant for garden ponds in Europe (PPP-Index 2017), for example, Germany (Hussner, Nehring, and Hilt 2014) and the U.K. (Figure 7).

Eichhornia crassipes has been promoted as a relatively cheap and environmentally friendly tool for the decontamination of wastewater because of its rapid growth rate and high rate of heavy metal and nutrient absorption since the 1940s (Penfound and Earle 1948), and even today is used to treat contaminated water, particularly in Asian countries (Yan, Song, and Guo 2017). More recently, it has been used to prepare elastic

cellulose-based aerogels with excellent oil sorption capacities, and reusability, which is very promising for cleaning oil spills (Yin et al. 2017). Sindhu et al. (2017) discuss new value added products and fuels which can be produced from water hyacinth, while its use in the production of supercapacitors, and to improve the immune resistance of plants and animals is promising (Guna et al. 2017; Wu et al. 2016).

However, the biggest factor mitigating against its utilisation is its very high water content (on average 95%) (Harley 1990). To gain 1 tonne of dry material, 9 tonnes of fresh material has to be collected (Julien et al. 1996), making the cost of drying for the paper and furniture industries not commercially viable (Julien, Griffiths, and Wright 1999). In addition, *E. crassipes* as fodder for horses and cattle is inferior, again due to its high water content, and it is also unpalatable due to the high potash and chlorine content (Edwards and Musil 1975). Therefore, utilisation of *E. crassipes* is not feasible as a control method due to the low demand for *E. crassipes* products, the inaccessibility of most *E. crassipes* infestations and the high cost of processing the raw material (Julien et al. 1996) (see 6.2. below). For these reasons, *E. crassipes* utilisation will remain restricted to small-scale cottage industries, which are highly unlikely to provide a viable method for controlling or managing the weed. Consideration of possible utilisation of *E. crassipes* should therefore not prevent the execution of control programmes against it. In addition, a reliance on *E. crassipes* should not be created, because this would in turn create a conflict of interest and lead to an increase in the spread of the weed.

5.2. Negative impacts

5.2.1. On biodiversity and ecosystem functioning
Eichhornia crassipes is regarded as the world's worst aquatic weed due to its documented socio-economic impacts, and its significant ecological impacts on aquatic ecosystem functioning. From an ecological perspective, drifting mats scour vegetation, destroying native plants and wildlife habitat. *Eichhornia crassipes* also competes with other plants, often displacing wildlife forage and habitat (Center et al. 2002). Increased detrital production and siltation occur under *E. crassipes* mats due to high sediment loading. Dense mats reduce light to submerged plants, thus depleting oxygen in aquatic communities (Mitchell 1985; Rommens et al. 2003; Ultsch and Anthony 1973). The resultant lack of phytoplankton (McVea and Boyd 1975) alters the composition of invertebrate communities (Brendonck et al. 2003; Hansen, Ruby, and Thompson 1971; O'Hara 1967). For example, Masifwa, Twongo, and Denny (2001) showed an increase in macroinvertebrate abundance at the edges of *E. crassipes* mats on Lake Victoria, Uganda, while Midgley, Hill, and Villet (2006) and Coetzee, Jones, and Hill (2014) showed that *E. crassipes* mats significantly

reduced the diversity and abundance of benthic invertebrates in impoundments in South Africa. In Spain, GIC (2006) reported significant reductions in the total density of phytoplankton, and zooplankton after invasion by *E. crassipes*. Changes in zooplankton communities were evidenced by the substitution of crustacean species for others (e.g. *Tropodiaptomus processifer* (Kiefer 1926), *T. kaepelini* (Poppe and Mrázek 1895) and *T. orientalis* (Brady 1886) by *Ceriodaphnia dubia* (Richard 1894), and *Daphnia dubia* (Herrick 1883)). In southern Europe, *E. crassipes* outcompetes a number of aquatic plant species, including species in the *Potamogeton* L., *Ranunculus* L., *Myriophyllum* L., *Nuphar* Sm., *Nymphea* L. and *Zanichellia* L. genera (GIC 2006). Elimination of these species alters the habitat of aquatic communities, effecting changes in aquatic biodiversity.

