Distribution, ecological and economic impacts and competition of the invasive alien aquatic weeds (*Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch. and *Azolla filiculoides* Lam.) in Madagascar

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Abstract

In Madagascar, as in several countries in the world, the invasion by four aquatic weeds (*Pontederia crassipes* Mart. (Pontederiaceae), *Pistia stratiotes* L. (Araceae), *Salvinia molesta* D.S. Mitch Salviniaceae) and *Azolla filiculoides* Lam. (Azollaceae) are among the drivers of environmental and socio-economic deterioration in aquatic ecosystems. *Pistia stratiotes* was first recorded on the island in the 19th century, and *P. crassipes* from the beginning of the 20th century, while *S. molesta* and *A. filiculoides* were only documented during in the 21st century. From the 1920s, botanists such as Henri Perrier de la Bathie and Raymond Decary were already aware of the dangers caused, in particular by *P. crassipes* in other countries, and raised the alarm, but little attention has been paid to these species. The aim of the research conducted for this thesis was to determine the distribution, socio-economic and ecological impacts of these four invasive alien aquatic weeds in Madagascar and to make recommendations for their control.

First, the distributions of these four aquatic weeds were mapped. This mapping exercise compiled data from different sources including herbarium records, online data and field visits across Madagascar. The mapping study was undertaken from August 2015 to June 2020. Except for mountainous areas above 1800 m (Tsaratanana Massif, Ankaratra Massif and Andringitra Massif) where no data were available, all of Madagascar's bioclimates were invaded by at least one of the four aquatic weeds. In total, at least one species was recorded in 18 of the 22 Regions. *Pontederia crassipes* was recorded in 13 Regions, *S. molesta* in 14 Regions, *P. stratiotes* in 12 Regions, and *A. filiculoides* in 13 Regions. Herbarium records revealed the oldest record for *P. stratiotes* to be 1847, 1931 for *P. crassipes*, 1995 for *S. molesta* and there were no herbarium specimens for *A. filiculoides* prior to the start of the current study in 2015. We now know where these four weeds occur and how abundant they are.

An objective of this research was to assess the impacts of the four invasive aquatic plants on the socio-economy of the island, mainly on rice production and fishing. Between 2016 and 2019, 102 households in three regions, Soanierana Ivongo, Foulpointe and Antananarivo, were randomly selected and questioned on the impact of these weeds in their aquatic ecosystems and their livelihoods such as fishing and rice growing. Surveys revealed that the four aquatic weeds significantly threatened household activities. On the east coast of Madagascar, the invasions of these four invasive species decreased fish and freshwater shrimp production by 82%. On the high plateau of Madagascar, they reduced rice yield by 30% despite requiring an additional expense of US$ 1,107/ha for control. Although farmers surveyed only used manual control to manage these weeds, they were receptive to other control methods, including integrated control using herbicides and biological control.

Another objective of this research was to determine the ecological impacts of the four weeds and specifically if freshwater ecosystem functioning would return after control. To assess the ecological impact, between February 2017 to August 2019, on Lake Antsokafina, the following abiotic and biotic factors were considered: physico-chemistry of water, succession of macrophyte community and animal diversity. With the exception of turbidity, the values of the physico-chemical parameters of the water (pH, electrical conductivity, water temperature and turbidity), were similar between the infested zone and cleared zone. A study on the invasion process of aquatic weeds showed that the plant community succession of the lake changed over time in the areas that had been cleared. The submerged species *Ceratophyllum demersum* was the pioneer, followed by creeping species such as *Echinochloa colona* and *Ipomoea aquatica,* before the area was recolonized by aquatic weeds. Among the aquatic weeds, *S. molesta* was the most aggressive, covering 92% of the area one year after the start of the experiment. For animal diversity, bird, shrimp and fish community were assessed. The cleaning of the plots in the lake allowed the resumption of fishing activity providing 50 to 200g/catch for shrimp and from 0.25 to 0.5kg/catch for fish per person per day, while no catch was obtained in the areas infested by aquatic weeds were fishermen still attempting to harvest fish/shrimp from the aquatic weed infested areas. Three species of birds, Humblot's Heron (*Ardea humbloti*), the white-faced whistling duck (*Dendrocygna viduata*) and red-billed teal (*Anas erythrorhyncha*) returned once the areas had been cleared.

A manipulated outdoor as descriptor for laboratory experiment was conducted to determine the level and nature of competition of four aquatic weeds species against the indigenous floating fern, *Salvinia hastata* Desv. (Salviniaceae), using an additive series density model. It was shown that all four invasive species outcompeted *S. hastata,* with *P. crassipes* being 24 times more dominant, followed by *P. stratiotes* at 12 times, *S. molesta* at 8 times, and finally *A. filiculoides* at 1.2 times more dominant. This study provided direct evidence of the biodiversity impact of these four species and thus also provided an environmental argument for their control.

Based on the findings of this study, a series of recommendations was formulated to manage the invasions of alien species in Madagascar with particular attention to invasive aquatic weeds. These recommendations mainly concern the establishment of management structures and legal instruments such as the creation of a lead government agency at national level and a cross-sectorial invasive species advisory committee, which should review legislation and regulations related to invasive species.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

1.1 Introduction

Biological invasions, the topic of this thesis, are known as one of the six components leading to global change (Vitousek *et al*., 1997). Globally, biological invasions are widespread and irreversible, with significant consequences for biodiversity, economics and human health (Vitousek *et al*., 1997; IUCN, 2000). Biological invasions are considered to be the second largest cause of global biodiversity loss after direct habitat destruction (Hequet *et al.,* 2009).

The terminology associated with invasion biology is often confusing, with many different terms being used for the same thing. For example, exotic species, introduced species, invasive species, naturalised species and weeds (in the case of plants) are used interchangeably (Colautti and MacIsaac, 2004). However, during the last few decades, several authors have tried to provide a more precise and generalised terminology. Biological invasion can be defined as a process by which propagules of non-indigenous species progress through a series of invasion barriers before becoming invasive in a new geographic area (Richardson *et al.,* 2000; Colautti and MacIsaac, 2004; IUCN, 2013; Sarat *et al.,* 2015a). Sarat *et al.,* (2015a) summarised the process of invasion into four categories of barriers, each of which can be an obstacle for the potential invasive organism. The first is the geographical barrier, which the species must first overcome to reach the border of the new area. Once at the border, the species can be detected if there are effective quarantine protocols in place, or pass through if these protocols are less than effective (Williams, 2003). However, many of the species that have become invasive have been intentionally introduced as they have valuable/usable attributes, and they are therefore not subject to border checks. When the potential invasive species reaches the new area, it must then overcome a range of abiotic (climate, habitats, resources) and biotic (trophic resources, predators, pathogens) barriers. The second barrier is that the potential invasive must adapt to the local climate if it is to survive and prosper. The likelihood that an introduced species will establish often depends on the quantity of propagules. When propagules are not abundant, then repeated attempts to become established may be necessary before success is achieved and to develop a viable population over the long term – this constitutes the third barrier, which is the "reproductive barrier" (Richardson *et al*., 2000). The stage at which establishment occurs and individuals of the potentially invasive species begin to reproduce and grow in natural environments, and in association with native species, is called naturalization. Following naturalization, initially not all suitable environments are colonised. The expansion of naturalized plant species more widely depends on a number of factors, including the success of pollination and seed dispersal (dispersal is recognised as the fourth barrier to invasion), and the degree of environmental disturbance. Environmental disturbance typically facilitates biological invasions, and landscapes dominated by intact natural habitats constitute a significant barrier to biological invasions (Richardson *et al.*, 2000; Colauttiand MacIsaac, 2004). The most successful invaders are those that function as ecosystem engineers and alter habitats and native fauna and flora assemblages (Richardson *et al.*, 2000).

It is important to distinguish the difference between the terms "naturalization" and "invasion". Invasion is the final stage of the process in which the naturalized species starts to impact native biodiversity, host ecosystems, the economy, and human health (IUCN, 2013; Thévenot *et al.*, 2013; RBG Kew, 2016). Hence, the definition given by IUCN (2000) is pertinent: "Alien invasive species means an alien species which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity". A more explicit definition has been reworked as: "an invasive alien species is an exotic species (allochthonous, non-indigenous species), introduced voluntarily or fortuitously, which has naturalized, spread and threatens ecosystems, habitats or native species, with adverse or potential ecological and/or economic and/or health consequences" (Soubeyran 2008; Sarat *et al.,* 2015a).

Intercontinental transport by humans plays an important role in invasion biology, and is reducing the importance of geographical barriers. For millennia, mountains, oceans, rivers and deserts have been barriers to species movement, enforcing the isolation of species to their natural habitats. With the development of increasingly effective methods of mass transport during the last few centuries, linked to trade and tourism, these barriers have become less effective, allowing species to cross long distances to settle in new habitats where they have the potential to become invasive alien species (Mack *et al.,* 2000; IUCN, 2000; Hulme, 2009; Turbelin *et al.,* 2017). The greater the degree of international trade to a region, the greater the number of invasive alien species that colonise the region (Westphal *et al.,* 2008). Few habitats and regions of the world are immune to biological invasion.

1.2 The role of climate change on invasive alien species

Climate change and biological invasions are two global phenomena that have been amplified over the past few centuries and have had an interaction of impacts from international scale down to local ecosystems and communities of species (Reiter, 2001; Burgiel and Muir, 2010). While biological invasions are favoured by trade exchanges and the movement of humans, and have been increasing for several centuries, climate change has been caused principally by the increase in the rate of greenhouse gases including carbon dioxide (CO_2) concentration. Atmospheric CO_2 contributes to 40% of the total greenhouse effect and its concentration has increased by 30% since the start of the industrial era (Sciama, 2010). The greenhouse effect is reflected in a temperature rise of 0.6°C observed at the global scale during the 20th century and a predicted increase of 1.1°C to 4.6°C by 2100 (Gitay *et al.*, 2002; Sciama, 2010). Temperature increase is inducing disturbance on climatic parameters, mainly on precipitation patterns (Seneviratne *et al.,* 2012). Biological invasions and climate change are seldom linked, yet, both have adverse impacts on socio-economic human livelihoods, e.g agriculture, human settlements, water scarcity, social tensions and human migration (Burgiel and Muir, 2010; Sciama, 2010).

The adverse impacts of climate change may affect several types of ecosystems, however, the most vulnerable are freshwater habitats like those included in this thesis, as well mangroves and coral reefs (CBD, 2009). These impacts can be direct or indirect. With respect to direct impacts, the rise of temperature and water availability causes significant changes to both the ecosystem as a whole and individual species (Burgiel and Muir, 2010). For example, several studies carried out in the arid and semi-arid zones of North America have shown that under the effect of climate change, invasive species become dominant to the detriment of native species. These include both invasive plants, as is the case of soft chess, *Bromus hordeaceus* L. (Poaceae) and sagebrush, *Artemisia tridentata* Nutt. (Asteraceae), and invasive animals, such as the case of Argentine ant, *Linepithema humile* Shattuck (Formicidae), and the zooplankton species water flea*, Daphnia lumholtzi* Sars (Daphniidae) (Hobbs and Mooney, 1991; Harte and Shaw, 1995; Dukes and Mooney, 1999; Engel *et al*., 2011).

It is thought that the effects of climate change are best studied at species and community levels. Climate change will induce a shift in the distribution of species and the interactions between them. Many species are shifting their distributions poleward or upward in elevation (Mooney and Hofgaard, 1999; Sciama, 2010; Engel *et al.*, 2011). This includes invasive species, as Shrestha *et al*. (2018) demonstrated when they studied the effects of climate change on the distribution of six of the most problematic invasive alien plants of Nepal. They found that by 2050, a clear shift toward higher elevation was predicted from 100-2100m above msl to 100-2300m above msl. Consequently, suitable habitats for *Ageratum houstonianum* Mill. (Asteraceae) (+70%), *Hyptis suaveolens* (L.) Poit. (Lamiaceae) (+66%), *Mikania micrantha*

Kunth (Asteraceae) (+14%), *Parthenium hysterophorus* L. (Asteraceae) (+3%), *Lantana camara* L. (Verbenaceae) (+10%) and *Chromolaena odorata* (L.) R.M. King & H. Rob. (Asteraceae) (+12%), will be expanded. Climate change will thus facilitate the spread and establishment of many alien species and create new opportunities for them to become invasive in the regions where they could not establish previously due to unsuitable climatic conditions (Dukes and Mooney, 1999; Mooney and Hofgaard, 1999; Burgiel and Muir, 2010; Engel *et al*., 2011; IUCN, 2017).

1.3 Plant invasions

Biological invasions occur across a range of taxonomic groups with some of the most damaging found in higher plants (IUCN, 2000), although invasions by non-vascular plants (algae and mosses) and fungi are poorly documented. For vascular plants (ferns and flowering plants), 13,168 species are reported as naturalised throughout the world due to human intervention (van Kleunen *et al*., 2015). This represents 3.36% of the total number of global vascular plant species, which is estimated at 391,000 (RBG Kew, 2016). The North American continent has the highest cumulative number of naturalised plant species (5,958 species), followed by the European continent (4,140 species) (van Kleunen *et al*., 2015). Fortunately, not all these naturalised species will become invasive. The probability of a given imported species transitioning through three important stages in the invasion process ranges from 5 to 20%, with an average of 10% for each of the three stages (Williamson and Fitter, 1996; Zanden**,** 2005). The transition from importation to a successful introduction is 10%, 10% of those successfully become established and 10% of established plant species become invasive. Thus, theoretically, the probability of an introduced species becoming invasive is in the order of 1 ‰. These values vary depending on numerous factors *viz.* type of habitat, climate of the site where the species is introduced, the characteristics of the species, and the native species communities present. The Royal Botanical Garden in Kew (2016) for example has counted 4,979 species of vascular plants that are recognised as invasive; this equates to 37.81% of naturalized species worldwide. For aquatic species introduced to Europe, the naturalisation rate has reached 63% (García-Berthou *et al.*, 2005). Among these invasive species ranked the most important include the vascular plant families Asteraceae (most numerous, including 541 species), followed by the Poaceae (with 528 species) (RBG Kew, 2016).

1.4 Aquatic weed invasions

While freshwater represents approximately 2.5% of the earth's water, only 0.01% is available as freshwater rivers and lakes and these habitats support 2.4% of all known vascular plant species in the world (McAllister *et al.,* 1997). The remaining freshwater is locked in polar ice caps or stored in underground aquifers. Freshwater ecosystems are divided into three major groups standing-water ecosystems (e.g. lakes and ponds), flowing-water ecosystems (e.g. rivers and streams), and fresh-dependent ecosystems that interface with the terrestrial world (e.g. wetlands and riparian areas) (Ciruna *et al.,* 2004) (Table 1.1).

Table 1.1: Distribution of inland water ecosystems by continent (modified from Korzun *et al.,* 1978 in Ciruna *et al*., 2004). All estimates are approximations and vary according to the methods used to derive them.

Ecosystem	Africa	Europe	Asia	Australia	North America	South America
Large lakes (km^3)	30,000	2,027	27,7S2	154	25,623	913
Rivers (km^3)	195	80	565	25	250	1,000
Wetlands (km^2)	341,000	'Eurasia' 925,000		4,000	180,000	1,232,000

Water is essential for all life to survive, and aquatic ecosystems play an important role as habitats for aquatic plants and animals. However, biological invasions are more important drivers of biodiversity change in freshwater ecosystems than in terrestrial systems (Sala *et al.,* 2000; Shea and Chesson, 2002). This is because water bodies are frequently close to human habitations, hence are prone to high disturbances such as hydrological alteration and enrichment through eutrophication that facilitate rapid expansion of invading species (Rejmánková, 2011). There is also a strong invasion pathway from the aquarium trade (Martin and Coetzee, 2011), and the macrophytic species are usually clonal and capable of rapid asexual reproduction. Globally, 19 pathways of entry have been identified for invaders of freshwater ecosystems, of which the most important are aquaculture, the ornamental aquarium trade, and fisheries (Ciruna *et al*., 2004). For the specific case of aquatic weeds, including the four target species included in this study, the main introduction pathway was as ornaments for ponds and aquaria (Coetzee and Hill, 2009; GISD, 2019a, b) (Table 1.2). When invasive aquatic plants arrive in new localities, in the absence of their natural enemies, they spread rapidly in freshwater bodies, especially in tropical and warm-temperate regions (Labrada and Fornasari, 2002).

Table 1.2: Major macrophitic aquatic weeds invading water bodies around the world (Coetzee and Hill, 2009).

Macrophyte biotype	**Scientific name**	**Family**	**Common name**	**Region of origin**
Free floating[1]	*Azolla filiculoides Lam.*	Azollaceae	Red water fern	South America
	Pontederia crassipes Mart.	Pontederiaceae	Water hyacinth	South America
	Pistia stratiotes L.	Araceae	Water lettuce	South America
	Salvinia molesta D.S. Mitch.	Salviniaceae	Giant salvinia	South America
	Stratiotes aloides L.	Hydrocharitaceae	Water soldier	Europe
Floating attached[2]	*Alternanthera philoxeroides* (Mart.) Griseb.	Amaranthaceae	Alligator weed	South America
	Myriophyllum aquaticum (Vell.) Verdc.	Haloragaceae	Parrot's feather	South America
	Nymphaea mexicana Zucc.	Nymphaeaceae	Yellow waterlily	North America
	Trapa natans L.	Lythraceae	Water chestnut	Eurasia
Emergent [3]	*Hydrocotyle ranunculoides* L. f.	Araliaceae	Pennywort	North America
Submerged[4]	Cambomba caroliniana A. Gray	*Cabombaceae*	Fanwort	Temperate and tropical America
	Egeria densa Planch.	Hydrocharitaceae	Dense aquatic weed	South America
	Elodea canadensis Michx	Hydrocharitaceae	Canadian aquatic weed	North America
	Hydrilla verticillata (L. f.) Royle	Hydrocharitaceae	Hydrilla	Asia, Australia, Europe, Central Africa
	Lagarosiphon major Moss ex Wager	Hydrocharitaceae	Curly aquatic weed	South Africa
	Myriophyllum spicatum L.	Haloragaceae	Spiked watermilfoil	Europe, Asia, North Africa

[1] : Free-floating macrophytes are aquatic plants that are found suspended on water surface with their root not attached to substrate, sediment, or bottom of the water body;
[2] : Floating-leaved macrophytes have root systems attached to the substrate or bottom of the body of water and with leaves that float on the water surface
[3] : Emergent macrophytes are plants that are rooted in shallow water with vegetative parts emerging above the water surface
[4] : Submerged macrophytes completely grow under water with roots attached to the substrate

1.5 Impacts of aquatic weed invasions

The main impacts of aquatic weeds can be classified as environmental, socio-economic and on human health (Rockwell, 2003; Hill and Coetzee, 2017). In terms of the environment, the impacts vary according to the invasive species and the vulnerability of the invaded ecosystems.

Several species of aquatic weeds, including four focus species of this study, form dense floating mats (Hill and Cilliers, 1999; Coetzee *et al.*, 2019; GISD, 2019a, b). These mats induce significant changes in the aquatic environment, and the effects can be measured at different levels, from the genetic, to the species population, the community, and the ecosystem as a whole (Ciruna *et al.,* 2004). At the genetic level, an invasion could result in the loss of genetic diversity (Templeton, 1980; Franks *et al*., 2011; Estoup *et al.,* 2016). At the population level, the aquatic weeds impose high levels of competition on native species with their rapid growth dense mats. Through high growth rates, these plants deprive the less competitive native species of light, nutrients and dissolved oxygen (Ciruna *et al.,* 2004; Coetzee *et al.*, 2017; GISD, 2019a, b; Kenfack Voukeng *et al*., 2019). At a broader scale, the process of homogenisation of the world's biota (Mooney and Hofgaard, 1999). At the biological community level, aquatic weed invasions cause a loss in specific diversity because of disturbance of the native species habitat and tropic chain as well (Thomaz and Da Cunha, 2010). In South Africa, at Lake Nsezi and the Nseleni River, in KwaZulu-Natal Province, 817 individuals of 13 families of benthic macroinvertebrates were collected under a water hyacinth mat, compared to 17,980 individuals of 27 families from open water (Coetzee *et al.,* 2014). Invasions cause physico-chemical perturbation of the water, including eutrophication by decantation of organic matter, blocking the re-diffusion of oxygen in water, and reducing the dissolved oxygen. These changes to the physicochemical parameters are harmful to the microfauna and microflora of the ecosystem (FCBN, 2012) leading to poor quality of drinking water in terms of colour, turbidity and odour (Hill and Cilliers, 1999). In relation to the hydrological regime, aquatic weed invasions can alter water flow, evapotranspiration, and groundwater (Penfound and Earle, 1948; Little,1966; Mitchell, 1970; Hill and Cilliers, 1999; Ciruna *et al.,* 2004). The creation of mats of aquatic weeds, combined with the alteration of the hydrological regime, can, in the long term, increase a high risk of aquatic ecosystem drying up through excessive evapotranspiration (Fraser *et al.*, 2016; Arp *et al*., 2017). A study conducted by Arp *et al.* (2017) at an impoundment in South Africa, showed that under 100% of water hyacinth cover, the annual net water loss was 5.6 million m^3 and if the half of the weir was covered, the value was 2.8 million m^3. The water lost due to evapotranspiration was thus not sustainable for agricultural development.

Socio-economically, aquatic weed invasions interfere with human activities by blocking the waterways for transport, reducing the efficiency and productivity of freshwater fishing, reducing water available for the irrigation of crops and reducing access to high-quality drinking water resources (Labrada and Fornasari, 2002; Ciruna *et al.,* 2004 ; Matthews and Brand , 2004;

Coetzee and Hill, 2009; Langa, 2013; Coetzee *et al.*, 2019). Socio-economic impacts can be classified into two main categories market impacts (e.g. changes in price) and non-market impacts (Ciruna *et al*., 2004). Market impacts result in the reduction of the quantity of goods going to market and difficulty in accessing these products. A study conducted on the Incomati River of Mozambique by Langa (2013) showed a significant reduction in the amount of fish caught per fisherman for periods when aquatic weeds were abundant compared to when they were rare. In another example from the southern part of Benin, where fishing is the main activity across the community (De Groote *et al.,* 2003), men fish and the women carry the fish to market, where it is then sold. This activity was negatively impacted by the invasion of water hyacinth because, when the weed was abundant, the time spent fishing was less productive and it took more time to carry the fish to market. Where this aquatic weed was rare, annual revenues were reported as US$ 1,984, however, where it was abundant, revenue fell to US$ 607. Women stated that during the periods of infestation, their income dropped from on average US$ 519 to US$ 137 per person. Non-market impacts can be described as the impacts of the change of ecosystem services on various activities related to aquatic ecosystems, e.g change in the ease of aquatic transportation, clogging of irrigation pumps, reduction of the aesthetic value of water bodies used for recreation (fishing, swimming, water-skiing) (Barrett, 1989; Hill and Cilliers, 1999; Labrada and Fornasari, 2002; GISD, 2019a) and reduction of water-storage capacities of reservoirs, tanks and ponds (Fraser *et al.,* 2016; Arp *et al*., 2017). Economic impacts on agriculture and livestock have also been recorded. The cheer biomass of severe aquatic weed infestations can destroy rice fields (GISD, 2019a) and also kill cattle (when trying to graze this vegetation, penetrated too deeply into the water body and ended up drowning (Lehavana, 2014a)), and cause destructive floods as they obstruct water flow (Coetzee *et al.,* 2019).

Invasion of aquatic weeds poses risks to human health. Standing water bodies and dense coverage by aquatic weeds favour the development of insects (mosquitoes in the genera *Aedes* and *Culex*) (Barror *et al.,* 1954), which may be the vectors for diseases such as dengue fever and malaria (Creagh, 1991/1992; Olivier, 1993; ISSG, 2013a), filariasis and elephantiasis (Pancho and Soerjani, 1978; Room *et al.,* 1989; Craig, 1993; ISSG, 2013a, b; Coetzee *et al.,* 2019). Invasion of water hyacinth also forms habitats for disease-carrying snail species, such as *Pseudosuccinea columella* (Say, 1817) *(*Lymnaeidae), which hosts *Fasciola cf. hepatica* Linnaeus *(*Fasciolidae) and *Fasciola* cf. *gigantica* Cobbold (Fasciolidae), causing fasciolosis, an important liver disease affecting both ruminants and humans and *Radix sp.* Rafinesque, (Lymnaeidae), hosting both amphistome and Fasciola (Carolus *et al.,* 2019). In the Incomati

River Basin of Mozambique, aquatic weed carpets increase the prevalence of malaria, bilharzia, diarrhoea and itching-skin problems (Langa, 2013; Coetzee *et al.,* 2019).

1.6 Management of aquatic weed invasions

An effective management strategy for aquatic weed invasions requires a plan that takes into account all stages of the invasion process (Figure 1.1). Prevention, prior to the introduction of a potential weed species, is the most cost-effective measure (Chippendale, 1991; Williams, 2003; Ciruna *et al.,* 2004).

All attempts of introducing a new species into a new country should be preceded by a Weed Risk Assessment (WRA) based on the application of national and international tools of regulation (Williams, 2003). For weed management, the risk assessment procedures must applied across different stages (pre-border, post border and protection of environnemental assets), helping to create systems that aim to prevent, eradicate, contain and protect assets from the effects of weed invasions (Downey *et al.,* 2010a). At the international level, regulation refers to the 1994 Agreement on the Application of Sanitary and Phytosanitary Measures (SPS agreement) of the World Trade Organization (WTO), and the International Plant Protection Convention (IPPC) (FAO, 2000a). At the national level, existing laws regulating the introduction of potential pests must be applied. In a weed risk assessment, it is crucial to start by identifying the species and the pathways of entry. Globally, the procedure consists of inspections of suspected materials at the borders (airports, border posts or ports), and prohibition or quarantine according to legal procedures. To be effective, those tasked with inspections must have easy access to reliable information on the identification of important potential invasives. The information related to such species can be obtained from the countries of origin and elsewhere (Williams, 2003).

Currently, many aquatic weeds, including the species of focus to this study, have spread to aquatic ecosystems around the world (Table 1.2). If these plants are already naturalized or invasive in a particular country, then preventative actions are too late. Once measures to prevent the entry of a plant at the border have failed, the next management action consists of eradicating the weed at an early stage of spread. If eradication fails, the next step is a containment strategy that aims to stop the spread of the species at a national level (Downey, *et al.,* 2010a; Howard, 2014). Eradication and containment require the development of an awareness-raising campaign, the establishment of a database (including monitoring, with the possibility of rapid intervention in the case of an alert (Ciruna *et al.,* 2004). Communication plays an important role in the engagement of stakeholders in campaigns to detect and control invasive species. This multi-layered approach requires coordinated accountability at the national, regional and local levels with a rapid response capacity across all relevant areas. Generally, eradication has rarely been successful in the case of aquatic weeds, because it is difficult to remove all fragments, buds or seeds once a water body is infested (Hill and Coetzee, 2008).

For a post-border context involving widespread weeds, the emphasis needs to move from three management strategies (prevention, eradication, containment) to protection of environmental assets and mitigation of the consequences of invasion (Downey *et al.,* 2010b; Sydes, 2012; Marbuah *et al.,* 2014). Downey *et al.* (2010b) described a triage approach as an effective system, based on (1) the urgency of control relative to the degree of threat posed to biodiversity, and (2) the likelihood of achieving a successful conservation outcome as a result of alien plant control. This approach has enabled long-term management priorities for management of widespread alien plants, considering the possibility of recoverability of the biodiversity following weed control and the likelihood of management success. This triage system uses three key assessment criteria for determining the species or biodiversity at risk from a weed species: (1) threat to the species or susceptibility of the habitat to invasion, (2) ability of the species to respond following control and (3) degree of match between the native and weed species' distribution (Downey *et al.,* 2010b). As one of the components of a weed management strategy, Blossey (1999) emphasized the importance of an effective monitoring system. This needs to provide for long-term monitoring, before and during the invasion, as well as during and after any control attempts, that assesses the changes in the abundance of species: not only the response of the weed to control, but importantly the species/biodiversity at risk and ecosystem properties as a whole.

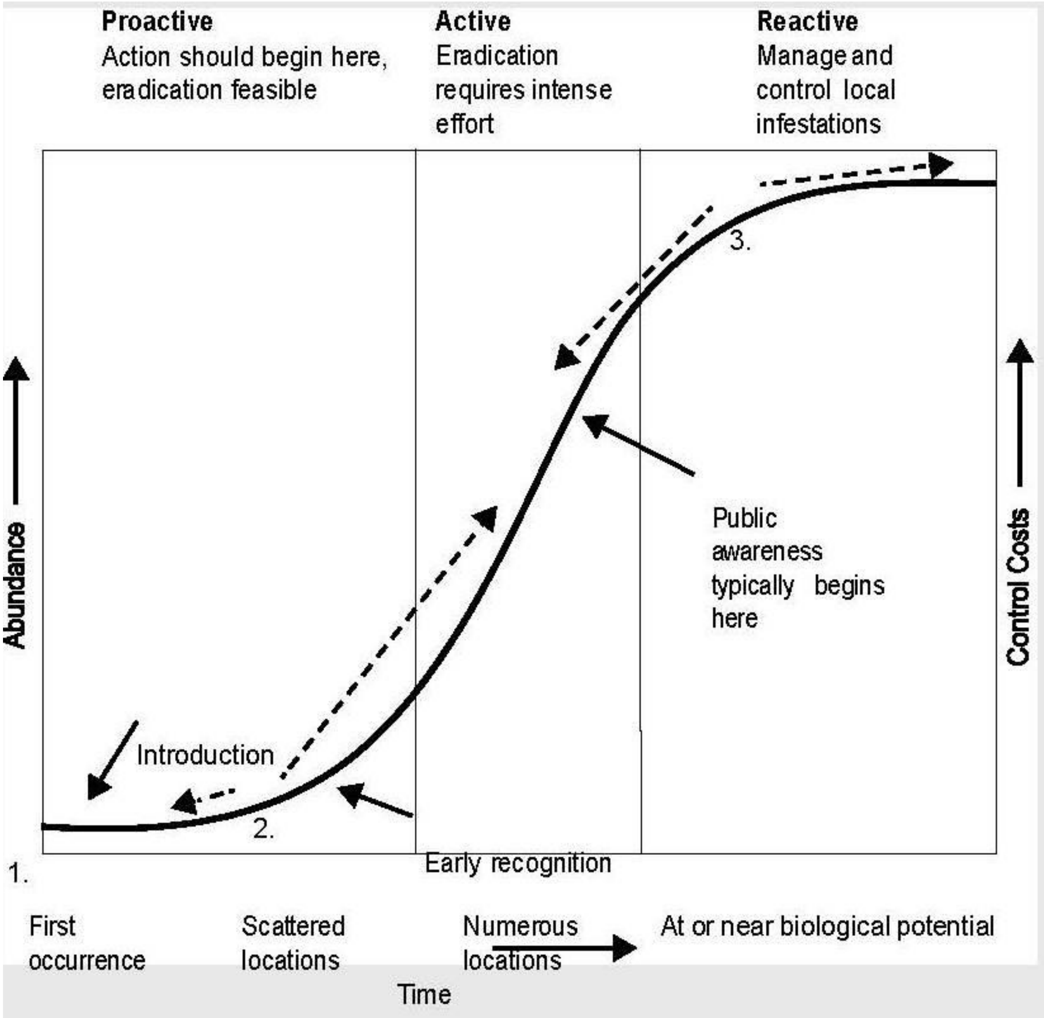

Figure 1.1: Phases of invasive species invasion and control. Numbers refer to: 1. prevention; 2. eradication; and 3. control techniques, in the context of freshwater invasive non-native species (from Chippendale, 1991, taken from Coetzee *et al.*, 2019).

For implementing control of aquatic weeds, several methods can be used, depending on the target species and water body characteristics (Coetzee and Hill, 2009; Akpabey, 2012). Before describing the control options, however, it is important to understand the global strategies employed in managing aquatic weeds (Figure 1.1). Williams (1997) described several approaches relating to the timing of an intervention to control an invasive species with its likely effectiveness and costs, during the earliest phases of colonisation, the required funds to extirpate a pest are low and these may be obtained as an adjunct to other pest control programmes. Once the pests begin to spread rapidly, the effort required to obtain the funds may be orders of magnitude greater.

The total cumulative costs over time include the investment required to obtain the required funds, the money spent on actual control, and the impacts of aquatic weeds on the economy and environment. These accumulated costs become progressively greater with time if control attempts are delayed. Whether or not a pest has established and spread, effective weed-risk assessment systems must be appropriate to the pest's biology and ecology, the values or resources being threatened, the extent to which it has or has not established in an area, and the technologies and resources available.

1.7 Aquatic weed control methods

Several methods can be used for controlling aquatic weeds, i.e utilisation, physical/mechanical control, chemical control, biological control and integrated control. The choice of options may depend on the species or on the local situation where actions will be implemented.

1.7.1 Utilisation

Utilisation is one of the proposed control methods used to limit the expansion of aquatic weeds and contribute to economic development. It consists of valorising biomass as a raw materials. Water hyacinth can be used to produce various products such as biogas, handicrafts, paper, rope, basket, fodder for livestock, mulch, compost for crop cultivation, and as a biological filter in water treatment schemes (Matthews and Brand, 2004; Rakotoarisoa *et al.*, 2015; Wang *et al.*, 2019). One of the most intelligent valorisations of water hyacinth was developed recently in Benin, where an enterprise uses water hyacinth to make absorbent materials for mopping up pollution (Roux, 2019). Their product can recover industrial oil spills by absorbing the oil into custom-designed cushions, rolls or carpets. The residues of this plant can absorb up to 17 times their weight in hydrocarbon, thus stopping the spread of a polluting liquid in case of leakage or following an oil spill (Roux, 2019). According to the same author, effluents released as a result of the treatment which are rich in nutrients, return to the crops to fertilize the soil. In addition, the valorisation of water hyacinth has enabled the company to offer jobs for communities. In the Badagry creeks west of Lagos, Nigeria, water hyacinth was first recorded in the early 1980s. Since 2011, a female entrepreneur has discovered an opportunity to transform biomass of water hyacinth to produce various products including blended cotton fabrics, open shoes, bags, and many other ornamental products, and her firm employs more than 300 women (https://www.africanews.com/2019/03/13/nigerian-entrepreneur-makes-handcraft-products-from-water-hyacinth/).

In several Asian countries, the biomass of giant salvinia (*Salvinia molesta* D.S. Mitch.) (Salviniaceae) has been used in composting, mulching and as a feed supplement for livestock (Olivier, 1993). Water lettuce (*Pistia stratiotes* L.) (Araceae) can be used in various ways, such as for biogas production, fodder for pigs, water purification, phytoremediation of metals, chemical products, oil, removal of pharmaceuticals and personal care products (Abbasi *et al.,* 1991; EPPO, 2017). In addition, water lettuce possesses properties that allow it to be used within Ayurvedic medicine as a diuretic, antidiabetic, antidermatophytic, antifungal and antimicrobial (Tripathi *et al*., 2010; Khan *et al.*, 2014). Red water fern (*Azolla filiculoides* Lam. (Azollaceae), due to its property of fixing atmospheric nitrogen, is widely used in several countries as a fertiliser. For example, in Ethiopia, inoculation of *Azolla filiculoides* by incorporating once into the soil has increased rice yield by 911 kg/ha (19%) (Feyisa *et al.,* 2013). However, no utilisation programme, no matter how successful, has resulted in the adequate control of these weeds (Center *et al*., 2002).

1.7.2 Physical control

Physical control of aquatic weeds may include both manual and mechanical control methods. While manual control consists of using hand tools to uproot, cut, bury, smother or burn, the mechanical method deploys more sophisticated approaches throught the use of machines to break, cut or tear plants (Holt, 2009; Osmond and Petroeschevsky, 2013; Sarat *et al.,* 2015a, b). The method is effective in the short term if infestations are still at a low level (Coetzee and Hill, 2009; Howard, 2014). Generally, physical control is environmentally safe and does not require sophisticated techniques. However, the method requires intensive labour (Sharp, 2014) and the operations must be frequently repeated due to fact that the target species cannot be completely removed from the treatment areas where fragments, buds or seeds of the species left remain in the water column or substrates which can regenerate very quickly. If the plants produce seeds, they are deposited in the hydrosoil and germinate as light penetrates the cleared zone (Coetzee and Hill, 2009; Howard, 2014). Research conducted on water hyacinth in water bodies in the Eastern, Western and the Northern Cape provinces, South Africa, shows high seed density which can reach 4,228 seeds/m^2 (Albano Pérez *et al*., 2011). As water hyacinth is hydrochorous, the disturbance caused by the removal of debris may cause these propagules to be released and distributed downstream.

1.7.3 Chemical control

Similar to physical control, chemical control is also only temporarily effective for small infestations and ineffective for large infestations (Coetzee and Hill, 2009). Nevertheless, the advantage of this method is that it acts quickly and less labour-intensive than physical control (van Wyk and van Wilgen, 2002). The most widely used products to control floating aquatic macrophytes such as water hyacinth, giant salvinia and water lettuce include: 2,4 D, glyphosate, paraquat and diquat, nitrophen (as coded compound, TOK E-25), and dalapon (McFarland *et al.,* 2004; Coetzee *et al*., 2019).

Although commonly used around the world in the fight against aquatic weeds, chemical control is expensive. At Hartbeespoort Dam, in South Africa, chemical control of water hyacinth costs on average ZAR1,481 per hectare of cleared area compared to ZAR309 per hectare for biological control (at 2001 rand values) (van Wyk and van Wilgen, 2002**)**. To maintain the infestation at an acceptable level, the spray operations must be repeated, which requires substantial investment.

The damages and the frequency of treatment required depends on the type of herbicide, the level of infestation, application method to be deployed and the local weather conditions. For glyphosate for treatment of hyacinth, it can take a number of weeks for weed to die and to sink (Osmond and Petroeschevsky, 2013). In any case, a post-sprayng follow-up must be planned to assess the damage and additional interventions that may be required at the site.

Chemical control poses environmental and human health risks. In rural parts of Africa, rivers are the main source of drinking water for humans and livestock, and contamination of these with chemicals poses significant health risks. The application of chemicals may also have an impact on the non-target species of fauna and flora living in the water ecosystems (van Wyk and van Wilgen, 2002).

1.7.4 Biological control

Biological control is a method of controlling pests, including waterweeds, using their natural enemies, termed ‘biological control agents’, whether parasitoids, pathogens, predators or competitors (Howard and Harley, 1998). Typically, this method requires an active human management role, particularly at early stages, although for aquatic weeds it is sometimes necessary to reintroduce the agents on an ongoing basis. The aim of biological control, when applied to a weed species, is to reduce a large population of the weed to manageable levels

(McFadyen, 1998). There are several categories of biological control, including conservation, augmentative and classical biological control, and weed biological control typically falls under the latter category. Classical biological control involves the release of an adequately host-specific natural enemy from the region of origin of the weed, in order to establish a permanent, self-sustaining populations of the natural enemy which will feed or develop on the weed and suppress the latter's population without further human intervention (McFadyen, 1998). When carefully conceived and implemented, this approach can be environmentally sound and economically cost-effective (van Wilgen and de Lange, 2011). A classical biological control programme includes several steps and can be summarised as follows (McFadyen 1998; PHPPS, 2006; Moran *et al.*, 2013):

Step 1. Accurate identification of the pest species and confirmation of the pest as a target for biological control.

Step 2. Surveys to identify natural enemies (generally insects, mites, nematodes and diseases) are conducted in the area of origin of the pest (usually overseas). Preliminary indications of host-range and impact of these natural enemies is often also made at this stage.

Step 3. Following approval from national regulatory officials, biological control agents are shipped to a domestic quarantine facility where they are examined to confirm species identity and to determine whether they themselves are free of parasites and diseases.

Step 4. Research is conducted in the quarantine laboratory to determine host-specificity of potential control organisms, in order to assess likely impact on non-target species and thus evaluate environmental risk. Further assessment of the amount of damage the candidate biological control agent can inflict on the target weed can also be made at this stage,

Step 5. If the natural enemy is shown to be adequately host specific and therefore poses low environmental risk, and judged to be adequately damaging to the target, and thus likely to be beneficial, an application to the relevant permitting authority is made for its release into the field in the country of introduction, usually in the form of a report indicating potential risks and benefits.

Step 6. If permission is granted for the release of the natural enemy as a biological control agent, the selected control agents can be mass-reared to high numbers and released at field sites established by the mandated Institution, with the aim of establishing a permanent, self-sustaining field population.

Step 7. Once released, each biological control agent is evaluated for establishment, spread, impact on the target species, and impact on non-target species and/or services. Careful, long-term evaluation studies provide scientific data that should be used to improve current and future programmes. Additional releases may be made to augment populations when the long-term stability of populations of the control agents is not feasible.

In some cases, if the biologists are confident of the specificity and efficacy of the control agents, on the basis of research and experience from other countries, it may be acceptable to skip some of these steps and to proceed directly to technology transfer. Such transfer or 'piggyback' projects have lower costs and higher success rates than projects that have to be started *de novo* (Olckers, 2004).

More than 2,000 biological control agents have been used worldwide in agriculture and conservation (Greathead and Greathead, 1992; Waterhouse and Sands, 2001; van Lenteren *et al*., 2017). Included in this number, 468 species of biological control agents have been released against 175 weeds worldwide (Winston *et al*., 2014; Schwarzländer *et al*., 2018). Within Africa, South Africa has the largest weed biological control programme (McFadyen, 1998; Moran *et al*., 2013; Zachariades *et al*., 2017). Other countries within Africa have benefited from these technological advances, including Kenya, Rwanda, Tanzania, Uganda, Benin, Mali, Niger, Nigeria, Burkina Faso, Ghana, Togo, Côte d'Ivoire, Mauritania and Senegal (Labrada and Fornasari, 2002). From 1913 onwards, the number of biological agents introduced and released in South Africa has continued to increase, especially since the 1970s. Of the 313 species of natural enemies considered for release in South Africa as biological control agents, 119 have been released, and of these, 87 have established on 66 invasive alien plant species (Zachariades, 2018).

There are now several excellent examples in which biological control of floating invasive aquatic plants has proven safe, sustainable, effective in the long-term and cost-effective, even potentially up to 400 times more than herbicidal control in certain cases (Labrada and Fornasari, 2002; van Wyk and van Wilgen, 2002; Coetzee and Hill, 2009; Coetzee *et al*., 2011; van Wilgen and de Lange, 2011). For example, in South Africa, McConnachie *et al.* (2003) evaluated the benefits, in terms of the return of investment, of using biological control against *A. filiculoides* as 2.5:1. Since then, this benefit to cost ratio can have only grown, as there have been few further costs associated with the project, with the benefits continue to increase, in terms of saving on other control methods and savings due to the weed being removed from agricultural systems where it was causing damage (Hill and McConnachie, 2009).

There are other examples of agents that have been shown to be effective in biological control of aquatic weeds in South Africa: *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) and *Neochetina bruchi* Hustache (Coleoptera: Curculionidae) for water hyacinth, *Cyrtobagous salviniae* Calder & Sands (Curculionidae) for giant salvinia, *Neohydronomus affinis* Hustache (Coleoptera: Curculionidae) for water lettuce and *Stenopelmus rufinasus* Gyllenhal (Coleoptera: Curculionidae) for red water fern (Klein, 2011; Zachariades *et al*., 2017). Besides the numerous advantages of biological control, the method may present drawbacks in cases where it is slow acting and where it doesn't always reduce populations of the target weeds adequately (van Wyk and van Wilgen, 2002).

1.7.5 Integrated management

Integrated control can be defined as a combination of two or more of the methods of control described above. In some cases, applying a single control method is rarely effective. Integrated control therefore aims to provide both short- and long-term results, suppressing populations of aquatic weeds in effective, economical and environmentally sound ways. Integrated management is a subset of integrated control which is used for planning and for managing weed infestations at sites, allowing decisions to be made of when and how to intervene when problems occur. An example of integrated control of aquatic weeds consist to consider the inflow of nutrients into the aquatic ecosystem to enhance biological control (Hill and Olckers, 2001). This approach involved habitat manipulation of water quality (nutrients, salinity), water levels, and current velocities (Osmond and Petroeschevsky, 2013; Sarat, *et al*., 2015a). The effort consisted of reducing eutrophication, nutrients. A key principle here is that it is necessary to take action only when infestations warrant it, not as a routine measure. In the case of applying integrated control of water hyacinth to the Nseleni/Mposa Rivers and Lake Nsezi, in South Africa, Jones (2001) described four main integrated management components, survey, plan, control and record. This requires the committed participation of key stakeholders to implement the programme.

Integrated control is often more cost-effective compared to a single method of control. For example, when combining chemical and biological control against water hyacinth in South Africa, the integrated control costs on average ZAR 277/Ha of cleared area compared to ZAR 309/Ha for biological control alone and ZAR 1,481/Ha for chemical methods (van Wyk and van Wilgen, 2002). Practically, the decision of choosing which methods will be combined in integrated control requires a good understanding of the local context. That is why it is crucial to start the programme with a survey of the local situation. However, when combining biological control and chemical control, it is important to consider the compatibility of the techniques, such as the choice of appropriate chemical products to avoid unexpected negative effects of these products on the biological control agents. For instance, Hill *et al.* (2012) found out that 2,4-D and diquat caused higher mortality of the weevil *N. eichhorniae* and the water hyacinth mirid, *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) (up to 80% for the mirid) than formulations containing glyphosate. Thus, in this case, it would be recommended to use glyphosate for successful integrated control.

1.8 Invasive species in Madagascar

The history of introduction of exotic species into Madagascar dates back to human colonization over 2,000 years ago. There are three main periods during which groups of people colonized the island. The first was by Indo-Malaysians at the beginning of the first millennium, followed by Arabs and Africans around the 10th century and finally by the Europeans, after their discovery of Madagascar in 1500 (Bingelli, 2003b; Kull *et al.,* 2012). Each of these groups brought with them useful exotic plants and animals, the main reasons of which were to provide food and raw materials for their survival (Bingelli, 2003b).

Concerning animal species, the data are still scattered. However, the compilation by Kull *et al*. (2012) gives an overview of the numbers of invasive species for each group, *ca.* 14 species for mammals, 3-14 species for reptiles, two species for amphibians, 11 species for birds and *circa* 24 species for freshwater fish. It is important to highlight the recent arrival of two invasive animal species that pose a serious threat to the economy, health and biodiversity of Madagascar, the marbled crayfish (*Procambarus* sp. or "Marmorkrebs") (Cambaridae), native to North America and the Asian toad (*Duttaphrynus melanostictus*) (Bufonidae) (Anastacio *et al*., 2005; Cruz and Rebelo, 2007; Volana, 2007; Jones *et al.,* 2008; Kearney *et al.*, 2008; DEWHA, 2010; Heimer, 2010; CI, 2011, 2014; Feria and Faulkes, 2011; Randrianantoandro and Randrianiaina, 2014; McClelland *et al.,* 2015; Moore *et al.*, 2015; Goodman *et al.,* 2017; MEEMF, 2017; Gutekunst *et al.*, 2018; Marshall *et al*., 2018; Reardon *et al.*, 2018).

For plants, the record of introduction reached a peak during the colonial period from 1896 to 1960 (Kull *et al*., 2012). During the 1920s, the French botanist J.M.H.A. Perrier de la Bathie was aware of the risks associated with the introduction of exotic species. However, he distinguished between introduced plant species, most of which were useful to the human population (a total of 524 species) and those that interfered with human activities or caused economic impacts, which he called plant pests (Perrier de la Bathie, 1928; 1931-1932). Since then, several other attempts have been made to enumerate the introduced plant species in Madagascar, especially for forestry tree species (Gachet, 1962, 1965, 1966; Chauvet, 1968; Sutter and Rakotonoely, 1989). The introduction of forestry tree species peaked between 1950 and 1956, during which 406 species were introduced into 31 arboreta or forest stations, of which 159 species now pose a risk of invasion (Tassin *et al.,* 2009). After independence in 1960, the rate of introduction of plant species decreased with some recent introductory trials for interests in agronomy, forestry and agroforestry (Kull *et al*., 2012). Kull *et al*. (2012) compiled data from different sources, resulting in the most complete and up-to-date work of listing the introduced species in Madagascar. According to their records, the total number of introduced plant species in Madagascar is estimated at 1,157 species, including 101 species with invasive behaviour. These introduced species represent 10.3% of the total of 11,220 vascular plant species in Madagascar (Callmander *et al.,* 2011).

1.9 People's perception of invasive species in Madagascar

Globally, the effects of invasive species can be both positive and negative. In Madagascar, the perception of a particular species is based on its socio-economic values and the judgments attributed to each of the species refer to the utility values which they bring to human livelihoods (Kull *et al*., 2014). The term "invasive species" is not seen as problematic (Binggeli, 2003b; Carriere *et al*., 2008). Indeed, people are only concerned with the species whose impacts interfere with socio-economic livelihoods, i.e. those species that Perrier de la Bathie (1928) call "Les pestes végétales". So far, very few studies have focused on the distribution and impacts of invasive species (Binggeli, 2003b; Kull *et al.*, 2014). However, several studies have demonstrated the usefulness of invasive species (Kull *et al.,* 2007; Carriere *et al.,* 2014; Gerard *et al.,* 2015; Kull *et al.*, 2014, 2019).

For plant species, the case of two Australian invasive species, *Grevillea banksii* R. Br. (Proteaceae) on the East Coast and *Acacia dealbata* Link. (Fabaceae) on the highlands of Madagascar, illustrate opposing views where these species are positively perceived by Malagasy people, despite the fairly advanced level of invasion (Kull *et al*., 2007, 2019) Very recently, Government set the goal of planting 60,000,000 plants across the island. During the official opening of the reforestation campaign, carried out in Firarazana, Ankazobe, around fifty species including invasive species such as *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) were planted (https://www.facebook.com/photo.php?fbid=2568014030186985&set=pcb.2568016633520058&type=3&theater).The selection of species was made by the Ministry of Environment and Sustainable Development, based on their socio-economic utility, without taking into account the risk of invasion.

Despite the late awakening on biological invasion in Madagascar, scientists and managers of natural resources are starting to become more sensitised to invasive species (Binggeli, 2003b; Kull *et al*. 2014, 2019). There is also increased regional awareness, such as WIO-IAS invasive species group (wio-ias@list.auckland.ac.nz) and some regional symposia around invasive species, Mayotte in 2012, Mauricius in 2014 and Reunion in 2014 (UICN-Comité francais, 2012; UICN and COI, 2014; https://www.especesinvasives.re/evenements/a-la-reunion/article/ecole-thematique-sur-les-invasions-1242). Research and sporadic actions exist. In 2013, a symposium on invasive species was held for the first time in Antananarivo, bringing together researchers and various environmentalists from the Indian Ocean region to discuss the problem of invasive alien species, and particularly to draw up an inventory, identify gaps, and capitalize on what has been learned about invasive species (Rakouth *et al.,* 2014).

1.10 Aquatic weed invasions in Madagascar

Madagascar has a large and dense network of freshwater ecosystems encompassing lotic ecosystems from five major watersheds (590,200 km^2) and lentic ecosystems including lakes, marshes, lagoons, ponds and wetlands (Elouard and Gibon, 2001; Raharimalala, 2007; MEEMF, 2017). The principal stagnant freshwater bodies are formed mainly by continental and coastal lakes occupying a total area of approximatly 2000 km^2 (CI, 2010). Aquatic biodiversity and the economy of both urban and rural households are highly dependent on the availability and health of freshwater ecosystems. The Malagasy government recognises the importance of water resources. Hence, in 1997, the Department of Water Services decared: [translation from French]: "*It becomes imperative to protect, conserve and use the water resources of the country in a rational and integrated way. Water is a vital resource, essential for people to stay alive, and we must allow everyone, especially the poorest, to access it. It is also an eminently economic good, requiring the mobilization of economic and financial measures to ensure the sustainability of services for its distribution to users in an effective manner, i.e. in quantity and quality requirements*" (MEEMF, 2017). However, this important resource is threatened through the invasion by aquatic weeds. Madagascar records 387 naturalised plants of which 52 (13.4%) occur in freshwater habitats (Phillipson *et al*., 2017, 2018). Aquatic ecosystems represent 9% of the total invaded areas by invasive alien species in Madagascar (Raharinaivo, 2012). The collection of data from different sources has resulted in the identification of 17 alien plant species that are invasive in aquatic, semi-aquatic and wetland ecosystems (Table 1.3) (Binggeli, 2003b; Kull *et al.,* 2012; Raharinaivo, 2012**;** GISD, 2019b)

Table 1.3: List of aquatic, semi-aquatic and wetland weeds in Madagascar, based on current literature.

Species	**Vernacular name**	**Family**	**Region of origin**
Achyranthes aspera L.	Chaff-flower, Prickly chaff flower, Devil's horsewhip	Amaranthaceae	South-east Asia and/or Africa
Centella asiatica (L.) Urb.	Centella, Asiatic pennywort	Apiaceae	Asia and northern Australia
Cleome hirta (Klotzsch) Oliv.	Sticky purple cleome/Sticky purple mousewhiskers	Cleomaceae	Africa
Cynodon dactylon (L.) Pers.	Couch grass, Bermuda grass, Quickgrass, Twitch grass	Poaceae	Probably from sub-Saharan Africa and/or on islands in the western parts of the Indian Ocean
Cyperus difformis L.	Small-flowered umbrella sedge, Smallflower umbrella plant	Cyperaceae	Old World and Mexico / New Caledonia
Cyperus esculentus L.	Chufa sedge, Nut grass, Yellow nutsedge, Tiger nut sedge, Edible galingale, Water grass or Earth almond	Cyperaceae	Tropical Africa, India
Cyperus rotundus L.	Coco-grass, Java grass, Nut grass, Purple nut sedge	Cyperaceae	Cosmopolitan (Africa, southern and central Europe (north to France and Austria), and southern Asia
Eclipta prostrata (L.) L.	False daisy	Asteraceae	Asia and northern Australia
Eleusine indica (L.) Gaertn.	Goosegrass, Yard-grass, Wiregrass, or Crowfootgrass	Poaceae	Africa
Ischaemum rugosum Salisb.	Murain grass	Poaceae	Tropics of the Old World / tropical Asia
Melaleuca quinquenervia (Cav.) S.T. Blake	Punk trees or paperbark tea trees	Myrtaceae	Australia, New Guinea, and the Solomon Islands
Mimosa pigra L.	Giant sensitive plant, Sleepy plant, Bashful plant	Fabacae	Tropical America
Oxycaryum cubense (Poepp. & Kunth) Palla	Burhead sedge, Capim-de-capivara, Cuban bulrush	Cyperaceae	North and South America
Paspalum conjugatum P.J. Bergius	Buffalo grass, Carabao grass	Poaceae	Tropical America

Pithecellobium dulce (Roxb.) Benth.	Madras thorn	Fabacae	Tropical and subtropical America
Pontederia crassipes Mart.	Water hyacinth	Pontederiaceae	South America
Salvinia molesta D.S. Mitch.	Giant salvinia	Salviniaceae	South America

1.11 Target species for the this thesis and current knowledge in Madagascar

For the purposes of this study, four floating aquatic macrophytes were selected, *P. crassipes* (water hyacinth), *S. molesta* (giant salvinia), *P. stratiotes* (water lettuce) and *A. filiculoides* (red water fern). The four target invasive species in this thesis are globally recognised as among the most formidable in terms of economic, health and environmental damage. Two of them, *Pontederia* (previously *Eichhornia*) *crassipes* Mart. (Pontederiaceae) and *S.molesta* are included in the list of the 100 worst invasive species in the world (GISD, 2018).