Effects of *E. crassipes* infestations on fish abundance and diversity depend on its impacts on invertebrate and plankton abundance and diversity as these are crucial links in the trophic ecology of aquatic ecosystems. Fish abundance and diversity will respond positively to an increase in epiphytic invertebrate community increases, for example, in Lake Chivero in Zimbabwe, *E. crassipes* mats generally have a positive effect on taxon diversity of fishes by providing shelter and feeding grounds for small fishes (Brendonck et al. 2003). Similarly, the increase in macroinvertebrate abundance at the edges of mats in Lake Victoria resulted in Nile tilapia shifting their diets to include a larger component of these species (Njiru et al. 2004). Conversely, a decrease in phytoplankton as a result of shading and increased turbidity may decrease dissolved oxygen concentrations and planktivorous fish abundance, subsequently affecting higher trophic levels.

Water bird communities also change in the presence of *E. crassipes* infestations. At moderate densities, bird communities may benefit if macroinvertebrate and fish abundances increase. In Florida, birds stalking in *E. crassipes* mats most often obtained prey located near the perimeter of mats, and rarely hunted for food in the interior of mats (Bartodziej and Weymouth 1995). However, when water hyacinth becomes dominant, outcompeting other vegetation types and preventing access to water, water bird diversity may be negatively affected when dense mats physically prevent water bird access to prey, or if dissolved oxygen reductions cause negative effects on prey populations (Villamagna and Murphy 2010).

5.2.2. Other impacts
In addition to the biodiversity impacts, the socio-economic impacts of *E. crassipes* have also been well documented. Dense impenetrable mats restrict access to water, negatively impacting fisheries and related commercial activities, the effectiveness of irrigation canals, navigation and transport, hydroelectric programmes, and tourism (Navarro and Phiri 2000). For example, the hydropower station at the Kafue Gorge Dam in Zambia is responsible for supplying 900 MW of power to the

country. At the height of the *E. crassipes* problem on the dam, at least one of the five turbines was forced to be shut down for a day per week. This was due to the increased concentration of nitrous oxides in the water that caused a certain amount of corrosion on the turbines. The hydropower dams on the Shire River in Malawi and the Owen Falls Dam at Jinja in Uganda on the Nile River are also frequently forced to stop production due to *E. crassipes* clogging the intakes for the water cooling system. No estimates of costs of this are available, but it must amount to several million USD per year (Wise et al. 2007). The impact of the plant in 2007/2008 on the Victoria Falls Power Station production of electricity amounted to US$946,822 (Nang'alelwa pers. comm. 2008). Other problems include property damage during floods as a result of *E. crassipes* building up against bridges, fences, walls, obstructing water flow and increasing flood levels. Arguably, the most affected are poverty-stricken communities in rural Africa, where the extent of these effects are yet to be fully measured. *Eichhornia crassipes* alters the livelihoods of any community with high dependence on freshwater waterways for food (subsistence or commercial), transport and clean water.

In many rice growing areas of the world, *E. crassipes* has hindered production through competition for nutrients, allelopathy and restricting accessibility, particularly in deepwater rice culture (Smith 1983). These problems have been reported from Bangladesh (Whitton et al. 1988), Sri Lanka (Room and Fernando 1992), and West Bengal in India (Datta and Banerjee 1978), as well as anecdotal evidence from Africa and South East Asian countries. In Europe, *E. crassipes* has invaded rice fields in Portugal (Figueiredo et al. 1984; Guerreiro 1976).