Pontederia crassipes was probably introduced to Madagascar around 1900 (Binggeli, 2003a) and Perrier de la Bathie (1928) described it as one of seven weeds in Madagascar. Today, this species is widespread across the country, including Imerina and Betsileo (high plateau), Betsiboka Bassin (Majunga), the Pangalanes Canal and Lake Alaotra (Toamasina) (Binggeli, 2003a). According to Ranarijaona (1999), *P. crassipes* has invaded all types of lentic lakes except those at an altitude above 2163m. On Lake Alaotra, *P. crassipes* is considered the second most abundant and damaging species for rice and fisheries after *Salvinia* spp. (Rakotoarisoa *et al.,* 2015). For Madagascar, Perrier de la Bathie had already sounded the alarm on *P. crassipes* in 1927 [translation from French]: "*This plant, that has been cultivated in Antananarivo, has not yet become a pest in Madagascar, but, if we are not careful, it will not be long in showing its usual misdeeds, such as the case observed in all the tropical countries. Water hyacinth exists today in Tamatave, Nossibé and Majunga, and there is great danger, if severe measures are not immediately taken, that it escapes from the cultivation to invade all the water bodies of the warm zones of the island. The adverse impacts caused by this plant in many tropical countries are too significant, so that the complete destruction of its population on the island has to be ordered*" (Perrier de la Bathie, 1928). Decary, (1965) repeated the warnings, describing in addition the case of *P. stratiotes.*

Although in 1928, a decree was issued prohibiting the hawking of *P. crassipes*, the species continued to spread across the island due to lack of surveillance and application of control actions. Control began only in 1947 in the region of Antananarivo and Lake Alaotra.

Variable results were achieved, ranging from 30-100% control, using 2-4-D or 2-4-dichlorophenoxyacetic compounds, which were reported to be harmless to fish and insects (Decary, 1965). Despite the alarming spread of the species across the island since then, no concrete, large-scale action has been undertaken to reduce the impact of these scourges at a national scale. Sporadic actions exist, but they are far from effective in managing or containing the progression of these biological invasions.

The first record of *S.molesta* in Madagascar was reported in the early 2000s (Binggeli, 2003b). For a long time, there was confusion between *S. molesta* and *Salvinia hastata* Desv., (Salviniaceae). The latter species is native to Madagascar (http://legacy.tropicos.org/Name/26600425?projectid=17) and can be recognised by its oblong leaves, undivided simple hairs on the upper surface, brown hair on the underside of the leaves and submerged leaves divided into 2-5 lobes (Henderson and Cilliers, 2002). It is the most closely related species to *S. molesta* in Madagascar. Based on the Tropicos database (http://www.tropicos.org/), before the start of our study, only four collections of *S. molesta* had been made in two provinces (Fianarantsoa and Toamasina). Notwithstanding the lack of records, *S.molesta* causes significant impacts on socio-economics and on biodiversity of Madagascar's freshwater ecosystems (Lehavana, 2014a, b).

The origin of *P. stratiotes* is still controversial. Authors have delineated the origin of the species variously as South America, Africa, Madagascar and Australia (Table 1.4). Decary (1965) included *P. stratiotes* on the list of invasive or harmful species in Madagascar, but no other publication mentions it as an introduced species on the island. The MadCAt database records ten collections, from all provinces except Toamasina. The species is widespread on the island, in the backwaters and lagoons of the eastern coast, and in Sakalava country regions at altitudes up to 1,200m (Decary, 1965; Ranarijaona, 1999). Some swampy areas, which could have been turned into rice fields, were abandoned due to the excessive abundance of *P. stratiotes* (Decary, 1965).

Finally, the existence of *A. filiculoides* on Madagascar has not been recorded in any databases or publications. However, Raharinaivo (2012) listed an unidentified species of Azolla as invasive. In addition, the indigenous species *Azolla pinnata* R. Br. (Azollaceae) (http://legacy.tropicos.org/Name/26600073?projectid=17) has been listed as an invasive species in Madagascar (MEEMF, 2017).

1.11.1 Description of the four target species of the study

Water hyacinth (*Pontederia crassipes*)

Order: Liliales

Family: Pontederiaceae

Scientific name: *Pontederia crassipes* Mart.

Synonyms: Historical synonyms include *Pontederia crassipes* Martius, Nov. Gen.; *Eichhornia speciosa* Kunth; *Heteranthera formosa* Miquel, *Pontederia azurea* Hook, non Sw; *Eichhornia cordifolia* Gandoger, *Eichhornia crassipes* (Mart.) Solms.

Pontederia crassipes is a perennial free-floating aquatic macrophyte growing, generally from 10 to 50 cm in height (Gopal, 1987; Henderson and Cilliers, 2002). The growth form of this plant is variable. When growing at the edge of an infestation or otherwise not in dense mats, they are generally short (<30 cm tall) with inflated bulbous petioles, while in dense mats, the plants characteristically have elongated petioles up to 1.5 m in length. Each plant consists of a rosette of six to ten leaves attached to a rhizome with a well-developed fibrous root system (Hill *et al.,* 2011). *Pontederia crassipes* forms a shoot consisting of a branched, stoloniferous rhizome, six centimeters in diameter and up to 30 cm in length, with several short internodes. Each node bears a leaf and roots. Its roots are purplish black and feathery (Gopal, 1987). Leaves are petiolated with a glossy sheen, and are arranged spirally, appearing to be in a rosette. Each leaf consists of a petiole, isthmus (between petiole and blade) and blade. The petiole bears a large membranous stipule, which forms a sheath around the next younger leaf. Petioles are spongy and measure up to five centimeters in diameter and 30-50cm in length (maximum 125cm). They may be elongated, swollen in the middle and tapering towards the blade or they may form a bulbous float, containing air-filled lacunate tissue. Its leaves are thick, waxy, rounded, and glossy and rise well above the water surface on stalks. They are broadly ovate to circular, 10-20 cm in diameter, with gently incurved, often undulate sides. Leaf veins are dense, numerous, fine and longitudinal. Leaf stalks are bulbous and spongy. The stalk is erect, and carries at the top a single spike. Each spike has 4-25 showy flowers (maximum 35) with 8-15 being the most common (GISD, 2019a). The flowers have six petals which are purplish blue or lavender to pinkish, with the uppermost petal containing a yellow, blue-bordered central splotch. The perianth tube is 1.5-1.75 cm long with a green base and pale top. Tepals are ovate to oblong, thin, lilac and up to 4 cm long. The posterior tepal (labellum) has a central bright yellow diamond-shaped region, surrounded by a deep blue border with bright red radiating lines. When young, this labellum has a green spot. There are six stamens (sometimes five or seven) having curved filaments with glandular hairs. Three are small and close to the perianth tube. Anthers are violet and measure 1.4-2.2mm long.

After pollination, the flower spike bends to position the seed capsule below the surface of the water, where the seeds are released. Each seed capsule contains up to 50 seeds, which sink and remain viable in the sediment for 15 to 20 years (Gopal, 1987; Hill *et al*., 2011). The fruit is a thin-walled capsule, enclosed in a relatively thick-walled hypanthium, developed from the perianth tube. However, it has been reported that sexual reproduction is limited, and although the plant flowers profusely, few observers have seen seeds or seedlings in the field (GISD, 2019a). Vegetative reproduction is more important, with *P. crassipes* growing and spreading rapidly under favourable temperature and nutrient conditions, doubling every 11–18 days (Hill *et al*., 2011). Stolon buds develop that bear offshoots from axillary buds, and stolons are readily distributed by water currents, winds and boat traffic.

Optimum temperature for growth of *E. crassipes* is 25-27.5°C (Gopal, 1987). Growth ceases when water temperature is above 40°C or below 10°C. However, it has been observed that even at temperatures below 10°C, ramets are still produced and from 5-0°C, there is a significant decrease in regrowth (Gopal, 1987; Owens and Madsen, 1995). The plant can survive freezing temperatures ranging from 0 to -16°C for at least 24 hours (Owens and Madsen, 1995). *Pontederia crassipes* grows well in water with high nutrients (nitrogen and phosphorus), and high light intensities. There is a hyperbolic relationship between the growth rate and the nutrient concentration in the water and solar radiation (Aoyama *et al.,* 1986). The growth is best in neutral pH, and it tolerates pH levels from 4.0 to 10.0 (Haller and Sutton, 1973), but it tolerates only low level of salinity, not more than 20 to 25% sea water and at 3.33 ‰ the plant died (Haller *et al.,* 1974; Muramoto *et al.,*1991). *Pontederia crassipes* is very responsive to nutrients (especially nitrogen and phosphorus) and high growth rates are always associated with eutrophic, nutrient-rich conditions.

The species was discovered in 1823 by the German naturalist C. von Martius who was studying the flora of Brazil. He named it *Pontederia crassipes*. Sixty years later, Solms included it in the *Eichhornia* genus as described by Kuntz in 1829 (Téllez *et al*., 2008). A recent taxonomic revision of the Pontederiaceae family using phylogenic evidence places the genus *Eichhornia* back into *Pontederia* (Pellegrini *et al*., 2018). The centre of origin of *P. crassipes* is the Amazon basin in Brazil and Peru (Barrett and Forno, 1982; Hill *et al*., 2011). The first authenticated record of *P. crassipes* outside South America is in New Orleans in 1884 (Penfound and Earle, 1948; Hill *et al*., 2011). On the African continent, the first introduction was made in Egypt between 1879 and 1892 (Edwards and Musil, 1975; Hill *et al.,* 2011) and it is now present in more than 30 countries (see Figure.1.2). At the present time, it is distributed throughout the world, flourishing in tropical and subtropical regions (EPPO, 2008).

Giant Salvinia (*Salvinia molesta*)

Order: Salviniales

Family: Salviniaceae

Scientific name: *Salvinia molesta* D. S. Mitchell

Synonyms: *Salvinia auriculata* Aubl.

Salvinia molesta is a perennial, free-floating aquatic fern. Initially identified as a form of *S. auriculata*, *S. molesta* was reclassified in 1972 based on details of the male sporocarps or fruiting bodies (Mitchell, 1972). It produces a horizontal rhizome 60-250 mm long (Henderson, 2001) that lies below the water surface, and two types of fronds (buoyant and submerged). Buoyancy is facilitated by the formation of aerenchyma tissue in the stems and leaves (Barrett, 1989). A pair of leaves are green to yellow-green, oval 10-60 mm wide, emergent or floating, and ovate to oblong, while the third is a modified leaf, which occurs at each node, is brown and highly dissected, and hangs underwater, forming a "root"; together (the node and its leaves and "root") they form a ramet. A single ramet or, usually, a cluster of joined ramets forms a plant (Julien *et al*., 2009). It lacks true roots but its submerged fronds function as roots (Smith *et al*., 2006). The floating fronds are positioned at an opposite orientation to each other and are round to oblong in shape. The upper surface of each floating leaf has a prominent midrib and is covered by rows of white, bristly hairs (trichomes), topped with four branches united distally to form a structure resembling an "eggbeater" or "kitchen whisk" which is characteristic of *S. molesta* (Henderson, 2001; Henderson and Cilliers, 2002; McFarland *et al.,* 2004; Julien *et al*., 2009). These hairs give the leaves a velvety appearance and serve as air traps to repel water and aid in flotation. This plant shows considerable phenotypic plasticity, mainly because of environmental conditions such as crowding and nutrient availability (Julien *et al*., 2009). There are three basic forms, associated with degrees of crowding:

Primary (or primary-invading) form; plants with a small leaf, typical of those invading open water. At this stage, the plants produce small, delicate, oval leaves, observed mostly in uncrowded conditions in shade or when grown in a nutrient-rich ecosystem (Harley and Mitchell, 1981).

Secondary (or open water-colonizing) form; stem internodes are longer and larger than in the primary stage, leaves are slightly cupped but do not overlap, and the entire lower leaf surface is in contact with the water. Sizes of the leaves vary widely from about 20 to 50 mm in diameter (McFarland *et al*., 2004).

Tertiary (or mat) form; occurs under crowded conditions typically associated with a mature infestation. This form is a relatively robust with short internodes; the leaves are large (up to 60 mm in diameter), heart shaped or oblong, and deeply keeled. As crowding increases, the leaves are pushed upward to erect and may become packed into mats up to one meter thick (McFarland *et al.,* 2004).

As a reproductive system, the mature plant produces egg-shaped, slender-tipped sporocarps that develop in elongated chains along the submerged fronds (GISD, 2019b) but spores are rarely found, and when present, the spores are generally deformed and nonviable because it is pentaploid (2n=45) (Loyal and Grewal, 1966; McFarland, *et al*., 2004; GISD, 2019b). As a consequence, *S. molesta* is sterile and can only reproduce asexually (Coetzee and Hill, 2009). Rhizomes of the plant can break very easily, and daughter plants arise from buds. In calm waters, fragmentation occurs when older ramets senesce, causing the plant to break, or due to mechanical damage such as from human activities, winds or water currents (Harley and Mitchell, 1981; Room, 1983, 1990).

Temperature and nutrients are the key factors affecting growth of *S.molesta* (Julien *et al*., 2009). However, other factors such as pH and conductivity also affect its growth (McFarland *et al*., 2004). The optimal temperature for growth is 30°C, and below 10°C or above 40°C, growth stops (Room, 1986a, b). Temperatures below 3°C and above 43°C are lethal to buds during exposures of over 2 hours (Whiteman and Room, 1991). Dissolved nutrients, especially Nitrogen (N) and Phosphorus (P), play an important role in determining the growth rate and morphological characteristics of the species (Julien and Bourne, 1986; Room and Thomas, 1986a, b; Coetzee *et al*., 2019). If tissue concentrations reach approximately 5 % or more for N and 0.5 % or more for P, growth ceases (Cary and Weerts, 1983a, b; Room, 1986b).

In Australia and Papua New Guinea, N tissue concentrations ranged from 0.62 to 4.0 % and P tissue from 0.03 to 1.07 % dry weight (Room and Thomas, 1986a, b).

Salvinia molesta is native to south-eastern Brazil, in the subtropical zone, in the States of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (between latitudes 24º05'S and 32º05'S), extending inland to an elevation of about 900 m (Forno and Harley, 1979; Forno, 1983), and also in Argentina, Colombia and Guyana (GISD, 2019b). It was first observed outside its native range in Sri Lanka in 1939 (Williams, 1956) and since then has become widespread and poses a serious problem for aquatic ecosystems in more than a hundred countries (Figure.1.2).

Water lettuce (*Pistia stratiotes*)

Order: Arales

Family: Araceae

Subfamily: Aroideae

Scientific name: *Pistia stratiotes* L.

Synonyms: *Pistia spathulata* Michaux, *P. stratiotes* var. cuneata Engl., *P. stratiotes var. linguiformis* Engl., *P. stratiotes var. obcordata* (Schleid.) Engl., *P. stratiotes var. spathulata* (Michx.) Engl., *Zala asiatica* Loureiro, *Apiospermum obcordatum* (Schleiden) Klotzsch, *Limnonesis commutata* (Schleiden) Klotzsch, *Limnonesis friedrichsthaliana* Klotzsch, *Pistia aegyptiaca* Schleiden, *Pistia aethiopica* Fenzl ex Klotzsch, *Pistia africana* C. Presl, *Pistia amazonica* C. Presl, *Pistia brasiliensis* Klotzsch, *Pistia commutata* Schleiden, *Pistia crispata* Blume, *Pistia cumingii* Klotzsch, *Pistia gardneri* Klotzsch, *Pistia horkeliana* Miquel, *Pistia leprieurii* Blume, *Pistia linguaeformis* Blume, *Pistia minor* Blume, *Pistia natalensis* Klotzsch, *Pistia obcordata* Schleiden, *Pistia occidentalis* Blume, *Pistia schleideniana* Klotzsch, *P. stratiotes* Linnaeus, *var. obcordata* (Schleiden) Engler, *Pistia texensis* Klotzsch, *Pistia turpinii* Blume, *Pistia weigeltiana* C. Presl. (http://www.theplantlist.org; http://florida.plantatlas.usf.edu/Plant.aspx?id=4002#synonym; EPPO, 2017).

Pistia stratiotes is a perennial herb, free-floating, stoloniferous plant with sessile leaves in rosettes. The upper sides of the leaves are light green, while the undersides are almost white, up to 40 cm long, covered by short hairs, mostly spatulate to broadly obovate with a rounded to truncate apex, with 7-15 prominent veins radiating fanwise from the base. Both surfaces, in particular the lower surface, are covered by a dense mat of white woolly hairs which trap air bubbles and thus enable buoyancy (Cook *et al.,* 1974; Aston, 1977; Neuenschwander *et al.,* 2009; EPPO, 2017). Root systems are large and feathery, hanging freely in the water. Inflorescences are axillary, solitary and inconspicuous (7–12.5 mm) with short peduncles in the centre of the rosette, growing on a stem. The spadix, enclosed in a whitish spathe, is pale green, hairy outside and glabrous inside. The spathe generally shows a constriction between the groups of male and the female flowers (Neuenschwander *et al*., 2009). Flowers are unisexual, pale green or white. They contain two stamens, one locular ovary (with numerous ovules), a slender style and penicillate stigma. Fruits are thin-walled andmany-seeded. Seeds are cylindrical and rugulose (Henderson, 2001; Acevedo-Rodríguez and Nicolson, 2005).

The plant reproduces both sexually and through vegetative budding (Coetzee and Hill, 2009), but in many parts of its adventive range the plant does not reproduce sexually (Neuenschwander *et al*., 2009). In the case of sexual reproduction, a dense layer of seeds, which can reach 4,000 seeds/m^2 at the bottom of the water column, can germinate at a lower temperature limit of 20°C, although vegetative reproduction is thought to be the primary means of propagation. The plant reproduces rapidly by vegetative fragmentation from offshoots on short, brittle stolons (Thayer *et al*., 2018).

Pistia stratiotes grows in a very wide variety of aquatic habitats, it prefers relatively stagnant water. Plant growth is optimal at temperatures between 22 and 30°C and high-nutrient conditions (Pieterse *et al*., 1981; Henry-Silva *et al*., 2008). However, the plant still develops at temperatures as low as 10°C (Pieterse *et al*., 1981; Hussner, 2014), although its seeds can survive submerged in water that is 4°C for at least 2 months and a few weeks in ice at -5°C (Parsons and Cuthbertson, 2001). *Pistia stratiotes* has a low salinity tolerance, at 2.5 ‰, plants died (Haller *et al*., 1974). Chadwick and Obeid (1966) reported that pH 4 is approximately the optimal growth of *Pistia* stratiotes. However, Pieterse *et al.* (1981) found that the growth optimum of *P. stratiotes* was at pH 7.

According to Holm *et al.* (1977), *Pistia stratiotes* is one of the most widely distributed hydrophytes. It has a cosmopolitan distribution throughout tropical and sub-tropical regions. Several authors have attempted to delineate the status of *P. stratiotes* in various parts of the world, and these sometimes give conflicting information regarding its origin. Information based on fossil and phylogenetic analysis revealed the status of *Pistia stratiotes* as native to Madagascar (Renner and Zhang, 2004). The oldest records of the genus *Pistia* date back to the Late

Cretaceous period, between 90 and 85 million years (my) ago, and the genus likely originated in the Tethys region (Renner and Zhang, 2004). The first fossil of *Pistia* known from seeds was recorded from the Late Oligocene/Early Miocene and mid-Miocene (18 to 16 my) (Friis, 1985; Kvacek, 1998). The isolation of the Seychelles archipelago from Madagascar and India in the Late Cretaceous period (85 my ago), and the close genetic relationship between *P. stratiotes* (a pantropical species) and *Protarum sechellarum* Engl. (Araceae) (a species endemic to the Seychelles), provide evidence for the ancient origin and common evolutionary pathway of these two species (Renner and Zhang, 2004). The U.S. Fish and Wildlife Service (2018) compiled a list indicating status, based on several references, which is summarized in Table 1.4.

Table 1.4. Biogeographical status of *Pistia stratiotes* around the world, according to several authors.

Status	Countries	References
Native	Pantropical, occurring on all continents except Antarctica	Holm *et al.* (1977); Adebayo *et al*. (2011); Thayer *et al*. (2018).
	South America (Brazil and Argentina)	Henderson and Cilliers (2002); Center *et al*. (2002); Coetzee and Hill (2009); Neuenschwander *et al.* (2009).
	Madagascar, Comoros, Africa, New World	MBG (http://www.tropicos.org/Name/2103622?projectid=17)
	Northern Territory of Australia	Parsons and Cuthbertson (2001)
Introduced	Australia	Blake (1954)
Introduced and invasive	Central America, Africa and South-East Asia Brazil, Chile, and the Solomon Islands. Botswana, Brunei Darussalam, Cambodia, Canary Islands, China, Cook Islands, Cuba, French Polynesia, Indonesia, Laos, New Caledonia, New Zealand, Palau, Réunion, Slovenia, and Taiwan	CABI (2018)
Introduced	India, Kazakhstan, Portugal, Romania, Russian Federation, Seychelles, Saint Lucia, and Ukraine	CABI (2018)
Alien, invasive, and established	Australia, Burkina Faso, Reunion, and Eswatini	GISD (2017)
Alien, established and invasiveness unspecified	Bermuda, French Polynesia, Papua New Guinea, and Saint Lucia	GISD (2017)
Alien and eradicated	New Zealand	GISD (2017)
Introduced	Bangladesh and Pakistan	Pallewatta *et al.* (2003)
Introduced	Okinawa and Ogasawara [Japan].	NIES (2018)

Introduced	Serbia	Živković *et al.* (2019)
Ephemeral population	Netherlands, the Erie Canal in upstate New York and in Lake Erie in northern Ohio, southeast of the Hague	Dray and Center (2002); Pieterse *et al.* (1981)
Uncertain (present but without an indication of native or introduced status)	Afghanistan, Angola, Antigua and Barbuda, Argentina, Australia, Bangladesh, Belize, Bolivia, Burundi, Cameroon, Canada, Central African Republic, Chad, Colombia, Comoros, Democratic Republic of Congo, Costa Rica, Dominican Republic, Ecuador, Egypt, El Salvador, Equatorial Guinea, Ethiopia, France, French Guiana, Gabon, Gambia, Germany (formerly present), Ghana, Guadeloupe, Guatemala, Guinea, Guinea-Bissau, Guyana, Haiti, Honduras, Israel, Jamaica, Japan, Lesotho, Liberia, Madagascar, Malawi, Martinique, Mauritania, Mauritius, Mexico, Montserrat, Morocco, Mozambique, Myanmar, Namibia, Nepal, Nicaragua, Niger, Nigeria, Pakistan, Panama, Papua New Guinea, Paraguay, Peru, Rwanda, Saint Vincent and the Grenadines, Senegal, Sierra Leone, Singapore, Somalia, Spain, Sri Lanka, Sudan, Suriname, Eswatini, Tanzania, Togo, Trinidad and Tobago, Uruguay, Venezuela, Vietnam, Zambia	CABI (2018)
Uncertain (present and invasive but without an indication of native or introduced status)	Benin, Burkina Faso, Côte d'Ivoire, Kenya, Malaysia, Philippines, South Africa, Thailand, Uganda, Vanuatu, and Zimbabwe.	CABI (2018)
Uncertain (cryptogenic, established, and invasiveness unspecified)	Cambodia, China, Cook Islands, Indonesia, Malaysia, New Caledonia, New Guinea, Philippines, Seychelles, Solomon Islands, Thailand, Vanuatu, and Vietnam	GISD (2017)
Uncertain (established with both status and invasiveness unspecified)	Guadeloupe, Martinique	GISD (2017)

Red water fern (*Azolla filiculoides*)

Order: Salviniales

Family: Azollaceae

Scientific name: *Azolla filiculoides* Lamarck

Synonyms: *Azolla caroliniana* Willd., *Azolla majellanica* Willd., *Azolla arbuscula* Desv., *Azolla squamosa* Molina (Cambron *et al.,* 2017)

Azolla filiculoides is a very small perennial aquatic fern, about 1-2 cm in overall width, and rarely more than 2.5 cm (Hill and McConnachie, 2009). It has a branched rhizome, with small, alternate, overlapping leaves called fronds, and roots hanging in the water (Ashton, 1974). Fronds are hydrophobic on their upper part. They spread horizontally on the surface of the water as the plant grows. These fronds are small, green or sometimes pink, orange or red. Their underside is covered with hair. Like other Azolla species, *A. filiculoides* has a symbiotic relationship with the cyanobacterium *Anabaena azollae*; it can therefore fix atmospheric nitrogen. These bacteria play a role in explaining the nitrogen-binding capabilities that allow the plant to grow even in low Nitrogen habitats (Hill and McConnachie, 2009). The plant reproduces both vegetatively by plant fragmentation and sexually by spores (Coetzee and Hill, 2009). It produces heterospores, which are able to resist extreme desiccation and allow the plant to resume its lifecycle after adverse conditions (Hill and McConnachie, 2009).

Combined effects of temperature and light intensity determine the growth rate and the activity of nitrogenenase for nitrogen fixation in symbiosis with blue-green alga *Anabaena azollae* Strasburger (Nostocaceae). In South Africa, Ashton (1982) found that the maximum value growth rates of *A. filiculoides* rangers from 22.5°C at 15 kLux to 27.5°C at 45 kLux and at 45°C, *A. filiculoides* ceases to grow. The experiments conducted by Espinar *et al.* (2015) in the Doñana marshland (Spain) confirms the positive correlation between temperature and the growth rate of *A. filiculoides*. In temperate regions, at -2°C, the plant remains alive and the lethal temperature is -4°C (Janes, 1998). Because *A. filiculoides* has the ability to fix N through its symbiotic relationship with Anabaena, the availability of P is the major limiting factor in its growth (Chakrabortty and Kushari, 1986; Kitoh *et al*., 1993). Regarding pH requirement, the growth rate is optimal and equal over pH range from 5 to 8, and both above and below this range, the growth of *A. filiculoides* declines and reaches zero at pH 3 and 10 (Ashton, 1982).

Azolla filiculoides is native to South America and western North America (Campbell, 1893; Hill and Cilliers, 1999; Hill and McConnachie, 2009). The species has been introduced into many areas outside its native range (Ashton, 1982), including the Old World, and has sometimes become invasive (in several areas of Western Europe, southern Africa, tropical Asia, Australia, New Zealand). According to Szczesniak *et al*. (2009), *A. filiculoides* was first recorded in Europe around the end of the 19th century (1870s-1880s). The plant was introduced to Africa in 1948 as an aquarium plant (Oosthuizen and Walters, 1961; Jacot-Guillarmod, 1979).

1.11.2 Distribution of four invasive alien aquatic weed species in Africa

The four focus species of this dissertation are widespread in all continents, and they are present in almost all African countries, with the exception of Algeria, Djibouti, Tunisia and Western Sahara (Figure.1.2). Globally, *P. crassipes* is present in 110 countries, including 38 in Africa (Labrada and Fornasari, 2002; Dagno *et al.,* 2007; Wise *et al.,* 2007; EPPO, 2008; Coetzee *et al.,* 2017; GISD, 2019a). *Salvinia molesta* occurs in 100 countries including 23 African countries (McFarland *et al.,* 2004; Labrada and Fornasari, 2002; Julien *et al.,* 2009; GISD, 2019b). *Pistia stratiotes* is distributed in 115 countries around the world including 45 countries in Africa (Labrada and Fornasari, 2002; EPPO, 2017; GISD, 2017). Finally, *A. filiculoides* is found in Europe, eastern, central and southern Africa, tropical Asia, North America, Australia and New Zealand and in eight countries in Africa (Lumpkin and Plucknett, 1980; Hill and Cilliers, 1999; Serag *et al.,* 2000; Gratwicke and Marshall, 2001; Henderson 2001; Langa, 2013).

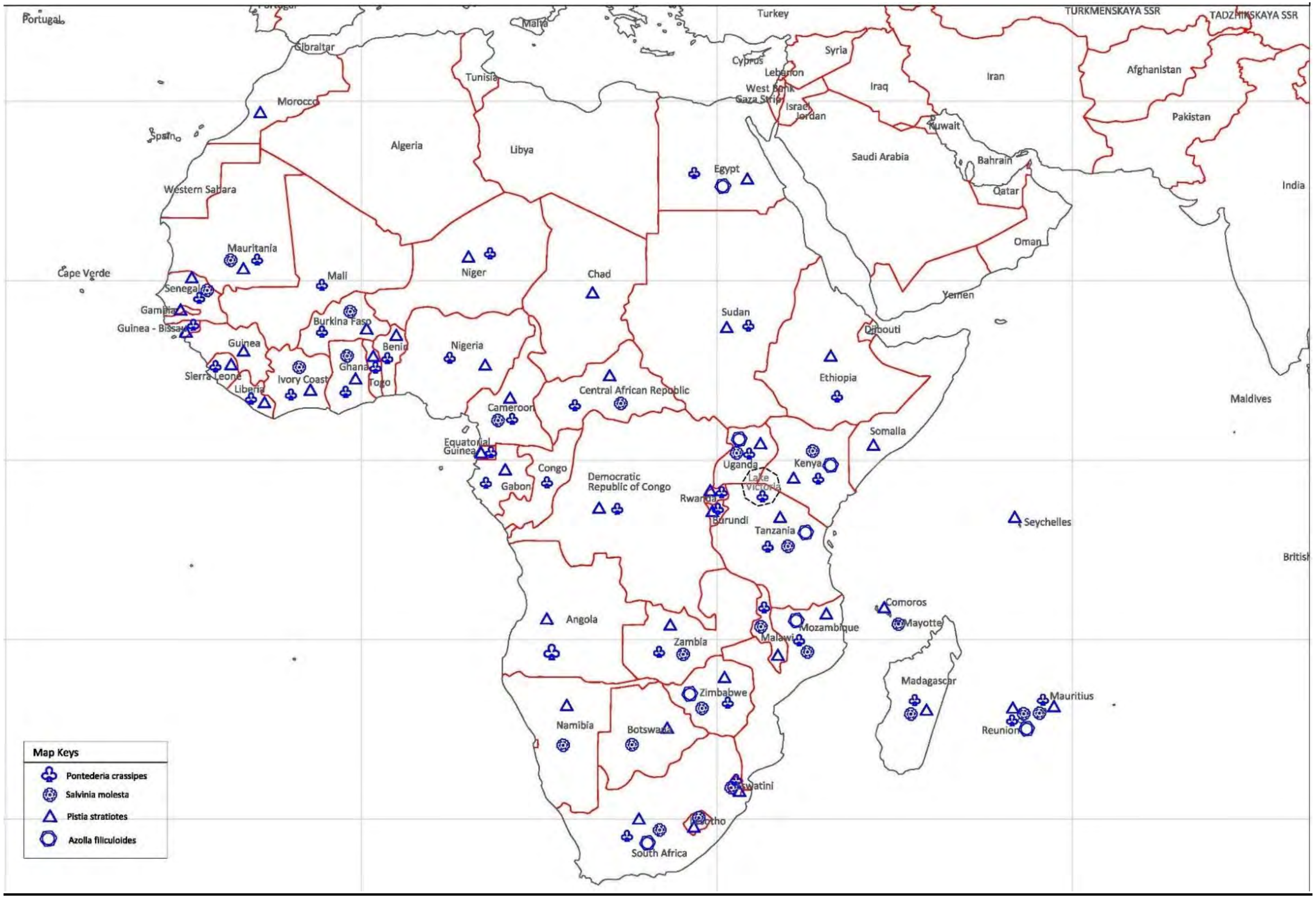

Figure 1.2: Distribution of four invasive alien target species in Africa

1.12 Justification for this research in Madagascar

Nearly a century ago, scientists such as Perrier de la Bathie were aware of the issues related to the presence of aquatic invasive species in Madagascar. It is clear that the 17 invasive plant species associated with wetland ecosystems (Table 1.3), representing 17% of all invasive species, constitute a proven threat to these ecosystems and contribute to the deterioration of the living conditions of the people who depend on them. Aquatic ecosystems offer diverse services such as human food, livestock feed, agriculture, raw materials for handicrafts, pharmacopoeia, fishing, hunting, hydroelectric, drinking water and leisure (Ranarijaona, 1999). Fishing, for example, including both sea- and freshwater fishing, contributes 7% to Madagascar's Gross Domestic Product (GDP) and accounts for around 500,000 direct and indirect jobs (MPRH, 2012; Gyre, 2013). However, these direct benefits and the services provided by aquatic ecosystems are increasingly under threat, as with the case of the blockage of a 645 km length of the Pangalanes canal, from Farafangana to Mahavelona, by *P. crassipes* (among other species), blocking navigation and reducing fishing productivity (Canal des Pangalanes, 2010; Ranarijaona *et al.,* 2013; Ratsirinony, 2018; Acaciasbungalows, 2020). In terms of biodiversity, a few case studies have demonstrated the threats posed by these invasive aquatic species on native Madagascar species, such as at Lake Ravalobe, on an endemic species of freshwater turtle, *Erymnochelys madagascariensis* (Podocnemididae), the fish *Paretroplus maculatus* (damba) (Cichlidae), the birds *Haliaetus vociferoides (*Accipitridae), *Butorides striatus (*Ardeidae) and *Amaurornis olivaceus* (Rallidae) and the golden-brown mouse lemur, *Microcebus ravelobensis* (Cheirogaleidae) (Ranarijaona *et al*., 2013). A study undertaken by the IUCN revealed that more than 40% of Madagascar’s freshwater specis are now being pushed to the edge of extinction, and that competition by aquatic invasive species with native species is one of the main drivers leading to this situation (Máiz-Tomé *et al.,* 2018).

Madagascar positions its invasive species management strategy as a part of the National Strategy and Action Plans for Biodiversity defined by Decree N° 2016-128 of 23 February 2016, adopting the National Biodiversity Strategy and Action Plans projected from 2015 to 2025 (Rabarison *et al*., 2015). The strategic objective 9 states that: "By 2025, alien and invasive species and pathways of entry are identified and prioritised, priority species are controlled or eradicated; management measures are in place to prevent the introduction, manage the pathways and mitigate the establishment of these species and value the beneficial species”. For the strategic objective 9, four actions were defined:

1. Capitalize the knowledge on invasive species at national and regional levels and develop the related database.

2. Develop and implement a National Strategy and programmes to combat the invasive species, emphasising prevention and control while involving the local community in these processes.

3. Promote a regulatory and governance mechanism for invasive species: development of legal and regulatory texts and institutional arrangements.

4. Encourage research for the valorisation of invasive species and set up dissemination/extension programmes.

Madagascar has a strategic plan to promote the control of the invasive species. It was assigned to the National Commission for Biodiversity Coordination (CNCB) to formulate the implementation and monitoring plans. The goals align with those of Aichi,target 9 stating that "*By 2020, invasive alien species and pathways are identified and prioritised, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment*" (CBD, 2013). However, the availability of implementation funding remains one of the challenges in meeting these goals by 2025. To achieve goal 9, Madagascar needs US$ 2 million for 10 years from 2015 to 2025 (Rabarison *et al*., 2015).

It is recognised that there is an urgency of the actions to tackle the risk related to invasive species in Madagascar. Also, stakeholders, including both national and international researchers are fully encouraged to participate in improving the knowledge defined in the actions 1 and 4 described above. This study contributes to the implementation of Strategic Action number 2 of Objective 9, technically and financially. While there is agreement that there are already sporadic data available, especially for the four aquatic invasive species, the information available is not sufficient to formulate effective management plans for these species. To meet target 9 of Aichi, the Convention on Biological Diversity (CBD) states that research and prioritisation will be imperative in order to fill gaps of understanding of current invasions, as well as with new invasions (Turpie *et al.,* 2012).

1.13 Aims of the study and chapter of the thesis

The aim of this research was to determine the distribution, socio-economic, ecological and biological impacts of four invasive alien aquatic weeds in Madagascar and make recommendations for their control. To achieve this aim, a series of studies with set objectives were undertaken which are reported in Chapters 2-5:

Chapter 2: The distribution of invasive alien aquatic weed species in Madagascar. This part of the research assessed the range and stage of invasion throughout the country and attempted to formulate appropriate management strategies for each species.

Chapter 3: The socio-economic impacts of invasive alien aquatic weed species in Madagascar. This study aimed to determine the impacts of the four study on the socio-economic worth and biodiversity of freshwater ecosystems.

Chapter 4: Ecological impacts of aquatic weeds. This study was undertaken at Lake Antsokafina, nearby the village of Andrangazaha, rural commune of Antanifotsy in the District of Soanierana Ivongo. Research was undertaken to determine whether freshwater ecosystem function returned after the control of the three aquatic focus weeds (*P. crassipes*, *S. molesta*, *P. stratiotes)*, with respect to socio-economic and biodiversity components. The dynamics of the vegetation and species were evaluated, taking into account the physico-chemical and biological attributes of the lake.

Chapter 5: Competitive interactions between *S. hastata* and *P. crassipes*, *S. molesta*, *P. stratiotes* and *A. filiculoides.* As *S. hastata* is native to Madagascar, it was important to understand how this species interacts with the invasive species, to determine whether populations of the native species were threatened through interspecific competition.

The Chapter 6: General Discussion and Recommandations places our findings into a global context, acts as a conclusion of the study, and puts forward recommendations for appropriate actions to align with the national strategic plan going forward.

Chapter 2: Distribution of the invasive alien aquatic weed species *Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch. and *Azolla filiculoides* Lam. in Madagascar

2.1 Introduction

As soon as an invasive species has crossed the various barriers (see Chapter 1) and has become naturalised or invasive, the use of post-border early detection and rapid response (EDRR) is the first important intervention to limit its expansion and is the key to successful and cost-effective eradication (ISSG, 2000; Wittenberg and Cock, 2001; Lizzio *et al.*, 2009). According to Wittenberg and Cock (2001), in this phase, the strategy should first include both species and site-specific studies before moving on to an eradication attempt. Site-specific studies allow us to understand the weed's current distribution, the potential ratio, i.e. the percentage of the distribution which is currently occupied by the weed and its maximum potential for spread, and future potential distribution based on various climate change scenarios (FAO, 2006; Lizzio *et al.,* 2009). Sometimes EDRR interventions are too late, or are not undertaken, and the species can spread. In this case, a strategic intervention plan is needed to reduce or eliminate the impacts of the established invasive species. These interventions may include containment and/or control (Wittenberg and Cock, 2001; Lancar and Krake, 2002; Soubeyran, 2008; IUCN, 2018).

For these actions, mapping of the extent of the invasive alien plant (IAP) is essential. Mapping allows managers to know where the species is or likely to be found, as well as informing the prioritisation for interventions, before the population becomes established and spreads to all suitable areas (FAO, 2012). The goal of mapping is to obtain the data necessary to decide how to manage IAPs at local, regional and national levels (ISSG, 2000; Rawlins *et al.*, 2018). Mapping is also vital in assessing the success of any control interventions (Holcombe *et al.*, 2007; FAO, 2012; Rawlins *et al.*, 2018; Riva-Torres *et al.*, 2018), and can also serve as an effective tool in efforts to educate the public about the species (ISSG, 2000; FAO, 2012; CBD, 2014). In mapping IAPs, several methods can be used, depending on the objectives of the program, the level of detail required, and the availability of technical, financial and human resources (Wittenberg and Cock, 2001; FAO, 2012).

2.1.1 Remote sensing

Satellite-based remote sensing may be used to obtain high resolution imagery of IAPs. Remote sensing analyses the vegetation using reflected light across a spectrum from visible to nearinfrared, with wavelengths from 330nm to 2500nm (Schowengerdt, 2007; Thenkabail *et al.*, 2011; Jakubauskas *et al.*, 2012). Spectrum sensors are then able to discriminate the reflected wavelengths, which are different for each plant species depending on physical properties such as chlorophyll absorption and leaf structure (Jakubauskas *et al.*, 2012; Chance, 2014). With ground-truthing, different spectral signals can be associated with a specific plant species.

Several studies have used this technology to map populations of IAPs. For example, Hamilton *et al*. (2013) mapped *Myriophyllum spicatum* L. (Haloragaceae) on Fish Lake in the mountains of south-central Utah, USA with an accuracy of up to 94%[1]. In the Sacramento-San Joaquin Delta in Central Valley, California, Underwood *et al.* (2006) used hyperspectral images to map *Egeria densa* Planch. (Hydrocharitaceae) and *Pontederia crassipes* Mart. (Pontederiaceae) with a precision level of 93% and 73% respectively. Further, Riva-Torres *et al.* (2018) mapped native and invasive plant species in the Galápagos Islands using Landsat8 and high-resolution drone imagery. Finally, Chance (2014) used both hyperspectral images, light detection and ranking data to map the distribution of two understorey invasive plant species in the city of Surrey, British Columbia, Canada with a level of accuracy of 76% for *Rubus armeniacus* Focke (Rosaceae) and 80% for *Hedera helix* L. (Araliaceae).

The benefits of using such technology are: a) it can sample areas that may be inaccessible for field sampling; b) it allows for the detection of rapid changes in plant extent and density (useful for aquatic species) because the images can be easily repeated; c) it can be used to document seasonal and inter-annual changes in the density of the infestation (Jakubauskas *et al.*, 2012). However, the technology is expensive and requires considerable expertise in using the dedicated software to process and interpret the images.

2.1.2 Global Positioning System (GPS)

An alternative for mapping IAPs employs the use of simple tools, such as Global Positioning System (GPS) technology (Rawlins *et al.*, 2018). The approach consists of pinpointing the presence (or absence) of the target species from its geographic coordinates (latitude and longitude), then importing the data into Geographical Information System (GIS) specific thematic layers (e.g. bioclimates, water plans, vegetation types or administrative divisions) and displaying it (Holcombe *et al*., 2007). Software programs such as Arcview or ArcGIS can be

[1]This indicates the degree to which the spectrum can be used to positively discriminate between the target species and the coexisting plants/objects, depending on the pixel values when analysing the images by the object-oriented classification process (segmentation and classification).

used for processing and presenting the data (Holcombe *et al*. 2007), as can programs such as Google Earth. The advantage of this technique is that it is relatively easy to gather and analyse this data and generate maps using a variety of layers. The technique thus allows for public involvement in the mapping process especially since smart phones with GPS facilities are now widespread, which can assist in the early detection of the presence of an invasive species in a previously unrecorded location.

Several data sources are available as initial input informatio, e.g. field trips, and herbarium and online records. In California, USA, for example, the CalWeedMapper program was initiated to build a database for IAP mapping which allowed for public participation (https://www.cal-ipc.org/solutions/mapping/). The approach is very simple, because all that is needed is a smartphone to allow for a photograph of the presumed IAP to be taken, and its geographic coordinates to be recorded. A simple technical guide was developed so that everyone could immediately transmit data from field observations to the database management centre (http://www.calflora.org/entry/poe.html). A similar program was established by the Washington State Department of Agriculture (https://www.nwcb.wa.gov/mapping-noxious-weeds), however, the target area included the entire United States. In addition to the inventories and the online mapping and reporting system, the program accepts herbarium records. This program collaborates with the University of Washington herbarium at the Burke Museum (WTU) to enrich the database.

2.1.3 Bioclimates of Madagascar

Bioclimatic characteristics are principal parameters in determining the classification of ecofloristic zones in Madagascar and the geographical distribution of plant species (Cornet, 1974; Rajeriarison and Faramalala, 1999; Schatz, 2001; Gautier *et al.,* 2018) and can be important in explaining the distribution of IAP species. For Madagascar, Cornet (1974) defined five basic bioclimatic regions subdivided into several bioclimatic zones, based on temperature, altitude, precipitation, water deficits and number of dry months (Table 2.1). These different zones have been simplified by Schatz (2001) into five bioclimatic regions.

Table 2.1.: Bioclimates and ecofloristic zones of Madagascar

Simplified bioclimatic regions (Cornet, 1974; Schatz, 2001)	Bioclimates of ecofloristic zones (Rajeriarison and Faramalala, 1999; Gautier *et al.* 2018)	Mean annual temperature (°C)	Mean annual minimum temperature (°C)	Mean annual precipitation (mm)	Number of dry months	Climax vegetation
Humid	Equatorial warm, humid and perhumid of low altitude (0-800m asl) (e.g. location Toamasina)	24	>20	>2000	0	Lowland moist, evergreen, humid forest
Sub-humid	Equatorial warm, humid of middle altitude (800-1800m) (e.g. location Mantasoa)	15	10 -15	1500 - 2000	0 - 2	Medium altitude moist, evergreen forest
	Tropical warm, humid of Sambirano region (0-800m) (e.g. location Ambanja)	26	>20	>2000	3 - 4	Lowland moist, evergreen, humid forest
Dry	Tropical warm, sub-humid and semi-arid (0-800m) (e.g. location Maevatanana)	27	>20	500 - 1500	6 - 7	Deciduous forest
	Tropical sub-humid of western slopes (800-1800m) (e.g. location Ambatofinandrahana)	18	15 - 20	1000 - 1500	5 - 7	Savanna and sclerophyllous woodland
Sub-arid	Dry sub- and semi-arid (e.g. location Toliara)	24	15 - 20	<400	8 - 11	Spiny thicket (special vegetation type of Didiereaceae and Euphorbia)
Mountain	Cool to cold, humid, high elevation (1800-2000m) (e.g. location Manjakatompo)	15	10	1000 - 1500	0 - 1	Mountain sclerophyllous forest and bamboo
	Cold, perhumid and high mountainous (>2000m) (e.g. location Andringitra)	10	<0	>2000	0	Mountain thicket

2.2 Aim of the study

The main aim of this study was to assess the distribution of the four targeted aquatic weed species *Pontederia crassipes*, *Salvinia molesta, Pistia stratiotes* and *Azolla filiculoides* across Madagascar. The specific objectives were to:

a) determine the current distribution of the target aquatic weeds;

b) provide a historical account of the introduction of the species;

c) provide useful tools for managing the invasion of the target aquatic weeds for decision-makers and land managers.

2.3 Methodology

The mapping of the four target species was carried out across Madagascar. We chose to use the simple method of capturing of species presence data using a GPS unit during fieldtrips to different parts of the island. In addition, we gathered additional data by consulting herbarium records from Madagascar's national herbarium at the *Parc Botanique et Zoologique de Tsimbazaza* (TAN) and searching other botanical databases available online. This approach based on specis presence, was adopted because it is inexpensive and its simplicity also allowed data collected by colleagues to be integrated into the data set. The data collected could also be utilised in models such as MAXENT to predict suitable areas for the target species (Phillips *et al.,* 2004; 2005; 2006; 2008; Martin, 2013; Martin *et al.,* 2020).

2.3.1 Field trips

Four major field trips were undertaken between August 2015 and June 2020. The first one was undertaken in the northwest of the island, in the vicinity of Mahajanga; the second was in the north towards Antsiranana; the third towards was undertaken in the south-east; and the fourth occurred around the central part of eastern Madagascar in the vicinity of Fenerive-Est (Figure 2.1).

Figure 2.1.: Route of the four planned trips for mapping distribution of the target aquatic species following national roads (in red trace).

Eutrophication, which favours the development of aquatic weeds, is mostly found in association with dwellings (Julien and Bourne, 1986; Room and Thomas, 1986a, b; Coetzee *et al.,* 2019). In Madagascar, large villages and towns are generally located along roads, thus we concentrated our survey efforts along main roads (following Kosaka *et al*., 2010; Wabuyele *et al.*, 2014) to maximise the likelihood of encountering the target aquatic weed species.

When a species was detected, the geographic coordinates (latitude and longitude, elevation) were recorded and photographs and herbarium specimens were taken for verification of identification. In addition, for each encounter, we estimated the Gross Area (extent of occurrence), which was defined as of the extent of waterbody area, not necessarily occupied by invasive species, and the Infested Area (area of occupancy), which was the area within the Gross Area that was actually covered by the invasive species (Rawlins *et al.*, 2018).

The survey intervals (distance) used between sampling points for roadside surveys in the literature is varibale (Thapa *et al.*, 2018). In East Africa, Wabuyele *et al.* (2014) used 25 km intervals for *P. hysterophorus* (Asteraceae); in Arunachal Himalaya, India, Kosaka *et al.* (2010) used 5-30 km intervals for 18 invasive alien plants and in Western Himalaya, in Nepal and India, Thapa *et al.* (2018) used 5-10 km intervals for their survey for 11 invasive plants. In our study, the distance chosen was 5-10 km between survey points. However, if the elevation changed dramatically within a short distance, the survey interval distance was reduced, as little as 1 km.

2.3.2. Herbarium records

In Madagascar, two herbaria are available: the TAN herbarium, located in the *Parc Botanique et Zoologique de Tsimbazaza* (PBZT); and the TEF herbarium at Ambatobe, both in the capital city of Antananarivo. At TEF, only specimens of woody plants are stored. Thus, research was only conducted at the TAN herbarium. In this herbarium, plant specimens are classified by Family, which made searches for the target species of this study quick and easy. We recorded all the information pertaining relating to the collection data (date of collection, geographic coordinates, description of locality, names of the collectors) and all the specimens were photographed for infield reference.

2.3.3. Online data

The TROPICOS website (https://www.tropicos.org/home), managed by Missouri Botanical Garden (MBG), constitutes the main database of plants in Madagascar. A large proportion of the specimens from earlier botanical collecting were sent abroad, mainly to the *Muséum National d'Histoire Naturelle* (MNHN) in Paris and to the MBG herbarium in Missouri. All the more recent specimens are available online in the TROPICOS database. If a greater level of detail on each species was required, the Tropicos to the Catalog of the Plants of Madagascar (http://legacy.tropicos.org/Name/26100027?projectid=17) was consulted.

2.3.4 Data analysis

All datasets of the four invasive species derived from fieldtrips, the herbarium, colleagues and online databases were represented in a spatial format to facilitate visualization of species distribution (Holcombe *et al.,* 2007). Using the QGIS 2.18 visualization software and superimposing the data onto the databases (bioclimatic data of Cornet (1974); water bodies; administrative divisions), we obtained various spatial representation maps for each species. The data-processing actions that were performed are indicated in Figure 2.2.

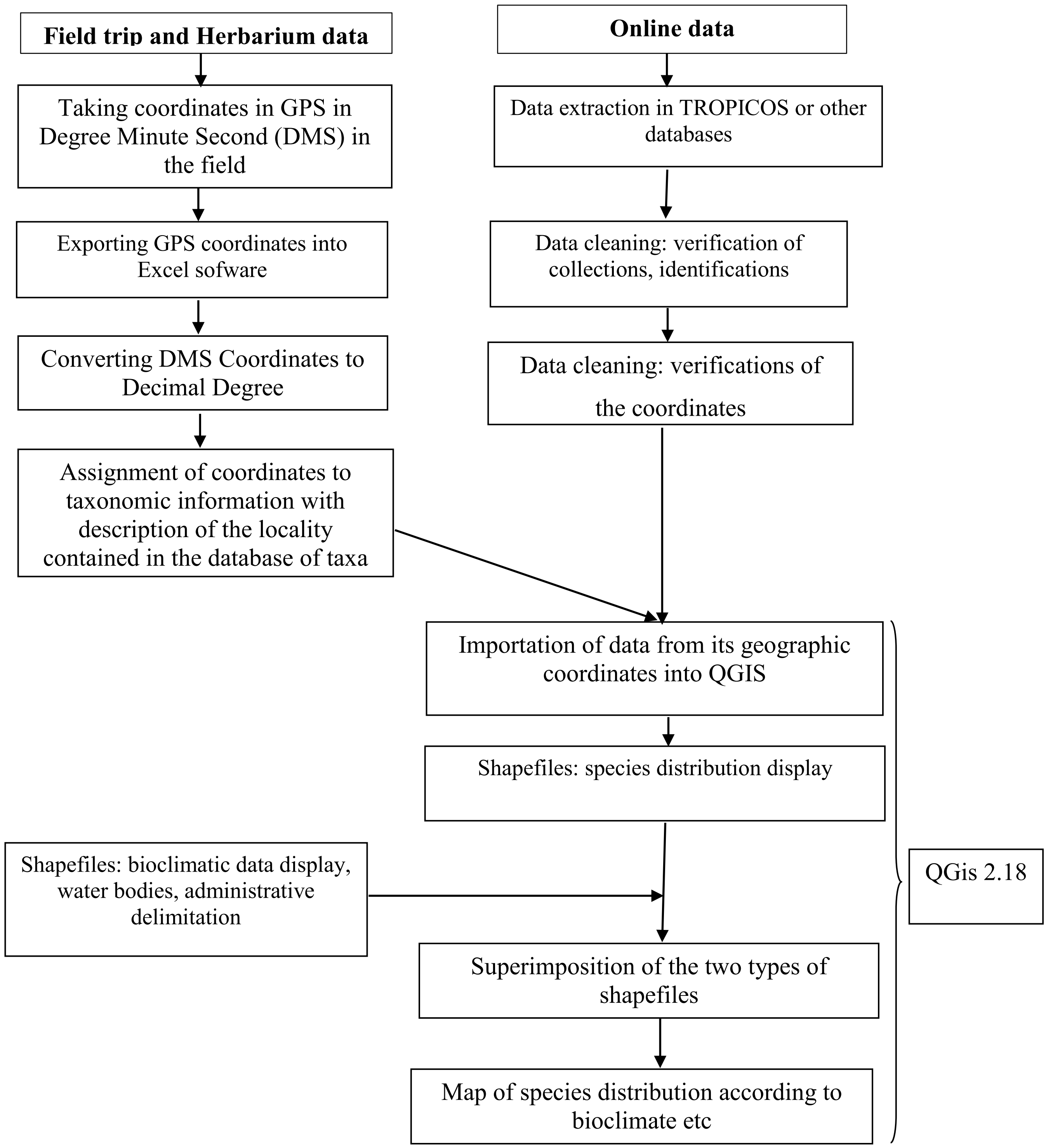

Figure 2.2.: Process of data analysis for invasive species in Madagascar

2.4. Results

2.4.1 Overall distribution of the four target invasive aquatic species in Madagascar

The data compilation from three sources discussed above (field trips, herbarium, online information) provided a general overview of the distribution of the four target aquatic weed species in Madagascar (Figure 2.4). In total, 18 of the 22 Regions[2] in Madagascar were recorded as being infested with at least one of the target aquatic weed species. There were only four Regions, namely Melaky, Bongolava, Androy and Atsimo-Atsinanana, where the target species were not recorded. Of the 18 Regions, six were invaded by all four species, five by three species, six by two species, and there was one Region where only one species was recorded (Table 2.2). No data were available for mountainous areas > 1800 m above sea level (asl), i.e. the Tsaratanana Massif (that overlaps across three regions: Diana, Sava and Sofia), Ankaratra Massif (overlaps across two Regions, Vakinankaratra and Itasy) and Andringitra (overlaps across the regions of Haute-Matsiatra and Ihorombe) (Figure 2.3).

Most of the data used for these maps came from the data collection trips along roads that were designated as part of this study. These included the *Route Nationale* 4 (RN4, Antananarivo to Mahajanga), RN6 (Antananarivo to Antsiranana), RN7 (portion of road from Antananarivo to Alakamisy-Ambohimaha), RN25 (Alakamisy-Ambohimaha to Mananjary), RN12-A (portion of road from Irondro to Vohipeno), RN5 (Foulpointe to Soanierana-Ivongo) and RN22 (Antsokafoka to Vavatenina). Remarkably few herbarium specimens for these species existed and thus few data were obtained from TAN and from online botanical databases.

Table 2.2.: Number of aquatic weeds present in the Regions of Madagascar. For placement of Regions and bioclimates, see Figure 2.3.

Region	Number of aquatic weeds present	Species	Bioclimate
Alaotra-Mangoro	3	*S. molesta, P. crassipes, A. filiculoides*	Humid and sub-humid
Amoron'i Mania	2	*S. molesta, A. filiculoides*	Sub-humid and humid
Analamanga	4	*P. crassipes, S. molesta, P. stratiotes, A. filiculoides*	Sub-humid
Analanjirofo	4	*P. crassipes, S. molesta, P.stratiotes, A. filiculoides*	Humid and a small part sub-humid

[2]Madagascar is divided into twenty-two administrative Regions with each, currently led by a governor and technical staff who plan and implement all regional development programs.

Anosy	1	*P. stratiotes*	Subarid, sub-humid, humid
Atsinanana	4	*P. crassipes, S. molesta, P. stratiotes, A. filiculoides*	Humid and a small part sub-humid
Atsimo-Andrefana	2	*P. crassipes, A. filiculoides*	Subarid, dry and a small part sub-humid and humid
Betsiboka	3	*P. crassipes, S. molesta, A. filiculoides*	Dry and sub-humid
Boeny	3	*P. crassipes, S. molesta, P.stratiotes*	Dry
Diana	4	*P. crassipes, S. molesta, P. stratiotes, A. filiculoides*	Dry and sub-humid and a small part of the region is mountainous
Haute Matsiatra	2	*S.molesta, A. filiculoides*	Sub-humid and a small part dry and mountainous
Ihorombe	3	*S. molesta, P. stratiotes, A. filiculoides*	Humid and mountainous
Itasy	3	*P. crassipes, S. molesta, P. stratiotes*	Sub-humid and a small part mountainous
Menabe	2	*P. crassipes, P. stratiotes*	Dry, sub-arid and a small part sub-humid
Sava	2	*P.crassipes, S. molesta*	Humid, dry and a small part mountainous
Sofia	4	*P. crassipes, S. molesta, P. stratiotes, A. filiculoides*	Humid and dry and a small part mountainous
Vakinankaratra	2	*S.molesta, A.filiculoides*	Sub-humid and a small part dry and mountainous
Vatovavy-Fitovinany	4	*P. crassipes, S. molesta, P. stratiotes, A. filiculoides*	Humid and a small part sub-humid

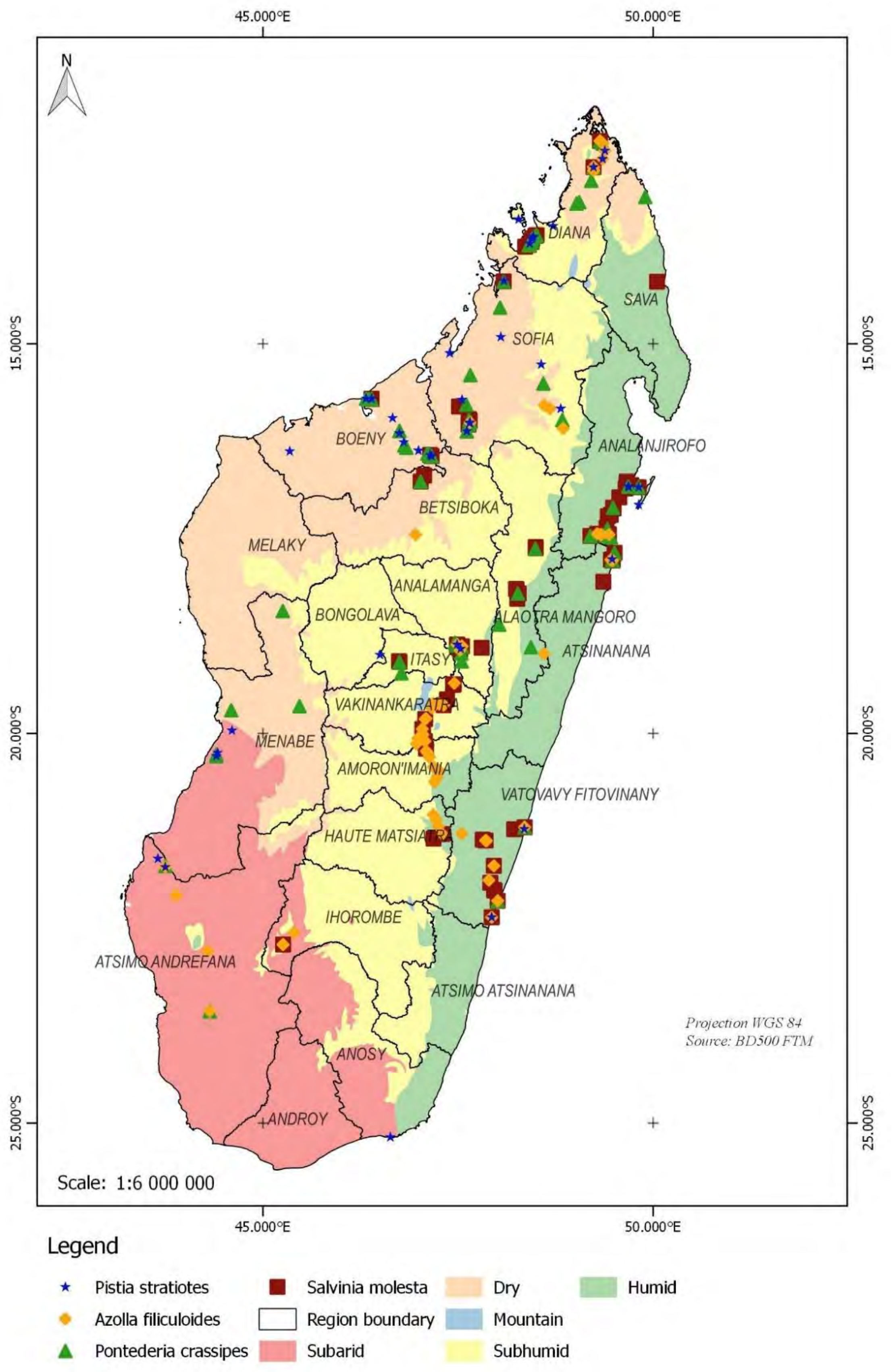

Figure 2.3.: Distribution of the four target invasive aquatic weeds according to the Regions and bioclimates of Madagascar.

2.4.2 Distribution and history of spread of *Pontederia crassipes*

Pontederia crassipes was recorded in 13 Regions of Madagascar, namely Alaotra-Mangoro, Analamanga, Analanjirofo, Atsinanana, Atsimo-Andrefana, Betsiboka, Boeny, Diana, Itasy, Menabe, Sava, Sofia and Vatovavy-Fitovinany. This species was found in all bioclimates, except in the mountainous region, extending over a range of elevations from 0 to 1429m asl (Figure 2.4). Most of the records of the species were derived from field trips.

In moving water bodies, especially in rural areas, the infested area (area of occupancy) was small, ranging from less than half a hectare to a few square metres, while for lentic water bodies (lakes, swamps etc.), infestations were sometimes very large, even covering several hectares. Examples included (i) Lake Ambondromifehy (12°54′23.2″S 049°12′29.5″E), in the rural municipality of Anivorano, Diana Region, where almost half of the lake (about 1.5ha) was infested; (ii) Lake Manompa (18°25′44.5″S 045°15′15.4″E), in the rural town of Ankijabe, Boeny Region, and Lake Amparihely (16°07′25.2″S 047°36′48.7″E), in the municipality of Mampikony, Sofia Region, which each had an invaded area of more than 50ha, with infestations being seasonal and sometimes very heavy. In urban areas, such as in the capital Antananarivo, and in several towns like Mahajanga, Ambilobe and Maromandia, many sporadic lakes were heavily infested by *P. crassipes*. Sewers discharging into the water bodies of these cities, made conditions very favourable for the growth water hyacinth due to eutrophication. In the Pangalanes canal, connecting the town of Farafangana to Foulpointe, the water hyacinth biomass contributed significantly to the plugging of the canal, especially in the northern part of Toamasina. In Antananarivo, the species invaded large rice fields, resulting in their abandonment in several cases, due to excessive biomass.

With regards the history of *P. crassipes* in Madagascar, the earliest collection of the species dates from 1931, when a specimen was collected by the agricultural service in the vicinity of Antananarivo. This specimen is conserved in the Tsimbazaza herbarium. From this date to 2010, only six botanical specimens were collected, all from the vicinity of Antananarivo. From 2010 to 2016, a Madagascar Aquatic Plant Inventory Program was initiated by the Missouri Botanical Garden. Through this program, the surveys and collections were expanded beyond Antananarivo, gathering 10 additional records across different regions of the island. The largest proportion of the data used in the current distribution-mapping exercise came from the mapping missions executed during the current study, which added 54 new localities. Thus, in total, in Madagascar, this species has now been recorded at 70 locations throughout Madagascar.

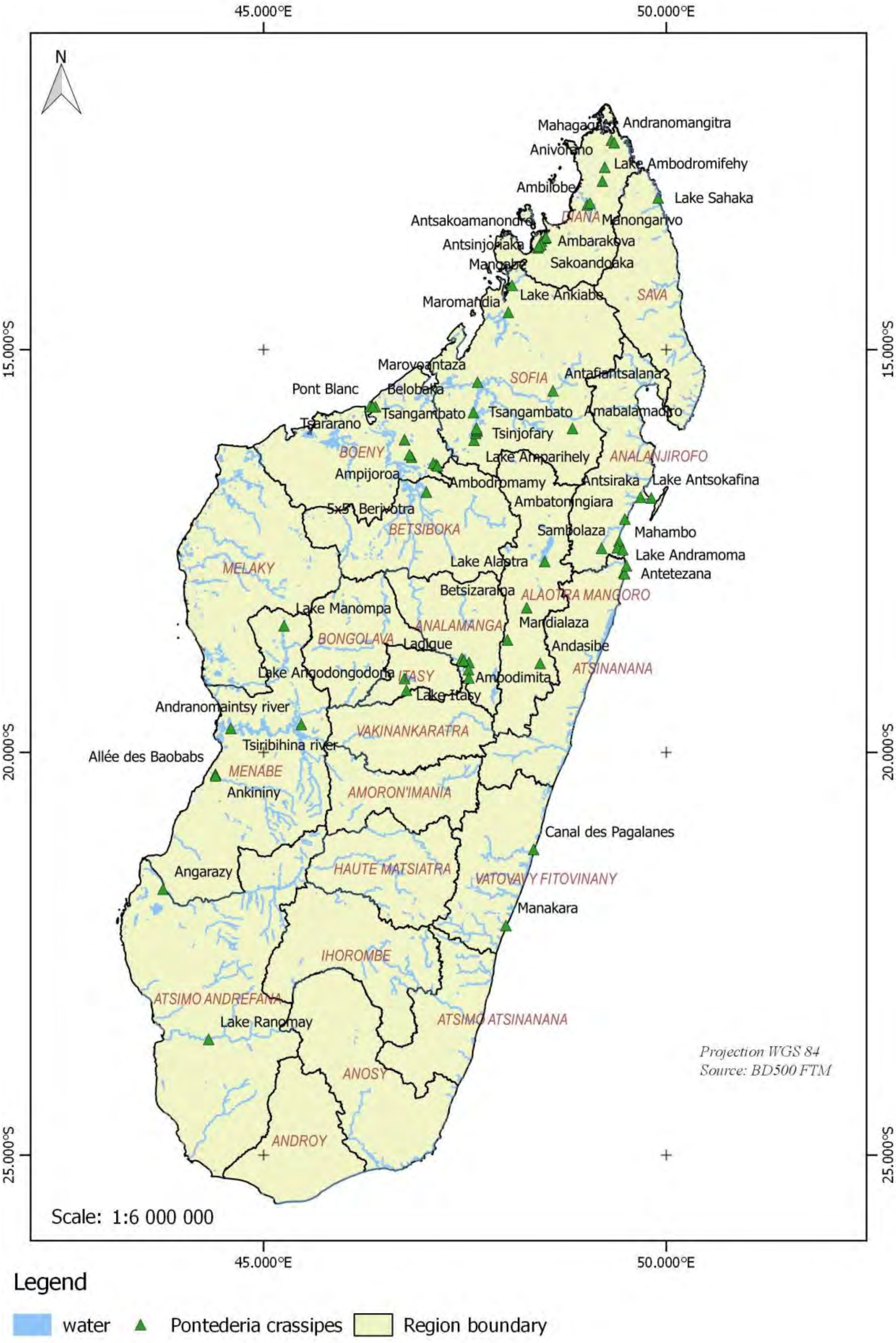

Figure 2.4.: Distribution of *Pontederia crassipes* in Madagascar

2.4.3 Distribution and history of spread of *Salvinia molesta*

Using the three data types of sources (herbarium, online data and fieldtrip), *S. molesta* was recorded in 14 Regions in Madagascar, namely Alaotra-Mangoro, Analamanga, Analanjirofo, Atsinanana, Betsiboka, Boeny, Diana, Haute-Matsiatra, Ihorombe, Itasy, Sava, Sofia, Vakinankaratra and Vatovavy-Fitovinany. These Regions included four bioclimates (humid, sub-humid, dry and sub-arid), over altitudes ranging from 0 to 1579m asl (Figure. 2.5). In all areas where *S. molesta* was present, it was observed that many different types of water bodies were invaded, especially lentic ecosystems and rice fields. Here, it rapidly expanded to cover the entire body of water (gross area). As the fragments of the plant are readily dispersed, even by a small streams of water, the species is able to colonise large areas. In Antananarivo, *S. molesta* was ranked by rice growers as the most noxious among aquatic weed (Chapter 3). In all the ecosystems conducive to its development (lakes, marshes, ponds, rice fields, etc.), it can cover several tens of hectares (up to one hundred hectares). Examples of colonised zones included Lake Andramoma (17°45′59.9″S 049°28′31.6″E), rural commune of Foulpointe, Atsinanana Region, Lake Sarondrano (15°48′25.7″S 047°30′44.6″E), in the rural commune of Ankiririky, District of Mampikony, Sofia Region, and Lake Antsokafina (16°50'20.5"S, 049°41'17.0"E), Rural Municipality of Antanifotsy, District of Soanierana Ivongo, Analanjirofo Region. The carpets formed by the species also contributed to the plugging of the Pangalanes canal (17°46′54.1″S 049°28′56.9″E), making transport difficult or even impossible, on the portion from Toamasina to Foulpointe. Among the four target species of the present study, *S. molesta* was found to be the most widespread in Madagascar.

Regarding the history records of its occurence in Madagascar, its introduction appears to have been much more recent than that of *P. crassipes*. The first collection was made on 03 April 1995 by K. Amstein (Botanist, Prof. and plant Curator, Department of Botany and Nature Conservation, Agriculture, University of Norway) and R. Solohery (Plant Curator, Chief of botanical department at *Parc Botanique et Zoologique de Tsimbazaza*, Madagacar) in shallow water at the western shore of Lake Itasy (19°05′S 046°45″E), Itasy Region. Examination of this herbarium specimen at Tsimbazaza Herbarium revealed that the species was misidentified as *Salvinia hastata* Desv. (Salviniaceae), a closely related, indigenous species. The MBG program inventorying aquatic plants in Madagascar, from 2010 to 2016, resulted in 12 additional collections. However, confusion with the identification of *S. molesta* and *S. hastata,* was not resolved until 2015, when this study was initiated. The majority (67) of records for *S. molesta* of this species were made during fieldtrips conducted during this study along various roads in different parts of the island. The compilation of all records from different data sources gave a total number of 80 locations in Madagascar.

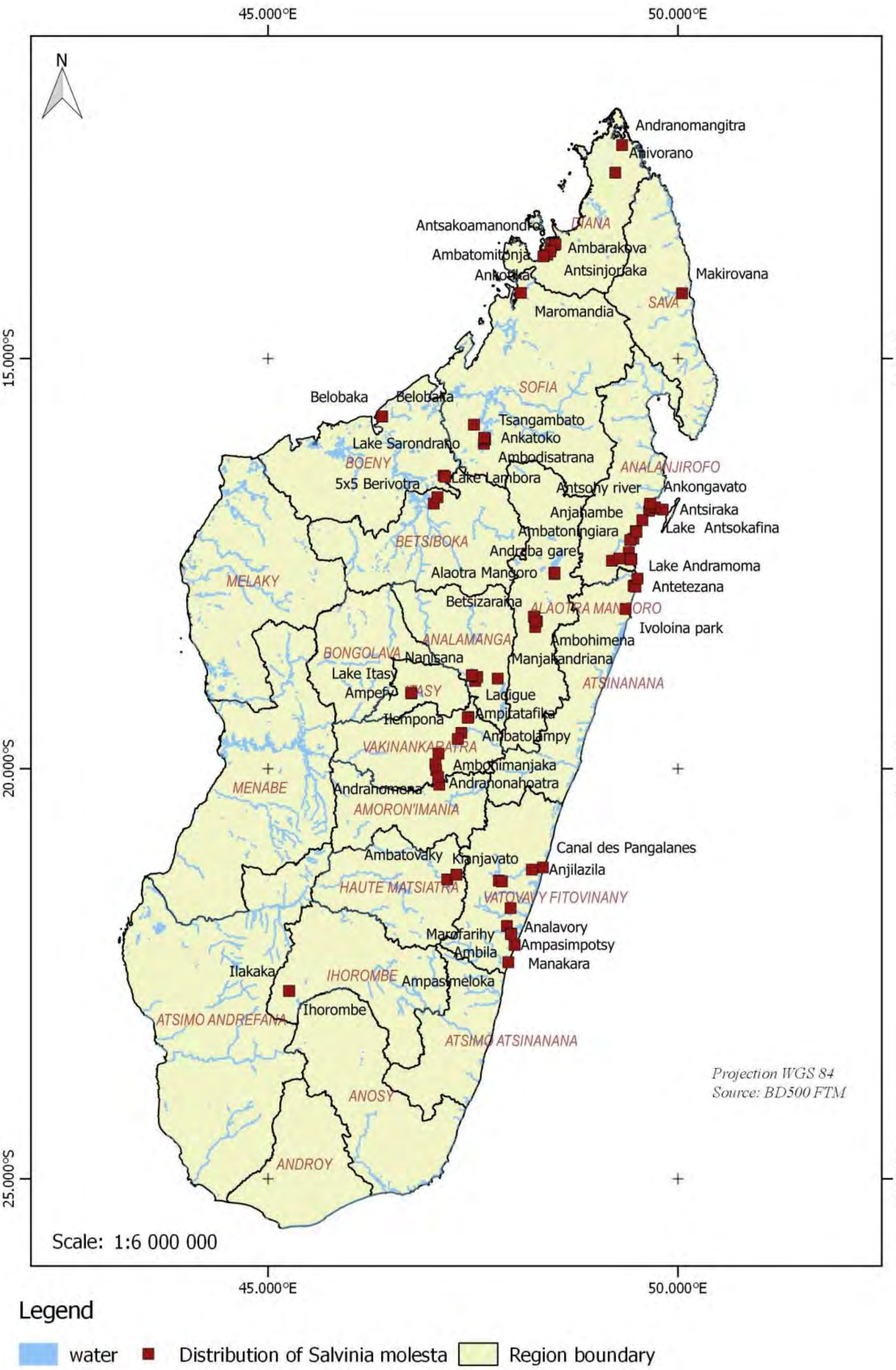

Figure 2.5.: Distribution of *Salvinia molesta* in Madagascar

2.4.4 Distribution and history of spread of *Pistia stratiotes*

The various sources of data regarding the distribution of *P. stratiotes* in Madagascar revealed the presence of the species in 12 Regions: Analamanga, Analanjirofo, Anosy, Atsinanana, Betsiboka, Boeny, Diana, Ihorombe, Itasy, Menabe, Sofia and Vatovavy-Fitovinany. These invaded Regions encompassed all bioclimates, except the mountains, extending over an altitude ranging from 0 to 1255m asl (Figure 2.6). The *P. stratiotes* collection made in January 1905 in Betsiboka region, by J.M.H.A. Perrier de la Bâthie (Botanist, geologist, and explorer of Madagascar, Natural History Museum, Paris), contained no geographic coordinates. Although this species tolerates a wide bioclimatic range, there were very few locations where it was observed behaving as an aggressive invader. However, at Lake Antsokafina, *P. stratiotes* was observed as a primary invader of this water body. This observation merits further investigation to better understand the bioclimatic conditions or physicochemical parameters of the water body under which *P. stratiotes* becomes highly competitive and aggressively invasive.

Regarding the history of spread of the species in Madagascar, *P. stratiotes* has the earliest collection records for the target species investigated in this study. It was first collected in March 1847 by L.H. Boivin (Botanist and explorer, Natural History Museum, Paris) on Sainte-Marie Island (Nosy Boraha). The second collection was in September 1879 by J.M. Hildebrandt (German botanist and explorer of Madagascar, Horticultural Society, Berlin, Germany) on the island of Nosy Be. Subsequently, at least seven botanical collections were made in different localities: in January 1905 in Betsiboka by J.M.H.A. Perrier de la Bâthie; in April 1909 in Mananjary by M. F. Geay (French pharmacist, naturalist, plant collector of Natural Histoy Museaum of Paris); in April 1921 in Antananarivo, in September 1932 in Fort-Dauphin and in July 1939 in Mandritsara, all three collections by R. Decary (French Colonies Administrator in Madagascar, historian, geographer, ethnographer, ethnologist, linguist and naturalist, and contributor to the Paris National Natural History Museum's Malagasy herbarium) and in April 1942 in Befadriana-Avaratra by the Botanical Garden of Antananarivo. As part of an inventory program of aquatic plants in Madagascar by MBG from 2010 to 2016, seven collections were made. During the current study, 30 new localities were identified, giving a total number of 43 records for Madagascar.

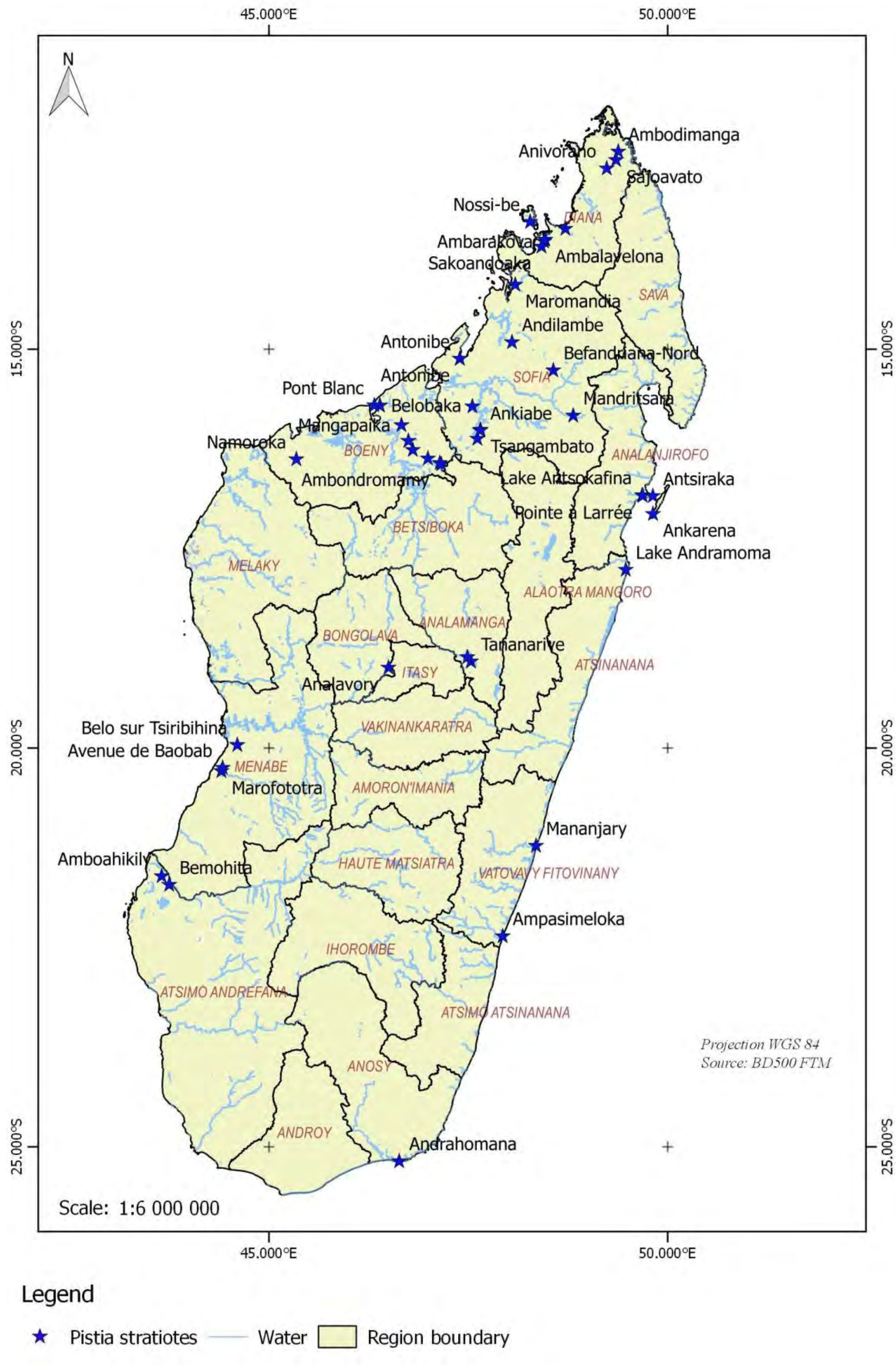

Figure 2.6.: Distribution of *Pistia stratiotes* in Madagascar

2.4.5 Distribution and history of spread of *Azolla filiculoides*

Azolla filiculoides was recorded in 13 Regions of Madagascar, Alaotra-Mangoro, Amoron'i Mania, Analamanga, Analanjirofo, Antsimo-Andrefana, Atsinanana, Betsiboka, Diana, Haute-Matsiatra, Ihorombe, Sofia, Vakinankaratra and Vatovavy-Fitovinany. This species grows in four bioclimates (humid, sub-humid, dry and sub-arid) ranging in altitude from 0 to 1663m asl (Figure 2.7). Our field observations revealed that *A. filiculoides* thrived in almost all types of water bodies, even in slow-moving rivers, e.g a river near the village of Ampisavankaratra (17°27′S 046°57′E), close to the road to Mahajanga, in the rural commune of Antanimbarinandriana, District of Maevatanana, Betsiboka Region. In the Regions of Vakinankaratra, Amoron'i Mania, Vatovavy-Fitovinany and Haute-Matsiatra, the species was recorded occupying large expanses in rice fields, up to several hundred hectares in size. For example, close to Manandona, District of Antsirabe II, Vakinankaratra Region, *A. filiculoides* covered more than 60% of the rice fields starting from the villages of Andranomena and Ampasindava (20°01′05.1″S 047°03′05.3″E) to the village of Beronono (20°15′00.9″S 047°06′29.6″E), Rural Municipality of Ilaka, District of Ambositra, Amorin'i Mania Region. On the High Plateau, where rice growers usually fertilize the soil, they sometimes intentionally spread *A. filiculoides* into non-colonised rice fields, in order to increase soil fertility. As the species is easily carried away, even with the slightest current of water, this practice has contributed to the acceleration of spread of the species. In contrast, in coastal areas where the soil generally remains rich in nutrients, rice growers complain about the *A. filiculoides* infestations as it adds too many nutrients to the soil. This reduces the rice crop yield, because the rice grows excessively lush vegetative parts while producing very little grain for harvest. This problem was mentioned many times by rice growers in the Regions of Vatovavy-Fitovinany and Analanjirofo.

With respect to the history of introduction of *A. filiculoides*, prior the start of the current study in 2015, no herbarium specimen of the species had been collected (no specimens found either in the Tsimbazaza herbarium nor using the online data). A few collections of the genus *Azolla* are conserved at Tsimbazaza herbarium, but our verification confirmed that all of them are the indigenous *Azolla pinnata* R.Br (Azollaceae). In 2015, as part of the Inventory of Aquatic Species in Madagascar program, the MBG team made 6 botanical collections of *A. filiculoides* in the Regions of Ihorombe and Antsimo-Andrefana. At this time, however, researchers confused the species with *A. pinnata*. Therefore, a verification was performed, during the current study, on all previously collected specimens. For this species, 62 geographic locations were recorded including all site records; six records on online data (TROPICOS data base) and 56 records from fieldtrips of the current study.

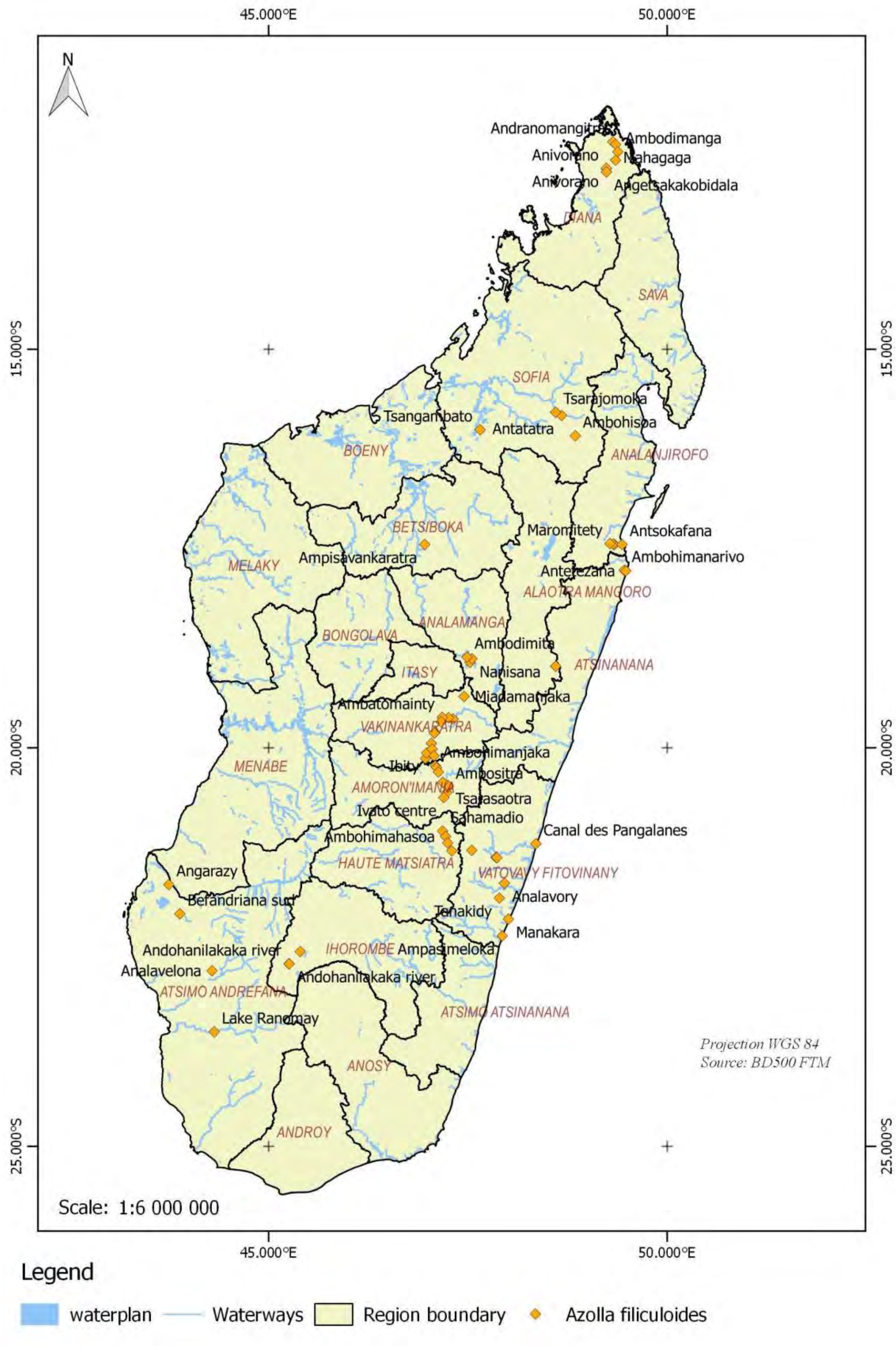

Figure 2.7.: Distribution of *Azolla filiculoides* in Madagascar.

2.5 Discussion

The current study provides a preliminary maps of the distribution of the four invasive alien aquatic species in Madagascar. The approach consisted of gathering data from different sources (herbaria, online data and fieldtrips). A total of 255 records were assimilated, of which 81% were collected during fieldtrips, forming part of this study. These records vary from species to species, with 70 for *P. crassipes*, 80 for *S. molesta*, 43 for *P. stratiotes* and 62 for *A. filiculoides*. Before 2010, the number of botanical collections of aquatic plant species in Madagascar was estimated to be less than 1000 specimens, representing about 0.5% of the total collections at the National Herbarium at Tsimbazaza (TAN), and included fewer than 20 collections for the four invasive aquatic weed species forming part of this study (Manjato *et al.*, 2020, 'manuscript in preparation'). Between 2010 and 2016, the number of collections of aquatic plant species increased due to aquatic species inventory program led by the Missouri Botanical Garden team, resulting in an additional 31 confirmed records for the four aquatic invasive species that form the subject of this thesis. For the current study, it is recognised that there is a lack of quantitative data related to recorded locations of the four target species, especially in Melaky, Bongolava, Androy and Atsimo-Atsinanana, where no records of these species have yet been made. The absence of collections in these areas does not mean that the species are not present there, but rather that no focussed surveys have been carried out in these localities. For the effective management of these invasive species, improved qualitative and quantitative data is highly desirable (following FAO, 2006; Grice, 2009). Nevertheless, the admittedly incomplete data currently available can already inform control of the target species.

Despite their tropical origins, all species were present in all bioclimates of Madagascar, with the exception of the mountain bioclimate – although this bioclimate is rare and little inventoried. Overall, *A. filiculoides* was particularly widespread, especially in the highlands. Although the growth rate of *A. filiculoides* is positively correlated with increasing temperature, the plant can survive temperatures that are close to, and even below, freezing (0°C) (Janes, 1998; Espinar *et al.*, 2015). In Madagascar, this weed thrives under the cooler temperature regime of the sub-humid bioclimate which mainly stretches along the highlands, from south to north (Cornet, 1974). The species was most abundant and widespread in large rice fields and small ponds in Vakinankaratra, Amoron'i Mania, Vatovavy-Fitovinany, Haute-Matsiatra, in the District of Mandritsara, Anivorano in the District of Antsiranana II as well along littoral zones from Toamasina to Fenerive-Est.

For *S. molesta*, the bioclimates favourable to its development were similar to those of *A. filiculoides*, viz. humid or sub-humid, but *S. molesta* thrived best at higher temperatures and in nutrient-rich ecosystems, especially near villages or towns where there was sewage discharge. The optimal temperature for growth of *S. molesta* is 30°C; below 10°C and above 40°C, growth stops, while temperatures below 3°C are lethal to the vegetative buds of the plants (Room, 1986a; Whiteman and Room, 1991). In addition, the species is characterized by rapid growth in nutrient-rich aquatic habitats (Mitchell, 1974; Julien and Bourne, 1986; Room and Thomas, 1986a, b; Coetzee *et al*., 2019). So, the distribution and infestation levels of *S. molesta* are largely determined by the combined effect of temperature, humidity and nutrient level. While *A. filiculoides* was especially abundant in the highland regions, *S. molesta* was abundant both in the highlands and in the coastal lands, invading nutrient-rich water bodies including lentic, lotic and rice-field ecosystems.

The ecological conditions determining the distribution of *P. crassipes* are similar to those of *S. molesta* as both originate from tropical bioclimates (Forno, 1983; Center *et al.,* 2002; EPPO, 2008). In the laboratory, the growth rate is higher for *S. molesta* than *P. crassipes*, with leaf doubling time from about 2 to 4 days (Gaudet, 1973; Mitchell and Tur, 1975; Mitchell, 1979), and from about 1 to 8 days under field conditions (Finlayson, 1984; Room, 1986b), while that of *P. crassipes* is estimated at 11 to 18 days under field conditions (Penfound and Earle, 1948; Parsons, 1963; Mitchell, 1974; Hill *et al.,* 2011). Results from an experiment in Lake Antsokafina, Soanierana Ivongo (see Chapter4), with a humid bioclimate (Cornet 1974), confirmed the high growth rate of *S. molesta* compared to *P. crassipes*. Under field conditions, after one year, *S. molesta* covered 92.13% of the experimental surfaces whereas *P. crassipes* covered only 1.25%. This could partly explain why *S. molesta* was more abundant across the island and that in the places where it occurs, its impacts are significant (see Chapter 3). In addition, the characteristics of the plant, *viz*. high mobility owing to aerenchyma tissue that increases buoyancy and enables movement, and reproduction by fragments, facilitate long distance dispersal of the species, by dispersal vectors such as water level during flooding, humans, wind, fishing equipment, boats, trailers, or other vehicles (Mitchell and Thomas, 1972; Barrett, 1989; Oliver, 1993; Chilton *et al.,* 2002).

Concerning *P. stratiotes*, the species appears to be widely adapted to the different climates of the island, but it was never recorded to form large infestations comparable to those of the other target species. At Lake Antsokafina, Soanierana-Ivongo, the weed was observed to in the process of covering the lake after it had been cleaned, but after a few months, its dominance gradually decreased in favour of *S. molesta* and *P. crassipes*. In Madagascar, *P. stratiotes* is considered a native and non-introduced species (http://legacy.tropicos.org/Name/2103622?projectid=17) and it has never appeared on the list of introduced or invasive species of Madagascar (except in Decary, 1965). In some regions of the island such as Analamanga and Sofia, *P. stratiotes* is called "Tsikafona gasy", which means "Malagasy aquatic weed", as opposed to introduced aquatic weeds (*P. crassipes, S. molesta*). Moreover, some Malagasy people attribute an important spiritual value to this species, especially in the Regions of Sofia and Diana (see Chapter 3).

In many African countries, the origin of *P. stratiotes* is also uncertain (present but without an indication of native or introduced status). These include Angola, Burundi, Cameroon, Central African Republic, Chad, Comoros, Democratic Republic of Congo, Egypt, Equatorial Guinea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau, Lesotho, Liberia, Madagascar, Malawi, Mauritania, Mauritius, Morocco, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, Sudan, Tanzania, Togo, and Zambia (CABI, 2018). Egyptian hieroglyphics and the ancient Greek botanists Dioscorides and Theophrastus record the species from the Nile River, suggesting an African origin (Stoddard, 1989).

In Australia, the origin of the species is also debated. Some authors like Blake (1954) indicated that the species was introduced into Australia some 50 years ago, while others like Gillett *et al.* (1988) presented evidence for it being indigenous in the Northern Territory of Australia. The presence of natural enemies that regulate its population, and the fact that the species has not become a nuisance to the natural habitat in which it grows, constitute evidence that northern Australia may be part of the plant's native range (Parsons and Cuthbertson, 2001). In Madagascar, we suggest that this species should be treated differently, not being of the same status as the three other target species and it needs to be monitored further in Madagascar to ascertain its invasive potential.

The current distribution study of the four target species was carried out based on information from available records which did not completely cover the entire island. This information should be supplemented with modelling of the current and predicted distributions under both current and future climate scearios. Projections of the future range of invasive species based on climate niche models have become increasingly prevalent and useful (Thuiller *et al.,* 2005; Jiménez-Valverde *et al*., 2011). This approach provides a crucial tool for comprehensive assessment and study of aquatic alien plant species distribution and for adopting appropriate measures to control their spread (Pearson and Dawson, 2003). Worldwide, predictive studies based on current and climate change scenarios for the three target species (*P. crassipes, S. molesta* and *A. filiculoides*) have been carried out, which could serve as examples illustrating the importance of models in both present and future management for these species (Kelly *et al.,* 2014).

Kelly *et al.* (2014) studied the changes in the invasive range of 15 invasive aquatic plant species within Ireland, including three of the target species, *viz. A. filiculoides*, *P. crassipes* and *S. molesta* by using regional and global climate niche models. *Azolla filiculoides* is already established as an invasive species in Ireland, while *P. crassipes* and *S. molesta* were listed as potentially high-risk species for establishment in the country. By using MAXENT software, under global climate niche models, and modelling under a predicted climate change regime for 2080, the authors showed that while *A. filiculoides* is likely to expand its suitable range by 7% compared to its current range in Ireland, neither the current nor future climates were predicted to be suitable for *P. crassipes* or *S. molesta*. This study also showed that climate was the single most important variable associated with the range of *A. filiculoides*.

The effects of climate change manifest differently in southern and northern of Madagascar. From 1970 to 2000, in the southern part of the country, with an arid and sub-arid bioclimate, the average temperature increased by approximately 0.2°C, while in the north, with a humid and dry bioclimate, the average temperature increase is estimated to be less than 0.1°C (Rabefitia *et al.,* 2008). The same authors made future climate projections for Madagascar as a whole for the period from 2046 to 2065, averaged over 20 years, confirming that average annual temperatures will increase from 1.1°C to 2.6°C compared to the average for the period 1961-1990. Annual precipitation is predicated to decrease by 6.4% and 7.5% for the climate scenarios of RCP 4.5 and 8.5 respectively by 2050 (Raholijao *et al*., 2019). The changes in these climatic parameters are likely to result in extreme events such as drought and frequent flooding. These climate-change trends will alter the future distribution of aquatic invasive species. For aquatic weeds, temperature is the most defining parameter in predicting potential distribution (FAO, 2006), while Heneidy *et al.* (2019) found that isothermality, temperature seasonality, annual precipitation and precipitation of the driest month were major contributors to the models predicting distribution of *Hydrocotyle umbellata* L. (Araliaceae) and *Salvinia auriculata Aubl. (Salviniaceae)*.

Carrying out a study based on climate-change information in Madagascar is essential and highly recommended for the future, to enable effective and proactive management of these four target species, currently in the saturation phase (see Chapter 3). Although currently these aquatic weeds are already widespread in Madagascar and only mountainous ecosystems above 1800m asl are not infested (at least no records were taken from there), the projected temperature increases of 1.1-2.6°C in 2055 would probably result in an upward extension in the distribution and density of these aquatic weeds (Sciama, 2010; Mooney and Hofgaard, 1999; Engel *et al*., 2011). In a study undertaken by Shrestha *et al.* (2018) on six of the most problematic invasive alien plants of Nepal, a clear shift toward higher elevation was predicted, from 100-2100m asl to 100-2300m asl. Climate-modelling programmes such as Maxent, where the known localities of current infestations for a given species (in Madagascar, or even globally) can be used to obtain potential distribution maps for Madagascar under current and future climate scenarios would enable, (i) predictions of where they are likely currently to occur, and (ii) predictions of where they are likely to spread (Phillips *et al.,* 2004; 2005; 2006; 2008; Martin, 2013; Martin *et al.,* 2020).

An increase in temperature would positively enhance the competitive abilities of aquatic weeds. Due to the enhanced development of their root systems, aquatic weeds would be able to increase their nutrient uptake to the detriment of native species (Coelho *et al.,* 2000; Fan *et al.,* 2013; Zhou *et al.,* 2017). From a socio-economic point of view, the potential impacts of aquatic weeds under the effect of a rise in temperature would be more important. Two phenomena would be responsible for this. Firstly, several studies have argued that the relative growth rates of the four target aquatic weeds are correlated with increasing temperature (Knipling *et al.,* 1970; Room, 1986a; Whiteman and Room, 1991; Janes, 1998; Santamaria and van Vierssen, 1997; Espinar *et al.,* 2015; Eid and Shaltout, 2016). For example, in the Nile Delta, Egypt, Eid and Shaltout (2016) found that relative growth rates of water hyacinth were lowest during the cooler months, October and November (-0.017 g/DM/g/day), whereas highest yields were recorded during the spring months, April and May (up to 0.044 g/DM/g/day). Secondly, urbanization caused by human population increase will amplify eutrophication, and wastewater rich in P and N is favourable to the development of aquatic weeds (Mitchell, 1974; Julien and Bourne, 1986; Room and Thomas, 1986a, b; Gopal, 1987; Wilson *et al*., 2005; Eid and Shaltout, 2016; Coetzee *et al.,* 2019). The combined effect of temperature rise and eutrophication will thus exacerbate the competitive performance of aquatic weeds. The end result would be an increased negative impact on various socio-economic sectors, especially freshwater fishing, rice cultivation and transport. These negative socio-economic impacts would require additional resources and investment into control measures. This in turn would weaken social structures and the broader economy of affected areas, both for rural communities and for the country as a whole. For this reason, it was important to evaluate the current impacts of each of the target species and combined effects on Madagascar's socio-economic aspects in order to propose appropriate measures that had been undertaken in chapter 3.

Chapter 3: The socio-economic impacts of invasive alien aquatic weeds (*Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch. and *Azolla filiculoides* Lam.) in Madagascar

3.1 Introduction

Nature provides humans with a huge number of services, which are referred to as 'ecosystem services'. These services can be used directly, in which case they have 'use values', which can be further divided into 'direct use values' (consumptive use values and non-consumptive use values) and 'indirect use values'. Besides these 'use values', ecosystems provide 'non-use values' services, such as 'existence values', 'option values' and 'bequest values' (Charles and Dukes, 2006). The 'direct use values' involve interaction with nature, including both consumptive use, which refers to products consumed locally or sold in markets, and non-consumptive use, which typically refers to cultural services such as recreation, tourism, and aesthetic, educational and/or scientific value (Charles and Dukes, 2006). These use values are generated by the products resulting from the provisioning services of ecosystems, and include food (e.g. crops, livestock, fisheries), fresh water, fuel and biochemical/pharmaceutical/natural medicines. Indirect use values encompass all values provided through regulating services such as climate regulation, air purification, water regulation (extent of flooding and runoff), water purification, natural pest control, pollination, erosion control and supporting services (e.g. photosynthesis, nutrient cycling, water cycling, maintenance of soil fertility).

The impacts of invasive species can be viewed from three aspects, *viz.* economic, environmental and social. Economic impacts are those of direct consequence to humans, in terms of monetary losses. Environmental impacts are those affecting ecosystem structure and function, relating to the loss of biodiversity and habitat. Social impacts are those that focus on human health, safety, quality of life, recreational opportunities, cultural heritage and other aspects of social structure (Ciruna *et al.*, 2004; Charles and Dukes, 2006). The economic and social impacts can also be classified into two broad categories: market impacts (e.g. changes in prices) and non-market impacts (e.g. changes in ecosystems services) (Ciruna *et al.*, 2004).

The market impacts of invasive species refer to decreases in 'use values', and includes the reduction of property values, agricultural productivity, native fisheries, and tourism, a decrease in the availability and accessibility of water production, a decrease in the commercial and recreational navigability of lakes and rivers, and negative effects on public utility operations through the clogging of turbines and penstocks, which increases costs of electricity to consumers (Getsinger *et al.,* 2014). The non-market impacts may include changes in ecosystem services and potential risks to human capital, such as a decrease in social capital[3] (Ciruna *et al.,* 2004). Estimating the value of these non-market impacts can be difficult and costly because they do not have an explicit market price (Ciruna *et al.,* 2004).

Studies on the socio-economic impacts of invasive species consist of assessing changes in the values of ecosystem services following a biological invasion (GISP, 2007). These studies are difficult to conduct and are rare, especially regarding 'non-use values'. It has been argued that 'non-use values' are much smaller than 'use values' (De Groote *et al.,* 2003). Globally, biological invasions cost the world economy nearly 5% of its value (Pimentel *et al.,* 2001), which equates to some US$ 6.5 trillion per annum (Turpie *et al.,* 2012). Aquatic ecosystems are more prone to invasion because introduced freshwater aquatic and semi-aquatic plants are more likely to become invasive than terrestrial plants, due to trade and their ability to respond to disturbance such as eutrophication, and also due to the high frequency of vegetative reproduction among aquatic plants (Gordon *et al.,* 2012).

Biological invasions induce changes in the values of the goods and services provided by natural ecosystems. These values can be measured by considering the quantity of products and any changes in prices or costs of services before and after the invasion, and again, after removal of the invasion. These costs include control and damage costs from the uncontrolled or remaining invasive alien species when eradication has not been obtained (Gren *et al.,* 2007, 2009). To measure change, we must consider the quantities of products available at two defined periods at the producer level and the quantity of demand at the consumer level (Charles and Dukes, 2006).

3.1.1 Socio-economic impacts of aquatic weeds in Africa

Salvinia molesta, *Pistia stratiotes* and *Pontederia crassipes* are the main widespread aquatic weeds in Africa that cause significant socio-economic impacts (Table 3.1). The nature of impacts caused by infestations of these weeds is expected to be similar due to their similar habit and form (floating, mat-forming aquatic weeds), although impacts may vary in degree (GISP, 2007). In Africa, nine different socio-economic impacts of invasive alien aquatic weeds have

[3] Social capital is typically thought of as the relationships between people integral to sustaining trust in societies. These relationships facilitate the building of social institutions, such as non-governmental organizations, new government institutions, etc. IAS reduce ecosystem services and can cause greater demands on governments, as a result weakening social capital. This can have adverse impacts in countries that are already weak in social capital.

been identified affecting several sectors of activity: agriculture, tourism, transport, fishing, wood trading for fuels, infrastructure, health, unemployment and overall income. Globally, impacts on sectors of fishing, transport and agriculture are the most studied (Table 3.1).

Table 3.1.: Evidence of economic impacts of aquatic weeds in Africa

Economic impact	**Estimated degree of negative impact**	**Country**	**Species of concern**	**Reference**
Agriculture				
Decrease of income from vegetable-growing in the Oti River Arm of Lake Volta	35%	Ghana	*P. crassipes*	Akpabey (2012)
Labour costs of removing Invasive Alien Species on agriculture in the Oti River Arm of Lake Volta	US$30/ha (US$ 2012)	Ghana	*P. crassipes*	Akpabey (2012)
Annual economic cost for rice cultivation in the Lower Senegal Delta (cost/ha)	US$19/ha (US$ of the year 2005)	Senegal	*S. molesta*	GISP (2007)
Country-wide loss of water supply for domestic, stock and agricultural purposes	US$0.35 million per annum	Uganda	*P. crassipes*	Mailu (2001)
Tourism				
Annual economic cost on tourism in the Lower Senegal Delta	US$268/ha (US$ of the year 2005)	Senegal	*S. molesta*	GISP (2007)
Transport				
Decrease of monthly income from water transportation in the Wouri River Basin	Average of US$50 US$200 per family	Cameroon	*P. crassipes*	Kenfack Voukeng *et al.* (2019)
Reduction in the ease of river transportation for palm wine producers	Average decrease in productivity of 14% per operator	Central African Republic	*P. crassipes*	Wise *et al.* (2007)
Reduction in the ease of transport from food crop trading in southern Benin	Average decrease in yearly income of 95% per operator	Benin	*P. crassipes*	De Groote *et al.* (2003)
Maintaining a clear passage for ships to dock	US$3-5 million per annum for the whole country	Uganda	*P. crassipes*	Mailu (2001)

Fishing				
Decrease in fish catch for the Incomati River	36%	Mozambique	Aquatic weeds in general (mostly water hyacinth, water lettuce, and water fern: *Azolla cristata*)	Langa (2013)
Decrease in general fishing income for the Wouri River Basin	75%	Cameroon	*P. crassipes*	Kenfack Voukeng *et al*. (2019)
Reduction of fish catch in the Oti River arm of Lake Volta	80-90%	Ghana	*P. crassipes*	Akpabey (2012)
Decrease in fish catch from gill net fishing	26%	Central African Republic	*P. crassipes*	Wise *et al.* (2007)
Reduction in fishcatch in the Lower Senegal Delta	US$12/ha ($US of the year 2005) annual economic cost	Senegal	*S.molesta*	GISP (2007)
Decrease in yearly income from fishing for men in southern Benin	69%	Benin	*P. crassipes*	De Groote *et al.* (2003)
Decrease in annual fish-trading income (missed market attendance due to aquatic weed) in southern Benin	74%	Benin	*P. crassipes*	De Groote *et al.* (2003)
Losses in local fisheries and landing sites around the lake for the whole country	US$0.2 million per annum for entire country	Uganda	*P. crassipes*	Mailu (2001)
Reduction in fishing yields	40-50%	Niger and Malawi	*P. crassipes*	Joffe and Cooke (1997)
Fuel				
Decrease in yearly income from wood trading (fuel) in southern Benin	78%	Benin	*P. crassipes*	De Groote *et al.* (2003)
Infrastructure				
Damage to river weir in Nseleni River	Washed away due to pressure from water hyacinth	South Africa	*P. crassipes*	Wise *et al.* (2007)
More frequent cleaning of the intake screens at the Owen Falls	US$1 million per annum	Uganda	*P.crassipes*	Mailu (2001)

hydroelectric power plant				
Health				
Impacts on human health in the Wouri River Basin	Increase in the prevalence of malaria and typhoid	Cameroon	*P. crassipes*	Kenfack Voukeng *et al.* (2019)
Impacts on human health in the Homa Bay District western Kenya	Increase in incidence of malaria and cholera	Kenya	*P. crassipes*	Mailu (2001)
Unemployment				
Reduction in jobs - fishermen from Asukro on Nveye Lagoon	30%	Ghana	*P. crassipes*	Akpabey (2012)
Impact on overall income				
Decrease in income (average of four activities: fishing, trading fish, trading food crops, trading wood)in Southern Benin	Reduction in yearly overall household income: 70% for men and 60% for women	Benin	*P. crassipes*	De Groote *et al.* (2003)

3.1.2 Sectors affected by aquatic weeds in Madagascar

3.1.2.1 Rice growing

Rice is the staple food in Madagascar. Traditionally, Malagasy people eat rice three times a day. This places the Malagasy among the major consumers of rice per capita in the world, at on average 130 kg per person per year (data collected in 1998) (FAO, 2000b). In Madagascar, the role of rice is not limited to food security, but also plays an important role at political, social and cultural level (Dabat *et al.,* 2008). Around 80% of Malagasy people work in the agricultural sector and 85% of farmers cultivate rice. Direct economic added-value due to rice production, calculated in 1999, contributes to 12% of national GDP and to 43% of agricultural GDP (Dabat, 2002). Across the island, two main cropping systems are practiced, *viz.* irrigated rice and rain-fed rice including (slash-and-burn rice cultivation called tavy), which occupy 79% and 21% respectively of cultivated area (PAM, 2019). Between 2013 and 2018, the country's annual average white rice production was 2.4 million tons, with an average consumption of 2.7 million tons. During this period, the country imported an average of 374,000 tons annually (PAM, 2019).

Rice production has not kept pace with population growth. Between 1960 and 2000, the rice yield hardly changed (from 1.8t/ha to 2t/ha), while in other countries such as Mali and Indonesia, the yields more than doubled (Minten, 2006). From 1960, rice production has increased at an average annual rate of 1.8%, while between 1975 and 2018, the annual average growth rate of the Malagasy population was 2.87% (Minten, 2006, Rajaonera *et al.,* 2019). Although leaders are looking for ways to achieve rice self-sufficiency, this remains a big challenge. Since 1990, the export of rice has been non-existent, while the volume of imported rice continues to increase (PAM, 2019). In 2017, the country produced only 2,041,000 tons of white rice, while the volume of imported rice was 250,000 tons in 2016, which doubled to 570,000 tons in 2017 (Razafindrazaka, 2018).

3.1.2.2 Freshwater fisheries

Madagascar has large and abundant freshwater ecosystems including lotic and lentic water bodies, distributed in all phytogeographic areas of Madagascar (Rajeriarison et Faramalala, 1999; Elouard and Gibon, 2001). The lotic ecosystems encompass the rivers and streams, while the lentic ecosystems include lakes, marshes, and ponds (Ranarijaona, 1999; Elouard and Gibon, 2001; Raharimalala, 2007). Madagascar's littoral lakes alone comprise 3429 waterbodies (Ferry *et al.*, 1999). From an economic perspective, the published national statistics documents, with regards specifically to freshwater fisheries are poorly presented. Most of the available documents mix data on freshwater fisheries with sea fisheries, including traditional and industrial fisheries. The fishing industry contributes 7% of the island's GDP and provides around 500,000 direct jobs (MPRH, 2013). The maritime and continental production of fishing and aquaculture for the year 2014 amounted to 126,000 tons, of which a quarter was provided by freshwater fisheries production (inland fishing, fish farming in ponds and rice fish farming) (Randrianarison *et al.*, 2016).