Eichhornia crassipes infestations intensify mosquito problems by hindering insecticide application, interfering with predators such as fish, increasing habitat for species that attach to plants, and impeding runoff and water circulation (Seabrook 1962). Despite there being numerous references attributing an increase in malaria to *E. crassipes* infestations, in one of the quantified surveys, Mailu (2001) was unable to show a correlation between the explosion of *E. crassipes* on Lake Victoria and an increase in the disease. *Eichhornia crassipes* provides the ideal habitat for the snail vectors (*Biomphalaria* spp. (Preston 1910) and *Bulinus* spp. (O. F. Müller 1801)) of the bilharzia schistosome, and there is some evidence from Ghana that increased infestations of *E. crassipes* are linked to an increase in the prevalence of this disease (Navarro and Phiri 2000). It also blocks access to water points and, as such, has been linked to an increase in cholera and typhoid (Navarro and Phiri 2000). Furthermore, *E. crassipes* harbours venomous snakes, crocodiles and hippos, making the collection of water dangerous, sometimes fatal (Gopal 1987; Navarro and Phiri 2000).

In Europe, *E. crassipes* has invaded irrigation canals fed by the Guadiana River reducing water supply to important fruit growing areas. Further, the weed in this river system has had an impact on cross-border tourism from Portugal as the river and the Spanish–Portuguese Alqueva Reservoir attracts many tourists annually, who do not wish to see the waterbodies covered by the weed (Ruiz Téllez et al. 2016).

6. Legislation and management

6.1. Legislation

Eichhornia crassipes is on the 100 of the World's Worst Invasive Alien Species List. These 100 species are a selection from the Global Invasive Species Database, published by the Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission of the International Union for Conservation of Nature, as a contribution to the Global Invasive Species Programme. Many countries have legislation regulating *E. crassipes*: it is on the USDA/APHIS noxious weeds list, and it is a class 1 noxious weed in Australia, a prohibited weed in New Zealand, a declared invader in Botswana and a Category 1b weed in South Africa. All of these regulations prohibit the importation and sale of the weed and require land users and water authorities to control infestations in an appropriate manner. On the Asian continent, there are several pieces of legislation preventing the possession and trade of *E. crassipes*, but most of these date back to the early twentieth century, e.g. the Water Hyacinth Act of 1917, Burma (Gutter 2001), 1908 Act in China, Agricultural Pests and Diseases Act of 1919 in Madras, the Water Hyacinth Act of 1926 in Assam, and the Water Hyacinth Act of 1936 in Bengal (Iqbal 2010). Although no recent legislation is in place, this plant is still considered a threat, and governments consider it an unwanted non-native species.

After completion and approval of the EPPO PRA on *E. crassipes*, in 2008, the species was recommended for regulation within European and Mediterranean countries. Because of its negative impacts, the species is subject to various legal restraints. In addition to general rules concerning the use of alien plants like the prohibition to cause them to grow in the wild that is present in the nature conservation acts of several European countries, some legal texts mention the species explicitly: the recent EU Regulation No. 1143/2014 'on the prevention and management of the introduction and spread of invasive alien species' (EU 2014) contains a catalogue of restrictions for the use of alien species. According to this regulation "invasive alien species of Union concern" may not be brought into the territory of the Union, kept, bred, transported to, from or within the Union, placed on the market, etc. Invasive species are assigned to this list on the basis of detailed risk assessments. The first list of 37 animal and plant species was published by the European Commission in July, 2016. It contains *E. crassipes*, which was listed based on the EPPO PRA (EPPO 2008). Commercial owners may continue selling listed species for one year after coming into force.

In Portugal and Spain, legal restrictions to the use of *E. crassipes* were in place before the EU Regulation based on national and/or communal laws, e.g. the Portuguese Decreto – Lei no. 565/99 of December, 1999; or the Spanish Real Decreto 630/2013 of August, 2013 (Ministerio de Agricultura, Alimentación y Medio Ambiente 2013).

6.2. Management

Several control methods have been implemented against *E. crassipes*, utilisation, manual removal and mechanical control, hydrological manipulation, the application of herbicides and biological control, and more recently attempts have been made to integrate these control methods (Hill and Coetzee 2008). The EPPO standard describes the procedures for control of *E. crassipes* in the EU (EPPO 2009). Unfortunately, this plant is well adapted to surviving the many procedures that have been used for aquatic weed management such as the removal or killing of plants, draw down or flushing downstream.