The consumption rate of fishery products is around 7 to 8 kg per capita per year. A national framework survey carried out by the previous Ministry of Fishery Resources and Fisheries, on 18 out of the total of 22 Regions in Madagascar identified 84,000 fishermen, 85% of which were full-time and 15% who choose fishing as a secondary activity. Of these fishermen, three-quarters used canoes and one-quarter engaged in shore fishing (MPRH, 2013).

3.1.2.3 River transportation

River and coastal transport play very important roles in the development of internal trade in certain regions, both on the east and west coast of Madagascar. They are practiced in various bodies of water including rivers, streams, lakes, inlets, canals and costal routes, and they contribute to the opening up of regions by improving the accessibility of the population to basic services and facilitating traffic of goods and people (Rakotomalala *et al.*, 2001). On the east coast of Madagascar, Pangalanes canal is the best known, connecting the town of Farafangana in the south to Foulpointe in the north over a total length of 665 km, connecting ten Districts, and crossing lakes, lagoons, and rivers (Ratsirinony, 2018; Acaciasbungalows, 2020). Its creation started in 1896 and was completed in 1904 (Ratsirinony, 2018; Acaciasbungalows, 2020). For the Antsokafina canal, no official documents exist with only oral accounts of its history, and as a result the precise date of its creation is unknown.

The exact period of abandonment of the two canals (Pangalanes and Antsokafina) was less precise. Since the extension of the Pangalanes canal was continued until the 1950s, it is likely that it was abandoned from 1960 onwards due to silting up and the invasion of water hyacinth (Ratsirinony, 2018; Acaciasbungalows, 2020). Considering the economic and social interests associated with the Pangalanes canal, its dredging was undertaken by the State, in several portions from 1980 to 1991, and entrusted to IMI (Malagasy Institute of Innovation) (Ratsirinony, 2018). For the Antsokafina canal, according to the accounts of the elders of the village of Andrangazaha, it seems that this canal was abandoned earlier, around the 1940s. Subsequently, the waterways of this canal were quickly invaded by aquatic species including water hyacinth. Since then, no formal dredging action has been carried out for the Antsokafina canal.

Currently, the management of the river transport network is part of the responsibility of the APMF (Maritime and Fluvial Port Agency). It is a public industrial and commercial establishment, created by Decree No. 2003-659 of 4 June 2003, which is administratively, technically and financially autonomous. It is the authority responsible for ensuring the regulation of the port, maritime and river sub-sector, in order to implement the general policy of the State according to the strategies adopted by the Ministry of Transport.

3.2 Aim and objective of the study

The aim of the study was to evaluate the socio-economic impacts of aquatic weeds on riparian community livelihoods in three specific locations (Soanierana-Ivongo, Foulpointe and Antananarivo). The specific objectives of the study were to:

⇨Evaluate the socio-economic costs resulting from the invasions of aquatic weeds in the sectors deemed to be of major importance in the Malagasy economy.

⇨Provide reliable information to enable decision makers at all levels to act appropriately to deal with the impacts of invasive aquatic plant species.

3.3 Methodology

3.3.1 Choice of studied sectors (rice growing and fisheries)

The present study was aligned with the needs of the country, to achieve the objective of improving the livelihoods of the Malagasy people. Several framework documents and national policies refer to the objective, such as the Document for Poverty Reduction Strategy in Madagascar (DSRP, 2005) and Initiative for the Emergence of Madagascar (IEM). For the agricultural sector, the vision for Madagascar was defined by the Ministry of Agriculture, Livestock and Fisheries (MAEP) "*Towards food self-sufficiency and the emergence of a modern agricultural sector " (*Ranarivelo, 2020).

Regarding the rice sector, in 2019 the Government launched an initiative with the ambition to "*produce an additional 500,000 tons of paddy rice before 2024"* (Andriantefiarinesy, 2019; Navalona, 2020). To achieve this goal, for the year 2020, several strategies were adopted, (1) extension of rice-growing through the development of an additional paddy surface area by 14,155 ha, (2) popularisation of more efficient production techniques such as the PAPRIZ programme (phase III) for 76,000ha (Projet d'Appui pour l'Amélioration de la Productivité et de l'Industrialisation du Secteur Riz), and (3) promotion of hybrid rice for 20,000 ha (Ranarivelo, 2020). The strategies were based on strengthening the capacity of farmer organisations to form cooperatives, facilitating access to agricultural inputs (including quality seeds, agricultural mechanisation and post-harvest improvement) in 22 Regions of the country in cooperation with the Japanese International Co-operation Agency (Arh, 2019b; Navalona, 2020**,** Ranarivelo, 2020)**.** In terms of freshwater fishing, starting in 2020, the Ministry set an objective of producing 1500 tons of freshwater fish to satisfy national needs (Ranarivelo, 2020).

The implementation of these national ambitions requires not only technical expertise, leading to appropriate technical innovations, but also that the diverse factors hindering the development of these sectors are reduced or even eliminated. Field observations and some previously published studies demonstrate the importance of the socio-economic impacts of invasive aquatic species on rice and freshwater fish production. As stated above, irrigated rice occupies 79% of the total area of rice plantations, and this sector is prone to being severely compromised by invasive alien aquatic plants. Examples of studies describing the impacts on both the rice and fishery industries in Madagascar are those by Rakotoarisoa *et al.* (2015) with *P. crassipes* invasion at the Alaotra wetlands, by Lehavana (2014a) investigating *S. molesta* invasion on fisheries income at Lake Andramoma (Foulpointe), and by Lehavana (2014b) on rice production in Madagascar.

3.3.2 Choice of study sites

The selection of study sites was determined by the presence of the target species and that of sectors selected. Mapping the distribution of the four target species (Chapter 2) provided preliminary information on the zones where the socio-economic impacts of invasive aquatic weeds were present. For each of these zones, the level of infestation and the existence of local control organizations were important, with a preference being given to sites with high levels of infestation and where there was a local organization that actively combatted invasive alien plants. Compared to other regions in Madagascar, the Highlands and eastern regions were characterized by a deficit in rice production compared to needs (FAO, 2000b). Thus, a choice was made to establish three sites here. Both of these regions consume a large amount of the imported rice in Madagascar and supplement their needs other regions, making them particularly compelling choice for this study. Regarding fishing, the Analanjirofo and Atsinanana regions on the eastern coast of Madagascar, were classified as regions in the mid-range in terms of number of fishermen (MPRH, 2013). In two study sites (Soanierana-Ivongo, Foulpointe), data available in 2013 on the percentage of praticing fishermen varied from village to village, with an average of 18% (Table 3.2). These figures give an overview of the importance of the fishing industry for these areas, with the invasions of aquatic weeds posing a major threat for the sector.

Table 3.2.: Demographic characteristics of studied villages and fishing activities

Study site	Commune	Village	Population number	Number of fishermen	Percentage of fishing activity (%)
Site 1 (Soanierana-Ivongo)	Antanifotsy	Antanifotsy	1 017	121	12
		Rantabe	85	17	20
		Andrangazaha	1 937	241	12
	Manompana	Andakibe	72	66	92
Site 2 (Foulpointe)	Foulpointe	Antaratasy	172	31	18
		Antetezana	372	197	53
	Total		3 655	673	18

Source (MPRH, 2013)

3.3.3 Sampling areas of the study

The three sites chosen to conduct studies on the socio-economic impacts of aquatic weeds are shown in Figure 3.1 and each site is described below.

• Site 1 in Soanierana-Ivongo District, Region Analanjirofo, comprises three villages (Andrangazaha/Rantabe, Ambodimanga/Andakibe and Antanifotsy), located in the two rural communes of Antanifotsy and Manompana. These villages are on the periphery of Lake Antsokafina and the associated Antsokafina Canal which are heavily invaded by three invasive aquatic weeds: *P. crassipes, S. molesta* and *P. stratiotes*. The lake has an area of approximately 8 ha but the artificial canal, dug during French colonial times, is approximately 33 km long with a fork near the village of Ambodimanga. The socio-economic impacts of invasive aquatic weeds that were studied here included those on fishing and river transportation. In addition, the experiments on the interactions between invasions and physico-chemical parameters of the water (Chapter 4), were conducted on this lake.

• Site 2 in Foulpointe, District of Toamasina II, Atsinanana Region, including eight villages (Tanambao Iharana, Antaratasy, Antetezana, Anjambamaho, Ambohimanarivo, Ambodivoangy, Antanambaovao, Antsaribao), distributed in three Fokontany[4] (Antaratasy, Ambohimanarivo and Morarano), all in the rural community of Foulpointe. These villages surround Lake Andramoma and Lake Sahamare as well as the Pangalanes Canal. A part of this artificial canal connects the town of Toamasina to the terminus at Foulpointe. The lakes Andramoma and Sahamare are severely invaded by *S. molesta*, while the Pangalanes Canal is invaded by *P. crassipes*, *S. molesta* and *Azolla filiculoides* Lam. (Azollaceae). Andramoma and Sahamare are large marshes crossed in the middle by canals previously used for the transport

[4] : Fokontany is the smallest administrative municipality unit in Madagascar, just below the commune

of goods. During the rainy seasons in general, and especially during periods of heavy rainfall, the water floods from the bed of the canals and covers the adjacent marshes to an approximate area of 1022 ha. At this site, the impacts of aquatic weeds on the fishing and rice production sectors were the main foci of the study.

• Site 3 in Antananarivo, Analamanga Region, comprising two villages in Arrondissement V (Analamahitsy and Andranobevava) and five villages in Arrondissement VI (Ambodimita, Ambodiady, Amorona, Ambaravarankazo, Ambohimiavotra). Studies were conducted to assess the impacts of all target species (*P. crassipes, S. molesta, A. filiculoides* and *P. stratiotes*) on aquatic rice farming.

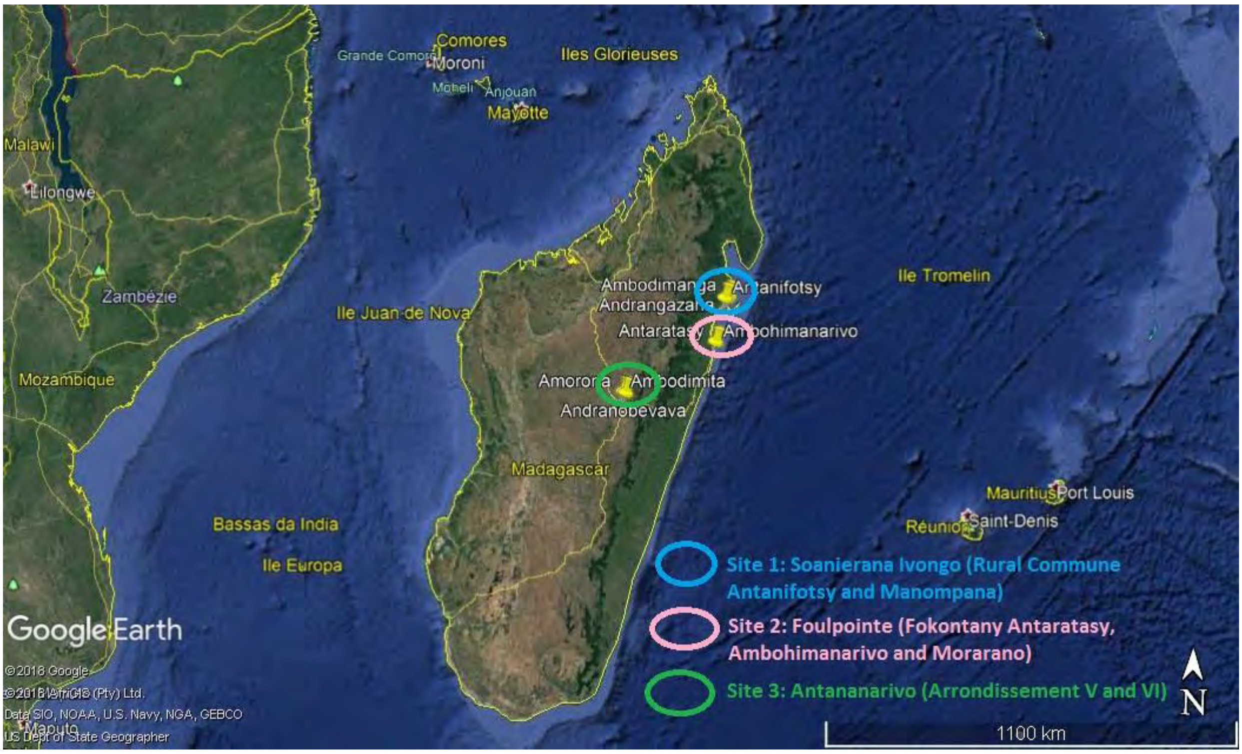

Figure 3.1.: Location of the aquatic weed socio-economic study sites in Madagascar

3.3.4 Questionnaire design and data collection

Using the method of simple random sampling (Chalmers and Parker, 1986; Wonnacott et Wonnacott, 2000), villagers were engaged throughout areas with aquatic weed infestations for face-to-face structured interviews, resulting in a total of 102 respondents (34 respondents at Site 1; 47 respondents at Site 2 and 21 respondents at Site 3). The surveys were carried out in two phases from July to November 2016 for Site 1 (Soanierana-Ivongo) and from November to December 2019 for Site 2 (Foulpointe) and Site 3 (Antananarivo). Each respondent was asked if he/she associated with any of the following activities: freshwater fishing, fish retailer, hotel owner, canoe transporter, rice grower. Sample sizes for surveys were capped at around 80% of the total numbers for each activity (fishermen, restaurant owners, transporters etc) per villages. Sample size is important for statistical accuracy. In general, increased sample size tends to decrease sampling error (Chalmers and Parker, 1986; Wonnacott et Wonnacott, 2000). The total numbers were estimated using local assistants who had been recruited at the start of the survey. Other characteristics of the samples, such as the age categories of the interviewees, and the gender were also taken into account. The questionnaire included common questions to be asked of all respondents including:

a) The respondent's knowledge and perception of aquatic weeds, including: a description of the plants, an assessment of the most troublesome among these species, their thoughts on how long the plant had been in the area, the origin of the plant, the level of the infestation now compared to the past, and finally, in the case that the plants were used, the nature of the usage and how much and how often do they use them. To facilitate this, we showed a photograph of each plant to the respondents.

b) The actions undertaken by respondents individually, or through community work to control aquatic weeds, including a description of the techniques used and how effective they were; what innovations they proposed that might improve the effectiveness of control, and an evaluation of their own and the community’s willingness to implement control measures against aquatic weeds.

c) Certain questions were more detailed with respect to activity sector, depending on that to which the respondent's activity impacted by aquatic weeds belonged, such as: how much did they earn before and during the peak of infestation, the price of the products (expressed in Ariary and in US$), the evaluation of expenditure associated with the control of aquatic weeds in the case of infestation, and the description of the types of materials used to perform the activity before and during the peak of infestation. As mentioned, the economic impacts were evaluated for activities related to fishing, river transportation and rice growing.

3.3.5 Method of data analysing for the sectors studied

For fishing sector, during data collection, the responses for the quantity and price of fish and shrimps during the two periods considered (viz. before and during the peak of infestation) were separated. As some fishermen engage in both fish and shrimp fishing, the weighted value “Qi” was used to adjust the sum of the quantity of fish and shrimp caught weekly per individual.

$$Q_i = Q_i \text{ fish} + Q_i \text{ shrimp}$$

For analysing the fishing-product worth, the Fisher value index was used. The growth of the economic value of a household's fishing activity as well as the gross domestic product (GDP) of a country, can be measured using two elements: a "price effect", or the part of the growth linked to inflation, and a "volume effect", which covers the change in quantity of a product. The Fisher value index was used to calculate the change (increase or decrease in the economic value) under the aggregate effects of price and quantity between two consecutive periods of time (Wonnacott and Wonnacott, 2000; Chevalier, 2003). In this study, fish and shrimp were the main fishery products, the only ones considered as fishermen's economy (Chevalier, 2003). The change or variation in economic value between two periods (initial period t0 and final period t1) can therefore be expressed in index[2] form by:

$$I_{V\,1/0} = \frac{\sum p_1 q_1}{\sum p_0 q_0}$$

Where

I_V: Fisher value Index

p_0: Price at T_0 (before the saturation phase of infestation)

p_1: Price at T_1 (at the saturation phase of infestation)

q_0: Quantity at T_0

q_1: Quantity at T_1

To assess trend of fishermen's income growth between two periods, T_0 (2000) and T_1 (2016 or 2019), percentage growth was obtained by subtracting 1 from the ratio given by the index and by multiplying the result by 100. In addition, fishing frequency parameter was considered which influenced the amount of weekly catch. This method was used to calculate the elasticity[5] of fish and shrimp products as impacts of the invasion.

While collecting data in the rice sector, rice producers were asked to estimate the yield for a paddy infested by aquatic weeds compared to another of the same size free from infestation. Similarly, for weeding work, we asked questions about additional cost and frequency of cleaning an infested rice paddy, per unit area. So, the total cost of the invasion

[5] *:* In economics, **elasticity** is the measurement of the percentage change of one economic variable in response to a change in another (https://en.wikipedia.org/wiki/Elasticity_(economics))

was calculated as the sum of the difference in yield (damage cost caused by reinvasion after cleaning) plus the expenses related to weeding in the infested areas (control cost) (Gren *et al*., 2007; 2009).

$$\boxed{\text{Total Cost} = \Delta\ (\text{yield + weeding costs})}$$

In Foulpointe, after the reopening of the canal in 2018, the benefit was evaluated by subtracting rice production during the peak of invasion from production after the reopening of the canal.

$$\boxed{\text{Benefit = Production after opening of the canal – Production during peak of invasion}}$$

3.3.6 Statistical analysis for socio-economical study

The data from the surveys were analysed using two statistical software pachages: CSPro (Census and Survey Processing System) version 7.2 and SPSS (Statistical Package for the Social Sciences) version SPSS 18 (IBM SPSS 18). The former is free software for census or survey data capture, modification and tabulation. Developed by the United States Census Bureau, it is designed to be as user-friendly as possible, yet powerful enough to handle the most complex applications. Due to the facilities it offers in the creation of data capture and consistency of control applications, CSPro has become the most recommended software of its type in terms of input interface (U.S. Census Bureau 2019a; b; c). The SPSS software package allows the user to carry out all the statistical analyses routinely performed in the social sciences. It is a very complete tool, with a single integrated interface which is simple to use for all operations (Greasley, 2008).

For data capture and processing, the two software packages were used in combination (CSPro for capturing and SPSS for data processing, both tools were used successively). The following steps were adopted:

a) Using CSPro, we first created a data dictionary where we defined the data structure (database) for the survey. Using this dictionary we could automatically generate the data entering application, and customize it as needed.

b) Used the input form thus created, survey data was entered and managed.

c) Data captured in CSPro was exported in an intermediate database, format readable by SPSS.

d) This intermediate database file was converted into SPSS database.

e) The desired analyses were performed using SPSS.

All villages and households surveyed were coded, which made it possible to exploit descriptive statistical treatments by means of cross-tabulation. All quantitative data, from whichever sector surveyed, were statistically analyzed to obtain the mean and the variance.

The difference between the means of the independent samples relating to the quantity of fishery products at two different periods (before and during the saturation phase of infestation) was statistically tested using the Student test (t-test). The significance of the difference was calculated using a 95% confidence interval ($P < 0.05$). The volumes of rice produced in paddies with and without aquatic weed infestations and the quantities of rice harvested before and after opening the canal (case of Foulpointe), were statistically analysed using the mean and variance.

3.4 Results

3.4.1 Characteristics of surveyed households' activities

The economic activities of the interviewees were centered around agriculture, fishing and the breeding of pigs, cattle and poultry. Other activities were also practiced such as motorboat transportation, timber sales, charcoal sales, catering, and freshwater fish retailing. Some respondents also earned an income from the provision of retirement pensions. Generally, people engaged in two or more activities to provide for their family needs. Agriculture (excluding livestock husbandry) was stated as the most practiced economic activity, povided by 92% of respondents, followed by fishing (58%) and livestock farming (56%) (Table 3.3). It should also be noted that 50% of the respondents were engaged in agriculture as their primary financial activity, especially rice cultivation. In Antananarivo, 100% of the farmers surveyed grew rice but in Foulpointe and Soanierana-Ivongo, some farmers also cultivated other food crops such as cassava, corn, and sweet potato in addition to rice. At these latter two sites, cash crops such as cloves, vanilla, and lychees were also an important source of family income, in addition to fishing and livestock.

Table 3.3.: Financial activities of survey respondents at the three survey sites (n=102)

Activities*		Gender		Age				
		Male	**Female**	**< 30**	**30 <Age<45**	**Age ≥45**	**Total**	
Agriculture	1st	37	14	10	12	29	51	94
	2nd	29	9	5	12	21	38	
	3rd	5	0	0	2	3	5	
Fishing	1st	33	0	5	10	18	33	60
	2nd	20	2	4	6	12	22	
	3rd	5	0	1	0	4	5	
Livestock	1st	2	2	0	1	3	4	57
	2nd	17	3	2	7	11	20	
	3rd	26	7	5	10	18	33	
Transportation	1st	2	0	0	0	2	2	5
	2nd	1	1	0	0	2	2	
	3rd	1	0	0	0	1	1	
Timber sales	1st	0	0	0	0	0	0	3
	2nd	0	1	1	0	0	1	
	3rd	2	0	1	1	0	2	
Charcoal sales	1st	0	0	0	0	0	0	8
	2nd	2	0	1	0	1	2	
	3rd	6	0	1	2	3	6	
Restaurant owner	1st	0	4	0	3	1	4	4
	2nd	0	0	0	0	0	0	
	3rd	0	0	0	0	0	0	
Freshwater fish retailer	1st	0	2	0	1	1	2	3
	2nd	1	0	0	0	1	1	
	3rd	0	0	0	0	0	0	

*:Activities are ranked in order of importance for household's livelihoods from 1st to 3rd.

3.4.2 Knowledge of aquatic weeds

At the three study sites, all respondents knew *P. crassipes* and *S. molesta*, while *P. stratiotes* and *A. filiculoides* were known by 64% and 54% of the respondents respectively (Figure 3.2). *Pontederia crassipes* and *S. molesta* were very widespread and abundant at all sites, and thus it was to be expected that all people knew them. In Soanierana-Ivongo, *A. filiculoides* was not yet present, hence, only one person knew of it. In Foulpointe, *P. stratiotes* and *A. filiculoides* were present but localised on the west side of Lake Andramoma and close to the outlets of rivers, so they were little-known.

Overall, *S. molesta* ranked as the most troublesome aquatic weed (52%), followed by *P. crassipes* (43%) (Figure 3.2). However, in Soanierana-Ivongo and in Antananarivo, *P. crassipes* (65%) was identified by respondents as the most problematic. Very small percentages of respondents felt that *P. stratiotes* and *A. filiculoides* posed a problem. In Soanierana-Ivongo, *P. stratiotes* contributed significantly to blocking the Antsokafina canal, which explains why a few of the fishermen (9%) considered it the most troublesome species. In Antananarivo, *A. filiculoides,* even though it was never mentioned as being the most troublesome, several respondents explained that it often interfered significantly in rice planting, and was very difficult to remove.

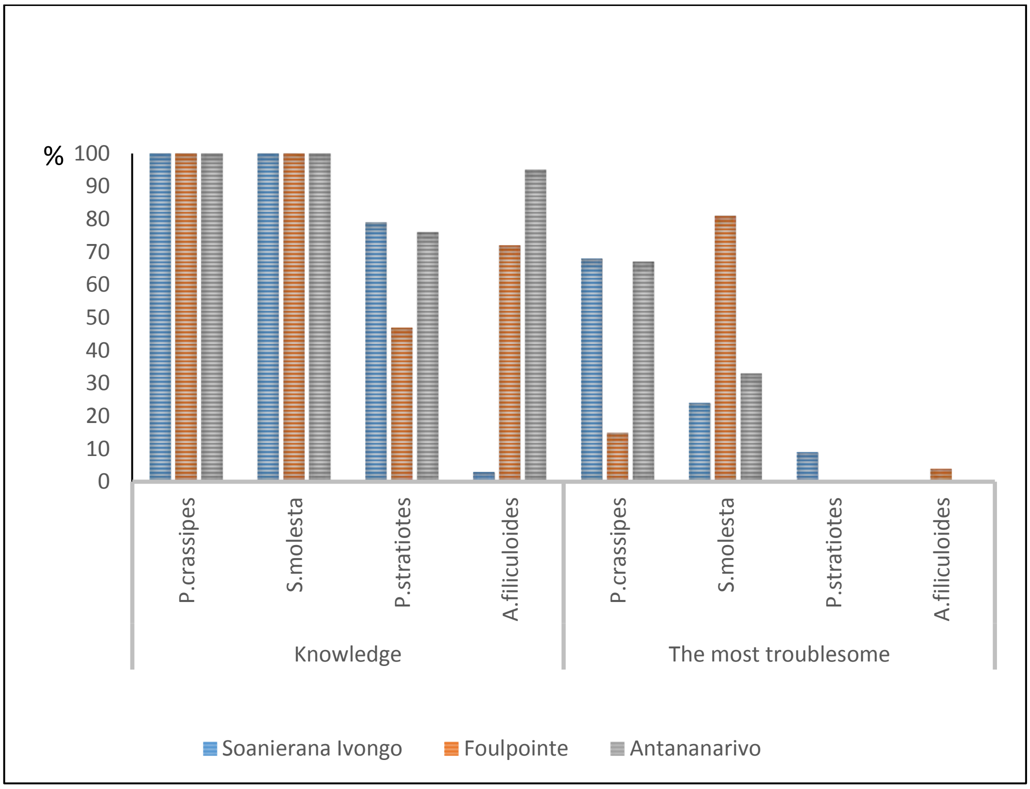

Figure 3.2.: Surveyed households' perception of four target aquatic weeds at the three sites surveyed

3.4.3 Knowledge of the presence of aquatic weeds

The responses of those surveyed about the periods of onset and saturation of the invasions depended on the number of years over which they had stayed in the village. Those who had lived in the village longer provided more details on the periods during which aquatic weeds appeared and the change in levels of infestation over time (Table 3.4).

In Soanierana-Ivongo, 32% of the respondents (n=34) observed that invasive aquatic weeds had been present in Lake Antsokafina for more than 40 years, that is to say before the 1980s. According to the accounts of the elders of the village of Andrangazaha, *P. crassipes* had arrived well before *P. stratiotes* and *S. molesta.* At this time, the species obstructed part of the artificial canal. This situation was confirmed by 19% of those interviewed at the site, while 29% of those interviewed confirmed the arrival of *P. stratiotes* and *S. molesta* between 30 and 40 years ago, i.e. during the 1980s. The arrival of these two last species accelerated the process of saturation of the canal and the lake of Antsokafina. At this site, 47% of the interviewees noticed that Lake Antsokafina was completely clogged up 10 to 30 years ago, that is to say around the 2000s.

In Foulpointe, 21% of people interviewed (n=47) said that invasive aquatic species had been present for more than 40 years, while 43% had noticed the presence of these species during the 1980s (Table 3.4). According to their account, similarly to Soanierana-Ivongo, *P. crassipes* had arrived first, before *S. molesta* and *A. filiculoides*. According to the interviewees, the latter two species appeared at the same period, during the 1980s. Forty-four percent of interviewees confirmed that the Sahamare Canal and Lake Andramoma were fully invaded less than 30 years ago, during the 2000s, and no one reported seeing the clogging more than 40 years ago. The closure of the Sahamare Canal and Lake Andramoma in Foulpointe is more recent than that of Lake Antsokafina in Soanierana-Ivongo.

In Antananarivo, 33% of respondents (n=21) had noticed the presence of invasive species for more than 40 years, while 48% first observed them during the 1980s (Table 3.4). Compared to the two other sites, the percentage of people who confirmed the arrival of these species in the period of the 1980s was higher. In Antananarivo, 14% of interviewees had seen invasive alien aquatic species blocking the canals and rice fields for more than 40 years, while 43% confirmed that this had happened during the 1980s. Those who had lived in the city for more than 40 years had noticed the presence of *P. crassipes* around 1975. An interviewee in the village of Andranobevava in Antananarivo remembered well, at the time of colonization (up to 1960) and the First Republic (1960 – 1972), those who could not pay their taxes were sent to remove *P. crassipes* in Antananarivo. The exact dates of the appearance of the other three species were not known.

As many of respondents were especially concerned about *S. molesta*, they were more precise about when it had first arrived (around 1980) at all three sites. Very few knew the origin of the weeds. In Soanierana-Ivongo, the elders of the villages said that these species arrived in the area by clinging to canoes. In Foulpointe, the village elders explained that the plants had originated in Toamasina when the canal was still navigable, before the 1980s. In Antananarivo, the origins were little known but some people around Ambodimita and Amorona claimed that these species come from the city of Antananarivo, which has a direct fluvial connection with Sector 1, Sector 2, and Sector 3 of District VI: the Andrianantany Canal, along which the sewage from Anosibe, Ampefiloha, and Andavamamba is carried. This canal was thought to transport aquatic weeds through these sectors, ultimately discharging towards Ampanindrona next to Ambohidratrimo. Thus, these areas are the most infested in the study area of District VI.

Overall, 95% of those surveyed said that during the years of survey (from 2016 to 2019), there were more aquatic weed invasions than at any other time. Only one respondent in Antananarivo said there was less aquatic invasion, following community control-interventions. This was the case in the western area of the Betsimitatatra, Antananarivo where the rice growers collaborated to control aquatic weeds. Moreover, according to their explanation, the canal which irrigates the area (Sector 4 of the District VI) was not very infested. This canal takes its source from the Ikopa River passing through Mafadatsa before flowing towards Sector 4, at the western part of the Dike.

Table 3.4.: Knowledge of the presence of aquatic weeds according to the number of years respondents had lived at the three survey sites[6]

Study site	**Number of years staying in the village**	**Noticed the first presence of aquatic weeds**				**Noticed that the zone was completely clogged up**			
		<10 year	**10-30 year**	**30-40 year**	**>40 year**	**<10 year**	**10-30 year**	**30- 40 years**	**>40 year**
Soanierana-Ivongo (n=34)	year <10	1	0	0	**1**	1	0	0	**1**
	10-25 year	1	10	0	**2**	4	8	0	**1**
	25-40 year	0	0	6	**3**	1	4	3	0
	>40 year	0	1	4	5	0	3	2	4
	Total	2	11	10	11	6	15	5	6
	%	6%	32%	29%	32%	19%	47%	16%	19%
Foulpointe (n=47)	<10 year	1	0	0	0	1	0	0	0
	10-25 years	2	5	0	0	4	3	0	0
	25-40 year	1	3	2	0	4	1	1	0
	>40 year	0	5	18	10	11	16	4	0

[6] Numbers in bold and blue in Table 3.4: as the duration of their stay in the village was shorter than the duration of their answer, it was assumed that they relied on information provided to them by people who had stayed in the village for longer or because they circulated in the zone before staying definitely.

	Total	4	13	20	10	20	20	5	0
	%	9%	28%	43%	21%	44%	44%	11%	0%
Antananarivo (n=21)	<10 year	1	0	0	0	1	0	0	0
	10-25year	0	1	0	0	0	1	0	0
	25-40 year	0	2	4	0	1	2	3	0
	>40 year	0	0	6	7	1	3	6	3
	Total	1	3	10	7	3	6	9	3
	%	5%	14%	48%	33%	14%	29%	43%	14%
Overall (n=102)	Total	7	27	40	28	29	41	19	9
	%	7%	26%	39%	27%	30%	42%	19%	9%

3.4.4 Economic and socio-cultural uses of target aquatic weeds

Aquatic weeds are used by the local communities in three main ways: fodder for animals, handicrafts and water purification. In addition, during our expedition to the north of the island, we identified several cultural uses of aquatic weeds. Out of the 102 people surveyed at the three sites, 17.6% valued two species: water hyacinth and water lettuce. Two people including one in Antananarivo and one in Foulpointe, tried to compost *S. molesta*, but after a single attempt, they stopped because of the low profitability.

In Antananarivo where 21 persons were interviewed, *P. crassipes* was commonly used to feed cattle, with 66.6% of those surveyed feeding zebus, 29% using it to feed pigs, and in rare cases, it was used as goose and duck feed. The amount of fresh biomass collected was on average 83 kg/day/head for zebus, 4.5 kg/day/head for pigs and a very small amount of 0.5 kg for geese and ducks. When forage became scarce, especially during May to November, zebu breeders turn to the collection of *P. crassipes* to feed their animals, with the plant being eaten as fresh biomass. For some, this practice was conducted throughout the year. Overall, it was estimated that 70% to 80% of forage per year in infested areas was *P. crassipes*. The number of zebus varies from two to eight per household, therefore at a rate of 83 kg/zebu/day, the amount of biomass used varied from 160 kg to 664 kg per household per day. A 25kg bag costs from Ar3,000 (US$ 0.8)[7] to Ar5,000 (US$ 1.3) (Figure 3.3a). Farmer therefore spends about Ar9,960 (US$ 2.7) to Ar16,600 (US$ 4.5)/day/zebu if they cannot personally collect the biomass in suitable places. The most common places for harvesting *P. crassipes* were Anosibe, Ambodimita and Andranobevava. Although *P. crassipes* fulfilled an important role in the feeding of the cattle in Antananarivo, the breeders did not perceive any conflict of interest with

[7] : US$ 1 = Ar3,663, exchange rate on 28/12/2019.

controlling the species because the weed has a low nutritive value and is less palatable than the other fodders. Thus, feeding cattle with *P. crassipes* becomes a necessary evil when there is no other fodder available. They said that the species was occupying more and more space in the rice fields to the detriment of other fodder species. They assumed that if *P. crassipes* was managed, the other species would replace the areas currently occupied by it and the cattle would be better nourished.

In Soanierana-Ivongo, and more precisely in Andragazaha, some households valued *P. stratiotes* for the purification of well water. For this a few individual plants were enough for a well. Also, of the 34 housewives surveyed in Soanierana-Ivongo, only one valued the *P. crassipes* to feed her single pig. She viewed it as a dietary supplement with an amount of about 1 kg/day/head being used (Figure 3.3b).

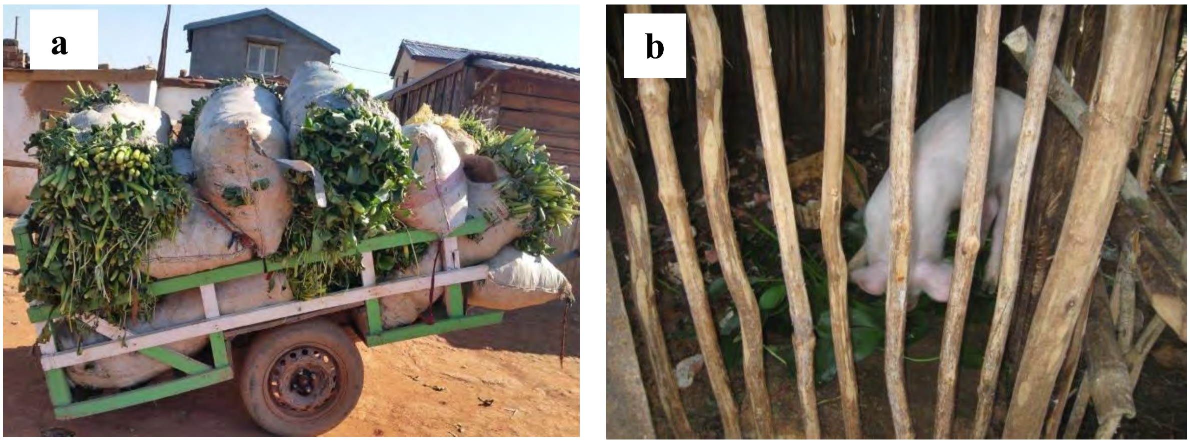

Figure 3.3.: Valorisation of aquatic weeds for feeding livestock: (a) harvest of water hyacinth for feeding zebus in Antananarivo; (b) use of water hyacinth for feeding pigs in Soanierana-Ivongo

In Foulpointe, as a relatively new initiative, a group of ten women had formed an association where they were making and trying to sell handicrafts made from *P. crassipes* (Figure 3.4a). They explained that in 2014, there was a woman from Antananarivo who was able to train several others on how to fashion the plant into several products. Currently, the people in this association were able to produce several types of products including hats, baskets, women's purses (Figure 3.4b, c, d) and bible covers. To sell their products, the association partnered with permanent hawkers in Toamasina, however, sales were limited. The reason behind this was thought to be that their prices were relatively expensive compared to products from other raw materials. For example, a basket (Figure 3.4c) cost Ar40,000 (US$ 11.4) and a hat (Figure 3.4b) cost Ar15,000 (US$ 4.5). The sale prices were high due to the time-consuming production process for weavers. First, the source of the *P. carssipes* was far from the village and the dry:fresh matter ratio was very low, at around 5%. To produce the type of basket illustrated in Figure 3.4c, 1 kg of dry matter was required (1kg of dry material is equivalent to about 20kg of wet material). To dry the raw materials, it took about two weeks, depending on the weather conditions. The weaving also took a longtime as the water hyacinth had to be carefully braided. Faced with the difficulty of producing these products on the one hand and the rather tight market on the other hand, weavers did not invest too much time in the weaving of *P. crassipes* products. Nevertheless, they try to maintain the know-how by supplying some products to hawkers in Toamasina. The biomass of water hyacinth used for this activity is limited; at a rate of 30 kg of fresh material per week per weaver, the removal of the biomass of the species hardly contributes to the its control.

Figure 3.4.: Valorisation of aquatic weeds for handicrafts, produced by a women's association of weavers at Anjambamaho, Foulpointe: (a) raw materials, dry stems of water hyacinth; (b) hat made from water hyacinth; (c) basket made from water hyacinth; (d) woman's purse made from water hyacinth

In the Sofia[8] (District of Mampikony and Port-Bergé) and Diana regions[9] (Ambilobe, Diego II and Diego city), traditional healers (mpimoasy) frequently used *P. stratiotes* mixed with the indigenous *Salvinia hastata* Desv. (Salviniaceae) and *Azolla pinnata* R. Br. (Azollaceae) to treat spiritual problems. In rare cases, *P. crassipes* and *S. molesta* are also used. The names of these plants varied from region to region, but the best known were those whose meanings were closely related to their roles: *P. stratiotes*, known by the local name "Ramanjaka", meaning "king", *S. hastata*, known as "Savalikipiky" means "horse" (powerful and rapid) and *A. pinnata*, known as "Ramilamina", meaning "making untroubled or peaceful". In society, if someone is sick because of swallowing something, or made a mistake that angered an ancestral spirit, he/she approaches a shaman, who often communicates with the deceased ancestors (mostly king ancestors) through the spirit of the tromba[10]. Afterwards, the tromba prescribes herbal recipes (*P. stratiotes, S. hastata* and *A. pinnata*) to treat the patients.

In the Diego area, we did not find any *S. hastata* plants during our expedition. In these dry areas, *P. stratiotes* was also very rare. To provide cultural needs, in several places *P. stratiotes* was cultivated either near the rice field or in the village, even in small containers (Figure 3.5a). Sometimes, people use *S. molesta* and *P. crassipes* for cultural purposes, but *P. stratiotes* was most widely used compared to other species. In the city of Diego, we also found *P. crassipes* and *S. molesta* for sale with *P. stratiotes* in the market (Figure 3.5b).

[8] Sofia region is in the central West of Madagascar and outside of the three studied sites. This information was collected during the distribution mapping of the target species, Chapter 2 of this thesis.
[9] Diana region is located in the North West of the island, outside of the three studied sites. Similarly as in Sofia region, information was collected during the distribution mapping of the target species (Chapter 2).
[10] The *"tromba"* is an ancestral Malagasy custom practiced until today, especially in the North-West region of Madagascar. During the ceremony, often during the evening through a medium, the deceased kings transmit specific messages to their descendants, or to anyone who needs help

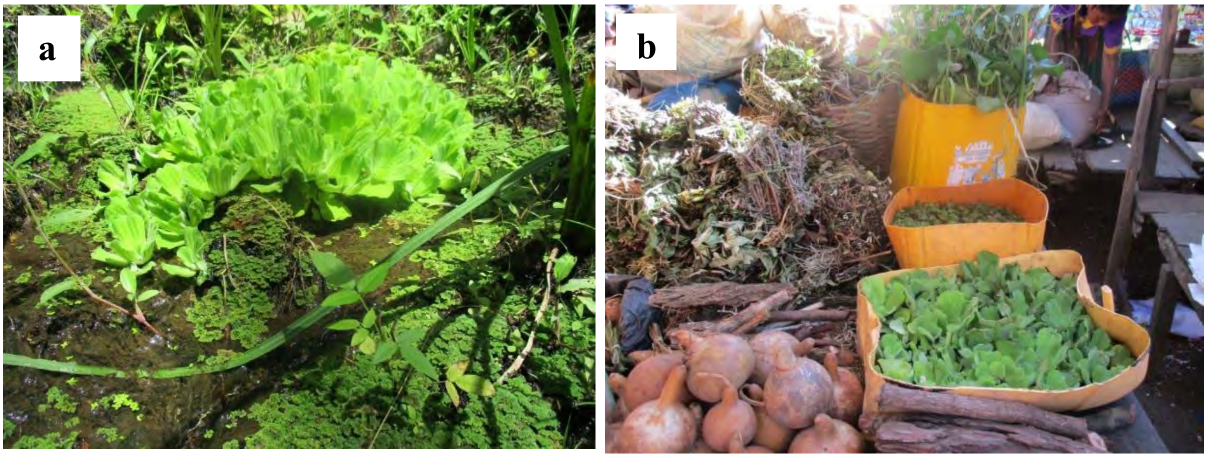

Figure 3.5.: Valorisation of aquatic weeds for cultural uses: (a) culture of *Pistia stratiotes* associated with *Azolla filiculoides*, at the village of Ambodimanga, in the vicinity of Anivorana, Diego II, Diana region; (b) sale of *Pistia stratiotes, Pontederia crassipes* and *Salvinia molesta* at the market in Antsiranana town, Diana region

3.4.5 Socio-economic impacts of water weeds

3.4.5.1 Fishing activity trends

In Sonierana-Ivongo, from 2000 to 2016, the number of fishermen increased. The average number of freshwater fishermen in the three villages (Ambodimanga, Andrangazaha and Antanifotsy) was 16 before the peak of the aquatic weed invasion in 2000 and this increased to 34 during the invasion peak in 2016 (Table 3.5). This increase in the number could be explained, on the one hand, by the high demographic growth of the zone and, on the other hand because the zone is increasingly flooded. These annual floods increased the risk associated with rice cultivation, causing most people to turn to fishing as a means of securing their livelihoods, even though the yields were decreasing. However, the frequency of fishing, that is the number of fishing days per week, reduced from an average of 5 days before the peak of invasion to 4 days during the saturation phase of invasion.

In contrast to Soanierana-Ivongo, in Foulpointe, from 2000 to 2019, the average number of fishermen from six villages (Tanambao Iharana, Antetezana, Anjambamaho, Antsaribao, Ambodivoangy and Antanambaovao) decreased from 87 fishermen before the peak of invasion to 45 during the peak of invasion. Due to water weeds blocking access to the fishing areas, many freshwater fishermen turned to other activities, such as agriculture, sea fishing, charcoal selling or weaving (for women). Similar to Soanierana-Ivongo, in Foulpointe the frequency of fishing per week dropped from 6 days per week to 5 days for those who had decided to continue with the activity.

Table 3.5.: Mean number of fishermen and frequency of fishing per week at the two study sites before and during the peak of invasion

Parameter	Site	Before the peak of invasion of water weeds	During the peak of invasion of water weeds
		Mean ± SD	Mean ± SD
Number of freshwater fishermen	Soanierana-Ivongo	16.32±18.8 (n=25)	34.00±24.61 (n=25)
	Foulpointe	86.88±50.43 (n=16)	44.69±27.96 (n=16)
	Total	**43.85±48.80 (n=41)**	**38.17±26.15 (n=41)**
Frequency of fishing (number of days/week)	Soanierana-Ivongo	5.31±2.26 (n=26)	4.08±2.43(n=24)
	Foulpointe	6.41±1.32 (n=29)	4.57±2.48 (n=21)
	Total	**5.89±1.89 (n=55)**	**4.31±2.44 (n=45)**

3.4.5.2 Fishing techniques

Different types of equipment were used for fish and shrimp fishing. For fish, four main fishing materials were used at the two sites (Table 3.6). Overall, gill nets and traps were used the most, at 47% and 39% respectively. For shrimp, we identified three types of traps: the shrimp trap “vovo taolankira” is used only in Foulpointe, the trap “Tritrampanga” was seen specifically in Soanierana-Ivongo (Figure 3.7a) and the third type of shrimp trap, “goninorana”, was used in both locations (Figure 3.7b).

Table 3.6.: Techniques and materials used for fishing at the study sites

Fishing techniques and equipment	% users (fishermen) before peak of invasion (n=55)	Description of the methods
Gill net = harato fandrika [fish]	47%	Gillnets were placed vertically in the water to catch fish by their gills and operculum without the body entering the mesh. This type of fishing was practiced day and night and the net was left in the water for at least 3 hours. The mesh size varied from 3 to 4 fingers (as local unit of measure) and the net was usually 100m long.
Cast net = harato atoraka [fish]	9%	This is a circular net with small weights attached at regular intervals around its edge. The net was thrown by hand so that it spreads over the water and sinks. The fish were caught while the net was being gathered up. The mesh diameter is quite small (1 finger) to catch even small fish.

Fishing line and fishhook [fish]	4%	Fish were caught with a fishing line by encouraging a fish to bite prey attached to a hook. The fishhook perforates the mouthparts of a fish.
Fish-trap (vovo) [fish]	39%	This fishing technique consisted of confining a trap in a delimited area with branches or leaves. There were two types of fish trap or vovo in the area. The first one was the real vovo, consisting of a fishing net and a funnel-like frame or a sort of box with a single funnel-shaped opening. This type of vovo is only used after floods. The second type is called "vovoharagna", made from woven flexible midribs of the leaflets of raffia.
Shrimp trap (vovo taolankira) (only in Foulpointe) [shrimp]	70 %	Bait such as fish or the cooked fruits of *Typhonodorum lindleayanum* were placed into a trap before being sunk into the water at the edge of water bodies. Traps were placed in the water at the start of evening and are collected the next day.
Tritrampanga (Figure 3.7a) (only in Soanierana-Ivongo) [shrimp]	50%	This is a trap for catching freshwater shrimp. It consisted of a bundle of leaves and stems of the fern *Dicranopteris linearis*, and was sunk into the water. The bunch was secured with a stick pushed into into the substrate, to hold it in one place. For this reason, the water where the bunch was placed had to be sufficiently shallow to allow the stick to secure it until it was collected. The shrimp, when seeking refuge or food in the tritrampanga, were trapped. The minimum exposure to maximise trapping was 4-5 days. For harvesting, the shrimp were released from tritrampanga and collected with another device called banabana (a woven basket made from principal nervures of Raphia (Figure 3.7a).
Goninorana (Figure 3.7b) (both in Soanierana-Ivongo and Foulpointe) [shrimp]	30%	This is a new shrimp trapping technique had been popularised since 2006. The main material called gony was not made in the area. It had to be purchased in cities like Soanierana-Ivongo. The fisherman poured rice bran into each bag (gony) through its circular opening, before placing all the bags in the fishing area. The bran served as shrimp bait and the trap could be collected after one hour. Currently, this type of trap was the most frequently used, because of its higher profitability compared to tritrampanga.

At the saturation phase of aquatic weed invasion, some of the fishermen who had been using gill nets and cast nets decided to change to using traps (vovo), with a slight increase in the percentage of fishing lines (Figure 3.6). This change was attributed to the difficulty of using gill and cast nets in quatic weed invaded areas. Originally, the fishermen only used tritrampanga and banabana methods for catching shrimp (Figure 3.7a), but in 2006 they found a new material which could be incorporated into a new type of equipment called "Goninorana" (Figure 3.7b), a much more profitable technique.

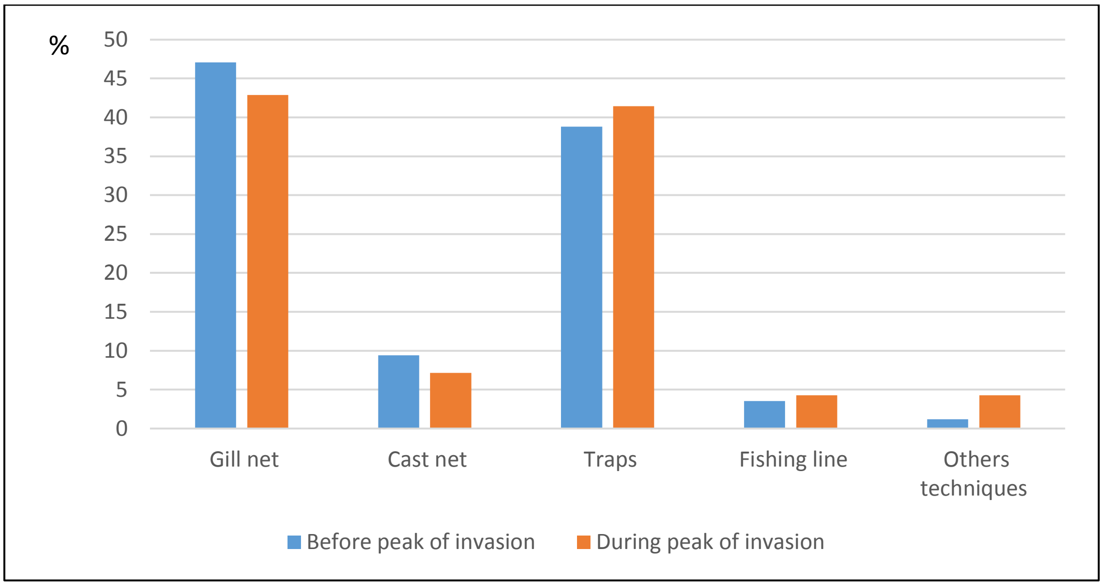

Figure 3.6.: Techniques used for catching fish before and during the peak aquatic weed invasion

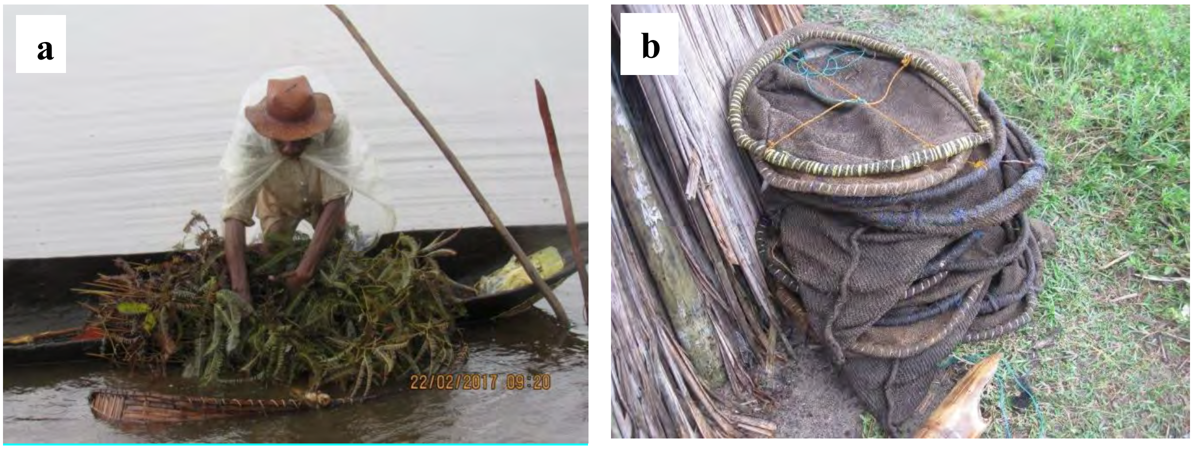

Figure 3.7.: Equipment used for shrimp fishing: (a) Tritrampanga (held bunch of plants) for trapping shrimp and banabana (equipment in the water below the tritrampanga) for collecting shrimp; (b) Goninorana, new material for trapping shrimp

3.4.5.3 Impacts of invasion on fishing revenue

None of the respondents indicated that the invasion of alien aquatic species at both sites had reached their saturation phase before the 2000s. In 2000, prior to invasion saturation, among the 102 households surveyed, 55 practiced fishing of which 42% targeted both fish and shrimp, while the remaining 58% of fishermen targeted a single product, either fish or shrimp. During the invasion saturation (from 2000 onwards continuing through the 2016-2019 survey period), ten respondents decided to abandon fishing altogether due to declining returns on effort. In addition, some of them who continued fishing reduced their frequency of fishing. Both these parameters, *viz.* a reduction in quantity and in the number of fishing days, induced a reduction in the quantity of both fish and shrimp per household. The invasion led to a decrease of fishery production from 117.26 kg/week to 21.03kg/week, a reduction of 82% which was statistically significant (Table 3.7).

Table 3.7.: Quantity of fishery production including fish and shrimp per week at Foulpointe and Soanierana-Ivongo

Statistical parameters with confidence interval 95% (*p<0.05*)	**Weight before the peak of invasion in 2000 (kg) (n=55)**	**Weight during the peak of the invasion (survey 2016 to 2019) (kg) (n=45)**
Mean of volume fishery production/week ± SD	117.26±33.32	21.03±10.60
t value	5.10 > ($t_{crit.}$=1.98)	
Difference of the means	96.23 ± 37.32	
Percentage of decrease of fishery caught	82%	

Although the prices of fish and shrimp increased significantly from the period before compared to during the saturation phase of the infestation, by 308% and 364% respectively, the income generated by fishermen continued to decrease to the reduction in volume caught. Before invasion saturation, the income generated from fishing averaged Ar101,112 (US$ 27.60) per week per fisherman, with this dropping to Ar74,330 (US$ 20.29) during the invasion saturation (Table 3.8). This resulted in a negative Fisher value index of 26.49% (I_v = -26.49%) for all fishermen surveyed. In monetary value, the income of these fishermen was reduced by 26.49% between these two periods.

The direct effects of the invasion were observed in the drop in the quantity of products and the fishermen did not recover to the pre-saturation phase values at conclusion of the interviews. This is mainly due to the blocking of navigation pathways and the difficulty in catching fish in infested areas. The invasive marbled crayfish (*Procambarus sp*), known locally by "Foza orana", was already present in Foulpointe, as was the Asian toad (*Duttaphrynus melanostictus*) or "Radaka boka" (Mr Adelin Mahefa, pers. comm.). According to fishermen's accounts, since the arrival of marbled crayfish in 2019, the quantity of shrimp catch had decreased further. Although the introduced shrimp constituted a significant source of income and protein in some invaded areas (Andriantsoa *et al.* 2019), in Foulpointe, *Procambarus sp* was not appreciated by local people in terms of palatability nor prioritised for sale compared to other species. Therefore, the quantity harvested was limited and the invasion of this species reinforced the deterioration of the freshwater fishing sector, already impacted by aquatic weeds.