6.2.1. Utilisation

Eichhornia crassipes utilisation is not commercially viable (see above), and its utilisation should not be considered as a control option, nor should it prevent the implementation of other control programmes. In addition, a reliance on *E. crassipes* utilisation would create a conflict of interest and lead to further spread of the weed, as has already been observed in some areas in Africa (see Section 5.1 above for details).

6.2.2. Manual removal

Manual removal through hand pulling or using pitch forks is used in a number of regions of the world, most notably, southern Africa, Europe and China. This method is very labour intensive, only effective for small infestations and essentially used as an employment creation exercise where labour is relatively inexpensive (Fig. 9). Zimbabwe initiated a manual removal programme on Lake Chivero, in the early 1980s (Chikwenhere and Phiri 1999). The manual removal team consisted of 500 workers, working an 8-hour day. Although almost 500 tonnes of water hyacinth was removed, the rapid regeneration of the weed made the effort slow and expensive, with no obvious impact 6 months later. It was then decided to implement mechanical control using a bulldozer, a boat, a conveyor and dump trucks. Even though almost 2 ha of plants was cleared daily, neither manual removal nor mechanical harvesting effectively reduced the amount of water hyacinth on the lake (Chikwenhere and Phiri 1999).

6.2.3. Mechanical control

Mechanical control, through the use of harvesters, has been used in many parts of the world to control *E. crassipes*. Again, the amount of biomass that needs to be removed, coupled with the growth rate of the plant, and the remoteness of some of the infested areas means that this option has limited applicability. For example, harvesters have been used at Port Bell and Owen Falls Dam on Lake Victoria, Uganda with limited success (Mailu 2001) and on the Liwonde Barrage in Malawi. Despite these problems, reasonably successful results were obtained in Mexico, where a combined chemical-mechanical programme, using the herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) and a mechanical harvester, was implemented to control water hyacinth on the Trigomil Dam (Gutiérrez et al. 1996). Furthermore, mechanical harvesting was successful on a series of small lakes in the Gauteng Province of South Africa, mainly because it was implemented in winter when the plant was not actively growing.

Despite the expense and limited applicability of mechanical harvesting, it is often the only solution available for the control of *E. crassipes* in rivers, impoundments and lakes in Europe. For example, some 8 km (560,000 m^2) of the River Mare 'e Foghe (central-eastern Sardinia) was covered by a dense mat of *E. crassipes* (mixed with *Hydrocotyle ranunculoides* L.f. (pennywort)) in 2010 (Brundu et al. 2012). Mechanical control was implemented using crane trucks with grapples and pushing boats. Sites that were difficult to access were cleaned using motor boats and manual extraction means, or boats equipped with cutting devices. By December 2010, some 6700 tonnes of plant biomass had been removed at a cost of €175,000. A 400–500 m (25,000 m^2) stretch of river invaded by the mat of *E. crassipes* remained, and an additional €400,000–500,000 was set aside to continue operations up to 2013.

E. crassipes was first recorded in the Lazio region, in the Pontine plains, in 1983 (Anzalone 1983). In the early colonisation phases, the species did not outcompete other species (Scoppola, Iberite, and Palazzi 1986); and until 1995, its populations were still small, limited to a few sites on the shores of the Rio Martino river near the Fogliano lake, sometimes even in brackish waters. In the following years, the populations of *E. crassipes* spread to other sites within the Pontine plains, covering a total surface of 5,000 m^2 in 2004 and 2005 (Iberite and Pelliccioni 2009). Every autumn, the weed is mechanically removed by the local authority responsible for water management (i.e. the Consorzio di Bonifica di Latina).

In 2006, mechanical harvesters were used to control *E. crassipes* in the lagoon system of Ria de Aveiro, Portugal that was approximately 50% covered by the weed. Since the operation began, the aquatic-harvester has removed more than 15,500 m^3 of mats from the lagoon, which, in accordance with the current legislation, has been transported to an old inactive quarry site. At present the lagoon remains free of *E. crassipes*, allowing navigation and the maintenance of traditional activities such as fishing and boating (Laranjeira and Nadais 2008).

One of the most prominent cases of *E. crassipes* invasion and control in Europe comes from the Guadiana River in Spain (Figure 8). The weed was first recorded on the river in 2004 (Ruiz Téllez et al. 2008). Measures carried out by Spain's Ministry of the Environment managed to retain the infestation to a 75 km section of the river. Control of the weed relied on physical methods with manual and mechanised extraction and the installation of floating booms to prevent the spread of the infestation downstream. By 2008, €8 million had been spent and 2,000 tonnes of biomass had been extracted. However, an EPPO International Workshop on the topic highlighted the river as a high re-infestation risk area (Martín de Rodrigo et al. 2008). *Eichhornia crassipes* did reinfest the river, most likely from seed, or scattered plants that the mechanical harvesting had missed, and in 2010, an additional 5 tonnes of the weed was removed, more than 51,000 tonnes was removed in 2012, and 170,000 tonnes was removed in 2016. Thus, in ten years of control (2005–2015), up to €26,000,000 had been spent (Duarte 2017). Despite this effort, scattered populations of *E. crassipes* had spread along 150 km of the river, just about reaching Portugal and Alqueva, the largest Reservoir in Europe. Management had thus failed, so a group from diverse social sectors travelled to the European Parliament in 2015 to raise the alarm about the situation. Community Union later included *E. crassipes* in the list of Invasive Alien Species of Union concern that required the relevant authorities to reinforce control strategies.

The above examples show that while mechanical control can be a useful tool in the control of *E. crassipes*, it is expensive and will not lead to the eradication of the weed, as it will recruit from a long-lived seed bank and thus requires a long-term commitment to this method (Ruiz Téllez et al. 2016). Furthermore, the remoteness of many infestations, and the shallowness of many of the invaded systems makes mechanical control unfeasible.

6.2.4. Hydrological manipulation

Water-level manipulation has been suggested for the control of *E. crassipes*. This method is appropriate for infestations on man-made impoundments where a drawdown of water is possible, stranding plans on the banks and allowing them to desiccate. Exposure of the sediments to sun, also allows for the top layer of soil containing seeds to be removed. Floods are very effective at controlling water hyacinth, especially in systems close to the ocean where salt water will kill the plants. Floods can be manipulated in river systems and canals downstream of impoundments, but only in areas where water scarcity is not an issue.

6.2.5. Herbicide application

The application of herbicides has been widely used in the control of water hyacinth throughout the world since the 1960s. Although herbicide application has the advantage of being fast acting, effective control depends on a long-term commitment to follow-up applications for possibly 20 years or more. Water hyacinth is very susceptible to herbicides such as 2,4-D, diquat, paraquat and glyphosate (Gopal 1987), which have resulted in successful control in small, single-purpose water systems such as irrigation canals and dams of around 1 hectare in size (Wright and Purcell 1995). In developing countries, many water hyacinth-infested sites are used for drinking water, for washing and for fishing, and so the use of chemical sprays contaminates these sites, and can threaten human health (Julien, Griffiths, and Wright 1999). The herbicide control of water hyacinth is often not appropriate in developing countries, as it is expensive and requires highly skilled personnel, and often herbicides are perceived as poisons. Furthermore, herbicides are not permitted for application onto waterways in Europe, so this control method is not an option against *E. crassipes* in the EU.

Figure 8. *Eichhornia crassipes* and *Nymphaea mexicana* Zucc. Guadiana River near the border of Portugal, in Badajoz, Spain. Photograph: Asociación Ciudadana Salvemos el Guadiana.