Table 3.8.: Revenue from fishing activities per week

Parameter	Revenue before the saturation of infestation , before 2000s (estimated from survey 2016 to 2019) (Mean ± SD)	Revenue during the saturation of the infestation (survey 2016 to 2019) (Mean ± SD)
Price of fish (per kg)	Ar1,275±795.25 (US$ 0.35± 0.22 (n=54)	Ar5,205 ±2,659.60 (US$ 1.42±0.72) (n=44)
Price of shrimp (per kg)	Ar1,367±939.49 (US$ 0.37±0.25) (n=23)	Ar6344±3,553.83 (US$ 1.73±0.97) (n=18)
Mean value of fishery products per fisherman	Ar101,112±78 138.77 (US$ 27.60±21.33)	Ar74,330±96 435.77 (US$ 20.29±26.32)
Fisher Value Index	-26.49%	

3.4.5.4 Impacts on the revenue of canoe transporters: case of Soanierana-Ivongo

According to the accounts by the elderly, on the Pointe à Larrée peninsula, Soanierana-Ivongo, the Antsokafina canal connecting the Simianona River and Antsohy, passing through Lake Antsokafina, was navigable before independence in 1960. However, in truth, nobody remembers the exact date of its closure. Its obstruction by invasive aquatic species (*P.crassipes, S.molesta, P. stratiotes*) resulted in only the portion connecting the Andranomena River and Lake Antsokafina being accessible by paddle canoe and despite several community efforts attempts to reopen it. Since it no longer serves as viable route between villages, the canal was not used as part of the public transport network. However, the fishermen, the owners of the rice fields around Lake Antsokafina and the charcoal producers used for access to their rice fields by means of paddle canoes. Since the Antsokafina Canal was no longer usable as a public transport route, the impacts of aquatic weeds on transport activities were instead evaluated through interviews conducted with motorboat operators between the village of Andrangazaha and the town of Soanierana-Ivongo along the Antarosa Canal.

The Antarosa Canal connects the Simianona and Marimbona rivers close to their outlets at their respective mouths at Andrangazaha and Soanierana-Ivongo. Like the Antsokafina Canal, the Antarosa Canal is also invaded by *P. crassipes* and *S. molesta*. As the Marimbona river connects directly to the sea, outside the peak season for rainfall from October to December, the seawater is able to intrude, contributing to a rise in salinity in the canal. In fact, the water becomes brackish, locally called "Fanasindrano". Freshwater invasive species do not tolerate this increase in salinity, resulting in a remarkable reduction in infestation along the canal. During the rainy seasons from January to September, the salinity of the water declines, thus favouring the development of these invasive species. Consequently, the existence of these alternating phenomena (low and brackish salinity), and the resulting fluctuations in levels of infestation by invasive aquatic species resulting in little effect on transport activity along the Antarosa Canal. When the infestation reaches a certain level, the salinity due to the rising sea wiped out the aquatic weed biomass. According to the transporters, the major factors that affect transportation activity are bad weather, floods and competition between motorboat operators.

At the time of interview, there were a total of nine motorboat operators in the village of Andrangazaha who provided daily transport, five of whom were interviewed. Of these one started less than one year ago, one had been in the business for six years and the other three for more than 10 years. They transported people and different kinds of goods, including fish, charcoal and poles. The frequency of travel depended on weather conditions, floods, competition level and varied from once a day to once a week. Profits ranged from Ar20,000 (US$ 5.5) to Ar60,000 (US$ 16.4) per day with an average Ar40,000 (US$ 10.9) per day. This illustrates the potential profits lost with regards transport on the Antsokafina Canal through blockage of the canal by invasive aquatic weeds.

3.4.5.5 Economic impacts of aquatic weeds on rice production

The impacts of aquatic weed invasions on rice production were studied at Site 2 in Foulpointe and Site 3 in Antananarivo. In Antananarivo, the 21 farmers surveyed were all rice producers and they all practiced irrigated rice cultivation, which was susceptible to aquatic weed invasion. For every cropping period, some farmers cleared the rice fields of all invasive aquatic weeds once, others twice, and some even up to three times (where the infestations were densest). At both sites, farmers cultivated rice once to three times a year and the cropping cycle lasted for three to four months. The first clearing of aquatic weeds was essential before transplanting of rice seedlings, otherwise, there was a risk of zero production in the infested plots. This first clearing accounted for 79% of the total clearing costs. The second and third operations clearings were optional, depending on the degree of infestation. However, in the case of re-infestation of aquatic weeds, neglect to clear could significantly reduce the yield of the rice plots. The total area of rice fields farmed by a family varied from 0.02 hectare (200m^2) to 0.7 hectare, with an average size of 0.22 hectare per household. The overall average expenditure of farmers per rice cycle to control the aquatic weeds was Ar2,909,500 (US$ 794)/Ha (Table 3.9).

Even where the rice fields were cleared regularly, the average yield reduction in the invaded plots was 30%, due to impacts by the remaining aquatic weeds in the rice fields. Given that the average rice field size was 0.22 hectare per farmer (our study), we could deduce that farmers lost an average of 211kg[11] of rice (141.3kg of white rice)[12] per planting season, which corresponded with a monetary value of Ar252,345[13] (US$ 68.9) per household, which corresponded to Ar1,147,022 (US$ 312.7)/Ha. As each household invested an additional average amount of Ar2,909,500/Ha for clearing (i.e. Ar640,100 for the total rice field of 0.22 hectare) the total costs caused by the infestation increased to Ar892,446 (US$ 243.7) per household per rice-planting season (Table 3.9). This was equivalent to Ar4,056,573 (US$ 1107) per Ha.

According to the rice growers' observations, while *P. crassipes* reduced the cultivable area, *S. molesta* was considered more harmful in terms of rice harvest reduction. *Pontederia crassipes* usually began its invasion from the edge of the plots and moved progressively to the middle of the rice field. The rice growers gradually abandoned the invaded plots because of the difficulty of removing *P.crassipes*. Consequently, each year, the cultivated area continued to reduce due to the invasion of *P. crassipes*. In contrast, *S. molesta* directly infested all parts of the plot and grew quickly between the rice seedlings. During flooding, the biomass of the two species piled up above the rice seedlings causing them eventually to die. Consequently, very little grain was harvested and sometimes nothing at all. Furthermore, according to the farmers' perception, the plots infested by *S. molesta* became very nutrient rich with rice growing excessively lush vegetation whilst producing very little harvestable grain.

Table 3.9.: Economic impacts of aquatic weeds on rice growing in Antananarivo (Arrondissement V and VI) (n=21)

Descriptive parameter	**Value (mean ± SD)**
Decrease in rice yield (damage costs)	Ar252,345±168,230 (US$ 68.9±45.93) per household per planting season, equivalent to Ar1,147,022 (US$ 312.7) per Ha
Additional expenses for clearing rice plots (control costs)	Ar640,100±697,709 (US$ 174.7±190.5) per household per planting season, equivalent to Ar2,909 500±3,174,000 (US$ 794.5±866.7) per Ha
Total costs by water weed invasion	Ar892,446 (US$ 243.7) per householdper rice-planting season, equivalent to Ar4,056,573 (US$ 1107.7) per Ha

In Foulpointe, in 2018, with the technical and financial support of the non-governmental organisation, Organe de Développement du DIocèse de Toamasina (ODDIT)[14], local

[11] : according to FAO (2000), yield of rice production is 3.2t/Ha in the study zone.
[12] : ratio of white rice/paddy is 67% (Totté, 1995).
[13] : 1kg of price of white rice is Ar 1785 (Arh, 2019a).
[14] : ODDIT is a religious national non- governmental organisation acting on development actions

communities undertook the cleaning of the Sahamare Canal. In the same year, rice producers at Andramoma (around the Sahamare Canal) benefited from increased production. According to the rice growers, before the cleanup, they harvested nothing because of the prolonged floods due to the obstruction of the canal. In 2018, the average yield of the farms amounted to 558 kg of paddy per household. This corresponds to a monetary value of Ar667,258/household/rice-planting season (Table 3.10).

The Pangalanes Canal crosses the studied area, including the village of Antetezana, south of Foulpointe. Before its closure, probably during the 1980s following the massive establishment of water weeds, rice growers used the canal as a means of both human and equipment transportation to reach the rice fields in the southern parts (Ifontsy, Ambodihazinina, Namandrahana) and especially to transport their agricultural production home. Others from southern Antetezana travelled to the Andramoma area where their rice plots are located. With the canal's closure, farmers had to use the bus to reach their rice fields and to transport their harvests. This type of extra expense was due to the invasion of aquatic weeds. The average annual expenditure of farmers related to bus fees travelling back and forth was estimated at Ar39,000 (US$ 11) per household. All four of the invasive aquatic weeds targeted by this study are found in the Pangalanes Canal (Table 3.10).

Table 3.10.: Benefits from removing aquatic weeds and the expenditure related to the closure of Pangalanes canal in Foulpointe

Descriptive parameter	**Value (Mean**±SD)
Rice production after cleaning of the Sahamare canal invaded by *S. molesta* (n = 29)	557.93±396.34 kg paddy per household per rice-planting season
Income generated from cleaning of the Sahamare canal invaded by *S. molesta*	Ar667,250 (US$ 182.14) per household per planting season, compared to Ar 978,000 = US$ 390*) as average annual farm income
Average annual expenditure (bus transport) linked to the closure of the Pangalanes Canal by aquatic weeds	Ar39,000±28,113 (US$ 11±8.7) per household per year

** : Equivalence considered by Randrianarison* et al. *(2016)*

3.4.5.6 Other economic impacts

Two other types of damage caused by aquatic weeds were identified, the effects of flooding on crops and the loss of livestock (zebu and pigs). In terms of flood effects, in Foulpointe, before 2018, when the canal was still obstructed, people complained about the flooding (Lehavana, 2014a), whereas only one person talked about this problem during the survey in 2019.

The Antsokafina Canal, in Soanierana-Ivongo, has a small catchment source from the Anjahamanintsy forest. Following the closure of the canal by carpets of invasive species, water quality was reduced as the mats of water weeds slowed down the water flow. In the event of excess water during the rainy season, the lack of a drainage system caused by the aquatic weeds lead to prolonged flooding, sometimes lasting up to a month. As a result, all rice plantations were destroyed.

Further, in Soanierana-Ivongo, more than 80% of the respondents complained about the disappearance of livestock that drowned after walking onto the floating aquatic weed mats of macrophytes to eat the grasses that grew on top of them. While currently this is not a concern among villagers at the Foulpointe study site, previously, in 2012, this problem affected cattle and pig rearing which accounted for 53% of households' overall income (Lehavana, 2014a).

3.4.6 Impacts on fish and shrimp biodiversity

In terms of biodiversity, at the two sites (Soanierana-Ivongo and Foulpointe), 32 species of fish and eight species of shrimp were identified, of which 26 species of fish and five species of shrimp were shown to be negatively affected by aquatic weed invasion during the surveys (Table 3.11). Before the saturation phase of invasion, all these species were reported by local people to be abundant in lakes. Currently, in Foulpointe, a species called Laokalava has not appeared in the fishermen's catch since 2000. From the description of the local fishermen, Laokalava was a big and long fish which, as an adult can reach 10 to 15 kg and 1 m in length. This fish prefers the surface of the water. Because we did not have any scientific reference, the description given by the fishermen is the only information known about the species. The endemic species, *Paratilapia* sp. (Cichlidae) (fony or zavaviantsohy) (Figure 3.8a) had also become extremely rare. We never found the species in Foulpointe, or at Antsokafina lake, but we did find an individual captured by a fisherman in an open area near the village of Rantabe (between village of Andrangazaha and Soanierana-Ivongo). *Ptychochromis* sp. (Teleostei: Cichlidae) (saroy) (Figure 3.8b) was also very rare at both sites. It had never been found in areas where there were aquatic weeds. However, some individuals still existed in the non-infested areas such as around the village of Ambodimanga, the village of Rantabe, both in Soanierana-Ivongo and in the western part of the Sahamare Canal in Foulpointe.

In addition to these three species, 23 other fish species were reported by local people to have declined (Table 3.11). Some of these species were still abundant in the catch of fishermen, but the numbers apparently continued to decline compared to the situation before the saturation phase of aquatic weed invasion. Five species remained stable, four of which are introduced species, including the invasive species *Channa maculata* (Lacepède, 1801) (Channidae) or fitaba. The introduced species *Coptodon zillii* (Gervais, 1848) (Cichlidae) according to respondents, had recently arrived at the study sites. In Foulpointe, according to fishermen, the species was found for the first time in 2014 and its population was currently growing quickly.

Concerning shrimp, eight species were routinely caught by fishermen. They were all still present at the time of the survey, but five of them were reported to have declined in abundance and two were stable (Table 3.11). It is also important to note the arrival of an invasive species, the marbled crayfish (*Procambarus* sp.) (Cambaridae), or foza orana in the Foulpointe area in 2019. At the time of survey, the species was not very abundant but populations are growing rapidly.

Table 3.11.: Trends in fish and shrimp abundance during the peak of invasion of aquatic weeds at Antsokafina and Andramoma lakes

Group	Vernacular name	Scientific name (Kiener, 1963 ; Andrianaivojaona *et al.,* 1992; Rham, 1996)	Family	Status (Kiener, 1963 ; Rham, 1996)	Situation during the saturation phase of invasion		Site
					Abundance	Trend	
Fish	Laokalava (trotisy)	*Unidentified*	Unidentified	Unidentified	Zero	Disappeared	Site 2
	Fony (Zavaviantsohy)	*Paratilapia* sp. Heckel	Cichlidae	Endemic	Rare	Highly decreased	Site 1, 2
	Saroy	*Ptychochromis* sp. Steindachner	Cichlidae	Endemic	Rare	Highly decreased	Site 1, 2
	Amalona	Anguilla sp Garsault	Anguillidae	Unidentified	Abundant	Decreased	Site 1, 2
	Ambarababaka	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Amboroka	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Ankavy	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Barahoa	*Unidentified*	Unidentified.	Unidentified	Abundant	Decreased	Site 1, 2
	Bikalanana	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 2
	Debo	Bedotia madagascariensis Regan	Melanotaeniidae	Endemic	Abundant	Decreased	Site 1, 2
	Fiampotsy	*Unidentified*	Unidentified.	Unidentified.	Rare Site 2, abundant Site 1	Decreased	Site 1, 2
	Fiagnambato	*Unidentified*	Unidentfified.	Unidentified.	Rare	Decreased	Site 1, 2
	Hintana	*Scatophagus cf. tetracanthus* Lacépède	Scatophagidae	Native but not endemic	Rare	Decreased	Site 1, 2
	Jebojebo	*Mugil sp.* Linnæus	Mugilidae	Unidentified	Rare	Decreased	Site 1, 2
	Lagnorana	*Caranx sp.* Lacépède	Carangidae	Unidentified	Abundant	Decreased	Site 1, 2
	Laobazaha	Osphronemus goramy Lacépède	Osphronemidae	Introduced	Rare	Decreased	Site 2
	Malemiloha (Kalibasy)	*Tilapia macrochir* (Boulenger, 1912)	Cichlidae	Introduced	Rare	Decreased	Site 2

	Masovoatoka	Paretroplus polyactis Bleeker	Cichlidae	Endemic	Abundant	Decreased	Site 1, 2
	Mikaosa	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1
	Angaravoha	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Tilapia	*Oreochromis niloticus* Linnæus	Cichlidae	Introduced	Rare	Decreased	Site 1, 2
	Toho	Glossogobius giurus F-Hamilton	Gobiidae	Endemic	Rare	Decreased	Site 1, 2
	Tsimisaraka (zono)	*Rheocles* sp. D. S. Jordan & C. L. Hubbs,	*Bedotiidae*	Native	Rare	Decreased	Site 1, 2
	Varivaragna	*Unidentified*	Unidentfified.	Unidentified	Rare	Decreased	Site 1, 2
	Vilivary (fotsy)	Teratamulus waterloti Pellegrin	Atherinidae	Endemic	Rare	Decreased	Site 2
	Zompona na henalahy	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Ambatsy	*Ambassis ambassis* Lacépède	Ambassidae	Native but not endemic	Abundant	Stable	Site 2
	Carpe	*Cyprinus carpio* Linnæus	Cyprinidae	Introduced	Abundant	Stable	Site 1, 2
	Fibata	*Channa maculata* Lacépède	Channidae	Introduced and invasive	Abundant	Stable	Site 1, 2
	Makrosera na dialava	*Tilapia sp* Smith	Cichlidae	Introduced	Abundant	Stable	Site 2
	Vily (maintimainty)	*Cf Bedotia sp*	*Bedotiidae*	Endemic	Abundant	Stable	Site 1, 2
	Tandrondromena	Coptodon zillii Gervais	Cichlidae	Introduced	Abundant	Newcomer as of 2014, increased	Site 1, 2
Shrimp	Horambe	*Macrobrachium* spa Spence Bate	Palaemonidae	Not endemic	Rare	Decreased	Site 1, 2
	Sahabetaifaka	*Macrobrachium* sp2 Spence Bate	Palaemonidae	Not endemic	Rare	Decreased	Site 2
	Oramilay	*Unidentified*	Unidentified.	Unidentified	Abundant	Decreased	Site 1, 2
	Orantsotra	*Macrobrachium* sp.3 Spence Bate	Palaemonidae	Unidentified	Rare	Decreased	Site 1, 2
	Rangàza	*Unidentified*	Unidentified.	Unidentified	Rare	Decreased	Site 1, 2
	Horampotsy	*Fenneropenaeus indicus* H. Milne Edwards	Penaeidae	Not endemic	Abundant	Stable	Site 1, 2
	Orandava	*Unidentified*	Unidentified.	Unidentified	Abundant	Stable	Site 1, 2
	Foza orana	*Procambarus* sp. Ortmann	Cambaridae	Introduced and invasive	Quite abundant	Newcomer as of 2019, increased	Site 2

Site1= Soanierana-Ivongo; Site 2 = Foulpointe.

Figure 3.8.: Endemic fish species at the study sites: (a) *Paratilapia* sp. (fony or zavaviantsohy); (b) *Ptychochromis sp.* (saroy)

3.4.7 Management of infestation of aquatic weeds

3.4.7.1 Current management

Following the closure of the Antsokafina Canal in Soanierana-Ivongo and the Sahamare Canal in Foulpointe, during the 2000s, Associations of Water Users were created whose aim was to keep the canals clean. In Soanierana-Ivongo, the Association was formalised, called the FIZASIFA Association, Registration No. 395/DIST/SI/ASS. In Foulpointe, the Association had not yet been formalised. The Associations gathered together all users of water sharing a primary interest in controlling the invasive aquatic weeds: including fishermen, rice growers, and charcoal and timber sellers.

In terms of participation in control actions, the two sites (Soanierana-Ivongo and Foulpointe) had the same levels of commitment, with 85% (n=33 in Soanierana-Ivongo and n=47 in Foulpointe) of those surveyed having taken part (Figure 3.9). Alongside weekly community works, the members also participated in high labour-intensive works to remove aquatic weeds, supported by NGOs for example the Missouri Botanical Garden in Soanierana-Ivongo in 2012 and by ODDIT in Foulpointe in 2018. In Antananarivo, an Association was never formed. Instead, an informal arrangement existed that everyone took care of cleaning their own rice field. Actions were coordinated by rice growers themselves, so that they are carried out within a specific timeframe in order to control aquatic weed infestations as a whole.

To strengthen community actions, the NGO APIPA[15] supported similar labour-intensive work to clean up the Andriantany Canal in Antananarivo.

Two types of control techniques were practiced, manual and chemical. The manual control included:

a) Physical removal of the aquatic weed mats to the banks of the rice fields. This technique was used by 82% of survey respondents (n=100). For Antananarivo, the technique was used by 100% of the rice growers (n=21). Generally, they started cleaning from the edge, whether in the rice fields or the canal, and gradually moved towards the middle of the infested areas. The sticks was often more effective, especially to collect the biomass of *S. molesta*. The process consisted of using a wooden stick to push the biomass of the aquatic weeds towards the edge of the rice field before collecting it by hand. For control of *A. filiculoides*, nets were sometimes used to scoop the plants up because they are too small to be gathered by hand.

b) Break up the mat so that it could be flushed away by the flow of water. This was practiced by 17% of the total respondents surveyed at the three sites (n=100), with all of them in Soanierana-Ivongo.

For chemical control, only one rice grower in Antananarivo reported using 2,4-D as a selective herbicide, known by many Malagasy farmers as "deshormone" to try to kill *S.molesta*. However, the technique was not effective. Despite this failure, ten months post-surveys, the farmer was still motivated to try the product again to attenuate the damage on of *S. molesta* on his rice production.

According to the members of associations, the manual techniques were effective for short periods (a few months). Nevertheless, these interventions have made it possible to keep the lakes accessible by manual canoe or to produce rice for a season. For rice cultivation, the manual removal reduced the damage to rice yield. According to rice growers, if no control action was taken, nothing was harvested from the plot as it became too cold for the rice seedlings, due to shading by the aquatic weeds. They argued that rice seedlings needed heat from the sun to thrive. Two main inadequacies were identified by survey respondents for

[15] : APIPA stands for Autorité pour la Protection contre les Inondations de la Plaine d'Antananarivo, managing the works and equipment to ensure the defence of Antananarivo against floods, namely: protective dike; the Ambodimita pumping station; storm basins; the flood warning system.

physical and chemical techniques in the long term: a) the plants regrew very quickly (88%, n=83); and b) the seeds germinated very quickly (12%, n=83).

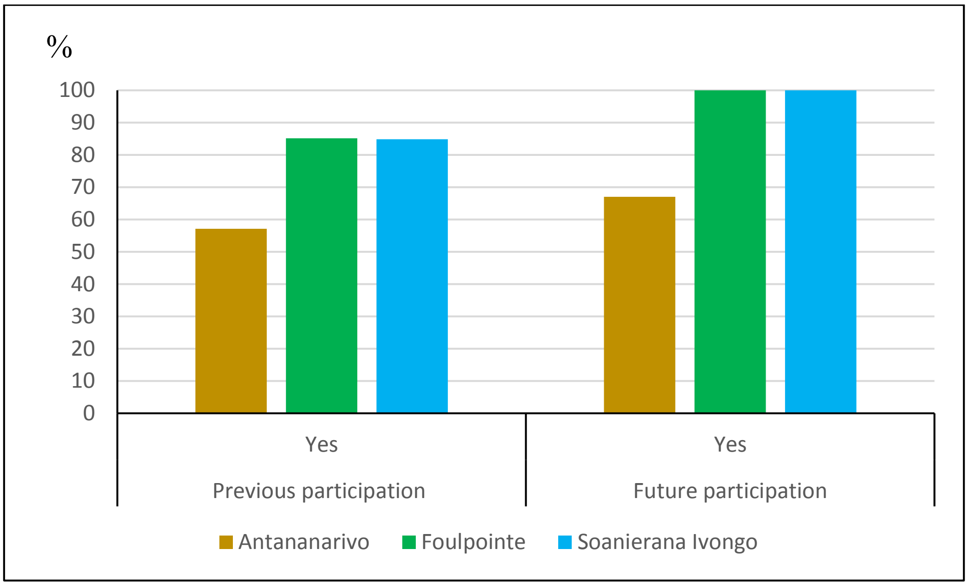

Figure 3.9.: Local community participation in the control of aquatic weeds

3.4.7.2 Management perspectives

When faced with the encroachment of aquatic weeds, seeking effective control techniques is essential. In Soanierana-Ivongo and Foulpointe, all those interviewed stated that they were in favour of participating in control actions. Some were willing to provide both physical and financial contribution concurrently. For the physical contribution, a majority opted for the frequency of once/week (80%); twice/month (5%); once/month (3%), twice a week (2%). The other options were less than 1% for each. Financial contribution values varied, ranging from Ar2,000 (US$ 0.55) to Ar30,000 (US$ 13.65)/year, with an average of Ar13,786 (US$3.76)/year. In Antananarivo, given that they have never organised such community actions, 32% of respondents were not ready for communal work (Figure 3.9).

From the five proposed techniques in the questionnaire, in descending order, the responses were as follows: a) use the correct dose of herbicides (50%); b) cut biomass followed by burning (26%); c) remove and leave with the water flow (20%); d) use natural enemies (4%); e) remove and use (0%) (n=100). Using the natural enemies implies using insects as agents for biological control. A majority of respondents opted to use chemical products because they were tired of continuing with manual practices, particularly for rice growers in Antananarivo who were already familiar with the use of chemical products such as NPK as fertilizer. However, some suspected that chemicals would have a negative effect on both human health and aquatic biodiversity such as fish and shrimp. Therefore, they insisted on reasonable application at the correct dose. For biological control, they were skeptical because: a) they were afraid that the insects would feed on the crops once they have eaten all of the target species; b) some thought that it will take a long time for the insects to eliminate the biomass; c) they were afraid that when living in the water, the insects will attack humans.

For valorisation of the biomass of aquatic weeds as a method of control, two rice growers including one in Antananarivo and one in Foulpointe had already tried to compost *S. molesta*. However, the yield was not worth the cost of production, so the exercise was abandoned. For *P. crassipes*, its use as zebu and pig feed was practiced by 67% and 29% of the interviewees respectively (n = 21), and was to contribute to limiting the spread of the species in the region of Antananarivo. Some propose integrated control, i.e combining mechanical and chemical control.

In order to improve the management of aquatic weed, infestations, several options were proposed to the respondents. The first one was to search for expertise from outside of the site or overseas. This was proposed primarily to share ideas or experiences from other areas throughout the island, where communities were faced with the same problem of biological invasion. This idea was supported by 12% of those interviewed (n=102). The percentage supporting this option seems low because most of the respondents want to see rapid, spontaneous actions rather than dragging around looking for ideas from outside their community. The other option was to seek financial support from NGOs (71% of responses) or support from the government (12%). A final proposal was to strengthen current techniques by increasing the frequency of intervention and the number of stakeholders. This idea was accepted by 5% of those surveyed. An idea also arose from survey respondents to plan and coordinate the actions better. For example, that interventions should be intensified during the dry season when water levels drop and water temperatures become warmer.

As a preventive measure, all the interviewees insisted that a system should be in place to prevent the new introduction of exotic, potentially damaging species in their areas. The main reasons were related to the potential threats to the access of water resources (60% of responses), reduction of fishing yield (10%), destruction of the environment (6%), health risk (4%), and risk of pest and disease (3%). Other reasons that were not proposed in the questionnaire and were frequently evoked by all interviewees in Antananarivo and by around 20% in the two other sites were the destruction of rice plantations and other crops, and their living conditions in general. Respondents commented that for any proposals to introduce alien species to their area, it should be mandatory to investigate the benefits and the risks beforehand.

3.5. Discussion

Through the results of this study, several points of discussion arose. First, regarding the freshwater fishing sector, *S. molesta* and *P. crassipes* were observed during this study as the most noxious species invading the lakes and canals of the two fishing areas studied. *Pontederia crassipes* arrived earlier, while the arrival of *S. molesta* coincided with the same period as that of the introduction of the carnivorous fish *C. maculata*, to Madagascar in 1978, which is well established in the west of the island as well as on the east coast including Pangalanes Canal (Masuda *et al.,* 1984; Huckstorf, 2012). So, it is difficult to identify whether the principal cause of the population declines reported for many native fish species was due to *S. molesta* or *C. maculata*. Despite this, aquatic weed infestations have caused a significant negative effect on aquatic ecosystem functioning. These species are mat-forming and lead to a disturbance of ecological conditions underwater by depriving other aquatic species of light and dissolved oxygen (Ciruna *et al.,* 2004; Dagno *et al.*, 2007; Coetzee *et al.*, 2017; Kenfack Voukeng *et al.*, 2019). It would also appear that endemic Malagasy native species are very sensitive to ecosystem change. For example, at Lake Ravelobe in Ankarafantsika, following a period when it was covered by *P. crassipes*, three endemic fish species, *Paratilapia polleni* Bleeker (Cichlidae), *Paretroplus kieneri* Arnoult (Cichlidae) and *Paretroplus maculatus* Kiener & Maugé (Cichlidae) disappeared and were replaced by the introduced tilapia (Sparks, 2011). Thus, it is very difficult to say with certainty whether the disappearance of certain species like Laokalava or the substantial population declines of endemic species like *Paratilapia* sp. and *Ptychochromis* sp. in the current study were due to water weeds or introduced fish species.

In Africa, there are several studies that provide evidence for the impacts of aquatic weeds on fisheries. In Cameroon, Kenfack-Voukeng *et al.* (2019) reported that, in the Wouri River Basin, Douala, fish catch decreased by 76% (compared to our study with 82%) due to aquatic weed invasion. However, in Cameroon, the percentage decrease in income was 75%, while our study found a much lower income loss of 26%. This can be explained by the fact that in Madagascar, the price of fish increased dramatically after the reduction of fish catch. In Zimbabwe, the situation was worse. A decrease in the quantity of fish caught was also reported by Chikwenhere and Phiri (1999) in Lake Chivero, where, before the invasion of water hyacinth, an average catch of 50–60 kg of fish a day was made, which reduced to just 2.5–3 kg per day, post-invasion.

The second point of discussion arising from our study centered around the transport sector, where rehabilitation programme for the Pangalanes Canal is currently underway (MTTM, 2019; Tribune, 2019). This 665 km long canal built in 1896, has long served as a transport route connecting lakes, lagoons and navigable rivers from Farafangana to Foulpointe. The current rehabilitation program consists of dredging the canal by removing the masses of sand and the biomass of aquatic species including the aquatic weeds. Currently, all the four target aquatic weeds are present along the canal (see Chapter 2). With an investment of Ar3,000,000,000 (US$ 819,000), it is proposed that a 433 km-long portion of the canal will be opened between Toamasina and Mananjary (Acaciasbungalows, 2020). The completion of works will contribute to improving the Malagasy economy, particularly in the transport and tourism sectors. This is the third investment in a long time, implemented by the government, that aims to control aquatic invasive species in Madagascar after the first attempt in 1947 and the second attempt in 1980 (Decary, 1965; Ratsirinony, 2018; Acaciasbungalows, 2020). In 1947, to control the infestation of water hyacinth in the region of Antananarivo and Lake Alaotra, the government used the herbicide 2-4-D product, which resulted in control ranging from 100% to 30% (Decary, 1965). Despite the alarming spread water hyacinth across the island since then, no concrete large-scale action has been taken to reduce the impacts of aquatic weeds. To be effective, any investment should be accompanied by an appropriate management system to mitigate or even to prevent the re-establishment of invasive aquatic species. When clean, the Pangalanes canal will have to be monitored to maximise the investment.

The third point of discussion arising from this study, with the average area of 0.22 hectare per rice farmer, the total cost of aquatic weed invasion was estimated at Ar892,446 (US$ 244)/household/rice-planting season, including harvest damage costs of 30% of harvest and control cost of Ar640,090/household/planting season. In an FAO study (2000b), it was found that the average size of rice plots in the highlands was 0.63 ha per rice farmer. So, if we used this figure as a basis for calculation, the loss due to the infestation amounts to Ar2,556,565 (US$ 697)/household/rice-planting season, while the average family income in Madagascar was US$ 390 per year (INSTAT, 2013; Randrianarison *et al.,* 2016). It is thus clear that with the current degree of infestation, aquatic weeds contribute significantly to the impoverishment of the Malagasy people, as around 80% of Malagasy people work in the agricultural sector and 85% of farmers cultivate rice. Irrigated rice, which is susceptible to invasion, occupies 79% of the total area under rice cultivation. In Senegal, the cost per hectare of *S. molesta* infestations on rice production is US$ 19 (GISP, 2007). This is much lower compared to the findings of this study, where the total cost of infestation was US$ 1107/ha. This significant difference can be best explained by the fact that in Senegal, the study focussed only on one species, *S. molesta*, while in our study, four aquatic weed species, and in particular *S. molesta* and *P. crassipes*, interfered with and induced impacts whose final costs were exorbitant.

The fourth point of discussion concerns the management of aquatic weed infestations. A project for cleaning up of Lake Ravelobe in Ankarafantsika national park, in 2007 by Madagascar National Parks (MNP), provided positive aquatic weed management experience in Madagascar. The lake offers a refuge area for several endemic species and has an important tourism value; however, it was severely invaded by water hyacinth, which covered almost half of the lake (Ranarijaona *et al.*, 2013). The impacts were observed as being both socio-economic (reduction of income, abandonment of the surrounding rice fields and hydraulic disturbance), and conservation-related, through a loss of wildlife biodiversity (Sparks, 2011; Ranarijaona *et al.,* 2013). Manual removal of *P. crassipes* was undertaken in 2007, using a total sum of 850 Euro, which allowed the hiring of labour for 810 person-days. The removed biomass was burnt and buried (Ranarijaona *et al.*, 2013). Two years after this intervention, in 2009, the species recolonised the lake. This demonstrates that the management system was not adequately effective. According to Park Agents, the reasons for ineffectiveness were as follows: 1) intermittent removal; 2) the completion period was different from one part to another, i.e. only part of the lake was cleared at any one time, which allowed re-infestation from the other parts; 3) incomplete removal; and 4) work poorly executed due to fear of crocodiles (Ranarijaona *et al.*, 2013). Although the manual removal technique on Lake Ravelobe in 2007 was not visibly effective, the experience provided an important learning experience, from amanagement perspective of such aquatic weed infestations. Because no monitoring of changes to water hyacinth biomass, after this intervention, was conducted, the inadequacy of the system could not be attributed only to the techniques used, but also to the lack of an appropriate monitoring system.

In 2016, the Durrell Wildlife Conservation Trust resumed cleaning work on Lake Ravelobe, across an infested area of 18 ha, by strengthening the actions of the local association FSR (Fikambanana Sakaizand-dRavelobe) with financial support of CEPF[16]. According to the

[16] : Critical Ecosystem Partnership Fund

technical report provided by Velosoa (2019), manual removing started in 2017. This continued until 2019 resulting in an infestation level of less than 1%. In total, 517 people including 214 women and 303 men took part in the actions. Currently, the lake, which is an important habitat for endemic species, has resumed its ecological functioning with viable populations of various species. With respect to the socio-economic aspect, the actions have improved the income of farmers in the riparian areas, including 2,166 farmer members of two local associations and 5,000 rice growers on the Marovoay plain, by improving the lake's water flow. The touristic circuits have been extended while providing benefits to 25 local guides and the Park manager. A revolving funding system is being negotiated between local stakeholders to make the actions sustainable.

During the three years of operations, the Durrell team, in conjunction with the local associations, carried out three participatory monitoring events per week, which made it possible to improve the infestation management system. *Phragmites* reed-beds often act as a refuge for individual of the water hyacinth plants. However, regular monitoring had been implemented to manage the species' population at a level of around 0.5%. Eradication has rarely been successful in the case of aquatic weeds due to the difficulty to completely removing all fragments; the remaining plant parts are the source of new mats (Hill and Coetzee, 2008). Importantly, a permanent monitoring system was put in place to keep the level of infestation at an acceptable level. Local stakeholders therefore agreed that each year, 525 person-days would be allocated to ensure ongoing monitoring. Post-control monitoring and continuous commitment are crucial for the success of the aquatic weed management programmes as it allows the implementing agent to better understand the impacts of interventions, to fine-tune their actions, to ensure better coordination and circulation of information between partners and to strengthen the training necessary for management (FAO, 2006; Dutartre *et al.,* 2008; Grice, 2009; Downey *et al.,* 2010a).

The final point of discussion concerns the perspective of a management strategy for invasive alien aquatic weeds in Madagascar. Faced with the massive challenges relating to aquatic weed invasions, the Malagasy government must prioritise actions. In Madagascar, sporadic control actions exist, undertaken by local communities, with or without support from NGOs or the government. For example, in the western part of the Digue Betsimitatatra, Antananarivo, in the villages of Anosivita and Ambohimiavotra, rice growers have made efforts to manage the infestations of *S. molesta* in rice cultivation. The results are palpable, for the past four years, the degree of infestation has dropped significantly. It is one of the few areas surveyed where farmers have reported having reduced the aquatic weeds. Likewise, in Foulpointe, the clean-up actions have brought tangible benefits to the communities. Such actions should be supported technically and financially with a coordinated programme of control by the State.

As the Malagasy government aims to be self-sufficient in rice and to increase fish production as well, it has to prioritise interventions to limit the loss of production. Grice (2009) emphasised that the evaluation of impacts of invasive weeds using quantitative data is important insofar as to justify any strategy as well as the investment in resources required. When analysing on one hand the available data on the current distribution of the four aquatic weeds forming the focus of this study, across the whole country (see Chapter 2) and on the other hand their socio-economic and environmental impacts, it is evident that it is too late to implement strategies prior to control (e.g. containment). So, control is suggested as the most appropriate strategy going forward, in an attempt to reduce the impacts of invasive species (Wittenberg and Cock, 2001; FAO, 2006; Grice, 2009).

A planning and implementing strategy for control requires a comprehensive understanding of the relationship between the abundance and impacts of an invasive species (Grice, 2009). The relationship between percentage yield loss (of a crop) and the abundance (density) of a weed has been described by a rectangular hyperbolic curve along with weed infestation phases (Figure 3.10). The abundance and the growth rate of aquatic weeds are determined by two main factors. First, they are influenced by a combination of biotic and abiotic factors such as interspecific competition, climatic factors and physico-chemical characteristics of the water bodies and secondly by the carrying capacity of the invaded water body and the stage to which the invasion has progressed (K in Figure 3.10) (FAO, 2006; Grice, 2009). The impacts of invasive species in general, increase with higher abundance, but at a decreasing rate. At low abundance, an invasive species induce negligible or undetectable impacts, while above some threshold, at saturation phase, further increases in abundance result in no greater impacts on the percentage of yield loss (Figure 3.10). Referring to this figure, currently, the three study sites fall in the situation to close to the carrying capacity and the country overall is assessed as being at the start of saturation phase. At this phase of saturation, practicing adequate controls, (e.g. containment) is the recommended action (Chippendale, 1991; Coetzee *et al.*, 2019).

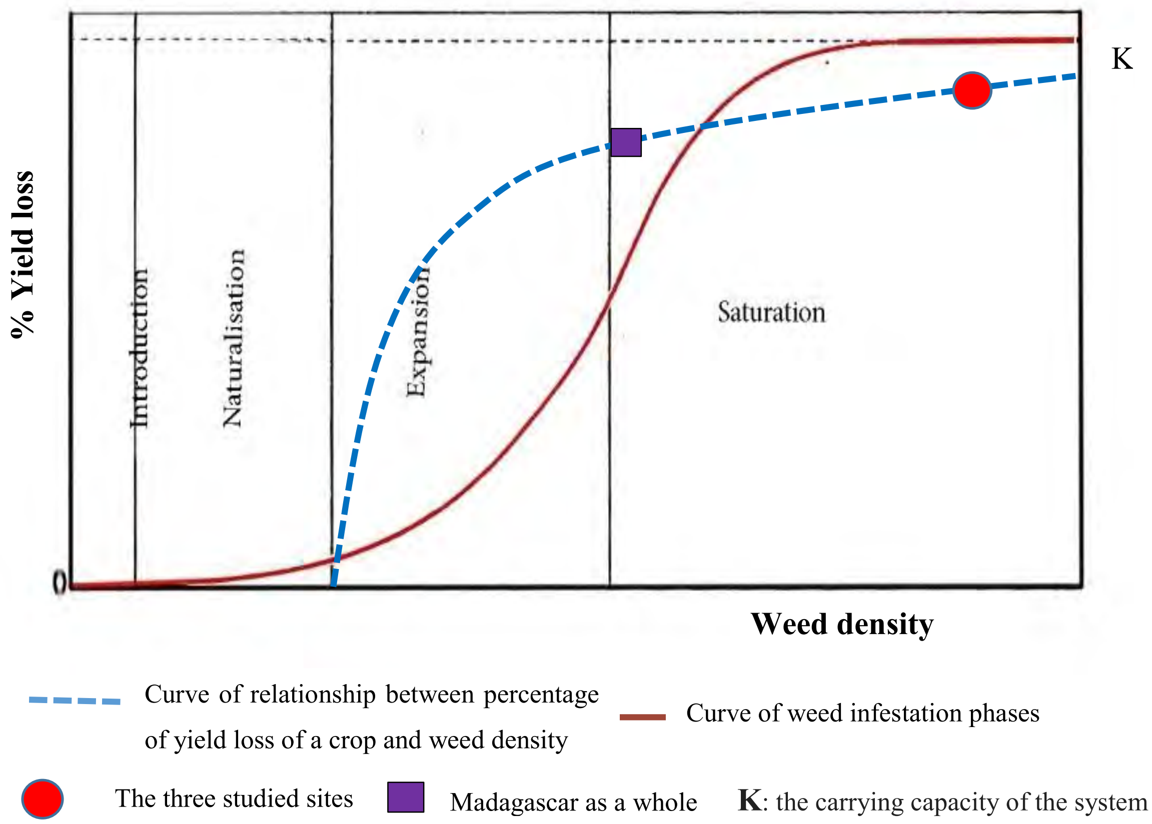

Figure 3.10.: The relationship between percentage yield loss (of a crop) and the abundance (density) of a weed (in dash and blue adapted from Cousens, 1985 in Grice, 2009); Four phases of invasion of invasive species (model adapted from Cousens and Mortimer, 1995; Grovers 1999; Colautti and MacIsaac 2004) (in Grice, 2009))

The benefit:cost ratio of intervention strongly depends on the timing of intervention relative to the different invasion phases. A strategic approach to the management of an invasive species can be defined as a temporal and spatial distribution of the effort that yields the greater benefit from the available resources (Grice, 2000). Taking no action or delaying action can increase the costs of control and decrease the changes of success (Downey *et al.,* 2010a). Early intervention, generally involves dealing with a lower overall density of the invasive aquatic weed which may be less expensive in the long run (Grice, 2009; Akpabey 2012). The decision of where to first intervene and inject resources is critical. This may be made with reference to local, regional or national scales and influenced by the measured and perceived costs, impacts and benefits of control actions (Gren *et al.,* 2007). Grice (2009) suggested that three scenarios can be considered when deciding on the prioritisation of implementing actions:

a) Effort is directed towards places where the invasive species is most abundant or having major impacts. The results of this study confirmed that *S. molesta* caused greater impacts on both fishery and rice growing sectors than did the other three aquatic weeds. Thus, planning of intervention should consider where this species is mostly distributed and abundant (refer to results of Chapter 2).

b) Effort is directed towards places where the invasive species is least abundant. This implies that an intervention requires fewer resources and prevents the species from reach high density, so that it induces fewer impacts. In this circumstance, it is important to maintain the abundance of invasive species at an acceptable level. This can be done through collecting information from the local level in several places and integrating it into the management programme in consultation with decision makers and stakeholders;

c) Effort is focused on areas of particular high value irrespective of the costs. Through this study, at least two sites (Lake Antsokafina and Lake Andramoma) were identified as sheltering endemic, rare and endangered species such as the case of *Paratilapia* sp. and *Ptychochromis* sp. Máiz-Tomé *et al.* (2018) delineated several aquatic sites across Madagascar as key biodiversity areas (KBA) which contain many endangered species. This included 133 species of plants, 60 species of fish, 16 species of molluscs, four species of crayfish, one species of shrimp, two species of crabs and six species of odonates (dragonflies and damselflies). These numbers give an overview of the importance of the biodiversity that deserves to be protected against the risk of aquatic weed invasions in Madagascar.

The results presented here allowed us to evaluate the magnitude of impacts incurred by aquatic weed invasions on the three main economic sectors of the Malagasy people, *viz.* rice cultivation, freshwater fishing and transportation. In addition, analyses of the current situation forecast the possible trajectory for aquatic weeds in the country if the appropriate measures are not taken. The available on-ground data collected will also help decision makers and stakeholders to finalise a management strategy, incorporating spatial and temporal interventions accordingly.

Chapter 4: Ecological impacts of invasive alien aquatic weeds (*Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch.) on Lake Antsokafina

4.1 Introduction

4.1.1 Aquatic macrophytes

Macrophytes can be loosely defined as all forms of macroscopic aquatic vegetation visible to the naked eye, including taxonomically very diverse representatives: macroalgae, mosses and liverworts, and vascular plants, that actively grow permanently or periodically submerged below, floating on, or growing up through the water surface (Chambers *et al.,* 2008). This is in contrast to microphytes, i.e., microscopic forms of aquatic plants, such as planktonic and periphytic algae. The fact that macrophytes live in aquatic environments, at least seasonally, makes them different from terrestrial plants that do not tolerate flooded environments (Rejmánková, 2011**).**

Ashton (1973), considering both lentic and lotic systems, distinguished three types of plants.

- Aquatic plants, called hydrophytes that grow permanently in water bodies. They can be submerged, free- floating or emergent.

- Semi-aquatic plants, or helophytes, that require a period of temporary floods. They live in temporarily flooded areas, the edges of permanently flooded environments, waterlogged environments or shallow-water environments.

- Hygrophytes, plants that are normally found in a waterlogged or humid environment and can only survive for a short time if the area is completely flooded.

4.1. 2. Importance of the physico-chemical parameters on invasive aquatic plant invasion

Aquatic ecosystem structure and functioning are perpetually changing, influenced by ecological and biological inputs. These inputs determine the properties and quality of the water and affect the type of plant- and animal life which it supports (Brooks, 1976; Thomaz and Da Cunha, 2010). For this study, some physicochemical parameters were taken into account in order to characterise the qualities of the water including the influences on IAPS invasions.

The pH which measures of the acidity or alkalinity of water and relates to the concentration of hydrogen ions. pH affects plant metabolism within the cell by affecting enzyme activity and externally by affecting the uptake of nutrients and carbon dioxide (Mitchell, 1974). Aquatic organisms, especially animals, are generally adapted to a very restricted range of pH values, and most of freshwater aquatic organisms prefer a pH range between 6.5 and 8.0 (Brooks, 1976; Svobodová *et al.,* 1993; Behar, 1997). pH below 4.0 and above 10.0 may alter or kill aquatic life (Mitchell, 1974). Thus, the presence or absence of certain invertebrates can be used to estimate the pH and pollution level of water bodies (Brooks, 1976).

The water temperature depends upon climate and this is affected by air temperature, storm-water runoff, groundwater inflows, turbidity, and exposure to sunlight (Behar, 1997). In considering the health of organisms, it is necessary to consider their minimum and maximum temperature thresholds, and optimum temperature. For example, the preferred temperature values of the fish *Tilapia* spp. are between 20 and 35°C, with reproduction taking place only between 25°C and 36°C, and feeding activity ceases when water temperature is below 16°C (Lim and Webster, 2006). Changes in temperature can also induce changes in species composition of plant communities by affecting the competitive ability of its components.

The conductivity is a measure of the capability of a solution such as water in a stream or lake to pass an electric current (Labrique, 1960; Felzines, 1977; Jeremie and Raynal-Roques, 1978). This is an indicator of the concentration of dissolved electrolyte ions in the water. Significant increases in conductivity may be an indicator that pollution discharges have entered the water. Higher conductivity will result from the presence of various ions including nitrate, phosphate, and sodium, increasing macrophyte growth.

The turbidity is a measure of how particles suspended in water affect water clarity. It is an important indicator of the concentration of suspended sediment and thus of erosion. Typically, it will increase sharply during and after a rainfall event, which causes sediment to be carried into water bodies. Elevated turbidity raises water temperature, lowers dissolved oxygen, prevents light from reaching aquatic plants (which reduces their ability to photosynthesize) and harms fish gills and eggs (Hollis *et al.,* 1964; Cumming and Herbert, 2016). Fish in particular become very stressed in waters that remain highly turbid for a long time and this may increase respiration rate, reduce growth and feeding rates, delay hatching and in severe cases, lead to death (Kjelland *et al.,* 2015; Cumming and Herbert, 2016). Turbidity levels can be evaluated by using Nephelometric Turbidity Units (NTU), which are a measure of the amount of light scattered by suspended material in the sample, and the value has to be converted to the Transparency Value using a conversion chart. High turbidity levels and duration of turbidity events influence the behaviour of aquatic organisms, particularly fish and invertebrates. Turbidity above 10,000 NTU for a few weeks is usually lethal to aquatic organisms (Water Action Volunteers, 2006).

Lacroix (1991) and Durantel and Enjelvin (1987) defined a lake as a natural or artificial waterbody that is deep enough to have a vertical gradient of temperature and to allow separation into a littoral area invaded by vegetation and a pelagic area that lacks vegetation. The depth of the pelagic area is always more than 1-1.5m on average in both the dry and wet seasons, and this zone essentially differentiates a lake from a pond.

Lakes are often subject to thermal stratification depending on the climate and the depth of the lake. Three zones can be distinguished along a vertical axis: the epilimnion, varying from 2 to 10m depth, followed by the intermediate thermocline zone and the lower zone (hypolimnion) below 20m depth (Vivier, 1934; Balasubramanian, 2015). During the course of a year, lake waters are characterized by variation in their tendency to mix, depending on a water-circulation pattern commonly known as the "turn-over cycle of the lake". Wind and temperature are the main factors determining the duration and period of lake-water mixing (Balasubramanian, 2015). Several types of mixing patterns of lakes are known throughout the world, but in the tropical environment, one generally encounters polymictic lakes, which show many mixing periods, even to the extent that the waters mix almost continuously throughout the year. These lakes are often small, shallow and in tropical or at least warmer climates. This contrasts with monomictic lakes, which have one regular period of mixing during the year, and of which Lake Victoria is an example. This lake is up to 80m deep and is characterized by thermo-stratification during the summer (September – May) and mixing during the winter (June – August) (Talling, 1966; Nyamweya *et al.,* 2016). During the turn-over of the lake's waters, nutrients from the lower water are brought to the upper surface and similarly oxygen is brought from the surface to the lower depths (Balasubramanian, 2015). This phenomenon brings uniformity of the temperature, and oxygen and nutrient levels, from the top to the bottom, and ultimately influences the biotic distribution and trophic structure of the lake.

Globally, the quality of freshwater resources around the globe continues to deteriorate because of anthropogenic activities including, among others, eutrophication and canalization. Phosphorus is the chemical element considered to be primarily responsible for eutrophication (Zhou *et al.,* 2001; Varjo *et al.,* 2003), but an increase in nitrogen concentration can also cause damage (Sampat, 2000). Eutrophication can be a natural process in which water becomes laden with nutrient salts leached out of the land by streams and formed by the decay of organic matter in the water (Britton *et al.*, 1975; Brooks, 1976; Yang *et al.*, 2008). It is a gradual process and the natural rate depends, amongst other factors, on the nature of the catchment area and depth of water bodies. However, this process has been accelerated through anthropogenic activities resulting in nutrients being added to the water by pollution from sewage, industrial effluent, fertilizer run-off and detergents (Britton *et al.*, 1975; Brooks, 1976; Yang *et al.*, 2008). These nutrients may cause the development of phytoplankton blooms, enhanced organic loading and the proliferation of aquatic macrophytes. These changes may hinder photosynthesis by submerged plants resulting in deoxygenation, and causing death of the ecosystem (Brooks, 1976; Klapper, 1991; Knockaert, 2019).

4.1. 3. Succession of macrophytes community during weed invasion

Macrophytes are represented by seven divisions including four macroalgae divisions (Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta), Bryophyta, Pteridophyta and Spermatophyta (Chambers *et al.,* 2008). Vacular plants represent the majority of taxa with 3457 species, 456 genera and 93 families (Murphy *et al.,* 2019). Spermaphytes are only represented by Angisperms, nearly 1% of the total number of vascular plants (Chambers *et al.,* 2008).
Macrophytes are grouped into four biotypes (Mitchell, 1974; Rejmánková, 1992, 2011; Petr, 2000):

1. Free-floating plants, which have leaves and reproductive organs that are aerial and/or floating, and since they are not rooted in the sediments, their nutrient absorption is solely from the water.

2. Submerged plants, which are generally attached to the bottom by roots, and which often have elongated, ribbon-like or dissected leaves.

3. Attached plants with floating leaves, which have long petioles with leaves adapted to mechanical stress, and reproductive organs that are floating or aerial.

4. Emergent aquatic plants rooted in the substrate with vegetative parts normally emerging above the surface of the water. This group can be categorised into two groups: a) erect emergent, e.g. *Typha* (Typhaceae)*, Phragmites* (Poaceae) and b) creeping emergent, e.g. *Myriophyllum aquaticum* (Vell.) Verdc (Haloragaceae) and, *Rorippa nasturtium-aquaticum* (L.) Hayek) (Brassicaceae).

Madagascar is included in the Afrotropical ecozone, which is characterised by having the second highest values of macrophyte diversity following to Neotropical ecozone (Chambers *et al.,* 2008; Murphy *et al.,* 2019). In terms of specific endemism, the Afrotropical ecozone is positioned ahead of the Neotropical ecozone, which have values reaching 64% and 61% respectively (Chambers *et al.*, 2008). However, the specific diversity values vary depending on the scale considered, viz. local, ecozone or global. Analyses by Murphy *et al.* (2019) using species pool per latitude band showed that the maximum macrophyte diversity occurs within the latitude bands of 10-30°, and Madagascar is included within these latitudes.

Madagascar records 489 species of vascular aquatic macrophytes, grouped in 233 genera and 89 plant families, representing 4.2% of the flora of the country (Manjato *et al.*, 2020, 'manuscript in preparation'). This includes 347 semi-aquatic species, 105 hydrophytes and 37 helophytes, with the species endemism rate reaching 49% (Manjato *et al.,* unpublished). A recent study undertaken by IUCN revealed that 133 aquatic plant species that were endemic to Madagascar were classified as threatened due to habitat loss as a result of agriculture and aquaculture (32.5%), pollution (8.7%), and invasive species (1.6%) (Phillipson *et al.,* 2018). This research recognised that there was a lack of knowledge on aquatic plants, especially the invasive species, and that effective restoration of aquatic ecosystems requires reliable information on the biological interactions within these systems.

Macrophyte diversity provides a complexity relationship between species in aquatic environments and this has been widely studied on various spatial scales of the ecosystems, ranging from a fine scale of centimeters (leaf level) to a large spatial scale(ecosystem level) , demonstrating the important role of macrophytes in structuring communities and the functioning of aquatic ecosystems (Thomaz and Da Cunha, 2010). However, aquatic environments are continually threatened by human activities and biological invasions (Lee *et al.*, 2016), and eutrophication is one of the drivers of macrophyte invasions (Srivastava *et al.*, 2008). Biological invasion leads to habitat homogenization when a single or a few species dominate the community, implying an alteration in physical structure and species composition and richness (Thomaz and Da Cunha, 2010). Changes brought about by eutrophication and biological invasions include those to the composition of the macrophyte assemblage itself, the taxonomic groups present and in biotic relationships among species (Mack *et al.*, 2000; Michelan *et al.*, 2010; Thomaz and Da Cunha, 2010).

4.1.4 Impacts of aquatic plant invasion on animal diversity

The relationship between macrophytes and aquatic fauna is determined by a complex mechanism which provides habitats where animal species can benefit from the assemblage of macrophytes by way of direct food, shelters, feeding sites, nesting materials, and spawning areas (Junk, 1973; Petr, 2000; Thomaz and Da Cunha, 2010). Several studies have demonstrated a positive correlation between macrophyte diversity and wildlife diversity (e.g. invertebrates and fish) per unit area (Gaudet 1974; Gomes *et al.,* 2012; Trindade *et al.,* 2018; Wolters *et al.,* 2018). Aquatic weed invasion may alter habitat complexity and lead to homogenization of physical and biological structures of ecosystems, resulting in a decrease in the availability of shelter and foraging sites, and food resource scarcity for aquatic animal species (Thomaz and Da Cunha, 2010). If a plant ecosystem with high species diversity could provide high levels of substrate heterogeneity, interstitial space habitats and food resources, thereby promoting a variety of types of niche to aquatic animal species, the aquatic plant invasion led to simplification of these structural assemblages (Townsend and Hildrew, 1994; Heino, 2000; Saulino and Trivinho-Strixino, 2017). In South Africa on the New Year's River, Midgley *et al.* (2006) found that the presence of water hyacinth mats had significant detrimental impacts on both the abundance and diversity of benthic invertebrates and algal biomass, and that this could lead to decreased stability in the functioning of the ecosystem because of a lack of interspecific interactions. Similar results were obtained by Coetzee *et al.* (2014) at Lake Nsezi-Nseleni River in the vicinity of Richards Bay, KwaZulu-Natal, South Africa, where 817 individuals (13 families) of aquatic macroinvertebrate were collected from sites located under water hyacinth mats, compared to 17,980 individuals (27 families) from open-water sites. The presence of water hyacinth altered both the diversity and assemblage structure of benthic macroinvertebrates.