Figure 9. Manual removal teams attempting to remove *Eichhornia crassipes* on the Vaal River, South Africa.

6.2.6. Biological control

It has often been suggested that biological control, or the release of host-specific natural enemies, is the only option that offers economical and sustainable control of the weed (Harley 1990). Research into the biological control of water hyacinth was initiated by the United States Department of Agriculture in 1961, and to date eight arthropod species including two weevils (*Neochetina eichhorniae* and *Neochetina bruchi*), two moths (*Niphographta albiguttalis* and *Xubida infusellus*), three sap-sucking bugs (*Eccritotarsus catarinensis*, *Eccritotarsus eichhorniae* and *Megamelus scutellaris*), one grasshopper (*Cornops aquaticum*) and one mite species (*Orthogalumna terebrantis*) have been released to control water hyacinth in its adventive range (Coetzee et al. 2011; Paterson et al. 2016; Winston et al. 2014) (Table 1). In addition, the fungal pathogen *Cercospora piaropi* (Tharp 1917) (Capnodiales) (Mycosphaerellales: Mycosphaerellaceae) has been released as a classical biological control agent for the weed in South Africa (Morris, Wood, and Den Breeÿen 1999). A programme (the International Mycoherbicide Programme for water hyacinth control in Africa (IMPECCA)), which was established to provide support for the discovery of a promising, acceptable and relevant fungi as mycoherbicides, ceased before any useful findings could be obtained (Ray and Hill 2012).

The arthropod agents have all been extensively studied and have been shown to be host-specific to the weed (Center et al. 2002). This control method has been widely accepted, and the two weevil species are the most commonly used with *N. eichhorniae* released in 39 countries, and *N. bruchi* in 36 counties around the world (Winston et al. 2014). The biological control of water hyacinth has been highly successful in a number of large tropical water bodies, mainly in Africa (Coetzee et al. 2011; Hill and Julien 2004), but also in Australia (Julien 2001) and Papua New Guinea (Orapa and Julien 2001).

Defining "control" and the length of time taken to achieve it is a fundamental issue in quantifying the benefits of control. Complete control of *E. crassipes* is considered to be reached when *E. crassipes* populations are reduced below an ecologically or economically viable threshold and are maintained at that threshold with no requirement of an additional intervention. Biological control is considered the most cost-effective method, but it takes a long time (3–5 years under ideal conditions), compared with manual control, which achieves instant success in a short period of time, but requires considerable human input to do so, and the results are not sustainable. Herbicidal control also achieves success in a short time period but is expensive, has negative environmental side effects and requires considerable follow-up.

Benefits relating to biological control of aquatic weeds have been assessed for Australia (Page and Lacey 2006). The costs of the biological control projects was approx. A\$5 million in 1974–1993. The *E. crassipes* project cost A\$636,000 in the period 1974–1991, and the combined cost–benefit ratio was 27.5:1. A much higher cost–benefit ratio was achieved for the biological control programme in southern Benin, due to the direct economic effects on the local people. At its peak of infestation, *E. crassipes* reduced the annual income of approximately 200,000 people by about US\$85 million, compared with the total cost of the control programme of about US\$2 million (in 1999 US\$ accrued at 6% p.a., for a total duration of 20 years), yielding a cost–benefit ratio of 124:1 (De Groote et al. 2003).

The lack of clear government policies that permit the use of biological control agents of weeds is a major constraint for the management of *E. crassipes* in Europe. Nearly 40 countries around the world practice biological control of *E. crassipes*, often with great success. It is encouraging that interest and impetus to use biological control for weed management in Europe are increasing (Djeddour et al. 2008; Shaw 2008) with intentional releases in three countries over the past five years (Shaw, Schaffner, and Marchante 2016).

6.2.7. Integrated control

Despite biological control having been highly successful in some regions of the world, in others acceptable levels of control have not been achieved through this method, or biological control is perceived to be too

Table 1. Characterisation of major arthropods associated with *Eichhornia crassipes* (modified and updated from Center et al. (2002)).