In the context of invasive species management, it is crucial to have a full understanding of the invasion mechanism and the influences of external factors as well as of the dynamic interactions of plant communities and the ecosystem as a whole. In the context of Madagascar, the appropriate management of aquatic ecosystems is becoming a major concern, considering the high dependence of riparian human communities on water resources and the degree of threats to these resources.

4.2 Study aims

The overall objective of the research presented here was to provide basic information on the biological invasion mechanism of three aquatic invasive species (*P. crassipes, S. molesta, P. stratiotes*) and their ecological interactions with the environment. The specific objectives were:

1) To understand the invasion process and the impacts of invasion on socio-economic indicators and on aquatic biodiversity of the study lake.

2) To determine the influence of physico-chemical parameter changes of water quality on biological diversity.

3) To provide a case study to determine if the functioning of aquatic ecosystems will return to the pre-invasion state after controlling invasive aquatic species.

The hypothesis is that restoration of ecological services in terms of biodiversity and local economy would be possible if the invasive species are removed and ecosystem functioning restored. The results obtained from this study will provide an effective management-plan model for other sites where there are similar problems.

4.3 Materials and Methods

4.3.1 Location of the study area

The experiment was conducted at Lake Antsokafina (16° 50' 20.5" S, 049° 41' 17.0" E), with an approximate area of 8ha, located 12km north of Soanierana Ivongo, in the Fokontany[17] of Andrangazaha, Madagascar. In this lake, only the western part (20,843m^2) was used for experimentation, and is referred to as Zone A. The area was subdivided into four sub-zones (Figure 4.1): (i) planned for control area (4,652m^2) which was 100% covered by aquatic plants; ii) area 100% infested with aquatic plants, which was subsequently cleared and kept clean (4,485m^2); iii) area 100% infested with invasive aquatic plants, which was cleared and then allowed to be re-invaded (4,731m^2); iv) area where less than 10% was infested, which was then cleared and kept clean (6,975m^2). Because all vegetation within Zone A was washed away by a cyclone at the start of the experiments, another zone, "Zone B", located 300m from Zone A, was demarcated. Zone B was 100% invaded by Invasive Alien Plants (IAP) and the vegetation

[17] Fokontany is the smallest unit of administrative territory in Madagascar below the commune

had been less impacted by the effects of cyclones. The area therefore served as a control for the treatment areas in Zone A. The data collected from Zone A and Zone B were compared with respect to floristic similarity and physico-chemical parameters of water quality.

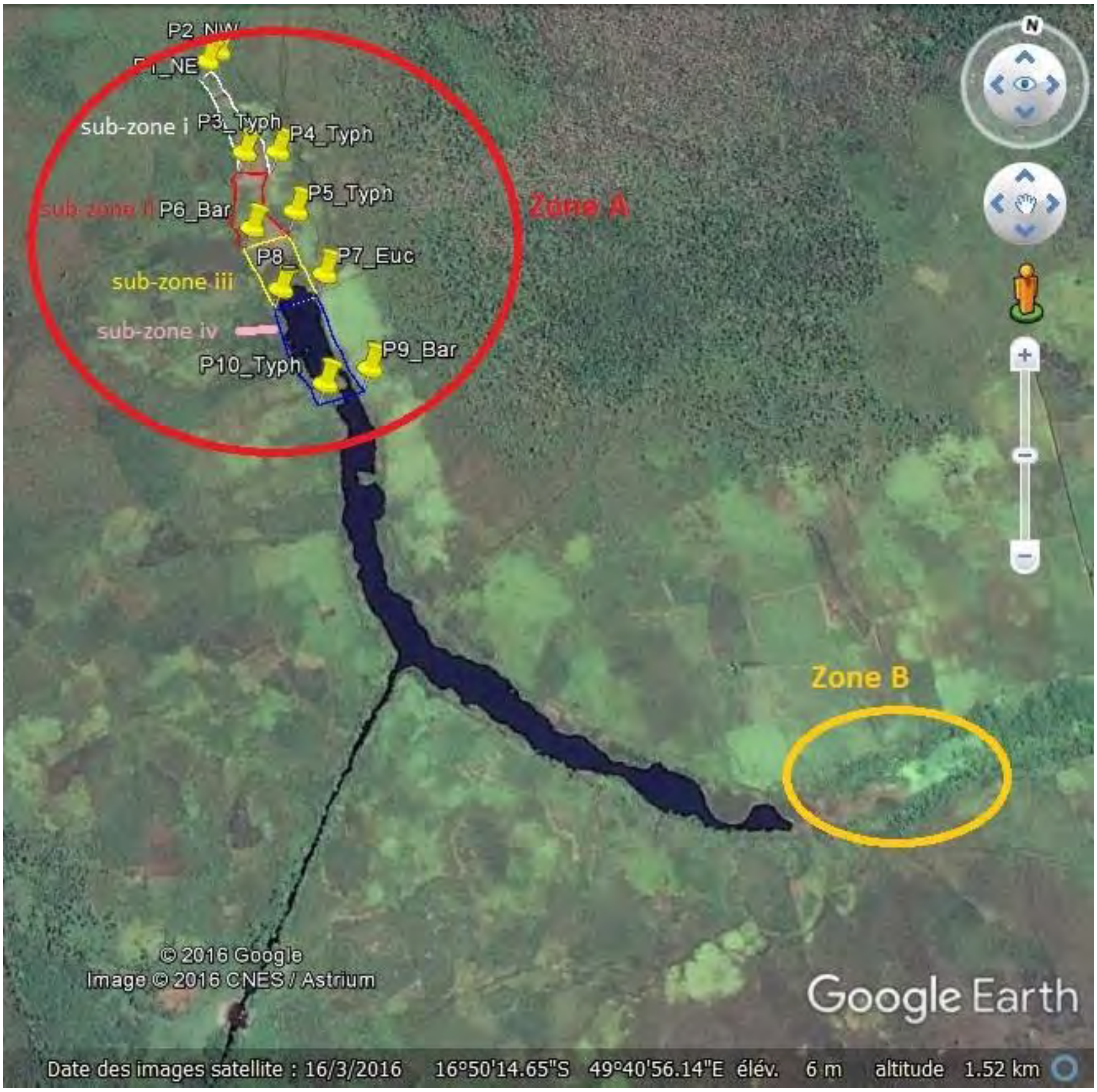

Figure 4.1.: Experimental plot design at Lake Antsokafina.

4.3.2 Physico-chemical measurements of the water

The physico-chemical parameters of the water were sampled every three months, as far as possible, from 05 April 2017 to 04 May 2019. However, this frequency could not always be achieved due to the level of the lake which sometimes prevented us from reaching the site (e.g.

samples prior to August 2018, where several samples were taken at irregular intervals due to the lake inaccessibility, while post August 2018, the sampling was regular).

In each zone, A (open water) and B (under mat of alien invasive aquatic plants), one litre of representative samples (from 12 to 31 samples) of water were taken for analysis. For each physical parameter, the following equipment was used to collect the data: an electronic pH meter calibrated using buffers to measure water pH, an EC/TDS meter to measure water electrical conductivity and temperature, expressed on the scale µS and °C, respectively, and a turbidity meter for measuring turbidity. The means of turbidity values collected in centimeter units were converted into Nephelometric Turbidity Units (NTU) using the Transparency Value Conversion Chart (Water Action Volunteers, 2006). These parameters were measured on the same occasions as shrimps were sampled (see below).

4.3.3. Floral inventory

Before clearing the experimental areas, a floristic inventory was undertaken, representing the T_0 measurements of the study (February 2017). In each subzone (i, ii, iii, iv), a stratified systematic method was applied in which three parallel lines of transect were laid at regular intervals of 15m. Using a rope, a transect line was laid out from one bank to the other. Following the transect line, equidistant quadrat units (2 x 2m) were demarcated, within which the presence/absence and cover/dominance of the species was recorded (Granville, 1976; Chalmers and Parker, 1986; Gillet, 1998).

It was not practical to count all individuals of each species in the lake, so the community was assessed in terms of the species per unit area including all divisions of aquatic macrophytes, except deeply submerged species invisible to the naked eye from the water surface (Begon *et al.,* 2006). The Shannon's diversity index was used as a measure of the character of the community, as it considers into account the total number of the species, their frequency and the species evenness.

To do this, cover-dominance of each species listed within the quadrat was evaluated based on the visual estimate of cover class using the Braun-Blanquet system (Poore, 1955) as follows:

5: any number of individuals, covering more than ¾ of the quadrat;

4: any number of individuals, covering ½ - ¾ of the quadrat;

3: any number of individuals, covering ¼ - ½ of the quadrat;

2: very numerous or covering at least 5% of the quadrat;

1: plentiful but of small cover value;

X: sparsely or very sparsely present, cover value very small.

For analysing the data, these codes of class cover were converted into percentage cover as shown in Table 4.1. When species cover was very small (code X), it was either put in the class "+" (where the cover was estimated to be less than 1%) or by "r" when the cover was insignificant.

Table 4.1.: Cover Classes of Braun-Blanquet (from Van der Maarel, 1979)

Class	Range of cover (%)	Mean
5	>75	87.5
4	51-75	62.5
3	26-50	37.5
2	6-25	15.0
1	1-5	2.5
+	<1	0.1
R	<<1	*

*Individuals occurring seldomly or only once; cover ignored and assumed to be insignificant.

As far as possible, the species encountered within the transect were identified in the field. For species without reliable field identifications, either herbarium specimens were collected and sent to specialists for identification, or information available in the Missouri Botanical Garden database of the plants of Madagascar (https://www.tropicos.org/Project/Madagascar) was used at a later stage to identify the plant. The biogeographical origins of all species were identified using information available through MBG's database.

4.3.4 Faunal inventory

Three types of animal biodiversity were inventoried birds, shrimps and fish. Abundance and diversity of aquatic birds were counted twice a week in the different zones surveyed. These inventories were conducted from 06 September 2018 to 06 August 2019. Each survey lasted approximately 3 hours, from 9 a.m. until 12 a.m. To identify the species from a distance, a pair of binoculars was used and then the species was identified by using Sinclair and Langrand (2013) field guide for birds.

For shrimp, the survey was conducted every three months. In each subzone (ii, iii, iv), 16 bunches of the fern *Dicranopteris linearis* (Burm. f.) Underw. *(*Gleicheniaceae*)*(used locally as shrimp traps known as *tritrampanga*) were used (Figure 4.2a) with a total of 48 *tritrampanga* for the three subzones. The bunches of fern were installed along the shoreline of the lake where the shallow depth allowed us to secure them with stakes. The shrimp traps were left in the lake for five days, as this was the recommended duration for the local method. On collection, the shrimp were collected using locally-made baskets called *banabana* (Figure 4.2b).

For fish sampling, it was not possible to use nets once bamboo poles had been placed in the area to demarcate quadrats, because the net length (usually 100m) exceeded the length of the quadrat (10m). We therefore used the data of catches made by fishermen just outside of the experimental areas.

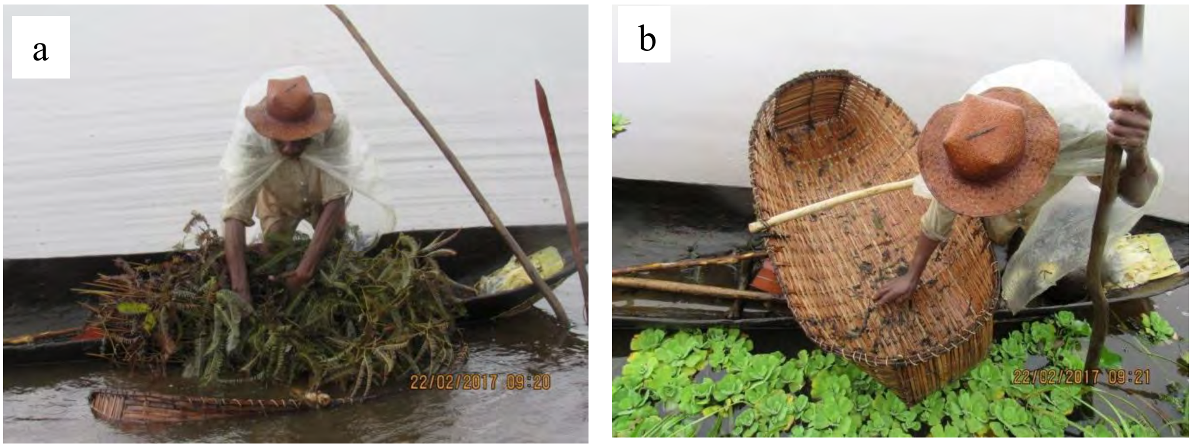

Figure 4.2.: Materials for shrimp fishing, (a) *Tritrampanga* used for trapping shrimp; (b) *Banabana* for collecting shrimp

4.3.5 Collection of meteorological data

At Andrangazaha, the village closest to the lake (3km from the lake), precipitation and atmospheric temperatures were collected daily. For this, we used a pluviometer and thermometer (minimum/average/maximum temperature), respectively. Rainfall data were collected once a day and the temperature was recorded three times a day, at 06h00, 12h00 and 18h00.

4.3.6 Reinvasion study

Monitoring of the reinvasion process was conducted in subzone A(iii), with the area being subdivided into 16 quadrats (Figure 4.3). To follow the reinvasion process, these 16 quadrats of 100m^2 (10 x10m) each were fenced using bamboo poles, along which were placed a line of stakes to separate adjoining quadrats, with the stakes 1m apart (Figure 4.4a, b). The fencing lines started from the edge of the lake and extended into the interior of the lake (perpendicular to the bank). Each stake was numbered to specify its position relative to the starting point. At the start and at the end of experiments, digital photos were captured of the vegetation that was created by populations of the various invasive aquatic species, which allowed a reference of changes of plant cover over time.

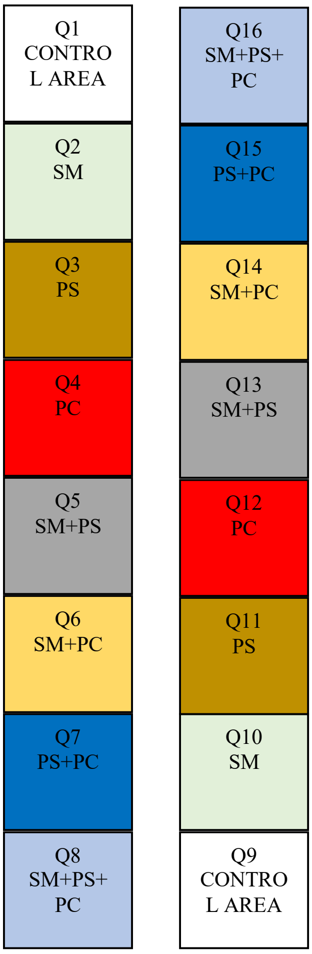

Figure 4.3.: Reinvasion study treatment for IAP (SM=*Salvinia molesta*, PS=*Pistia stratiotes*, PC=*Pontederia crassipes*)

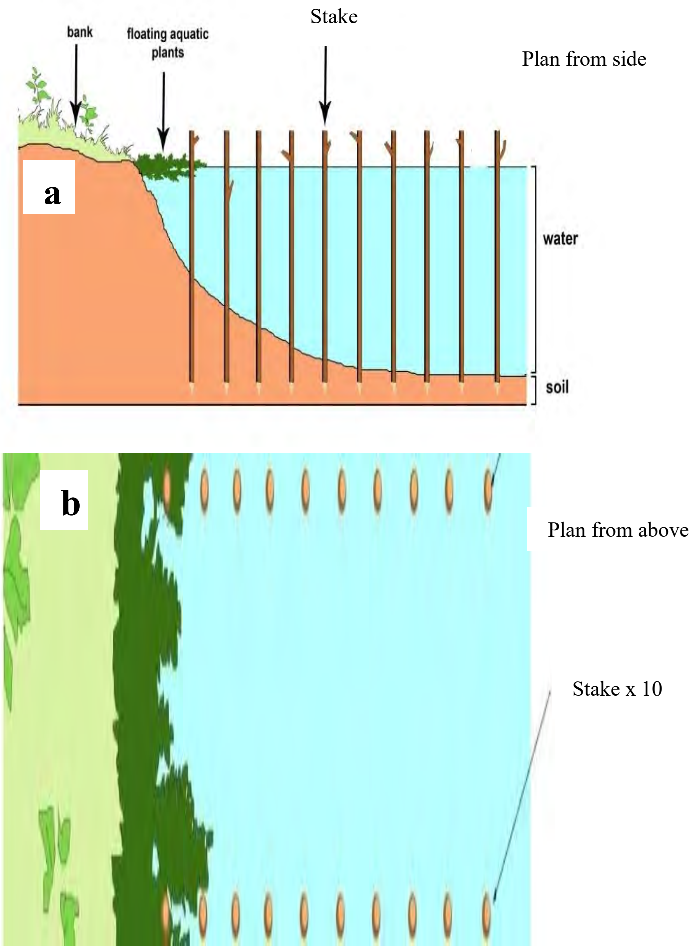

Figure 4.4.: Visual representation of the reinvasion process methodology : (a) side view (b) aerial view

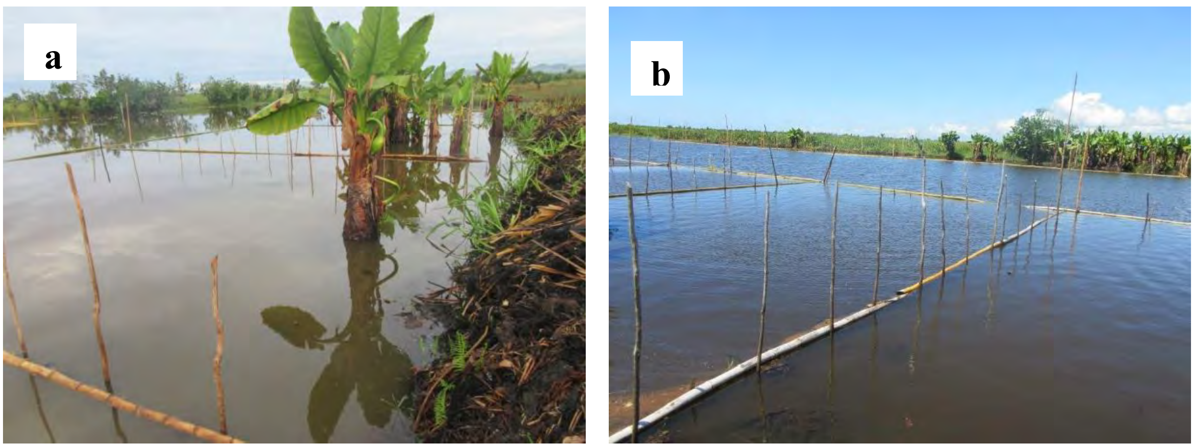

Figure 4.5.: Observation quadrat for monitoring the process of reinvasion of IAPs: (a) northern view; (b) side view

Each quadrat was allocated a specific treatment to represent the impact, control and reinvasion process of each plant species (Figure 4.3). Two individuals of each species (*S. molesta, P. stratiotes* and *P. crassipes*) were arbitrarily placed in each quadrat alone or in combinations of two or three with the other species (Figure 4.3). In total, there were seven treatments and a control area. This setup was duplicated, on the opposite bank of the lake, giving a total of 16 quadrats.

4.3.7 Site maps

To describe the fixed attributes of the sites, maps were used to supplement the information obtained from local villagers. To do this, four types of map were utilised:

- Aerial photos produced by F.T.M. (Foiben-Taosarintanin' i Madagasikara, National Geographic and Hydrographic Institute of Madagascar) in 1965;

- Geological map of Madagascar, sheet Fenerive 1962 (431-432), scale 1:200,000, produced by the Geology Department of Madagascar (Service Geologique de Madagascar, 1962);

- Topographic map of Madagascar, Sheet W-42, scale 1:100,000 (F.T.M., 1978);

- Hydrological map of Madagascar, scale 1:6,000,000. (Carte hydrologique de Madagascar, undated).

4.3.8 Statistical analyses

Recorded data were analysed using a variety of methods. The means and variances for each parameter (number, weight, frequency, diversity index, evenness and all physical and chemical parameters) were calculated for each subzone. The difference between the two means of the independent samples relating to values of physico-chemical parameters between Zone A and Zone B, were statistically tested using a Student's test (t-test). The significance of the difference was calculated using a 95% confidence interval ($P < 0.05$).

The Shannon's diversity index (H) (Shannon and Wiener, 1963) and Evenness index (Pielou, 1966) were applied to determine the characteristics of plant communities, according to biogeographical origin and plant life form at T_0, as well as for the dynamics of plant communities in the reinvasion experimental quadrats over one year of measurement (September 2018 to August 2019). For this, species were classified according to their status (endemic, native but not endemic, naturalized) and according to their biotype. While the Shannon index was used measure biodiversity, the Shannon entropy quantified the uncertainty in predicting the species identity of an individual that was taken at random from the dataset. Historically, the index has been used to measure the effects on habitat quality of factors such as pollution (Akpabey, 2012). In a modified ecosystem, as in the case of the lake where this experiment was conducted, the Shannon's diversity index provides a good tool for comparing two habitats, or changes in biodiversity over time, because it incorporates both species richness and evenness.

4.3.8.1 The Shannon's diversity index (H):

$$\boxed{H' = -\sum_{i=1}^{S} p_i \ln p_i}$$

Where

H': Shannon Biodiversity Index

i: a species from the study environment

p_i = n_i/N, the proportion of individuals belonging to the *i*th species in the dataset of interest, where n_i is the number of individuals for species i and N is the total number (individuals of all species). ln = natural logarithm.

This index allows the quantification of biodiversity, heterogeneity of the ecosystems in question and obeservable changes over time. It always varies from 0 to ln S, where *S* is the total species number in each subzone.

4.3.8.2 Evenness index (E):

$$\boxed{E = \frac{H}{lnS}}$$

The more abundant a taxon is (i.e. it dominates and excludes others), the lower the global diversity appears. This means that there is less evenness among species in communities and **E** is lower, and vice versa. Biodiversity is at a maximum when the total number of individuals at a location is evenly distributed among taxa. The regularity index (Evenness index) can be calculated by dividing H by H_{max} (here H_{max} = lnS). Equitability assumes a value between 0 and 1, with zero signifying no evenness and one a complete evenness.

4.3.8.3 The Simpson index of Dominance (D)

The Simpson's index (Simpson, 1949) is also used to quantify the biodiversity of a habitat. It takes into account the number of species present in the habitat, as well as the dominance of each species. In this study, we considered groups of plants defined according to their biogeographic status.

$$D_{Si} = 1 - \sum_{i=1}^{S} p_i^2$$

Where

D = Simpson index of dominance;

p_i = the proportion of the importance value of the i^{th} species ($p_i = n_i/N$, where n_i is the importance value index (IVI) of the i^{th} species and N is the IVI of all the species).

Importance Value Index = Relative dominance + Relative frequency (from Kalidass, 2014, adapted to herbaceous vegetation of the lake). In this study, we considered relative dominance to be a percentage of cover.

$$\text{Relative frequency (RF)} = \frac{\text{Number of occurrences of the species}}{\text{Number of occurrences of all species}} \times 100$$

The value of D varies from 0 to 1. The higher the index value, the greater the diversity of the sample.

4.3.8.4 Sorensen's index

Sorensen's similarity index (Sorensen, 1948) was performed to compare the similarities between plots in terms of floristic biodiversity. This method allowed us to evaluate the floristic affinities between the transects. For this study, it was used to compare floristic data between Zone A and Zone B, and within Zone A, the floristic affinity between subzone i, subzone ii, subzone iii and subzone iv. To do this, the similarity coefficient of Sorensen (1948) was adopted.

$$Ps = \left(\frac{2c}{a + b}\right)$$

Where:

c = number of species present in both zones

a = number of species present only in Zone A

b = number of species present only in Zone B

Ps: denotes the Sorensen coefficient of similarity, expressed as a percentage

Two zones are floristically similar if the similarity coefficient of Sorensen is greater than or equal to 50%.

4.4 Results

4.4.1 Description of the site

The study site is a natural lake with an elongated shape of about 80 m wide on average and 1km long, with an estimated surface area of 8ha. According to the topographic map of Madagascar, the lake was identified as a permanent watercourse (FTM, 1978). The original geology of the lake corresponds to the coastal sands (Service Géologique de Madagascar, 1962). Thus, the lake corresponds to a low sandy coast with lagoons (Battistini, 1996). According to this author, the small rivers generally end up in these low sandy lagoons and then they flow slowly before reaching an outlet to the sea.

The lake is crossed on its eastern part by an artificial canal, which connects the lake to Antsohy River in the northern part and to Simianina River in the southern part. The exact date of creation of this channel is not known. The older villagers at Andrangazaha reported that the canal was created by a Mr Clément before the 1950s as a freight transport route to the sea. It is also likely that the current canal was a small stream originating from the lake before spreading into the sea. If this is the case, Mr. Clément was only improving and widening the waterway to be navigable. The aerial photo in 1965 shows the artificial canal was already obstructed with dense vegetation (Figure 4.6a). According to a native of the village of Andrangazaha, during the period of 1960s, the canal was obstructed mainly by *Typhonodorum lindleyanum* Schott (Araceae) with some patches of water hyacinth in between (Jusline, a villager at Andrangazaha, pers. comm.). The topographic map of Madagascar indicates that the lake is surrounded by marshes which adjoin the natural forests of Anjahamanintsy in the northern part (FTM, 1978).

The aerial photograph taken in 1965 indicates that extensive forest cover existed on both sides of the artificial canal at that time. Mr Sary Fabien, a villager at Andrangazaha, remembers that the practice of slash-and-burn cultivation (tavy), which ended in 1985, was the principal cause of disappearance of these forests (pers. comm.). Currently, there is almost no forest on the east side of the lake, with degraded patches of forest on the west side (Figure 4.6b).

According to Perrier de la Bathie (1934), the soil type of the zone is classified in the category "swamp depression land". It is characterized by short vegetation of Cyperaceae and semi-aquatic ferns with peats, which makes cultivation very difficult because the peat, even under the tropical climate, can be used for agricultural purposes only after a thorough controlled burn to make rice cultivation easier. Until now, this practice, known as *écobuage*, has been pursued as a cultural technique for the area (Figure 4.7a, b). According to the same author, the area can be recognised by the presence of certain species of plants such as Viha (*T. lindleyanum*), Zozoro (*C. papyrus madagascariensis*) or Volotara (*Phragmites communis* Trin. (Poaceae)), thriving on soil similar to alluvial soils.

The hydrology of the lake is very complex. The main source (catchment) that feeds the lake comes from the marshy forest of Anjahamanintsy. According to Mr. Sary Fabien (a villager at Andrangazaha), this source often dries up during the dry season from October to December and the lake level drops to its minimum level. During the rainy season, runoff from the surrounding marshes supply water to the lake in the case of heavy rain, often causing flooding (Sary Fabien, pers. comm.). The Simianina River is the main outlet of the lake on its south side, forming part of the artificial canal (Hydrological Map of Madagascar, undated). As the canal continues along the northeast side of the lake before reaching the Antsohy River, the circulation of water flow seems unclear because for several decades this channel has been clogged with *T. lindleyanum* and water hyacinth.

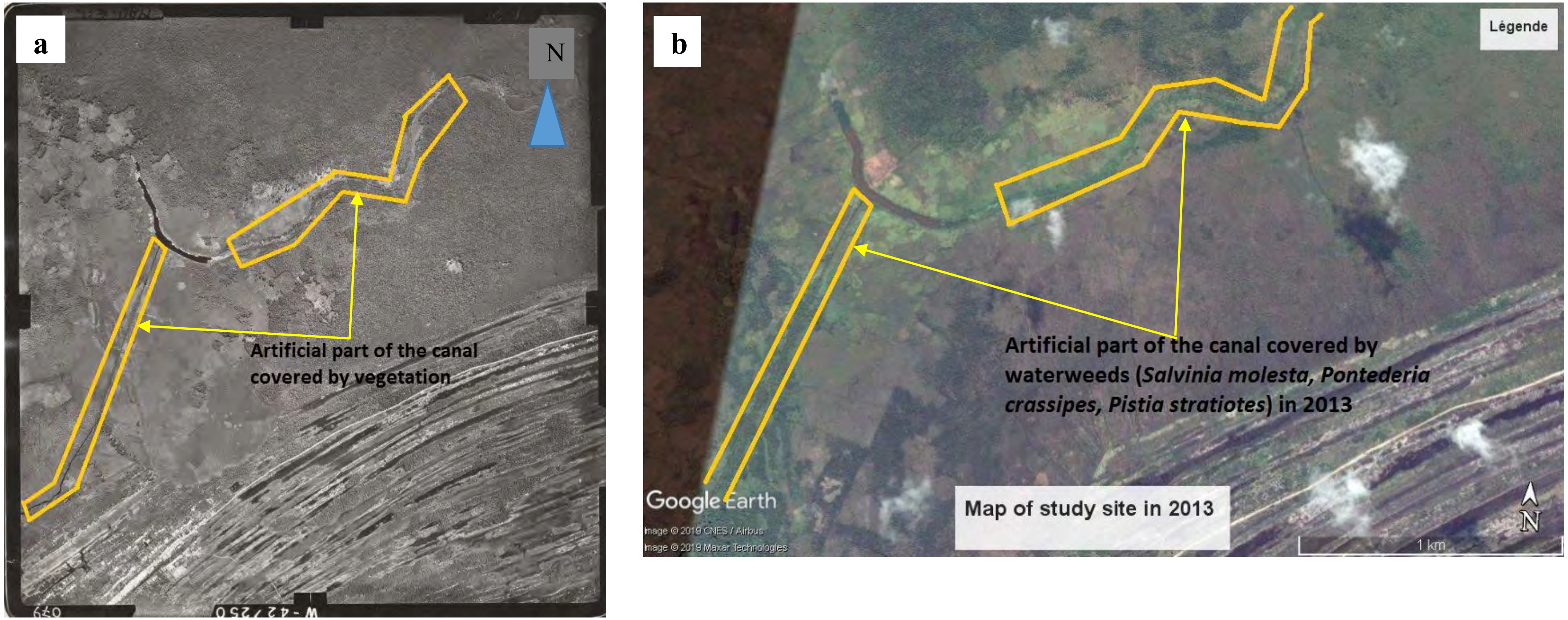

Figure 4.6.: Photos of the study area showing the artificial canal: (a) aerial photo in 1965 (reference W-42/250), (b) satellite image taken on 26/09/2013

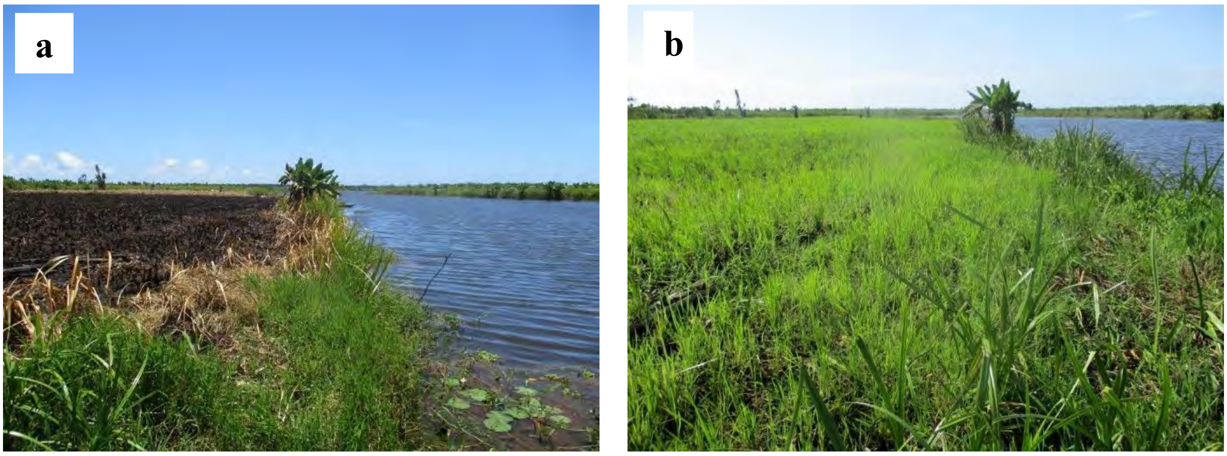

Figure 4.7.: Practice of controlled burn (*écobuage*) as rice plantation technique: (a) image on 08/12/2018 and (b) image on 02/02/2019

4.4.2 Climatic data collection for the zone

Temperature and precipitation sampling was carried out for 28 months from April 2017 to July 2019. The overall average of the temperatures was 26.79°C, with the maximum average temperature at 38.35°C and minimum average temperature at 20.62°C (Figure 4.8).

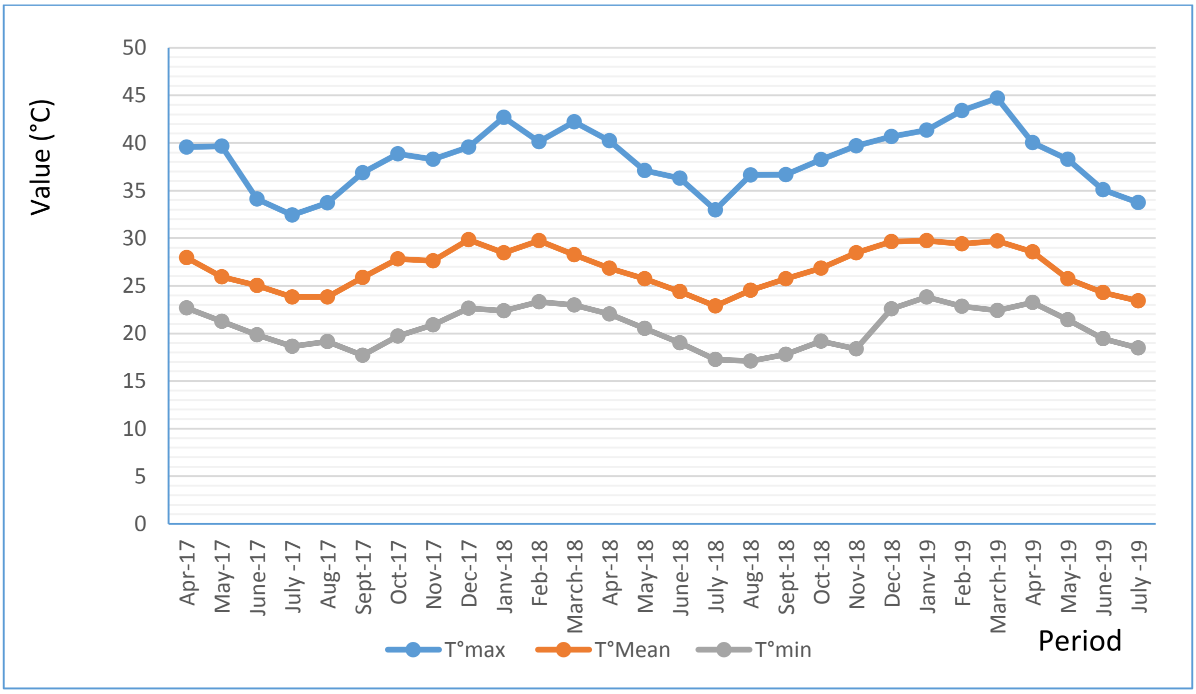

Figure 4.8.: Mean monthly local temperature during study period (April 2017-July 2019)

During the first year (April 2017 to March 2018), the total annual precipitation was 4,513 mm and during the second year (April 2018 to March 2019), it was 3,354 mm. The peak precipitation was in March 2018, during which two cyclones occurred, viz. Cyclone Domazile from 04 March 2018 and Tropical Depression Eliakim from 16 March 2018. The lowest monthly precipitation was recorded in September 2017 with 53.5mm. During the first year, there were 222 days of rain and in the second year, this number dropped to 197 days of rain. It is noticeable that the first year had more rain, with a greater number of rain days compared to the second year. This can be explained by the passage of three cyclones during the first year which brought a considerable amount of rain.

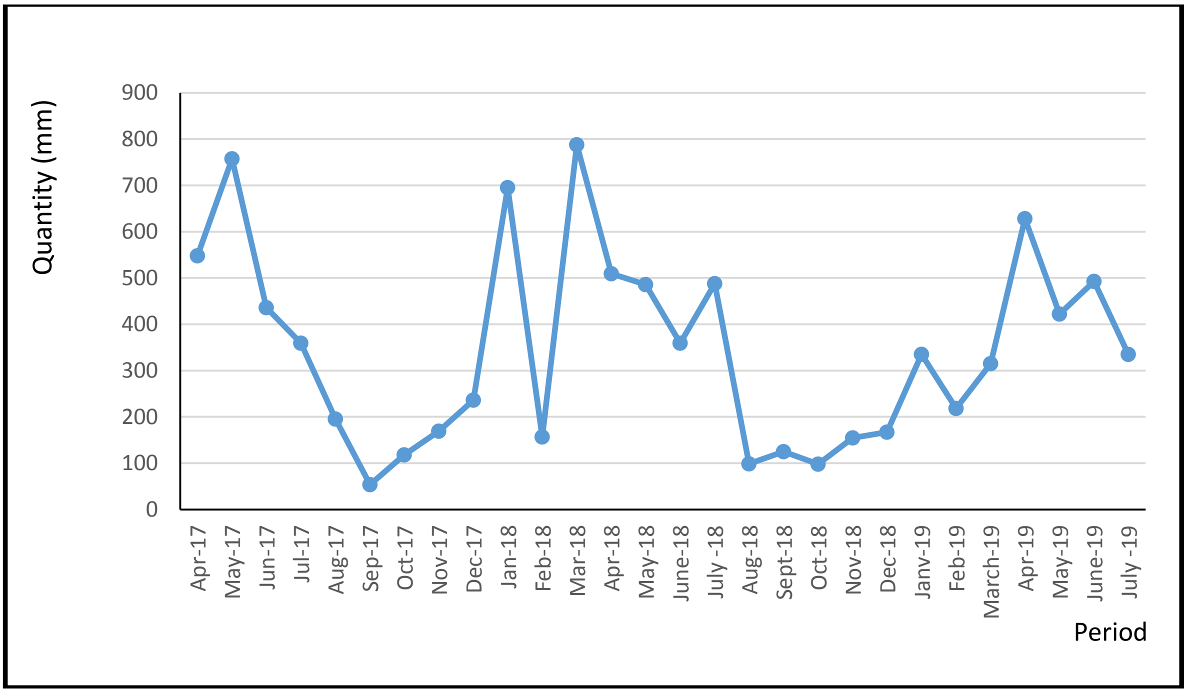

Figure 4.9.: Variation of local rainfall during the study period (April 2017-July 2019)

The comparison of the historical climatic data for the area with those of our samples showed a difference in temperature of 3.19°C, with the increased temperature from our data (Table 4.2). The average precipitation was also higher for our data. However, the number of rainy days was lower for our data compared to that of the local meteorological station, with a difference of 26 days. Since our data were collected over only two years, while the minimum period required to describe climate is considered to be 30 years (Rasolonjatovo, 2018), the differences between the two data sets should not be considered as indicating a changing climate. Nevertheless, it allows a comparison of climatic conditions during our sampling period with average climatic conditions for the area.

Table 4.2.: Comparison of mean temperature and precipitation from two sources

Parameters	**Source (data collected from April 2017-March 2019)**	**Source (weather station of Soanierana Ivongo from 1936 to 1970) (Lehavana *et al.*, 2015)**
Mean precipitation	3,933mm	3,587mm
Number of rainy days	209 days	235 days
Mean temperature	26.8°C	23.6°C

4.4.3 Physico-chemical parameters of the water

4.4.3.1 Physico-chemical parameters of zone A

Zone A, an open area encompassing subzone i, ii, iii and iv, was periodically cleaned (except the subzone iii) to prevent re-colonization of species during the study period. Data collected six times between 10 April 2017 and 04 May 2019, gave a pH range from 4.6 to 8. Generally, the values of the pH were slightly acidic, indicating that the open area was healthy for aquatic life. The pH averages varied from season to season. During the winter months, particularly May, the pH values was at its lowest (4.75). During this winter season, the water level frequently rose, causing the lake to overflow repeatedly. The highest pH value of 7.33 was in December 2018. This was possibly due to an increased in nutrients entering the water from surrounding rice fields. This period also coincided with the period of burning for rice cultivation around the lake (Figure 4.7a).

The values of the water conductivity of the zone A oscillated between 18.2 and 145 µS/cm. The conductivity averages were generally lower during the rainy months, with May having an average of 19.16 µS/cm. The conductivity reached its highest value during the dry months, with December 2018, having an average value of 139.84 µS/cm (Table 4.3).

With regards to the temperature of the water, the values varied from 25.4°C to 32.4°C as a maximum. There was a slight variation of mean temperature throughout the year. The lowest mean temperature was during winter in August 2018 (25.85°C) and the highest was recorded during summer in February 2018 (31.39°C) (Table 4.3). The recorded temperature ranges of the site aligned well with the ambient survival temperatures of living aquatic organisms and the reproduction of animal species (Dallas, 2008).

The turbidity values varied from 20.3 cm to over 60 cm, which corresponded to Nephelometric Turbidity Units (NTU) values of <10 to 27. The most turbid period was during the summer in February 2018 with 27 NTU. In general, turbidity values were low, and were viable for aquatic species. At 27 NTU, if the water stays turbid for a few days or weeks, the only likely symptoms that would appear might be some fish stress due to a reduction in photosynthesis (Water Action Volunteers, 2006). The longer the water remains at unusually high values, the greater the effect it has on fish and other aquatic organisms. However, data on the length of the turbid period were not collected during this study.

Table 4.3.: Characteristics of the physico-chemical parameters of Zone A (pH, electrical conductivity, water temperature and water turbidity) over the study period.

Parameter		**Date**					
		10/04/2017	15/02/2018	31/08/2018	08/12/2018	02/02/2019	04/05/2019
pH	Mean±SD (n=31)	5.92±0.08	7.29±0.25	6.90±0.11	7.33±0.20	6.42±0.09	4.75±0.12
TDS/EC (µS)	Mean±SD (n=31)	21.10±1.56	90.87±11.66	107.95±12.26	139.84±5.03	72.33±4.00	19.16±0.96
Water temperature (°C)	Mean±SD (n=31)	26.28±0.44	31.39±0.62	25.87±0.37	28.93±1.73	28.71±0.48	26.85±1.22
Turbidity (cm)	Mean±SD (n=31)	60.00±0.00	27.97±4.48	42.30±4.44	40.5±6.54	30.27±2.47	60.00±0.00
	Transparency value (NTU)	<10	27	14	15	24	<10

4.4.3.2 Physico-chemical parameters of Zone B

Zone B was sheltered from any disturbance, especially wind due to it being located in a narrow zone in the artificial canal, which is an area both far from the catchment and the outlet of the lake. In addition, in Zone B, the circulation of water was slow due to the presence of vegetation obstructing the canal. All of this reduced the wind and the effects of floods. Therefore, despite the frequent flooding of the site, the vegetation of Zone B was stable. Within Zone B, the physico-chemical parameters of the water were collected five times, i.e there was a lack of a data collected compared to zone A. This occurred due to a flood that prevented the collection of data in February 2018.

The pH values of Zone B varied from 4.8 to 7.4; the highest average pH (7.09), which was close to neutral, was recorded in December 2018, while the most acidic pH (5.33) was measured in May 2019 (Table 4.3). The lowest mean pH value (5.33) was slightly below the range preferred by aquatic organisms (6.5 to 8.0) (Behar, 1997). However, the values recorded from Zone B dit not exceed the thresholds for lethal values for aquatic organisms (<4.0 and >10.0, Mitchell, 1974).

The conductivity of the water in Lake Antsokafina from the zone B ranged from 17.8 to 167 µS/cm, with the mean varying from season to season. The lowest mean was in May 2019 (20.46 µS/cm) and the highest in December 2019 (147.65 µS/cm) (Table 4.4).

The minimum water temperature was 25.2°C and the maximum 32.4°C. During winter, the mean water temperature was the lowest (25.88°C) and during summer, the mean temperature was 30.48°C. These temperatures are considered optimal for the survival and reproduction of aquatic organisms, particularly fish (between 20 and 35°C, Lim and Webster, 2006).

The turbidity values varied widely from 5 cm to more than 60 cm. The lowest average was measured in August 2018 (15.28 cm) and the highest average in December 2018 (26.12 cm). These turbidity values corresponded to 65 NTU and 30 NTU respectively. These values are still far from lethal turbidity for aquatic organisms, which needs to be generally greater than 10,000 NTU for a few weeks (Water Action Volunteers, 2006).

Table 4.4.: Characteristics of physico-chemical parameters of Zone B

Parameter		Date				
		10/04/2017	**31/08/2018**	**08/12/2018**	**02/02/2019**	**04/05/2019**
pH	Mean±SD (n=31)	6.04±0.16	6.52±0.27	7.09±0.14	6.35±0.21	5.33±0.47
EC (µS/cm)	Mean± SD (n=31)	20.95±3.54	135.42±18.45	147.65±3.85	75.06±11.56	20.46±1.06
Water temperature (°C)	Mean± SD (n=31)	26.49±0.49	27.56±1.26	29.4±0.80	30.48±0.92	27.76±2.03
Turbidity (cm)	Mean± SD (n=31)	22.03±10.15	15.28±10.61	26.12±10.55	18.80±7.28	22.91±8.80
	Transparency value (NTU)	35	65	30	50	35

4.4.3.3 Comparison of the physico-chemical parameters of Zone A and Zone B

Except for turbidity, the physico-chemical parameter values of the water bodies seemed similar between Zone A and B. However, statistical tests of the data confirmed, that all measurements were significantly different, except for one pH, two electrical conductivity and two water-temperature readings (Table 4.5). Difference were more remarkable for the turbidity parameter for all measurements. Although the differences were statistically significant, both zones remained viable for all aquatic organisms, and the effects of the physico-chemical parameters were likely to be similar for all aquatic life.

Table 4.5.: Physico-chemical parameters and statistical tests for the Zone A and B at Antsokafina lake.

Parameters	**Zone**	**Statistical parameters with a 95% (p<0.05)**	**Date**				
			10/04/2017	**31/08/2018**	**08/12/2018**	**02/02/2019**	**04/05/2019**
pH	**A**	Mean±SD (n=31)	5.92±0.08	6.90±0.11	7.33±0.20	6.42±0.09	4.75±0.12
	B		6.04±0.16	6.52±0.27	7.09±0.14	6.35±0.21	5.33±0.47
		Difference of the means	0.12±0.06 8 (t=3.654)	0.38±0.11 (t=7.187)	0.24±0.09 (t=5.628)	0.07±0.08 (t=1.760)	0.58±0.17 (t=6.683)
		Significance of the difference	**Significant**	**Significant**	**Significant**	Not significant	**Significant**
EC (µS/cm)	**A**	Mean±SD (n=31)	21.10±1.56	107.95±12.26	139.84±5.03	72.33±4.00	19.16±0.96
	B		20.95±3.54	135.42±18.45	147.65±3.85	75.06±11.56	20.46±1.06
		Difference of the means	0.09±1.39 (t=0.130)	27.47±7.96 (t=6.906)	7.81±2.15 (t=7.253)	2.74±4.39 (t=1245)	1.31±0.51 (t=5.088)
		Significance of the difference	Not significant	**Significant**	**Significant**	Not significant	**Significant**
Water temperature (°C)	A	Mean±SD (n=31)	26.28±0.44	25.87±0.37	28.93±1.73	28.71±0.48	26.85±1.22
	B		26.49±0.49	27.56±1.26	29.4±0.80	30.48±0.92	27.76±2.03
		Difference of the means	0.18±0.24 (t=1.462)	1.69±0.47 (t=7.153)	0.47±0.69 (t=1.68)	1.77±0.37 (t=9.518)	0.91±0.84 (t=2.175)
		Significance of the difference	Not significant	**Significant**	Not significant	**Significant**	**Significant**
Turbidity (cm)	A	Mean±SD (n=31)	60.00±0.00	42.30±4.44	40.5±6.54	30.27±2.47	60.00±0.00
	B		22.03±10.15	15.28±10.61	26.12±10.55	18.80±7.28	22.91±8.80
		Difference of the means	37.97±3.65 (t=20.826)	27.02±4.13 (t=13.080)	14.34±4.46 (t=6.450)	11.47±2,76 (t8.311)	37,09±3,16 (t=23.456)
		Significance of the difference	**Significant**	**Significant**	**Significant**	**Significant**	**Significant**

4.4.3.4 Depth of the lake

During the survey period, in February 2017, the depth varied from 0 m to 6.1 m in the middle of the lake with an average depth of 4.5m. Outside of flooding time, it was observed that the the depth of the lake varied slightly. During the floods, the lake was overflowed and even invaded the ricefields around the lake. Even during the dry season, 10 m from the shore, towards the centre of the lake, the depth always measured more than 4 m. This was why emergent and attached plants with floating leaves rarely survived beyond 10 m from the edge of the lake, due to it being too deep for stems to reach the substrate.

4.4.4 Floristic diversity of the lake

In total, 39 aquatic and semi-aquatic plant species were inventoried in the lake, of which 33 were identified to species level and six species remained unidentified. Among the identified species, two were endemic to Madagascar (6%), 24 (72.72%) were native but not endemic and seven (21.21%) were naturalized/invasive species (Table 4.6).

Table 4.6.: List of aquatic and semi-aquatic plants species inventoried at Lake Antsokafina at T_0 (February 2017).

Species	**Family**	**Vernacular name**	**Status**	**Zone A**				**Zone B**
Emergent species				**i**	**ii**	**iii**	**iv**	
Adenochloa hymeniochila (Nees) Zuloaga	Poaceae	Anampody lahy	Native but not endemic				x	
Alloteropsis paniculata (Benth.) Stapf	Poaceae	Ankanimpodibe	Native but not endemic	x				
Bacopa monnieri (L.) Wettst.	Plantaginaceae	Popoko	Native but not endemic				x	
Barringtonia racemosa (L.) Spreng.	Lecythidaceae	Fotatra	Native but not endemic	x	x			x
Ceratopteris thalictroides (L.) Brongn.	Pteridaceae	Anambia	Native but not endemic				x	x
Commelina benghalensis L.	Commelinaceae	Ahibita	Naturalised	x				
Commelina diffusa Burm. f.	Commelinaceae	Ahilava	Naturalised	x	x	x	x	x
Cyperaceae1	Cyperaceae	Vazanomby antanety	Unknown	x				
Cyperaceae2	Cyperaceae	Unknown	Unknown	x				
Cyperus latifolius Poir.	Cyperaceae	Vendrana	Native but not endemic	x	x	x	x	x
Cyperus pectinatus Vahl	Cyperaceae	Bangoloha	Native but not endemic	x	x	x		
Cyperus prolifer Lam.	Cyperaceae	Beloha	Native but not endemic	x	x	x	x	x
Echinochloa colona (L.) Link	Poaceae	Tsingialivary	Native but not endemic	x	x	x	x	x
Echinochloa sp.	Poaceae	Tsimatinampanarivo	Native but not endemic	x	x	x		x
Eleocharis dulcis (Burm. f.) Trin. ex Hensch.	Cyperaceae	Horefo	Native but not endemic	x				
Ficus sp,	Moraceae	Aviavy	Unknown		x			x
Fuirena umbellata Rottb.	Cyperaceae	Vazanomby andrano	Native but not endemic			x	x	
Ipomoea aquatica Forssk.	Convolvulaceae	Bakiana	Native but not endemic	x	x	x		
Ipomoea aquatica Forssk.	Convolvulaceae	Anantarika	Native but not endemic				x	x
Lepironia articulata (Retz.) Domin	Cyperaceae	Penja	Native but not endemic		x			
Ludwigia octovalvis (Jacq.) P.H. Raven	Onagraceae	Tognombintsy kely	Native but not endemic	x				
Ludwigia adscendens subsp. *diffusa* (Forssk.) P.H. Raven	Onagraceae	Tognombintsy lehibe	Native but not endemic	x	x	x	x	
Mimosa pigra L.	Fabaceae	Anankoay	Native but not endemic			x		
Pandanus princeps B.C. Stone	Pandanaceae	Rambo	Endemic	x				

Panicum sp.1	Poaceae	Unknown	Unknown		x		x	
Panicum sp.2	Poaceae	Vilona	Unknown		x		x	
Persicaria mitis (Schrank) Assenov	Polygonaceae	Fotsivony	Naturalised	x	x	x	x	x
Phragmites australis (Cav.) Trin. ex Steud.	Poaceae	Bararata	Naturalised	x				
Pneumatopteris unita (Kunze) Holttum	Thelypetidaceae	Fitro	Native but not endemic	x	x	x	x	x
Pycreus cf. *polystachyos* (Rottb.) P. Beauv.	Cyperaceae	Tsivendrambendrana anatirano	Native but not endemic	x	x	x	x	x
Sesbania madagascariensis Du Puy & Labat	Fabaceae	Fanivana	Endemic					x
Trichanthecium parvifolium (Lam.) Zuloaga & Morrone	Poaceae	Lafomandotra	Native but not endemic	x				
Tristemma mauritianum J.F. Gmel.	Melastomataceae	Trotroka	Native but not endemic	x	x			
Typha domingensis Pers.	Typhaceae	Vondrona	Native but not endemic		x			
Typhonodorum lindleyanum Schott	Araceae	Via	Native but not endemic	x	x	x	x	x
Unknown	Unknown	Tananorana	Unknown					x
Free floating species								
Pontederia crassipes (Martius) Solms-Laubach	Pontederiaceae	Damozambody	Naturalised	x	x	x	x	x
Pistia stratiotes L.	Araceae	Hazafovavy	Naturalised		x	x	x	x
Salvinia molesta D.S. Mitch.	Salviniaceae	Hazafolahy	Naturalised	x	x	x	x	x
TOTAL				**25**	**22**	**17**	**19**	**18**
				37				**18**

4.4.4.1 Species diversity

The vegetation of sub-zone i was the oldest, at nine years (2008-2017) (Sary Fabien, pers. Comm.). It consisted of vegetation growing on a mat of IAP after a long process of invasion. The vegetation of sub-zone iv was the most recent, and was still establissing (Sary Fabien, pers.comm. and pers. observation). Moreover, for sub-zone iv, only 10% of the area was covered by thick vegetation and the remaining (90%) was open area. Therefore, the vegetation profiles of the four sub-zones differed in their ages and vegetation types. Zone B was 300 m east from Zone A and the history of its establishment was not well understood.

In terms of biogeographic affinity, among the subzones included in Zone A, sub-zone i had the highest biodiversity index (H = 0.959) with a species richness of S = 25, while sub-zone iii was the least diversified (S = 17; H = 0.606) (Table 4.7). The four subzones had similar species evenness indices (E = 0.214 to 0.298) dominated by native species. These indices were very far from 1 which is the ideal value of equilibrium. Similarly, the indices of evenness of plant biotype (0.099 to 0.165) were very low. This vegetation was dominated by emergent species; apart from free-floating species, other life forms were absent.

Zone B, although not very species rich (S = 18), had higher diversity indices for both biogeographic status and plant biotype (0.376 and 0.156 respectively). In Zone B the number of naturalised species was closer to that of native species than those of all subzones of Zone A.

Concerning the dominance of plant classes, Zone B had higher indices for both biogeographic status and plant biotype than Zone A (D = 0.529 and D = 0.500, respectively, Table 4.7). On the other hand, the lowest value was in subzone ii with D = 0.372 for biogeographic affinity and D = 0.348 for plant life form. This meant that in zone ii, native species strongly dominated naturalised species while in Zone B, native species were moderately dominant.

Table 4.7.: Plant diversity of the different zones at Antsokafina Lake.

Diversity Indices	Criteria for classification	Class/Parameter	Zone				
			A(i)	**A(ii)**	**A(iii)**	**A(iv)**	**B**
Shannon's diversity index	Biogeographical status	Endemic	1	0	0	0	1
		Native but not endemic	16	14	12	12	10
		Naturalised	6	5	5	5	5
		Unidentified	2	3	0	2	2
		S[18]	25	22	17	19	18

		H	0.959	0.896	0.606	0.879	1.087
		E	0.298	0.290	0.214	0.298	0.376
Simpson's index		D	0.408	0.372	0.500	0.512	0.529
Shannon's diversity index	Plant biotype	Emergent	23	19	14	16	14
		Free-floating	2	3	3	3	3
		S	25	22	17	19	
		H	0.279	0.398	0.466	0.436	0.451
		E	0.087	0.129	0.165	0.148	0.156
Simpson's index		D	0.375	0.348	0.499	0.499	0.500

S=total species number in each subzone; **H**= Shannon Biodiversity Index; **E**= Evenness index; **D**= Simpson index of dominance

4.4.4.2 Similarity of plant communities between zones and subzones

The Sorensen similarity index between Zone A and Zone B was 56.60%. Because the value was close to 50% (i.e. close to being similar), both areas were considered to be in the same plant community. Within Zone A, the value of the Sorensen index ranged from 55% to 72.73%. Overall, all subzones within Zone A (i, ii, iii, iv) were considered to be from the same plant community, although there were slight differences in Sorensen similarity values between subzones (Table 4.8). The age of the vegetation determined the degree of similarity between the subzones. According to the local community's account, the oldest vegetation (sub-zone i) was nine years old, i.e., it was formed after the passage of Cyclone Ivan in 2008. The youngest was the sub-zone iv which was developing, dominated by invasive aquatic weeds. The greater the age difference between areas, the lower was the value of the Sorensen index between these areas. For example, the ages of sub-zone i and sub-zone ii were very close, and they had the highest similarity index. In contrast, sub-zone i and sub-zone iv were very different in age, and the Sorensen index was lower.

Table 4.8.: Sorensen Similarity Indices between zones.

Zone/subzone	***Ps***
i & ii	72.73
i & iii	66.67
i & iv	55.00
ii & iii	71.79
ii & iv	70.00
iii & iv	71.79
A & B	56.60

4.4.5. Re-invasion by the three invasive aquatic species

Between December 2017 and July 2018, experimental equipment was washed away and destroyed several times, due to impacts of three cyclones and their accompanying floods: Cyclone Ava from 03-05 January 2018; Cyclone Domazile from 04 March 2018; the Tropical Depression Eliakim from 16 March 2018; and the last flood of 23 May 2018, causing a two-day overflow, which washed away all the plots. As a result, the experiment was not successfully initiated until 02 August 2018 and it lasted one year.

4.4.5.1 Change in number and coverage of species in all quadrats over time

When the three invasive alien species were deliberately introduced into the quadrats at the start of the experiment, they were the only species present on the surface of the water, and covered only 0.09% of the quadrat (Table 4.9). Four months later, 12 species had appeared, with a total surface cover of 49.84% of the quadrat. Subsequently, the number of species present as well as the area covered gradually increased, reaching its peak at 26 species in the 11th month of the experiment, with a surface cover reaching 170% (some species grew over others). At the end of the experiment (12th month), the number of species present dropped to 22 while the surface cover continued to increase, up to 178%.

Table 4.9.: List of inventoried species and surface area coverage from August 2018 to August 2019 (in 16 quadrats of subzone iii)

Scientific name	**Family**	**Vernacular name**	**02-Aug-2018**	**08-Dec-2018**	**13-Jan-2019**	**02-Feb-2019**	**09-March-2019**	**04-May-2019**	**13-July-2019**	**06-Aug-2019**
Alternanthera sessilis	Amaranthaceae	Anambala	0	0	0	0	0	0.01	0.01	0
Bacopa monnieri	Plantaginaceae	Popoka	0	0	0.01	0.01	0.03	0.03	0.08	0.03
Barringtonia racemosa	Lecythidaceae	Fotatra	0	0	0	0	0	0.02	0.05	0.03
Ceratophyllum demersum	Ceratophyllaceae	Horiagna	0	37.5	13.38	25.94	19.25	17.06	13.31	12.5
Ceratopteris thalictroides	Pteridaceae	Anambia	0	0.43	0.45	0.98	0.63	1.34	1.99	1.14
Commelina diffusa	Commelinaceae	Ahilava	0	0.02	0.06	0.07	0.26	0.6	0.46	0.45
Cyperus latifolius	Cyperaceae	Vendrana	0	0	0	0.15	0	0	0.02	0
Cyperus prolifer	Cyperaceae	Beloha	0	0.01	0	0.08	0.03	0.15	0.09	0.1
Echinochloa stagnina	Poaceae	Tsimatinampanarivo	0	0	0.06	0.31	0.57	0.31	0.93	0.34
Pontederia crassipes	Pontederiaceae	Damozambody	0.03	0.17	0.27	0.5	0.52	1.41	1.82	1.25
Eichnichloa colona	Poaceae	Tsingialivary	0	2.63	3.03	1.39	1.88	1.71	1.93	1.82
Eleocharis dulcis	Cyperaceae	Horefo	0	0	0.01	0.01	0.01	0.13	0.01	0
Fabaceae unknown	Fabaceae	Teloravina	0	0	0	0	0	0.01	0.1	0.03
Fuierena umbellata	Cyperaceae	Vazanomby andrano	0	0	0	0	0	0	0.02	0
Ipomoea aquatica1	Convolvulaceae	Anantarika	0	0.01	0.44	0.48	0.59	0.68	0.74	0.31
Ipomoea aquatica2	Convolvulaceae	Bakiana	0	0	0	0.01	0	0	0	0.01
Ludwigia octovalvis	Onagraceae	Tongobintsy madinika	0	0	0.01	0.14	0.09	0.08	0.21	0.13
Nymphaea nouchalii	Nympheaceae	Tatamo	0	1.51	2.47	2.98	2.72	1.69	0.08	0.09
Panicum sp.	Poaceae	Vilona	0	0	0	0	0.13	0.13	0.01	0.1
Persicaria mitis	Polygonaceae	Fotsivony	0	5.66	4.37	3.28	1.53	1.36	3.54	2.09
Pistia stratiotes	Araceae	Hazafo vavy	0.03	0.18	0.44	0.93	0.58	2.77	2.19	1.72
Pneumatopteris unita	Thelypteridaceae	Fitro	0	0.01	0	0	0	0	0.01	0
Pycreus cf. *polystachyos*	Cyperaceae	Tsivendrambendrana anatirano	0	0	0	0.15	0.22	5.16	48.88	64.25
Salvinia molesta	Salviniaceae	Hazafo lahy	0.03	1.71	11.2	25.13	54.38	87.81	93.44	92.13
Thrichanthecium parvifolium	Poaceae	Lafomandotra	0	0	0	0	0.01	0.01	0.01	0.01
Typhonodorum lindleyanum	Araceae	Via	0	0	0	0.13	0.06	0.1	0.16	0.06
Unknown	Unkown	Anambolo	0	0	0	0	0	0	0.01	0.04
	Surface cover (%)		**0.09**	**49.84**	**36.2**	**62.67**	**83.49**	**122.57**	**170.1**	**178.63**
	Number of species		**3**	**12**	**14**	**19**	**19**	**22**	**26**	**22**

4.4.5.2 Re-invasion process

Observations of the invasion process by the three invasive alien species (*S. molesta, P. stratiotes* and *P. crassipes*) began from September 2018, when they were placed alone in the quadrats which were clear of any other surface vegetation. In December 2018, four months after the start of experiment, other species colonised the quadrats. The re-invasion started from the edge of the lake. This was initiated by *C. demersum* which is a submerged species (figure 4.10a). The biomass of *C. demersum* allowed the three invasive species to anchor and multiply. *Nymphaea nouchalii*, which is an attached species with floating leaves, also grew in conjunction with *C. demersum*. Subsequently, other species such as the creeping species *E. colona* and *I. aquatica* clung to the target invasive species from the edge (figure 4.10b). All these species (IAPs, submerged species, creeping emergent species) had already appeared by December 2018. The entire plant community was interconnected and formed a system that stabilized the invasive alien species against the force of the wind. All species developed together and a few months later, other emerging species started to grow on the invasive alien species, using them as substrate, to the detriment of submerged species and those attached with floating leaves. Therefore, starting in March 2019 (eight months after reinvasion), the biomass of *C. demersum* and *I. aquatica* diminished gradually.

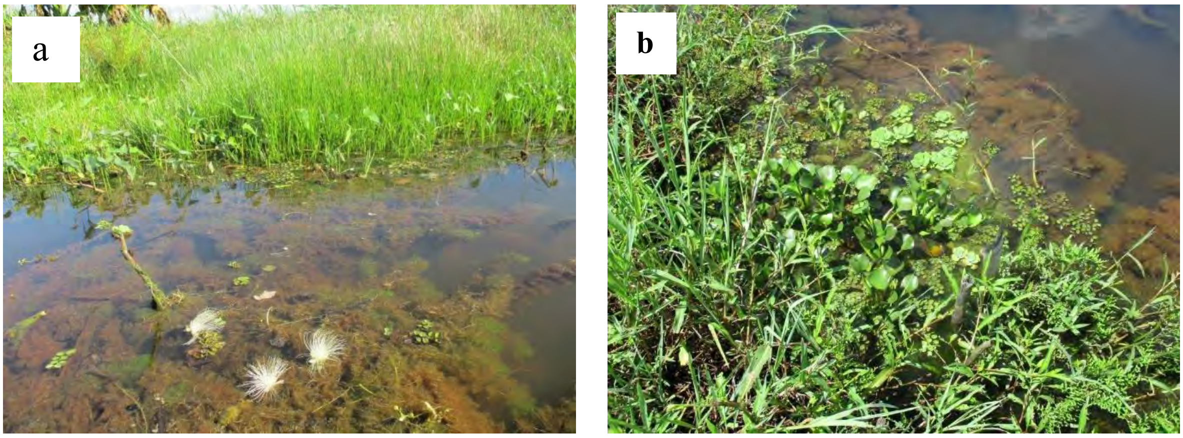

Figure 4.10.: Succession species invading the lake over time, (a) *Ceratophyllum demersum* (in front) initiating the invasion of the lake, followed by *Ipomoea aquatica* and so on; (b) other creeping plants interconnecting with invasive species

4.4.5.3 Dynamics of plant diversity over time

At the start of the experiment, only the three target weed species (*S. molesta, P. stratiotes* and *P. crassipes*) were found on the water surface of the quadrats. At the beginning of December 2018, four months after initial introduction of these target alien species, the number of species increased to 12, mainly due to the presence of submerged species, such as *C. demersum*, attached plants with floating leaves, such as *N. nouchalii*, and emergent creeping species, such as *E. colona*. From this point forward, the number of species continued to increase, reaching 26 species by July 2019. However, in August 2019, this number had dropped to 22 species (Figure 4.11). We did not find any plausible explanation for the disappearance of the four species (*A. sessilis, C. latifolius, F. umbellata* and *P. unita*). They may have been overlooked during the follow-up or may have disappeared naturally due to the succession of the vegetation or because they are seasonal in nature. The biomass of *I. aquatica* and *C. demersum* was also diminished. However, the number of naturalised species remained stable at five (*C. diffusa, P. mitis, P. crassipes, P. stratiotes, S. molesta*) between December 2018 and August 2019, and none of them gave any sign of disappearing.

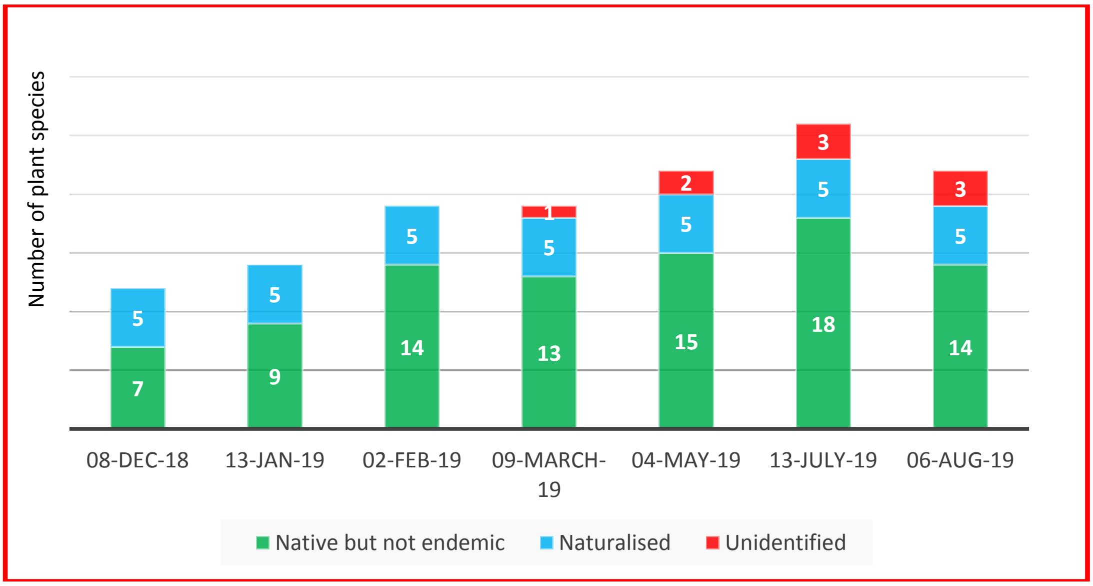

Figure 4.11.: Number of plant species over time at Antsokafina lake

Over time, there were significant changes in the relative dominance between the alien species and the native species. Prior to January 2019, native species predominated, but from this date onwards the growth of invasive species increased (Figure 4.12). In March 2019, the proportion balanced between the native and alien invasive species was balanced as indicated by Simpson's dominance index (D = 0.508, Table 4.10). Then, from March to July 2019, a progressive reduction in the dominance of invasive alien species was noticed in favour of the native *Pycreus* cf. *polystachyos*. At this stage, the structure of the vegetation was similar to that of subzone iii at T_0 in which *P.* cf. *polystachyos* and *S. molesta* were the two dominant species. Contrary to the example of *Pycreus* cf. *polystachyos*, a low level of dominance of *P. unita* was noticeable. In all subzones at T_0, this species was ubiquitous with a high percentage of coverage. However, in our experimental plots, it only constituted a small percentage.

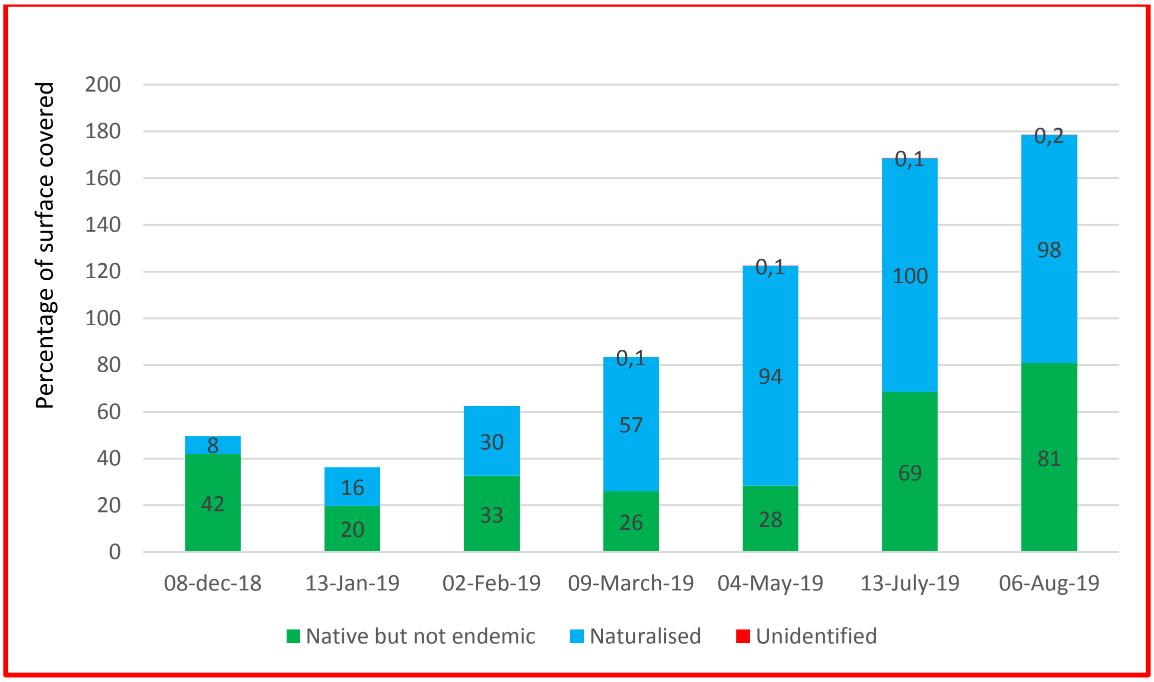

Figure 4.12.: Dominance of plant species over time at Antsokafina lake

Table 4.10.: Simpson's index of the dominance of plants grouped according to their status at Antsokafina lake over time (December 2018-August 2019)

Biogegraphical affinity	**08-Dec-18**	**13-Jan-19**	**02-Feb-19**	**09-March-19**	**04-May-19**	**13-July-19**	**06-Aug-19**
	Number of species						
Native but not endemic	7	9	14	13	15	18	14
Naturalised	5	5	5	5	5	5	5
Unidentified	0	0	0	1	2	3	3
Total	12	14	19	19	22	26	22
Simpson's Index (D)	0.4834	0.4994	0.4963	0.5082	0.4882	0.5137	0.5188

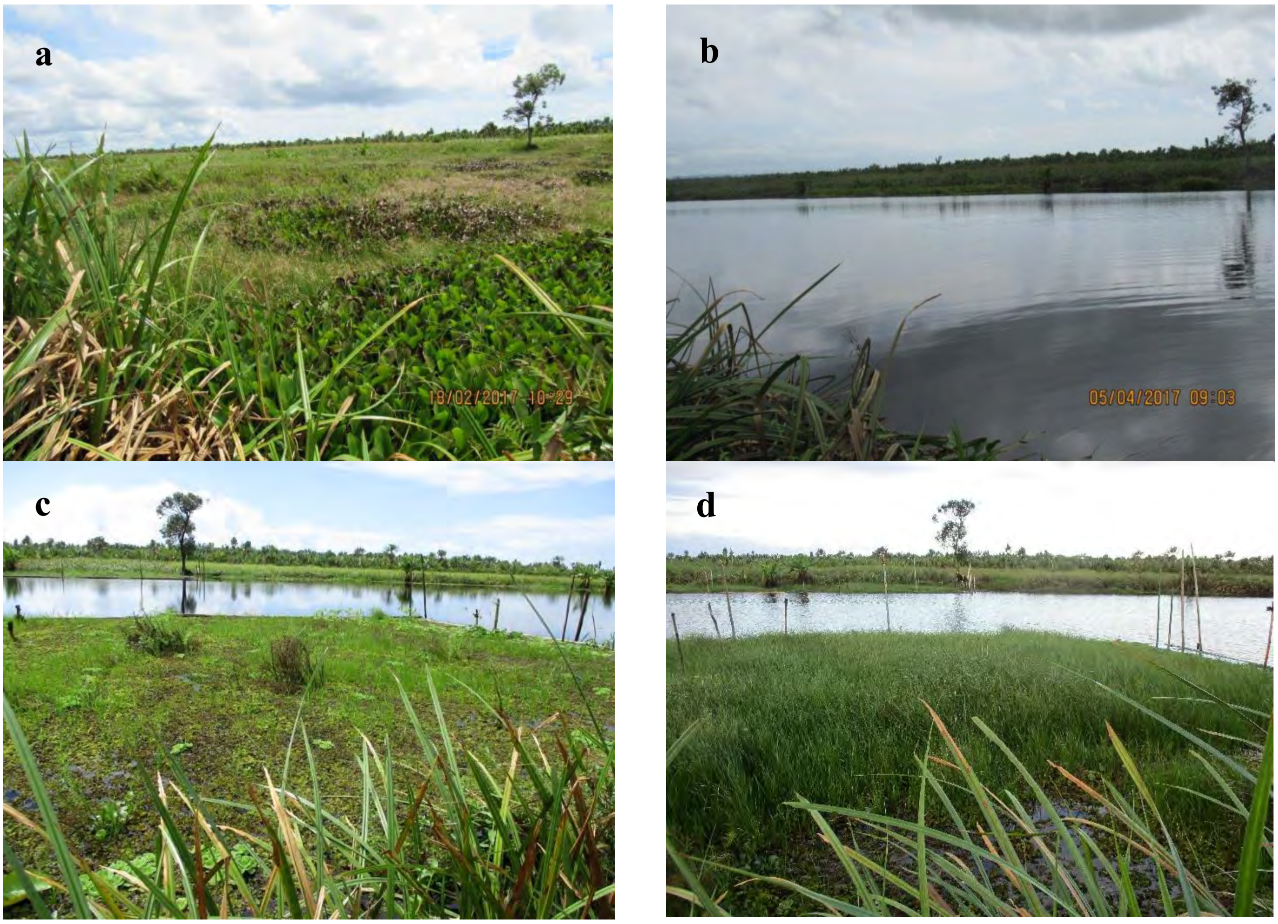

Figure 4.13.: Location for reinvasion study of subzone iii, Quadrat n°15: (a) before cyclone Domazile March 2017; (b) after cyclone Domazile; (c) reinvaded zone on 03/05/2019; (d) reinvaded zone on 06/08/2019.

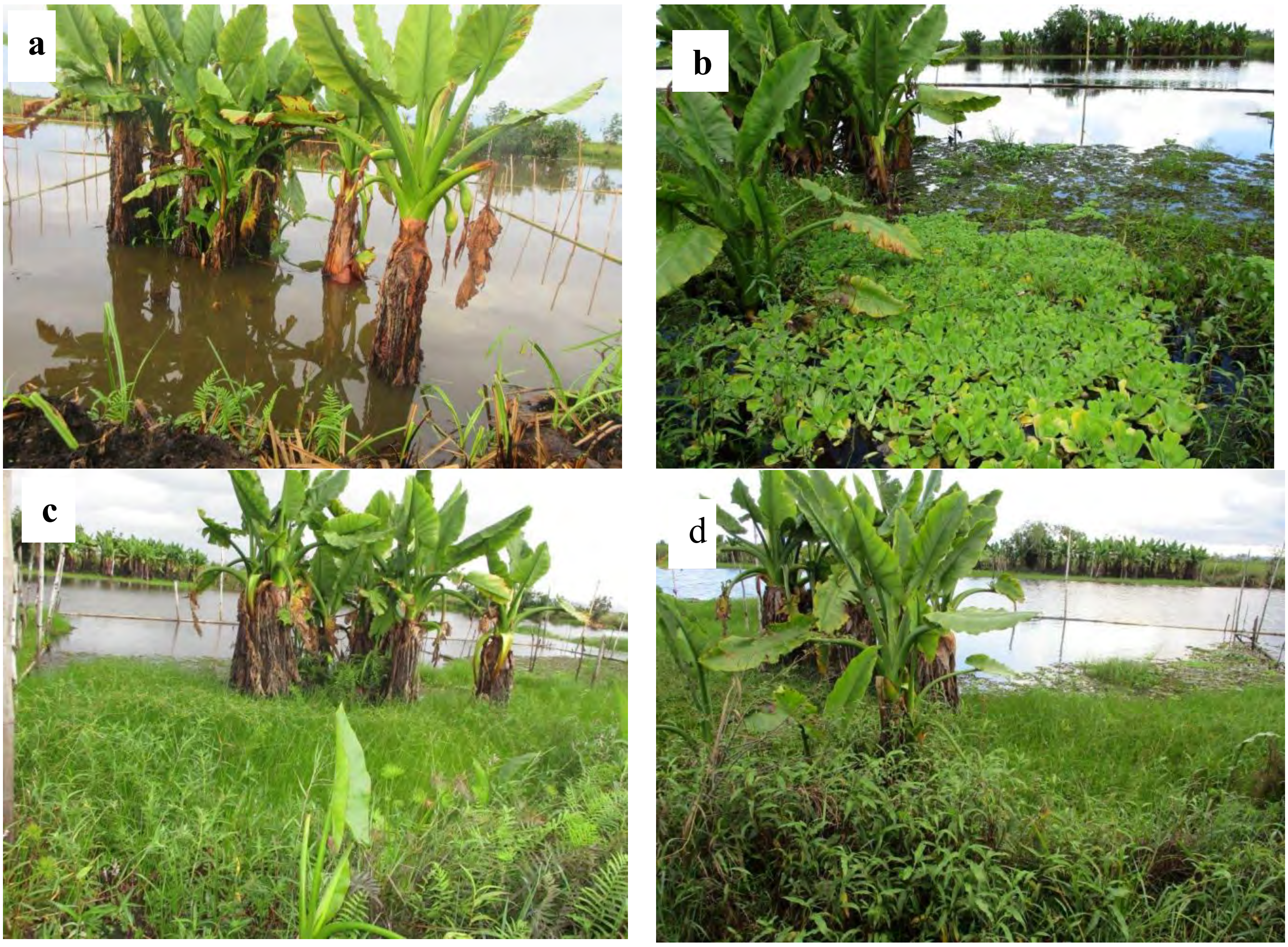

Figure 4.14.: Location for the reinvasion study of subzone iii, Quadrat n°7: (a) image on 02/08/2018; (b) image on 03/05/2019; (c) image on 13/07/2019; and (d) image on 06/08/2019.

4.4.5.4 Growth of Salvinia molesta

At the beginning of August 2018, two *S. molesta* plants were introduced for each treatment (monoculture and paired with *P. stratiotes* and *P. crassipes)* and a triple combination with both species (Figure 4.15). The growth rates of the species in the different treatments were not substantially different. In the control area, *S. molesta* appeared by itself, observed from December 2018, likely from the fragments of the species left in the quadrat during the cleaning. During the first four months, reproductive speed was slow and populations of the species covered less than 5% of each quadrat. From December 2018, the fourth month of experiment, the area covered rose rapidly, reaching 100% by May 2019.

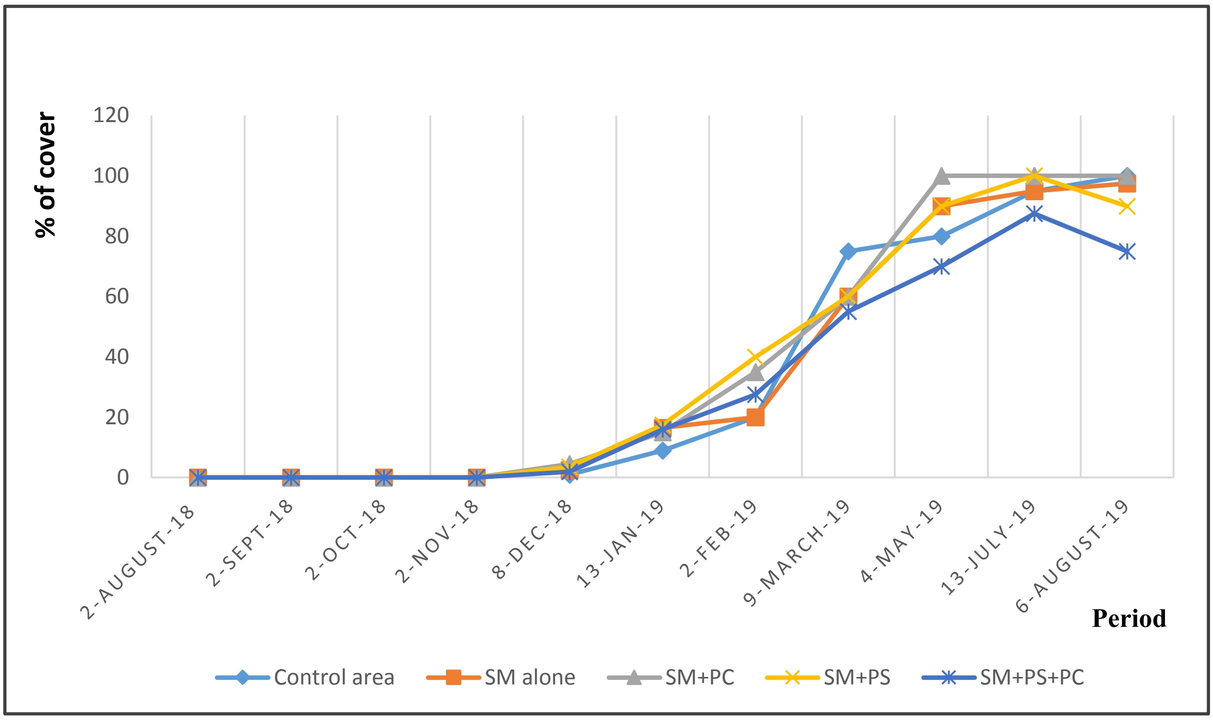

Figure 4.15.: Growth of *Salvinia molesta* in monoculture and in combination with other aquatic invasive species at Antsokafina lake

4.4.4.5 Growth of Pistia stratiotes

As for *S. molesta*, two individuals of *P. stratiotes* were introduced for each treatment. At the beginning of the experiment, the population grew rapidly (Figure 4.16). One month after the start of the experiment, in monoculture, the surface area covered by water lettuce had multiplied twenty times. By January 2019, i.e. five months after the start of experiment, *P. stratiotes* appeared by itself in the control area. In March 2019, the area covered was rapidly reduced. From this period, the population of the species was never stable. Our observations from the field suggest that no biomass of *P. stratiotes* was washed away. Although the *P. stratiotes* quadrats were not stocked with *S. molesta*, they were fully invaded by the *S. molesta.* Therefore, competition with other species, particularly *S. molesta*, could be a more plausible explanation for the reduction of f the *P. stratiotes* biomass. The maximum covered area was 6.5% at the end of the experiment.

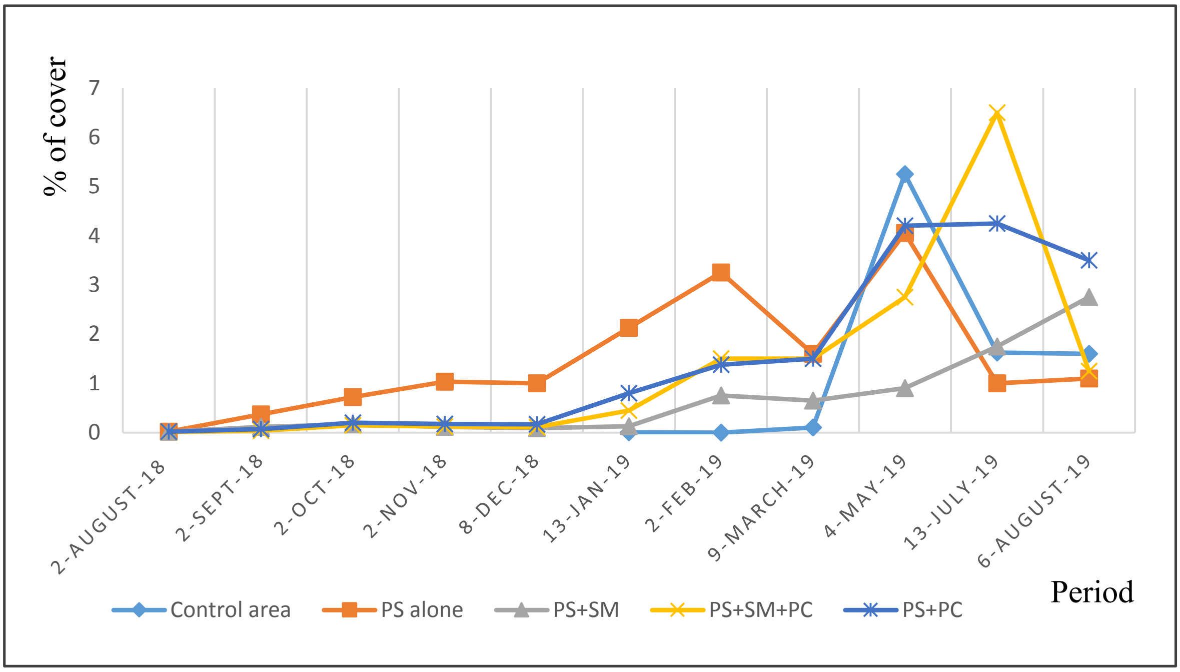

Figure 4.16.: Growth of *Pistia stratiotes* in monoculture and in combination with other aquatic invasive species at Antsokafina lake

4.4.4.6 Growth of Pontederia crassipes

As for *S. molesta* and *P stratiotes*, two individuals of *P. crassipes* were placed in culture in each treatment at the beginning of August 2018. During the first three months, the plants did not multiply. Slight growth was observed from November 2018 but this was reduced around March 2019 (Figure 4.17). As for *P. stratiotes*, the populations of the species may have suffered due to competition with the other plants in the quadrat, in particular *S. molesta*. By February 2019, i.e. sixth month after experiment, *P. crassipes* appeared by itself, likely from the fragments left in the quadrat during the cleaning.

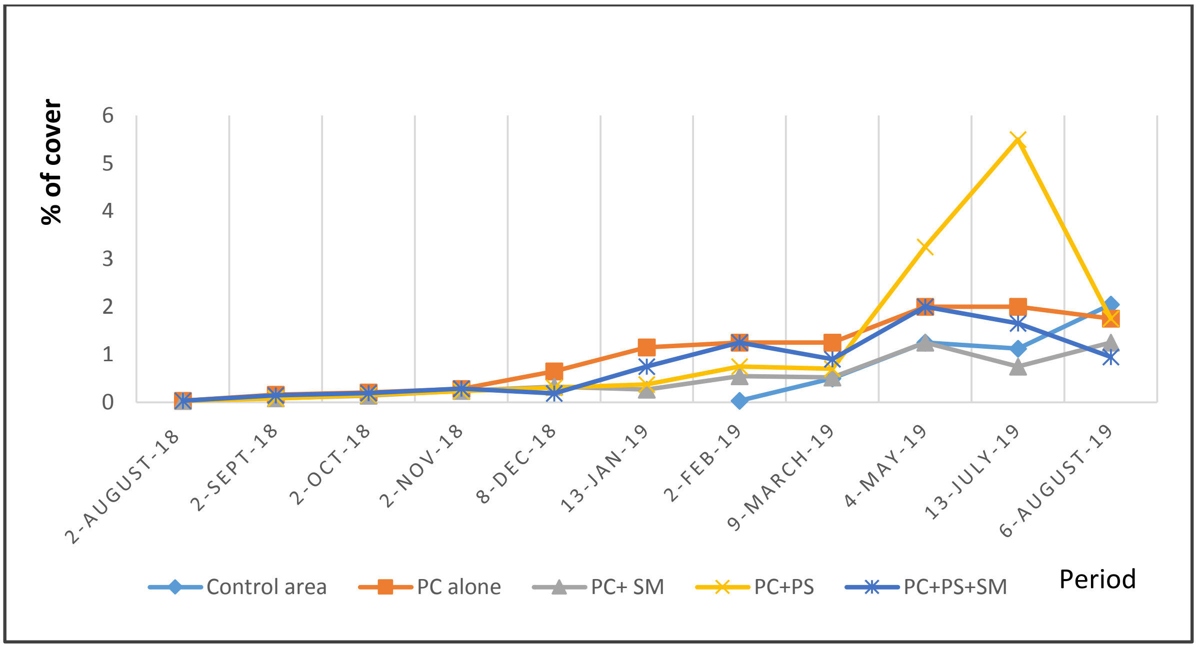

Figure 4.17.: Growth of *Pontederia crassipes* in monoculture and in combination with other aquatic invasive species at Antsokafina lake

4.4.4.7 Growth of the three species combined

During the first four months, all three species experienced a relatively slow growth rate. However, in December 2018, *S. molesta* started growing exponentially, covering 90% of the surface area by May 2019 (Figure 4.18). It was also noted that the monoculture of the species grew slightly faster than in association with *P. stratiotes* and *P. crassipes*. The area covered by *P. stratiotes* and *P. crassipes* remained below 7% until the end of the experiment. It appears that *S. molesta* is highly competitive when grown in combination with *P. stratiotes* and *P. crassipes*.

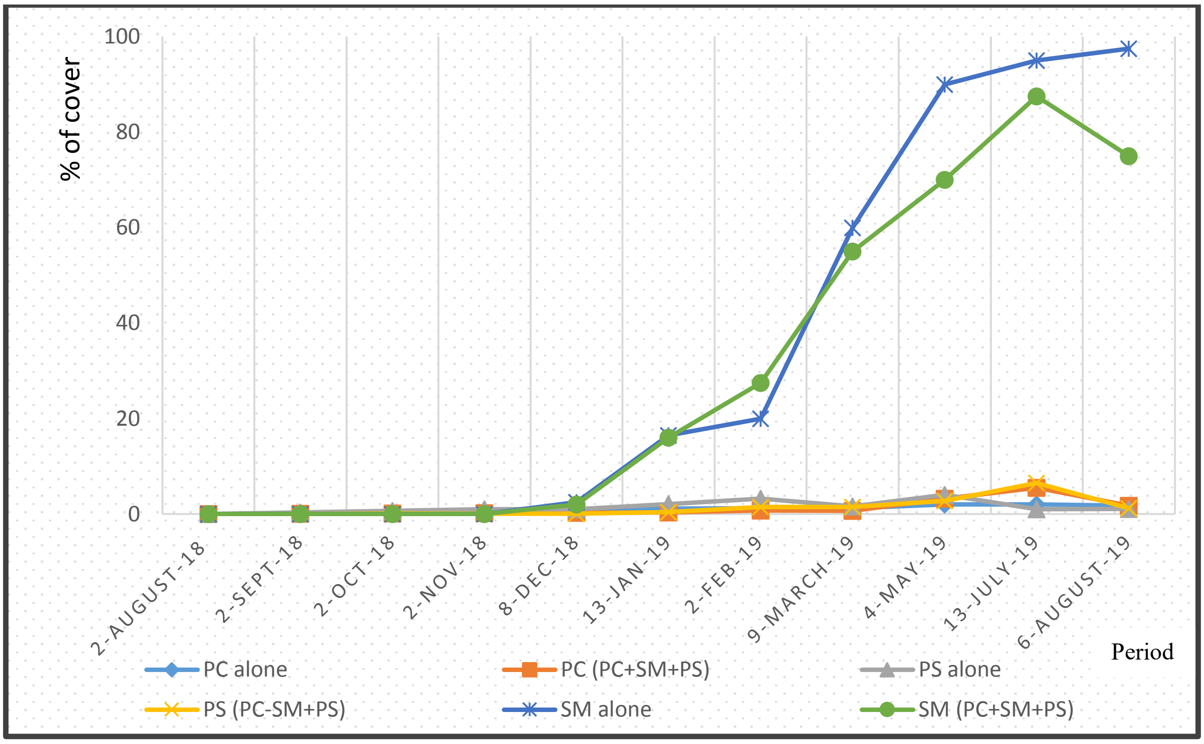

Figure 4.18.: Growth of the three aquatic invasive species in combination compared to monoculture at Antsokafina lake

4.4.6 Animal diversity

During this study, *M.* cf. *lepidactylus* was the only species of shrimp caught in the lake (Figure 4.19a). At T_0, no shrimp or fish were caught in the parts of the study area which were completely covered by invasive alien species, these areas were impossible for the fishermen to penetrate. Re-invasion experiments in this zone, encountered the challenge of not being able to install nets to catch fish. However, from April 2017, some fishermen started using the zones again (subzone ii and subzone iv) which were kept clear of IAP. From that time to the end of experimental trials, they reported that the daily yield were about 0.25kg to 0.50kg per catch. The most common fish species caught were *C. zillii* (Figure 4.19b) and *C. maculata*.

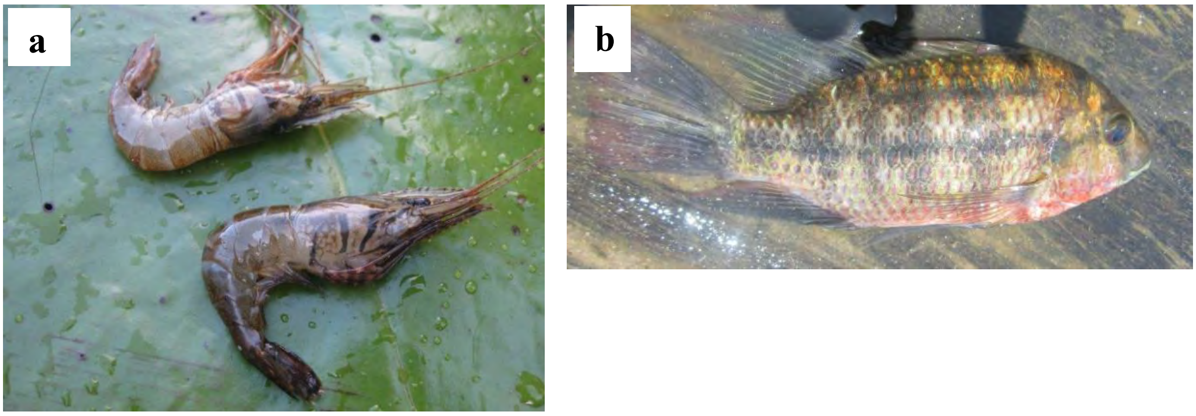

Figure 4.19.: Animal species found in the Antsokafina lake: (a) *Macrobrachium* cf. *lepidactylus* (horana); (b) *Coptodon zillii* (tilapia)

There was a remarkable variation in the quantity of shrimp caught (number and weight) but the maximum catch occurred in February 2018 just after Cyclone Ava (Figure 4.20). One possible explanation for this variation was the effect of the floods. According to Mr Edmond, a local expert on freshwater shrimp fishing at Ambodimanga, shrimp productivity depends on the movement of water. Generally, freshwater shrimp fishering is most productive following a decrease in water levels (Edmond, pers. comm). According to local climate data, precipitation levels dropped in February 2018, May 2018 and September 2018 (Figure 4.9). This probably explains the increase in the quantity of shrimp caught during these months.

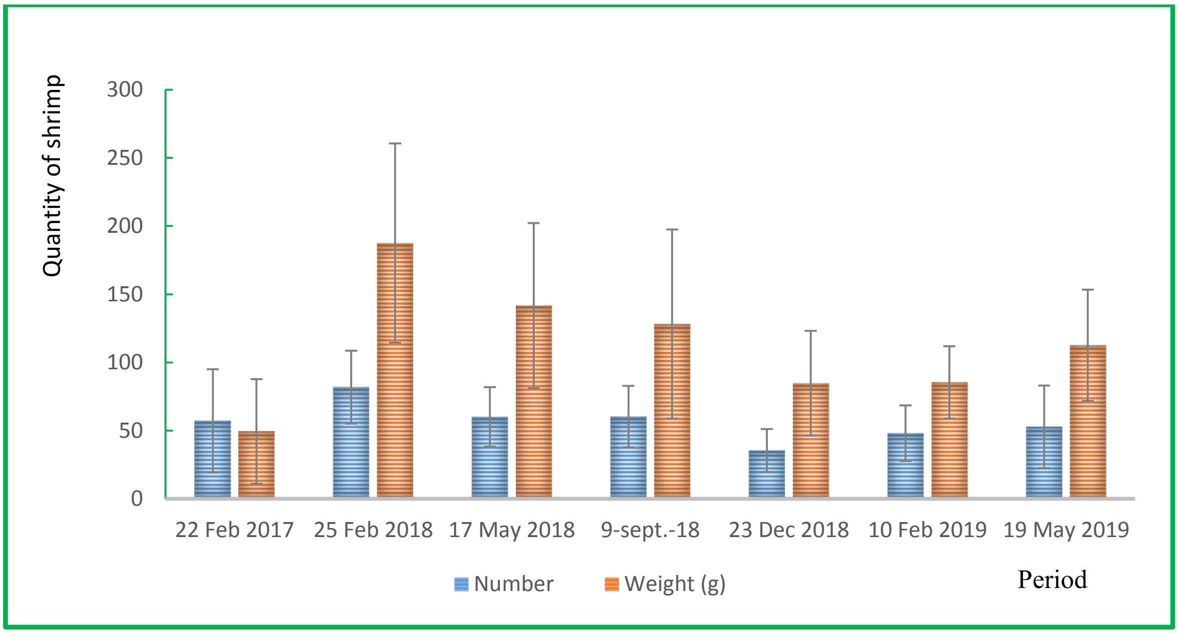

Figure 4.20.: Quantity of shrimp production in the lake over time

During the 11 months study period, from 6 September 2018 to 6 August 2019, 88 bird observations were made. Three species were seen frequenting the lake: Humblot's Heron (*Ardea humbloti* Milne-Edwards & Grandidier) (Ardeidae), White-faced whistling duck (*Dendrocygna viduata* (Linnaeus) (Anatidae) and Red-billed Teal (*Anas erythrorhyncha*) Gmelin (Anatidae) (Table 4.11). Although Humbolt's Heron occurs throughout the whole of Madagascar, it is classified as an endangered species (EN) (Sinclair and Langrand, 2013). The species was always seen at the edge of the lake where there were semi-aquatic plants. The number of White-Faced Whistling duck individuals varied from 2 to 15 individuals, never alone and they preferred the open area. White-faced whistling duck visit frequency was lower than Humblot's Heron. The third species, Red-billed Teal, was observed, as a pair, on just one occasion.

Table 4.11.: Bird diversity at Lake Antsokafina.

Species	**English name**	**Malagasy name**	**Number of individuals**	**Frequency***
Ardea humbloti	Humblot's Heron	Langoro	44	43
Dendrocygna virduata	White-faced whistling duck	Tsiriry	68	18
Anas erythrorhyncha	Red-billed Teal	Drakidrakirano mena molotro	2	1

* : Total observation=88

4.5 Discussion

In Madagascar, Lake Antsokafina lies within the 'Coastal Lakes and the Eastern Lagoon', according to the classification given by Ranarijaona (1999). This author included some lakes located along the Pangalanes canal in central-eastern of Madagascar, such as Lake Rasoamasay, Lake Rasoabe and Lake Laokangady, in this category. The results from Lake Antsokafina can be compared to these coastal lakes, knowing that they share the same type of bioclimate, being humid with precipitation greater than 2000mm, located in the low elevation, eastern ecofloristic zone (Faramalala, 1988). The climax vegetation surrounding these lakes is an evergreen moist forest in the east (Ranarijaona, 1999). Except for conductivity, the values of the physico-chemical parameters of Lake Antsokafina and Lake Rasoamasay are very close. The water conductivity of Lake Rasoamasay is much higher (1320 µS/cm) compared to that of Lake Antsokafina (67.43 µS/cm). This is because the conductivity of Lake Rasoamasay is influenced by marine intrusions (Ranarijaona, 1999; Feijoo and Lombardo, 2007). Lake Laokangady, which deviates from the series of lakes along the Pangalanes canal, is characterised by a lower conductivity of 370 µS/cm (Ranarijaona, 1999). The low value of the conductivity of Lake Antsokafina, with a maximum of 145 µS/cm in open water can probably be explained by its location away from the river mouth, about 4 km from the sea and therefore weakly influenced by marine intrusion.

In terms of biodiversity, the Antsokafina site (with 37 species of aquatic and semi-aquatic plants) was much richer than Lake Rasoamasay (which had only four species of macrophyte) and Lake Laokangady (with eight species) (Ranarijaona, 1999). It could be assumed that, as one moves away from the sea, the macrophyte diversity of the lake would increase due to decreased salinity.

In general, the values of the physico-chemical parameters of Lake Antsokafina were close to Lake Victoria on the African continent. In terms of biodiversity, Lake Victoria is much richer than Lake Antsokafina. As the inventories did not take into account the number of species per unit area, the comparison of two sites was not reasonable given that Lake Victoria has an area of 68,800 km^2 (Sitoki *et al.*, 2010) against 0.08km^2 for Lake Antsokafina.

This research revealed that the values of the physico-chemical parameters of the lake varied from season to season and that some of differences were significant between the areas invaded by invasive alien species and the open areas. Despite this, the water quality of the lake always remained favourable for the development of aquatic organisms.

Table 4.12.: Physico-chemical and biological parameters of the open areas of the three lakes, Lake Rasoamasay, Lake Antsokafina and Lake Victoria

Parameter	**Lake Antsokafina (study site in Madagascar) (source: Field measurement)**	**Lake Rasoamasay (central-East in Madagascar) (source: Ranarijaona,1999)**	**Lake Victoria in East Africa (sources: Gichuki *et al.*, 2012; Gophen, 2015; Sayer *et al.*, 2018; Sitoki *et al.*, 2018)**
pH	4.5-8 (Mean 6.27)	6.4	7.2-8.5 (Mean 7.8)
Conductivity (µS/cm)	18.2 -145 (Mean 67.43)	1320	106
Turbidity (NTU)	<10 -27	-	47.30-115.00 (Mean 71.1)
Water temperature (°C)	25.4 - 32.4 (Mean 28.1)	-	25.5–31.8 (Mean 27.7)
Macrophyte richness (number)	37	4	Around 82 species/sub-basin

The study showed that in a cleared area, four months after deliberate introduction of invasive aquatic species, submerged species (e.g. *C. demersum*), attached plants with floating leaves (e.g. *N. nouchalii*) and emergent creeping species (e.g. *E. colona*), colonized the zone with invasive alien species. Their development reached a peak in term of abundance six months after the start of the experiments. Being a submerged species, the biomass of *C. demersum* could be reduced by shading from floating and emergent species (Scheffer *et al.,* 2003; Khanna, *et al.,* 2012; Strange *et al*., 2018). After this time, the invasive aquatic species, particularly *S. molesta*, dominated dramatically until the end of experiments. However, the number of native species continued to increase, even though they represented only a small percentage of cover, from one month after the start of the experiment to the eleventh month.

In Lake Victoria, from September to December 2008, Gichuki *et al.* (2012) described the succession of plant communities in areas invaded by water hyacinth using four stages. In the first stage, the area was invaded by a pure water hyacinth population, followed by the second stage during which three species were added to the water hyacinth population: *Ipomoea aquatica* Forssk.(Convolvulaceae)*, Enydra fluctuans Lour.* (Asteraceae*)*, a species of Commelinaceae, with some scanty shoots of hippo grass, *Vossia cuspidata* (Roxb.) Griff. (Poaceae). During this stage, these species interconnected from the edge of the lake and stabilised the water hyacinth mat. During the third stage of succession, emergent plants developed further, to the detriment of water hyacinth. As for the fourth, climax stage, water hyacinth disappeared and *V. cuspidata (*hippo grass) reached its maximum development stage before dying off and sinking under water.

At our study site, a succession of similar plant communities was observed. However in all quadrats, *S. molesta* played the role that water hyacinth played in Lake Victoria. At the end of the trial (twelfth month), *S. molesta* remained the dominant species, covering on average 92% of the surface area of the quadrats. At this stage, *P.* cf. *polystachyos* (Cyperaceae) developed using *S. molesta* as a substrate. Although the emergent species occupied a significant proportion of the area (71% of the total covered area), *S. molesta* remained the most dominant (92% of total area covered). Therefore, this stage of plant succession corresponds most likely to the second stage of succession during which *S. molesta* was the most dominant (92% of total covered area), followed by *P.* cf. *polystachyos* (64% of total surface covered). Our results differed from those of Gichuki *et al.* (2012), on Lake Victoria, in that once the succession reached the climax stage, hippo grass died and the cycle restarted from the remaining fragments of water hyacinth. At Lake Antsokafina, in contrast, when examining the structure of the plant communities, assumed to be the climax stage (of subzone A(i), a nine-year-old site, at T_0), *S. molesta* still occupied significant proportions in terms of coverage (relative dominance of 22.69%). We assumed that the plant community structure similar to A(i) probably corresponds to the climax stage in which emergent species dominate at 75% against 22% for *S. molesta.* It should be noted that in subzone A(i) at T_0, among the emergent macrophytes, *Pneumatopteris unita* occupied the largest proportion (relative dominance of 22%), followed by *P.* cf. *polystachyos* (relative dominance of 20%). However, in our invasion experiment, *P. unita* did not appear in the plant succession, where the reinvasion process was only recorded for one year. During the plant community dynamics on Lake Antsokafina, this species probably came up at a later stage (> 1 year) in the development of the mats.

Gichuki *et al.* (2012) stated that, in Lake Victoria, macrophytes, predominantly hippo grass, died off due to the lack of nutrients following the disappearance of water hyacinth. On Lake Antsokafina, in a cyclonic zone, we assumed that cyclones renewed the mats. Also, the method of rice cultivation of surrounding areas (burning the rice fields) continuously supplied the nutrients necessary for the development of macrophytes in the lake. Without a cyclone, the mats of *S. molesta* would remain for at least nine years (as was the case in subzone A(i) from 2008 to 2017) without being naturally disturbed.

This study concentrated on plant species and their population dynamics. However, animal species were also observed as important elements in the ecosystem. As fish and shrimp were the main fishery products caught in the area, it is important to discuss the relationship between these animals and the aquatic macrophytes. Killgore *et al.* (1989) argued that the relationship between plant and fish abundance was an important management consideration when plant control strategies were developed, because it provided a basis to evaluate potential effects of the control program on the integrity of the fish community structure. In the USA, Borawa *et al*. (1979) found that fish densities increased from approximately 1 000 to more than 15 000 fish ha^{-1} after the establishment of the invasive plant *Myriophyllum spicatum* L. Welten & Sutter (Holoragaceae). Overall, the presence of macrophytes plays an important role in the enrichment of aquatic fauna (Junk, 1973; Petr, 2000). Given that *Macrobrachium* shrimps are omnivorous, eating aquatic insects, molluscs, other crustaceans, algae, leaves and stems of aquatic plants, plant seeds, detritus, and even fish (New, 1980; Lima *et al.,* 2014), it is likely that these observations would be valid for *M.* cf. *lepidactylus* present in the lake.

Thick mats of aquatic weeds reduce the dissolved oxygen concentration in the water, increase uptake of phosphorus and the concentration of carbon dioxide, and result in the formation of hydrogen sulphide underneath them (Petr, 2000). Lower oxygen concentrations, combined with increased amounts of organic detritus that collect beneath these floating mats, can increase sediment accumulation rates and accelerate the eutrophication processes (Britton *et al.*, 1975; Yang *et al.*, 2008; Chamier *et al.*, 2012). Increased eutrophication can be lethal to fish, cause algal blooms and render the water toxic and uninhabitable for native animal and plant species (Pieterse and Murphy, 1989). Invaded areas are therefore devoid of invertebrate fauna and have a benthos unsuitable for fish spawning (Bishai, 1960/61; Junk, 1977; Kongere, 1979; McLachlan, 1969; Poi de Neiff and Solis, 1994). On the one hand, knowing that aquatic macrophytes are essential for aquatic organisms and on the other hand, that aquatic weed mats are unfavourable for the survival of aquatic life, the strategic recovery plan for lake Antsokafina should specifically consider the management of invasive aquatic species and the functioning of the ecosystem as a whole.