Species	Attributes, limitations and current status of research
First priority – agents in use worldwide	
1. *Neochetina eichhorniae* (Warner, 1970) (Coleoptera: Curculionidae) I	In use in North America, Australia, Africa and Asia (Julien and Griffiths 1998)
2. *Neochetina bruchi* (Hustache, 1926) (Coleoptera: Curculionidae)	*Ibid.*
3. *Niphograpta albiguttalis* (Warren, 1889) (Lepidoptera: Crambidae)	*Ibid.*
4. *Orthogalumna terebrantis* (Wallwork, 1965) (Sarcoptiformes: Galumnidae)	*Ibid.*
Second priority – agents released in a few countries within the last 20 years	
5. *Eccritotarsus catarinensis* (Carvalho, 1948) (Hemiptera: Miridae)	In use in South Africa since 1996, released in Malawi, Benin, Ghana, Zambia and Zimbabwe in Africa, China (Winston et al. 2014). Rejected for release in Australia, U.S.A.
6. *Eccritotarsus eichhorniae* (Henry, 2017) (Hemiptera: Miridae)	In use in South Africa since 2007 (Taylor, Downie, and Paterson 2011)
7. *Xubida* (=*Acigona*) *infusellus* (Walker, 1863) (Lepidoptera: Crambidae)	Liberated in Australia September 1981; not established. Reimported in 1995 and liberated in 1996 (Julien and Griffiths 1998), and established.
8. *Cornops aquaticum* (Bruner, 1906) (Orth.: Acrididae, Leptysminae) R	Released in South Africa in 2011, not established (Coetzee et al. 2011).
9. *Megamelus scutellaris* (Berg, 1883) (Hemiptera: Delphacidae)	Released in the U.S.A. in 2010 (Tipping et al. 2014) and in South Africa in 2014 (Hill and Coetzee 2017). Rejected in Australia (Heard, Zonneveld, and Fichera 2014)
Third priority – candidates poorly known or of questionable specificity	
10. *Paracles* (=*Palustra*) *tenuis* (Berg, 1877) (Lepidoptera: Arctiidae)	Polyphagous in laboratory testing. It developed readily on *P. rotundifolia*, *Alternanthera*, *Canna*, *Limnobium*, and *Sagittaria*. Rejected for consideration (Cordo unpub. rpt.)
11. *Taosa longula* (Remes Lenicov & Hernandez, 2010) (Hemiptera: Dictyopharidae).	Host specific and damaging in native range (Hernández and Cabrera Walsh 2011)
12. *Brachinus* sp. (Weber, 1801) (Coleoptera: Carabidae)	Feeding on flowers (Silveira Guido 1965). May be the same as the *Callida* sp. found in Argentina (Cordo, Hill, and Center, unpubl.)
13. *Argyractis subornata* (Hampson, 1897) (Lepidoptera: Crambidae)	Root feeder; life history and biology studied by Forno (1983)
14. *Macocephala acuminata* Dallas (Hemiptera: Pentatomidae)*	Root feeder; a pest of rice (Silveira Guido 1965)
15. *Eugaurax setigena* (Sabrosky, 1974) (Diptera: Chloropidae)	Little known on food habits; *Eugaurax floridensis* Malloch reared from *Sagittaria falcata* Pursh. *Eugaurax quadrilineata* reared from eggplant (Sabrosky 1974)
16. *Chironomus falvipilus* (Rempel , 1939) (Diptera: Chironomidae)	In petioles of waterhyacinth in Surinam and Brazil. Undetermined chironomid from Uruguay (Silveira Guido 1965)
17. *Hydrellia* sp. (Robineau-Desvoidy, 1830) (Diptera: Ephydridae)	Common in Uruguay (Silveira Guido 1965)
**18. *Flechtmannia eichhorniae* (Keifer, 1979) Acarina: Eriophyidae)	Described for Brazil (Kiefer 1979). Mentioned from Uruguay (Silveira Guido 1965) as being a new species and genus; host specificity is promising. No studies conducted on this species
Herbivores rejected for release	
19. *Bellura densa* ((Walker, 1865) (Leptidotera: Noctuidae)	Rejected for release due to lack of host specificity (Center and Hill 2002)
20. *Thrypticus* spp. (Gerstäcker, 1864); seven species (Diptera: Dolichopodidae)	Despite host specificity, not sufficiently damaging and difficult to culture (Hernández, pers. comm.)

* Macocephala acuminata is frequently cited in the literature dealing with biocontrol of E. crassipes, but the name is taxonomically unconfirmed, it could represent actually Mecocephala acuminata (Dallas, 1851) (= M. (= M. holmbergi (Pirán, 1969))

** cited as such in literature dealing with biocontrol of E. crassipes; considered in genus Leipothrix (Keifer, 1979) (Prostigmata: Eriphydae) and a doubtful species by Gbif

slow acting. Thus an integrated management approach has been suggested for *E. crassipes*. An integrated management approach includes aspects of biological control, herbicide applications, manual removal and, possibly most importantly, the management of nutrients entering the aquatic ecosystem that drives *E. crassipes* growth (Hill and Olckers 2001). Jones and Cilliers (1999) and Jones (2001) developed an integrated management programme for the Nseleni River system, a subtropical region of South Africa, and this approach was further developed by Hill and Coetzee (2008). The key elements of this approach, which is applicable worldwide but pertinent to the European scenario, were to appoint one individual or organisation to drive the control programme; involve all interested and affected parties on the water body, including citizen science and volunteer groups; map the extent of the infestation to understand how big the infestation is; identify the cause of the infestation to determine where the infestation is coming from and what is driving its invasion; set the acceptable level of control; use appropriate control methods where applicable; evaluate the level of success of the control options; and adjust the management plan over time, depending on the outcomes of the evaluation.

7. Conclusion

In 2008, Julien outlined the challenges for the control of *E. crassipes* in Europe, and the outlook has not changed considerably, despite recent EU regulation of the species. The plant is already widely established in southern Europe, southwest of the Iberian Peninsula, and given the reality of global climate change, more areas will become suitable for establishment. Attempts to eradicate it have largely failed, while control options are limited. Herbicides are not permitted on most waterways, biological control has not been legislated

to date, manual and mechanical control has proven to be expensive and generally ineffective, and the plant is still traded within the borders of the EU. Even though the pathways for importation and dispersal within the EU have recently been regulated, and control options remain limited, *E. crassipes* is likely to become more problematic under current climatic conditions, and will no doubt increase its range under future climate change scenarios. Additionally, the plant thrives in eutrophic waters, which are typical of many European water bodies. Under the conditions outlined above, *E. crassipes* will become increasingly invasive and damaging in Europe, and until there is a change in legislation allowing for derogations for temporary herbicide use in waterways, and a more generalised use of classical biological control, prospects for the effective management of this weed remain poor. It is therefore crucial to address water quality and new introductions in the absence of effective control.

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Julie A. Coetzee is Associate Professor of Botany at Rhodes University, with a research focus on aquatic weed invasions and their control. *Contribution:* drafted the whole review.

Martin P. Hill is Professor of Entomology at Rhodes University, and his research focuses on the integrated management of invasive species. *Contribution:* co-contributed to the drafting of the review, in particular legislation and management.

Trinidad Ruiz-Téllez is Profesora Titular de Botánica at the Universidad de Extremadura. *Contribution:* provided additions and comments with regard to distribution, biology, phenology, impact and management of *E. crassipes* in Europe.

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Sarah Brunel is an agronomist with an interest in plant health; she currently works as Capacity Development Officer for the International Plant Protection Convention. *Contribution:* coordinated the EPPO PRA on *Eichhornia crassipes* while previously working for the European and Mediterranean Plant Protection Organization (EPPO), and provided comments on this paper.

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