The management plan for the lake should take into account the spatially two distinct zones, namely the littoral and the pelagic zones, that have different characteristics with respect to bio-physical parameters, and different ecological functions. The shallow, marginal littoral zone with aquatic macrophytes contains a greater diversity of aquatic animals than the offshore, open water areas. For example, in Lake George in Uganda, the vegetated littoral zone contained 19 fish species compared to around 10 species in the mid-lake (Burgis *et al*., 1973). Jayachandra and Joseph (1989) reported that decapod crustaceans including *Macrobrachium* as omnivorous species, take food from different trophic levels including fauna associated with submerged and shore vegetation in the water bodies that they inhabit. The littoral zones have to be managed, therefore, for colonization of macrophytes. In the artificial Lake Kariba, increased diversity within the inshore fish community was attributed to the development of a mosaic of new niches among the aquatic macrophytes, periphyton and submerged trees where a variety of benthic gastropods, molluscs, insects and other invertebrates provided a new food resource to fish (Karenge and Kolding, 1995). In Lake George, the development of a macrophyte belt enhanced the stocks of juvenile and small fish species such as *Serranochromis macrocephalus* Boulenger (Cichlidae) *Brycinus imberi* (Peters) (Alestiidae) and *Synodontis zambezensis* (Peters) (Mochokidae) which increased during the 1980s (Karenge and Kolding, 1995).

In the pelagic part of the lake, the surface of the water should be kept clear to allow fishermen to access the lake so that they can continue their activities. If the pelagic zone is kept open, it also becomes a niche for the animal species preferring open areas. These include aquatic birds such as of White-faced whistling duck (*D. virduata*) and Red-billed Teal (*A. erythrorhyncha*). Similarly, the shrimp *Caridina* H. Milne-Edwards (Atyidae) and larvae of the midge *Chaoborus* Edwards (Chaoboridae), which stay close to the bottom of the pelagic zone during the day, and at night swim up to the surface waters (Lehman, 1998), need open water. *M.* cf. *lepidactylus* probably displays the same behaviour. This requires further research.

The management strategy for Lake Antsokafina should further consider functional links between littoral and pelagic areas, for full integrity of ecosystems. Crowder *et al.* (1998) highlighted the need for linking the littoral and pelagic habitats, in terms of both prey consumption and translocation of nutrients, to include for example the transfer of epiphyte productivity to the pelagic habitat. Macrophytes, as a substrate for epiphyton, and fish, are the major components in such a simplified system, which shows the importance of a vegetated littoral zone for the entire ecosystem of a water body (Petr, 2000). Persson and Crowder (1998) described the habitat structure, the nutrient/organic transport, and the recruitment of juvenile and adult fish between littoral and pelagic zones as potential mechanisms by which fish may affect macrophyte abundance, littoral-pelagic coupling, and overall lake dynamics. If the lake is managed in such a way, the nuisance of invasive species is not the only risk to consider, because overfishing might become an important factor that threatens the integrity of the ecosystem as a whole. For example, in the Rawa Pening Reservoir in Java, Indonesia, control of water hyacinth led to overfishing, and only expansion of aquatic weeds due to the neglect of control measures led to rehabilitation of fish stocks (Carlander, 1980).

The final point of discussion concerns the relationship between cyclones and invasive aquatic species. According to the accounts of local villagers, the mat of invasive aquatic species that occupied the lake at the start of this study formed after Cyclone Ivan in 2008. This mat which traversed the entire lake, and was estimated to have a biomass of several tons, was completely removed by Cyclone Domazile in March 2017. This periodic clearing of the lake by cyclones probably explains why the lake was open in both 1965 and 2016, despite an almost 50-year period between them. In these two cases, we assumed that the lake had been previously cleared by strong cyclones, as was the case with Ivan in 2008 and Damazile in 2017. Nevertheless, if the period between the cyclones is long enough, then the mats have time to develop. Whenever cyclones sufficiently powerful to clear the mats occur, the strategic management plan after the cyclone should be to prevent invasive aquatic species from re-forming mats for as long as possible.

Chapter 5: A study of competition between the indigenous *Salvinia hastata* Desv and the four aquatic weed species (*Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch. *Azolla filiculoides* Lam.)

5.1 Introduction

Globally, biological invasion is recognised as the second biggest cause leading to the extinction of species after direct habitat loss (Sax and Gaines, 2008; Bellard *et al.* 2016). Of the 215 species listed as extinct on the IUCN Red list, Bellard *et al*. (2016) found that biological invasion was the cause of extinction for 58% of these species. For the biological invasion process, the resistance of native species is the last barrier that introduced species must overcome before being classified as invasive (Richardson *et al.,* 2000). According to Soubeyran (2008) and Sarat *et al.* (2015a), one of the criteria that is used to move the categorisation of an introduced species to the category of invasive species is the fact that they cause negative impacts on the socio-economy, health and/or biodiversity of the introduced range.

For habitat conservation, research focused on co-occurring invaders provides more evidence for the impacts of invasive species than focusing on a single invader (Kuebbing *et al.* 2013). Recent studies in 30 countries and on 5 continents, indicated that two-thirds of habitats were invaded by multiple species, and showed that the majority of highly competitive interactions were comprised of invader on – invader, while interactions of invaders with native species were more moderate (Callaway *et al.,* 2006; Schmidt *et al.,* 2008; Pfeifer-Meister *et al*., 2008; Jäger *et al.,* 2009; Rudgers and Orr, 2009; Metlen, 2010). In natural habitats, the effect of competition from invasive species, along with other threats such as biological resource use, increases the risk of the extinction of less competitive native species (Smith, 1992; Sax and Gaines, 2008; Bellard *et al.* 2016). Interspecific and intraspecific competition between species are important factors determining the specific composition, diversity and abundance in an ecosystem, and interspecific competition can lead to the elimination of one species (Barbault, 1983; Nabors, 2008). Several parameters determine the ability of invasive species to outcompete native species, including higher growth rates, high fecundity and exploitation of resources (Williamson and Fitter, 1996; IUCN, 2013; Sarat *et al.,* 2015a; Daehler, 2003).

Biological control, or the reuniting of the invasive species with its natural enemies, can reduce the competitive advantage of invasive species (Callaway *et al.,* 1999). Several studies have been conducted demonstrating the combined effect of competition and herbivory on reducing the competitive performance of invasive species including aquatic species (Pantone *et al*., 1989; Story *et al.,* 2000; Center *et al.,* 2001; Center *et al.,* 2005; Coetzee *et al.,* 2005; Mony *et al.,* 2007; Ajuonu *et al.,* 2009; Tipping *et al.,* 2009; Bownes *et al.,* 2010; Martin and Coetzee, 2014; Strange *et al.,* 2019). The degrees of competition depend on the biological control agent used, the presence or absence of density-dependent populations and nutrient concentrations. The model developed by Spitters (1983) is an appropriate way of quantifying competition between two species, and is based on an addition series of density and an inverse linear model (Spitters *et al.,* 1989; Pantone *et al.,* 1989; Van *et al.,* 1999; Coetzee *et al*., 2005; Mony *et al.,* 2007; Tipping *et al.,* 2009; Martin and Coetzee, 2014).

Currently, *Pontederia crassipes, S. molesta, P. stratiotes* and *A. filiculoides* co-occur in several African countries (Labrada and Fornasari, 2002). In Madagascar, coexistence has been recorded at several water bodies between *P. crassipes, P. stratiotes*, the indigenous fern *Azolla pinnata* R. Br. (Azollaceae) and *Salvinia hastata* Desv. (Salviniaceae) at Lake Ravelobe; and *P. crassipes* and *S. hastata* at Lake Alaotra (Ranarijaona, 1999, 2007; Ranarijaona *et al.,* 2013). But the impact of these weeds on *S. hastata* is unknown.

5.1.1 Taxonomy of *Salvinia*

The genus *Salvinia* belongs to the family Salviniaceae and is placed in the order Salviniales. Salviniaceae are a family of floating aquatic ferns, comprising two genera, *Azolla* with roots and *Salvinia* without roots (Smith *et al.,* 2008). For the genus *Salvinia*, the stems are dichotomously branched rhizomes, protostelic, aerenchymatous, bearing a whorl of three simple leaves, two of which are round and emergent while the third is submerged and finely divided to function as a root, blades round to oblong, entire, with water-repellent trichomes on upper surface. Sporangia in thin-walled sporocarps on submerged leaves (Taylor *et al.,* 2009).

The number of species recorded in the literature varies. A literature review as part of this sudy identified 24 species in the genus *Salvinia*, *viz.*: *Salvinia affinis* Desv., *Salvinia auriculata* Aubl., *Salvinia biloba* Raddi, *Salvinia braziliensis, Salvinia cucullata* Roxb, *Salvinia cyathiformis* Maxon, *Salvinia elegans* Hassk., *Salvinia europaea* Desv., *Salvinia hastata* Desv., *Salvinia michelii* Loefl., *Salvinia minima* Baker, *Salvinia martynii* Kopp, *Salvinia molesta* D.S. Mitch., *Salvinia natans* Pursh, *Salvinia nuriana* de la Sota & Cassa, *Salvinia nymphellula* Desv., *Salvinia oblongifolia* Mart., *Salvinia olfersiana* (Klotzsch) Klotzsch & Baker, *Salvinia reticulata* (Ettingsh.) Heer, *Salvinia pusilla* Liebman ex Herzog, *Salvinia sprengelii* Corda, *Salvinia sprucei* Kuhn, *Salvinia verticullata* Roxb., *Salvinia vulgaris*

(Micheli) Rupr. (Hounkanli, 1982; https://www.tropicos.org/nameSearch; https://fr.wikipedia.org/wiki/Salvinia).

5.1.2 Description of *Salvinia hastata*

Salvinia hastata is a yellow-green plant with a rhizome of about 1 mm in diameter, with dark brown multicellular hairs up to 2 mm long on the upper surface. Floating leaves are opposite, oblong, up to 2 cm long, 1.3 cm wide, sometimes slightly broadened towards the base, emarginate at the apex, cordate to truncate at the base, flat or infolded along the midrib, papillate on the upper surface with minute whitish multicellular hairs, pilose beneath with brownish multicellular hairs; submerged leaves are up to 6.5 cm long, dissected, the lobes have dense dark brown multicellular hairs up to 3 mm long. Sporocarps are spherical, hairy, up to 6, and are arranged in two rows along the midrib of each dissected leaf-lobe. This species differs from other species by having more oblong leaves with a truncated apex and heart-shaped base, the apex of the leaf-papilla does not have an open basket of 4 curved cells (Verdcourt, 2000; https://www.mozambiqueflora.com/speciesdata/species.php?species_id=175650). *Salvinia hastata* is a widely distributed species in East Africa (Kenya, Malawi, Mozambique, Tanzania), Mascarene Islands including Madagascar (https://www.mozambiqueflora.com/speciesdata/species.php?species_id=175650).

According to Ranarijaona (1999), the species is present in all phytogeographic of the divisions in eco-floristic zones of Madagascar. However, our research (with information from different sources e.g. herbarium at the Botanical and Zoological Park of Tsimbazaza, Tropicos website, field trips, literature) revealed that the natural habitat of the species is found in the low-elevation western eco-floristic zone from 0 to 800m asl (Faramalala, 1988) (Table 5.1). The area is a warm, semi-arid tropical sub-humid type, characterised by 6 to 7 months of dry period, annual rainfall varying from 500mm to 1500mm and with an average temperature of 27°C. Its distribution extends over the entire western region (low altitudes of 800m from the extreme north of Diego to Tulear) with a break in the Sambirano region. Outside of this zone, the species is also present in Lake Alaotra, which belongs to the eastern eco-floristic zone (of medium elevation from 800 to 1800m asl), characterised by a humid type temperate climate of 0 to 2 months dry, average temperature of 15°C, with rainfall between 1500mm to 2000mm (Rajeriarison and Faramalala, 1999).

Table 5.1.: Current distribution of *Salvinia hastata* in Madagascar (source Botanical and Zoological Park of Tsimbazaza herbarium, Tropicos.org, field trips)

Locality	Coordinates	Collector	Reference (collection number or photo)	Date	Source
Imerimandroso, Alaotra Lake, Alaotra Mangoro region	17°36ꞌ45.0″S 048°30ꞌ13.0″E	M.R Decary	325	24-June-1921	Herbarium ; Ranarijaona (1999)
RN8, Andranomavo, Soalala, Boeny Region		Conservation des Reserves Naturelles et Parcs Nationaux de Madagascar	4566 R.N.	4-Sept-1952	Herbarium
30km North-East of Morondava, Menabe Region			620A	19-june-1974	Herbarium
Tsimbazaza Lake, Tsimbazaza Botanical and Zoological Park		R. Bensist	141	19-Nov-1950	Herbarium
Manompa lake, 9km north-East of Ambatoboeny town, Betsiboka region	16°26ꞌ34.6″S 047°09ꞌ40.4″E	Adolphe Lehavana, Jacky Andriantiana, Costas Zachhariades	ALH 1135	16-Oct-2018	Tropicos
1km south of Andranofasika town, District Amboboeny, Betsiboka Region	16°20ꞌ37.2″S 046°50ꞌ40.7″E	Adolphe Lehavana, Jacky Andriantiana, Costas Zachhariades	Photo	17-Oct-2018	Fieldtrip
Ravelobe lake, Ankarafantsika National Park	16°18ꞌ16.7″S 046°48ꞌ42.9″E	Adolphe Lehavana, Jacky Andriantiana, Costas Zachhariades	Photo	18-Oct-2018	Fieldtrip
Amparihely lake, 4km south of Mampikony town, Sofia Region	16°7ꞌ25.2″S 047°36ꞌ48.7″E	Adolphe Lehavana, Jacky Andriantiana, Costas Zachhariades	Photo	18-Oct-2018	Fieldtrip
Creek Ambodisikidy, Fokontany AmpombibeIII, rural commune of Tsiningia, District Port Bergé, Sofia Region	16°32ꞌ45.5″S 047°33ꞌ16.8″E	Adolphe Lehavana	Photo	7-April-2019	Fieldtrip
Matsaborilava, Fokontany Ampandrianakanga, Andilabe, Antsohihy, Sofia Region	14°55ꞌ33.0″S 048°02ꞌ29.0″E	Adolphe Lehavana	Photo	8-April-2019	Fieldtrip
Kinkony lake, District Mitsinjo, Boeny Region	16°08ꞌS45°49ꞌE				Rabarisoa et Razafy (2012); Cabanis et *al.* (1969)

5.2 Aims of the study

The overall objective of this study was to determine the competitiveness of several species of aquatic weeds against the indigenous floating fern, *S. hastata,* as an indication of invasiveness. This study is based on the hypothesis that in absence of an insect herbivore in the introduced range, weeds are very competitive, to the detriment of *S. hastata*.

5.3 Methods and materials

The experiments were conducted under controlled outdoor conditions in the city of Fenerive-Est, Analanjirofo Region, Madagascar. The trials compared the competitiveness of *S. hastata* against the four target weed species (*P. crassipes, P. stratiotes, S. molesta* and *A. filiculoides).*

5.3.1 Macrophytes species and study site

In Madagascar, the stocks of *S. hastata* were collected in a small lake, located 1km south of the town of Andranofasika, District Amboboeny, Betsiboka Region (16°20'37.2″S 046°50'40.7″E). The stocks were brought to Fenerive-Est in a container containing water from the original lake. The stocks of three invasive aquatic species were collected from the water bodies in the vicinity of Fenerive-Est. *Salvinia molesta* and *A. filiculoides* were collected at Antsokafoka, 5km south of Fenerive-Est (17°26'42.6″S 049°26'01.6″E), while *P. crassipes* was harvested from a small pond in the town of Fenerive-Est (17°22'48.1″S 049°24'52.4″E). *Pistia stratiotes* was brought from Lake Antsokafina, near the village of Andrangazaha, Soanierana Ivongo (16°49'56.5″S 049°40'53.0″E).

Before conducting the experiments, the species were cultivated in plastic tubs (50cm diameter x 25cm deep) fertilized with NPK (11-16-22) at a dose of 10mg N/l ((Joubert and Coetzee, unpublished). All species were left outdoors for a couple of weeks before being used in the experiment. For *S. hastata, P. crassipes* and *P. stratiotes*, five culture tubs were used, while for *A. filiculoides* and *S. molesta*, two tubs of each were sufficient.

The experiment was conducted in the town of Fenerive-Est, where a staudy area (15m long and 10m wide) was set up. To regulate the amount of ambient sunlight, the site was covered with 35% shade cloth, below which the tubs were placed. The climate in Fenerive-Est is humid to perhumid, warm equatorial low altitude bioclimate, with an average monthly temperature of 24°C, average annual rain >2000mm and no dry months (Rajeriarison and Faramalala, 1999).

5.3.2 Experimental design

The experiment was initiated on 01 March 2020 concluded on 03 May, 2020. *Salvinia hastata* was propagated in monoculture and in mixture with one of the four invasive species studied as following: *S. hastata/P.crassipes; S. hastata/P. stratiotes; S. hastata/S. molesta* and *S. hastata/A. filiculoides*. Using an additive series model developed by Spitters (1983) for crops and weeds, extended to competition study of native and invasive aquatic plants, the species were planted in factorial combinations of different ratios (0:3, 0:9, 3:0, 3:3, 3:9, 9:0, 9:3). The adopted method is able to elucidate the effects of intraspecific and interspecific competition at a range of densities.

Depending on the plant densities described above, individual plants were randomly selected from the culture tubs for use in the experiment. Fresh biomass was weighed to calculate the stocking biomass before placing the individual plants in the smaller experimental tubs (30cm diameter x 12cm deep). Each tub was filled with 6 litres of water fertilized with NPK (11-16-22) at a dose of 10mg N/l (Joubert and Coetzee, unpublished). Fertilization was uniform for all tubs. Every two weeks, the water in the tubs was replaced to maintain the required fertilizer concentration. Each treatment was replicated five times. After 64 days, plants were harvested and then weighed separately. Before weighing, the plants were left in the open for one hour to allow the removal of excess water.

5.3.5 Data analysis

To assess biomass accumulation by species over the study period, relative growth rates (RGR) were calculated using the formula:

$$\boxed{\mathrm{RGR} = \frac{(\ln \mathrm{W}_2 - \ln \mathrm{W}_1)}{(\mathrm{t}_2 - \mathrm{t}_1)}}$$

where W_2 and W_1 are plant weight biomass at time t_2 and t_1 in days, respectively (Hunt, 1990; Poorter and Gamier, 1996). For this study, fresh biomass was analysed. The differences in RGR of each species under the various treatments were compared statistically using factorial Analysis of Variance (ANOVA) followed by Tukey Post-Hoc tests ($P<0.05$).

The effects of intraspecific and interspecific competition on the biomass yield of both *S. hastata* and the competing aquatic weed species were calculated using the model developed by Spitters (1983). Data were analysed using inverse linear models. Multiple regressions for each combination of species, using *S. hastata* density and the competing species density as regressors, and 1/mean end weight as the response variable were performed. The magnitude of the relationship was analysed using the reciprocal-yield model as follows:

$$1/W_{SH}= a_{s0} + a_{ss}d_s + a_{sw}d_w$$

$$1/W_W=a_{w0} + a_{ww}d_w + a_{ws}d_s$$

Where $1/W_{SH}$ and $1/W_W$ are the inverse of the average yields (end fresh weight) per plant for *S. hastata* (SH) and the competing weed species (W), respectively and d_s and d_w represent their densities. The coefficient a_{SS} measures the effect of intraspecific competition within *S. hastata*, whereas a_{sw} quantifies the effect of interspecific competition of the competing weed on *S. hastata*. The ratio of the coefficients a_{ss}/a_{sw} measures the relative competitive ability of *S. hastata* with respect to the weed and a_{ww}/a_{ws} represents the relative competitive ability of considered weed with respect to *S. hastata* (Coetzee *et al.* 2005). The results were presented in three-dimensional surface-response planes. All statistical analyses were conducted using Statistica V13 (Tibco Software Inc.).

5.4 Results

5.4.1 Competition between *Salvinia hastata* and *Salvinia molesta*

When *S. hastata* was grown in competition with *S. molesta, S. molesta* was 8 times more competitive than *S. hastata*. In other words, eight individual *S. hastata* plants would be required to reduce the biomass yield caused by a single individual of *S. molesta* on itself (Table 5.2). The regression model was significant (Table 5.3), implying a suitable fit. On the other hand, the regression model for *S. hastata* was not significant.

The analysis of three-dimensional graphs allows the interpretation of the influence of the competition coefficients on reciprocal yields. The higher the value of 1/w, the lower the yield; and the larger the slope, the larger the competitive coefficient. For the yield of *S. hastata,* the slope was gentle, indicating that neither intraspecific competition nor interspecific competition significantly influenced the yield of *S. hastata* (Figure 5.1a). For *S. molesta*, the slope of intraspecific competition was steep, while that of interspecific competition was flat, indicating that intraspecific competition resulted in a significant reduction in the yield of *S. molesta* (Figure 5.1b).

Table 5.2.: The outcome of multiple regression analysis of plant density on reciprocal yields (wet weight (g)) of *Salvinia hastata* (SH) and four aquatic invasive weeds, *Salvinia molesta* (SM), *Pontederia crassipes* (PC), *Pistia stratiotes* (PS), *Azolla filiculoides* (AF).

Considered weeds	Species	Regression equation	Intraspecific coef.	Interspecific coef.	Ratio
SM	SH	1/SH = -3.2643+0.525*x+0.8279*y	0.8279	0.525	1.576952
	SM	1/SM = 0.006+0.0064*x+0.0008*y	0.0064	0.0008	8
PC	SH	1/SH = -14.9609+2.2677*x+2.1384*y	2.1384	2.2677	0.94298
	PC	1/EC = 0.0071+0.0016*x+6.7854E-5*y	0.0016	6.79E-05	23.58004
PS	SH	1/SH = -1.6137+0.4981*x+0.2566*y	0.2566	0.4981	0.515158
	PS	1/PS = 0.0041+0.0108*x+0.0009*y	0.0108	0.0009	12
AF	SH	1/SHm = 0.0186+0.0133*x+0.007*y	0.007	0.0133	0.526316
	AF	1/AFm = 0.1811+0.0128*x+0.0111*y	0.0128	0.0111	1.153153

Table 5.3.: Multiple regression analysis of competition between *Salvinia hastata* (SH) and four invasive aquatic weeds *Salvinia molesta* (SM), *Pontederia crassipes* (PC), *Pistia stratiotes* (PS), *Azolla filiculoides* (AF).

Species combination	Dependent Variables	Multiple R^2	Df model	Df residual	F	*P* value
SH and SM	1/SH	0.074955	2	27	1.094	0.349
	1/SM	0.805598	2	27	55.944	0.0001
SH and PC	1/SH	0.268671	2	27	4.960	0.015
	1/PC	0.494812	2	27	13.223	0.0001
SH and PS	1/SH	0.178114	2	27	2.926	0.071
	1/PS	0.507042	2	27	13.886	0.0001
SH and AF	1/SH	0.528244	2	26	14.557	0.0001
	1/AF	0.032463	2	26	0.436	0.651

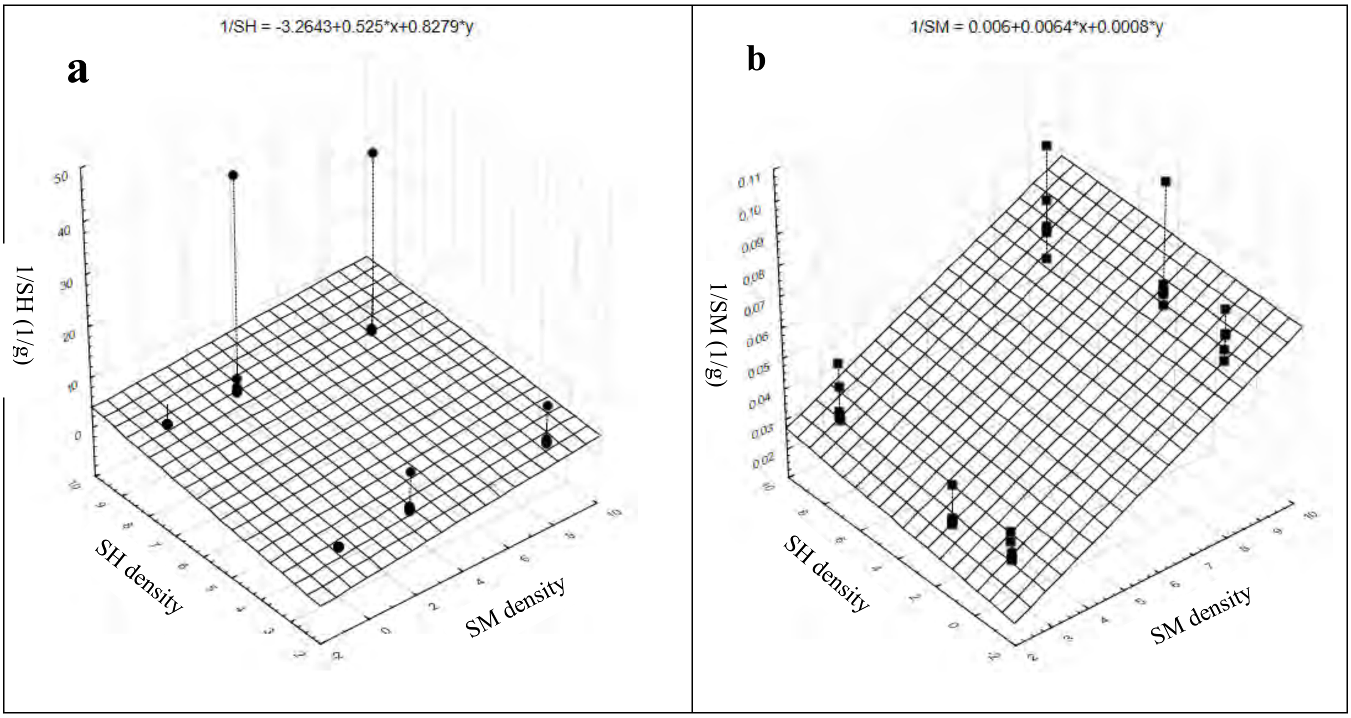

Figure 5.1.: Multiple regression plane indicating the combined effect of *Salvinia hastata* (SH) and *Salvinia molesta* (SM) on the reciprocal of the mean wet weight: (a) on *Salvinia hastata* (1/SH); (b) on *Salvinia molesta* (1/SM). Points indicate observations (n=30) and vertical lines between data points represent the residual value. Values on X and Y axes represent *S. hastata* and *S. molesta*, respectively for planting densities at the start of the experiment.

The relative growth rates of *S. hastata* and *S. molesta* were significantly affected by competition at different planting densities ($F_{(5,48)} = 11.26$, $P < 0.001$) (Figure5.2 and Table 5.4). *Salvinia hastata* planted in monoculture at low density (3:0) acquired a significantly higher growth rate of 0.076 g/day compared to high density monoculture (9:0) of 0.065 g/day. This could be explained by the influence of intraspecific competition. When planted in combination with *S. molesta*, growth rates of *S. hastata* were significantly reduced especially in the 9:3 treatment with a growth rate approaching zero (0.02 g/day).

The growth rate of *S. molesta* in monoculture at low density (3:0) was also significantly higher than the growth rate at high density (9:0) (0.064 g/day vs. 0.031 g/day, respectively). The growth rate of *S. hastata,* at a low density (3:3) and at high density combination (9:3), was significantly lower than the growth rates of *S. molesta* at the same planting densities (Fig.5.2).

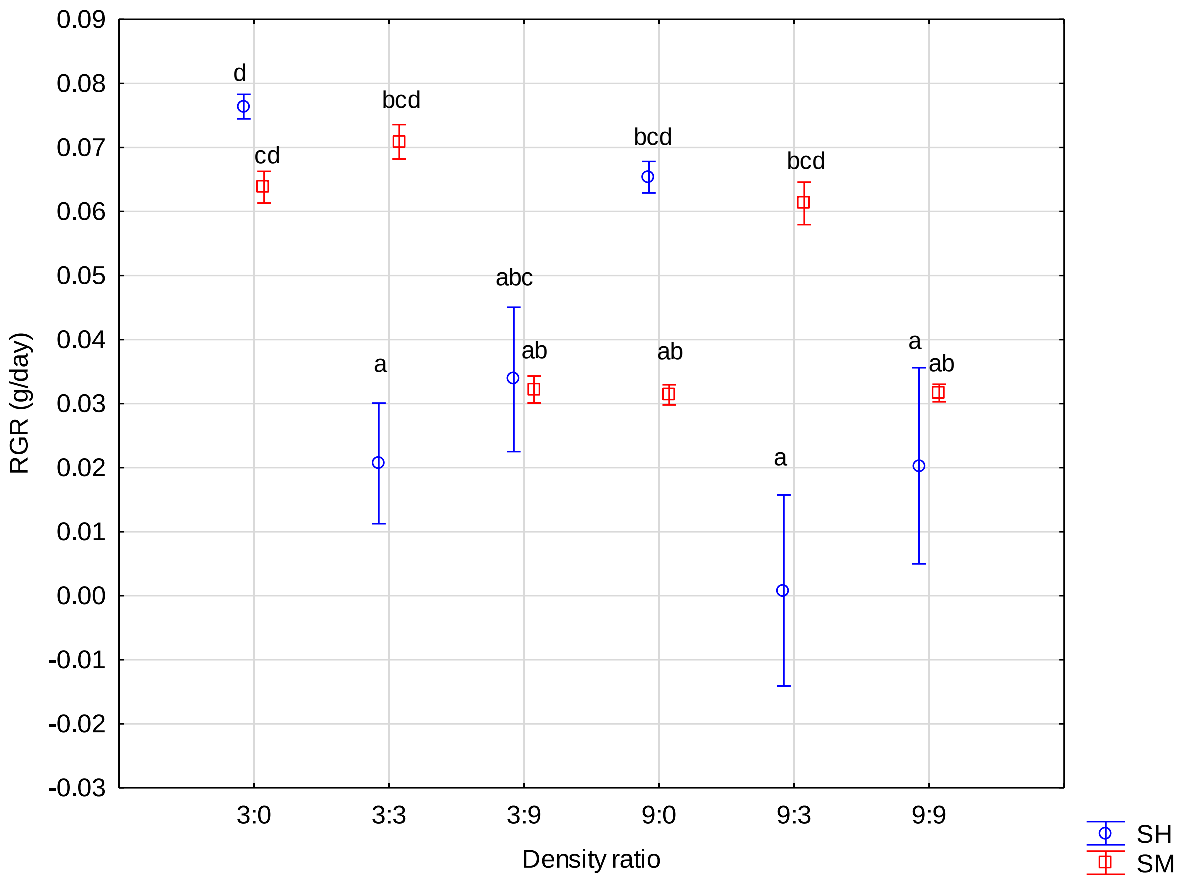

Figure 5.2.: Relative growth rate (RGR) of *Salvinia hastata* (SH) and *Salvinia molesta* (SM) at initial planting density ratios. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, $P<0.05$).

Table 5.4.: Factorial ANOVA analysis of relative growth rate (RGR) related to competition between *Salvinia hastata* and *Salvinia molesta*

Effect	**SS**	**Degrees of Freedom**	**MS**	**F**	***P***
Intercept	0.107723	1	0.107723	361.3733	0.0001
Density ratio	0.013012	5	0.002602	8.7303	0.0001
Species	0.002276	1	0.002276	7.6338	0.0081
Density ratio*Species	0.016780	5	0.003356	11.2580	0.0001
Error	0.014309	48	0.000298		

5.4.2 Competition between *Salvinia hastata* and *Pontederia crassipes*

Pontederia crassipes was 24 times more competitive than *S. hastata*, meaning that 24 individuals of *S. hastata* were needed to have the same competitive ability as an individual *P.*

crassipes (Table 5.2). The interspecific competition coefficient indicated that competition from *S. hastata* was almost negligible, which allowed *P. crassipes* to be highly competitive over *S. hastata*. The regression models for both, *S. hastata* and *P. crassipes* were significant ($F_{(2,27)}$ = 13.22 (*P*<0.05) (Table 5.3).

The three-dimensional graph of *S. hastata* yield supports these results, indicated by a fairly steep slope, implying significant effects of both intra- and interspecific competition with high constants ($F_{(2,27)}$ = 4.96), P<0.05) (Table 5.3; Figure 5.3). On the other hand, the slope for interspecific competition on *P. crassipes* is flat, as indicated by the small values of the coefficient for interspecific competition. The interspecific coefficient is almost negligible indicating that competition from *S. hastata* had a negligible effect on the yield of *P. crassipes*.

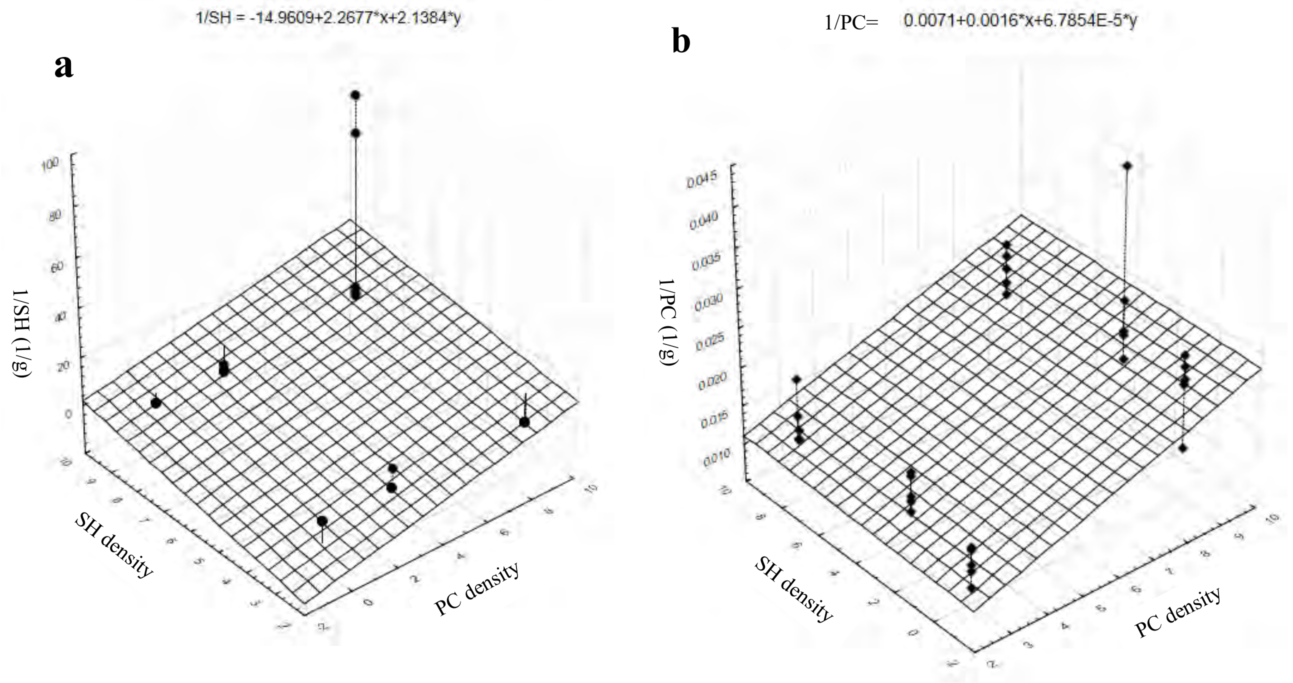

Figure 5.3.: Multiple regression plane indicating the combined effect of *Salvinia hastata* and *Pontederia crassipes* on the reciprocal of the mean wet weight: (**a**) on *Salvinia hastata (1/SH)*; (**b**) on *Pontederia crassipes* (1/PC). Points indicate observations (n=30) and vertical lines between data points represent the residual value. Values on X and Y axes represent *S. hastata* and *P. crassipes,* respectively for planting densities at the start of the experiment.

The relative growth rates of *S. hastata* and *P. crassipes* were significantly affected by competition at different planting densities ($F_{(5,48)}$ = 63.6, *P* < 0.0001) (Table 5.5). In monoculture, the relative growth rate of *S. hastata* was slightly higher (0.076 g/day) at low planting density (3:0), compared to those (0.065 g/day) at high density (9:0). When planted in association with *P. crassipes*, relative growth rates were significantly reduced at all densities especially with high densities of both species (9:9) procuring a negative relative growth rate (-0.02 g/day) (Figure 5.4). This means that the competition negatively affected the relative growth rate of *S. hastata*. Some individuals of *S. hastata* degenerated and eventually died by the end of the experiment.

In monoculture, the relative growth rates of *P. crassipes* were similar at both planting densisites, 0.024 g/day at 3: 0, and 0.017 g/day at 9:0. The presence of *S. hastata* did not significantly affect the relative growth *of P.crassipes* (Figure 5.4). This implies that the association with *S. hastata* did not have a great influence on the growth rate of *P. crassipes*, rather intraspecific competition was more important.

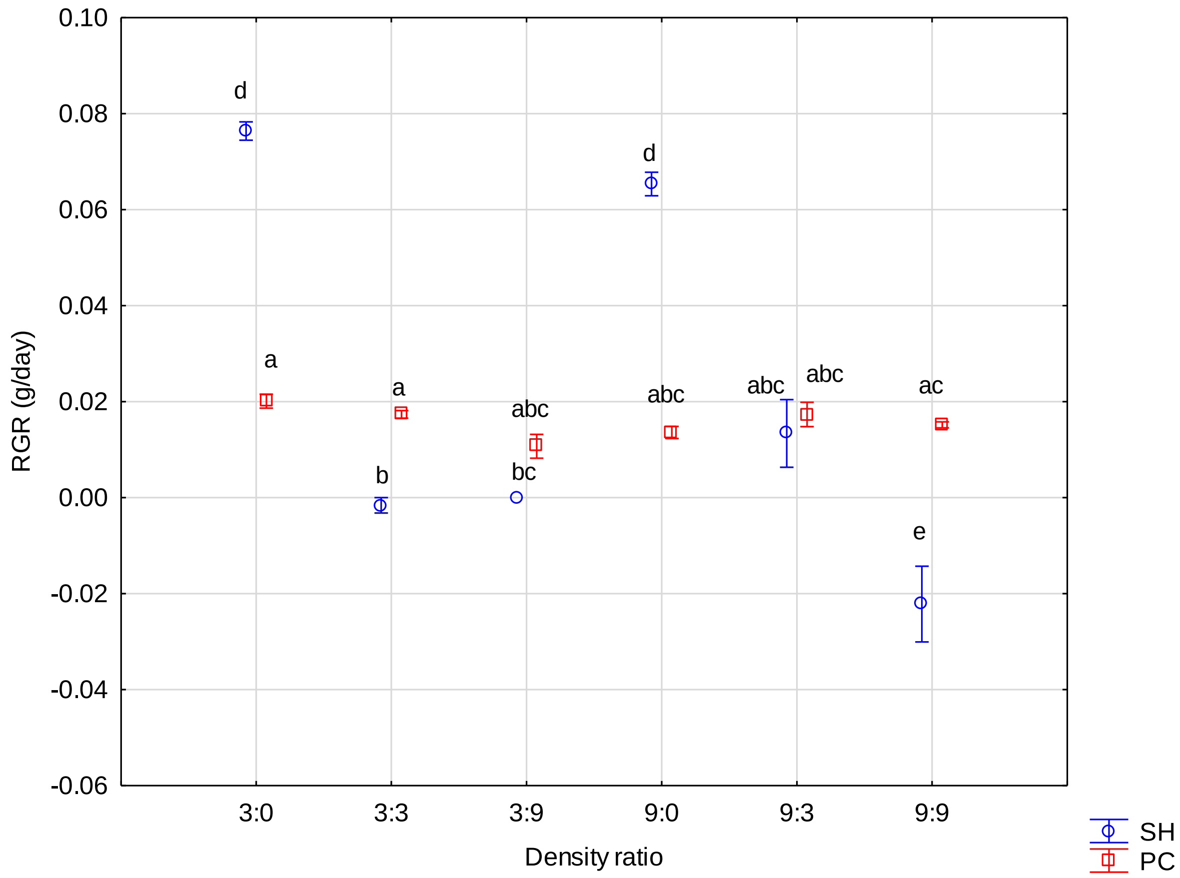

Figure 5.4.: Relative growth rate (RGR) of *Salvinia hastata* (SH) and *Pontederia crassipes* (PC) at select ratios of planting density. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, *P*<0.05).

Table 5.5.: Multiple regression analysis of relative growth rate (RGR) related to competition between *Salvinia hastata* and *Pontederia crassipes*

Effect	Degrees of Freedom	SS	MS	F	*P*
Intercept	1	0.021220	0.021220	359.9890	0.000000
Density ratio	5	0.021035	0.004207	71.3699	0.000000
Species	1	0.000572	0.000572	9.7027	0.003101
Density ratio*Species	5	0.018747	0.003749	63.6080	0.000000
Error	48	0.002829	0.000059		
Total	59	0.043183			

5.4.3 Competition between *Salvinia hastata* and *Pistia stratiotes*

Pistia stratiotes was 12 times more competitive than *S. hastata* (Table 5.2). The regression model for *P. stratiotes* was significant, indicating a suitable fit, however, that of *S. hastata* was not significant (Table 5.3).

The three-dimensional plane of *S. hastata* yield showed a fairly flat slope for intraspecific competition, indicating that it did not significantly affect the yield of *S. hastata* ($F_{(2,27)}$ = 2.92), P>0.05) (Table 5.3). The interspecific competition coefficient is almost twice that of the intraspecific coefficient, meaning that the competitive effect exerted by *P. stratiotes* has a larger influence on the reduction in yield of *S. hastata*. On the other hand, intraspecific competition had a significant effect on the reduction in the yield of *P. stratiotes* ($F_{(2,27)}$=13.89, P<0.05), while that for *S. hastata* had negligible influence on the yield of *P. stratiotes,* as indicated by the flat slope of the regression plane.

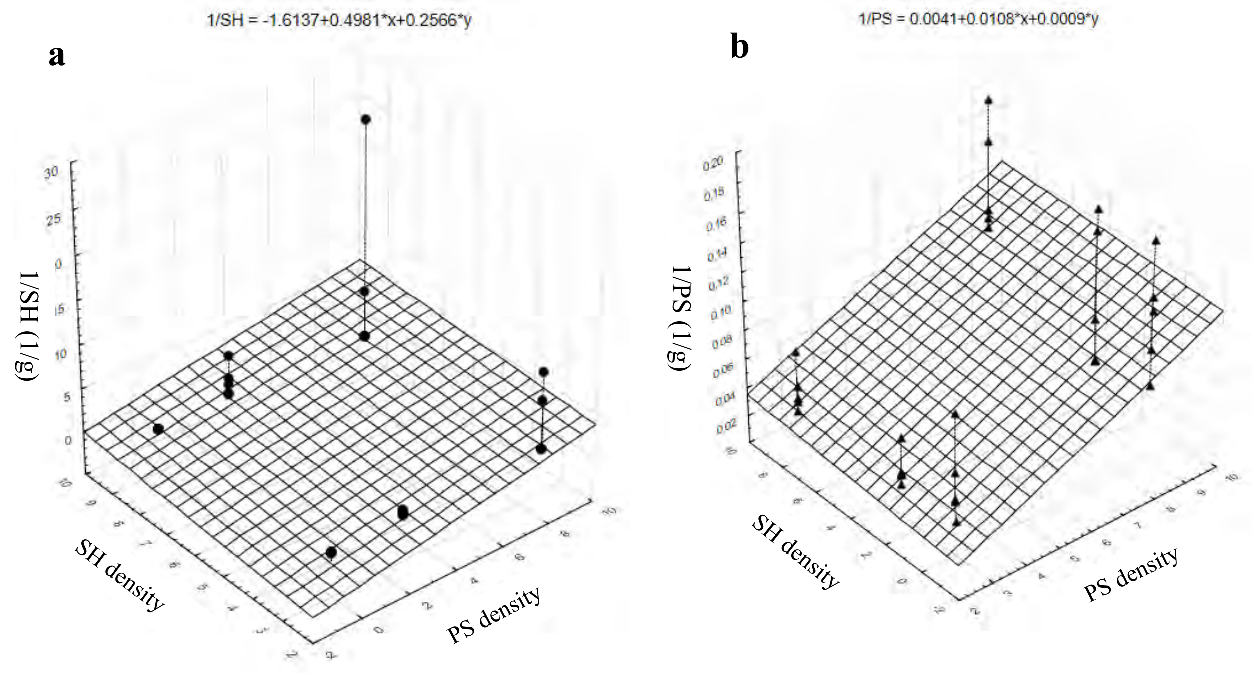

Figure 5.5.: Multiple regression plane indicating the combined effect of *Salvinia hastata* and *Pistia stratiotes* on the reciprocal of the mean wet weight: (**a**) on *Salvinia hastata (1/SH)*; (**b**) on *Pistia stratiotes* (1/PS). Points indicate observations (n=30) and vertical lines between data points represent the residual value. Values on X and Y axes represent *S. hastata* and *P. stratiotes,* respectively for planting densities at the start of the experiment.

The relative growth rates of *S. hastata* and *P. stratiotes* were significantly affected by competition at the different planting densities ($F_{(5,48)}$ =32.11, $P<0.0001$) (Table 5.6). In monoculture and at low density (3:0), *S. hastata* had a growth rate of 0.076 g/day compared to 0.065 g/day at high density (9:0). When planted in combination with *P. stratiotes*, relative growth rates of *S. hastata* were significantly reduced at all densities, but especially at high density of both species (9:9) where the growth rate became negative (-0.005 g/day) (Fig.5.6). This indicates that competition adversely affected the growth of *S. hastata*. Similarly, as was the case of *P. crassipes* treatment, some individuals of *S. hastata* died at the end of the experiment.

In monoculture, the growth rates of *P. stratiotes* were also very close to each other at planting densities of 3:0 and 9:0, corresponding to relative growth rates of 0.020 g/day and 0.014 g/day, respectively. By adding three individuals of *S. hastata* at these planting densities, the growth rates of *P. stratiotes* were higher than in monoculture (Fig.5.6). This indicates that the relative growth of *P. stratiotes* was not affected by competition with *S. hastata*, but rather by competition between individuals of the species. At high planting density (9:9), like *S. hastata*, the relative growth rate of *P. stratiotes* was lower compared to those of monoculture.

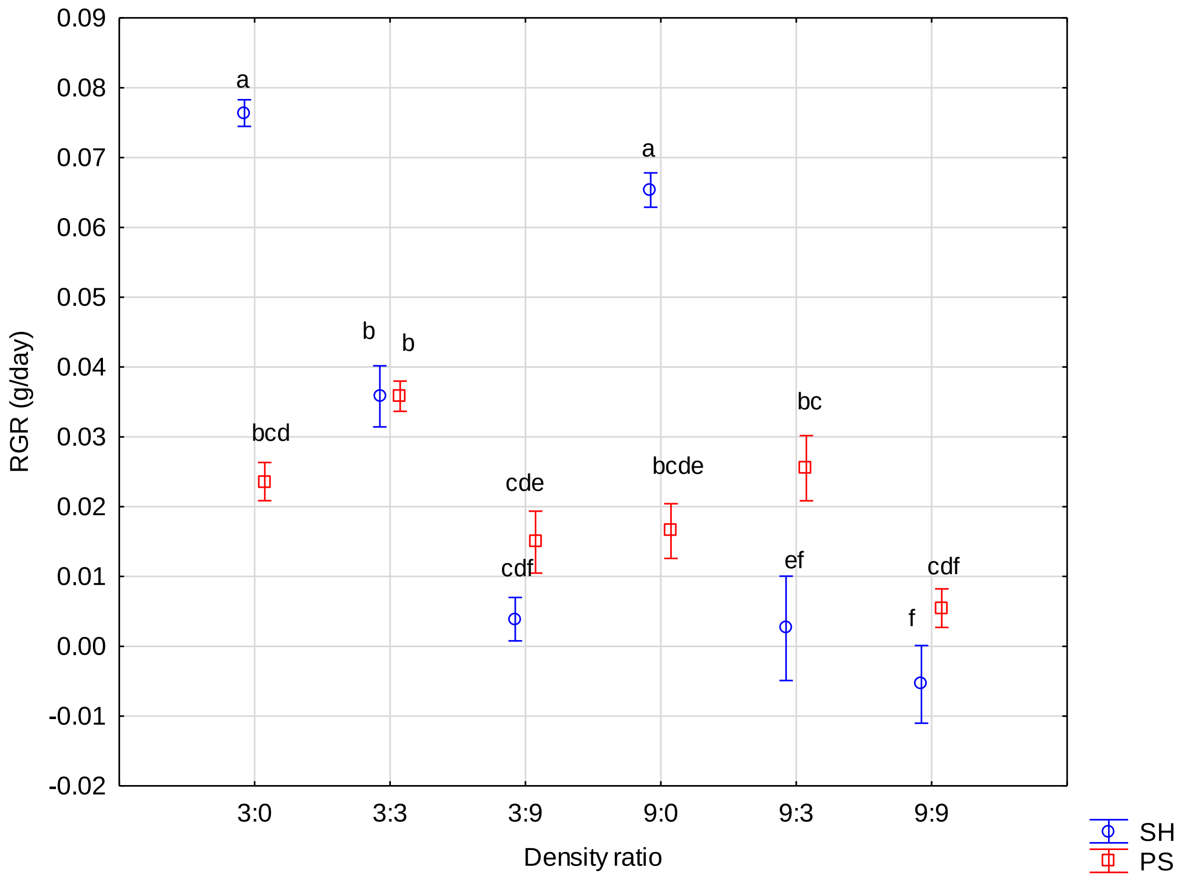

Figure 5.6.: Relative growth rate (RGR) of *Salvinia hastata* (SH) and *Pistia stratiotes* (PS) at select ratios of planting density. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, *P*<0.05).

Table 5.6.: Multiple regression analysis of relative growth rate (RGR) related to competition between *Salvinia hastata* and *Pistia stratiotes*

Effect	**Degrees of Freedom**	**SS**	**MS**	**F**	***P***
Intercept	1	0.037591	0.037591	446.7700	0.000000
Density ratio	5	0.019828	0.003966	47.1317	0.000000
Species	1	0.001341	0.001341	15.9390	0.000223
Density ratio*Species	5	0.013508	0.002702	32.1085	0.000000
Error	48	0.004039	0.000084		
Total	59	0.038716			

5.4.4 Competition between *Salvinia hastata* and *Azolla filiculoides*

In contrast to the other species, *A. filiculoides* was only 1.2 times more competitive than *S. hastata*. This indicates that overall, *S. hastata* and *A. filiculoides* have almost the same competitive performance with a slight advantage of around 20% for *A. filiculoides*. For *A. filiculoides*, the regression model was significant, indicating a suitable fit, however, that of *S. hastata* was not significant (Table 5.3).

The three-dimensional graph of yield of *S. hastata* showed a fairly flat slope for intraspecific competition, but a steep slope for interspecific competition, indicating that interspecific competition significantly affected the yield of *S. hastata* ($F_{(2,26)} = 14.56$, $P<0.05$) (Table 5.3). For *A. filiculoides*, the gradients for both axes were flat, meaning that both intra- and interspecific competition constants were similarly low, and not statistically significant for yield reduction of *A. filiculoides* ($F_{(2, 26)} = 0.44$, $P>0.005$) (Table 5.3, Figure 5.7).

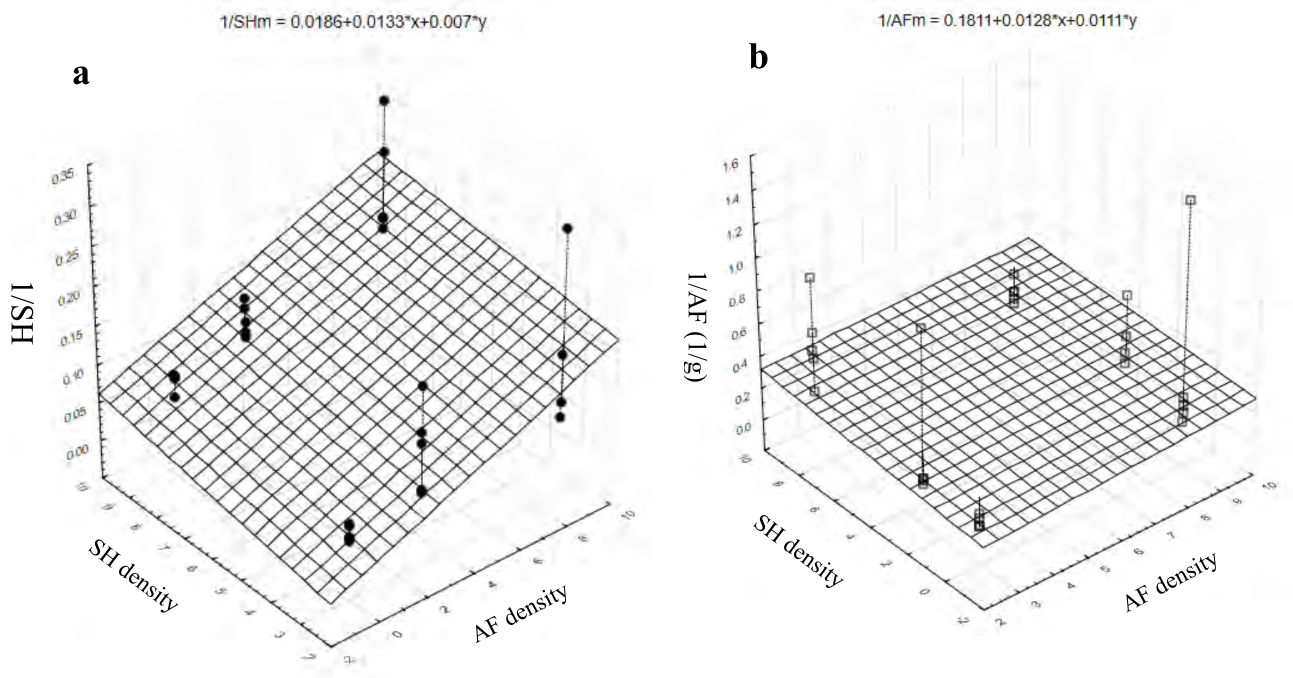

Figure 5.7.: Multiple regression plane indicating the combined effect of *Salvinia hastata* and *Azolla filiculoides* on the reciprocal of the mean wet weight: (**a**) on *Salvinia hastata (1/SH)*; (**b**) on *Pistia stratiotes* (1/AF). Points indicate observations (n=27) and vertical lines between data points represent the residual value. Values on X and Y axes represent *S. hastata* and *A. filiculoides,* respectively, for planting densities at the start of the experiment.

The relative growth rates of *S. hastata* and *A. filiculoides* were significantly affected by competition at different planting densities ($F_{(5,48)} = 7.616$, $P = 0.0002$) (Table 5. 7). Where *S. hastata* was planted as a low density monoculture (3:0), the relative growth rate was 0.076 g/day. This value increased to 0.087 g/day in association with a high density of *A. filiculoides* (3:9). However, if the competitor was planted at a low density, the relative growth rate of *S.*

hastata was reduced to 0.66 g/day. The relative growth rate of *S. hastata* was enhanced by the association with *A. filiculoides* which is a nitrogen fixer.

In contrast, the growth rates of *A. filiculoides* were lower when grown in association with *S. hastata* compared to monoculture. In monoculture and at low density (3:0), *A. filiculoides* had a relative growth rate of 0.089 g/day compared to 0.062 g/day at high density (9:0). When grown in association with *S. hastata*, the growth rates of both species were reduced except for the highest density (9:9) where the relative growth rate was close to that of the monoculture at the same density (0.064 g/day). Overall, competition did not significantly affect each species relative growth rates ($F_{(1,48)} = 0.037$, $P>0.005$) which was instead influenced by planting density ($F_{(5,48)} = 7.616$, $P<0.005$) (Table 5.7). It was deduced that interspecific interactions had a smaller effect on the relative growth rates of the two competitors, compared to densities, i.e. intraspecific competition was responsible for the reduction in relative growth rate. In the case of *S. hastata*, the presence of *A. filiculoides* even seemed to increase its relative growth rate.

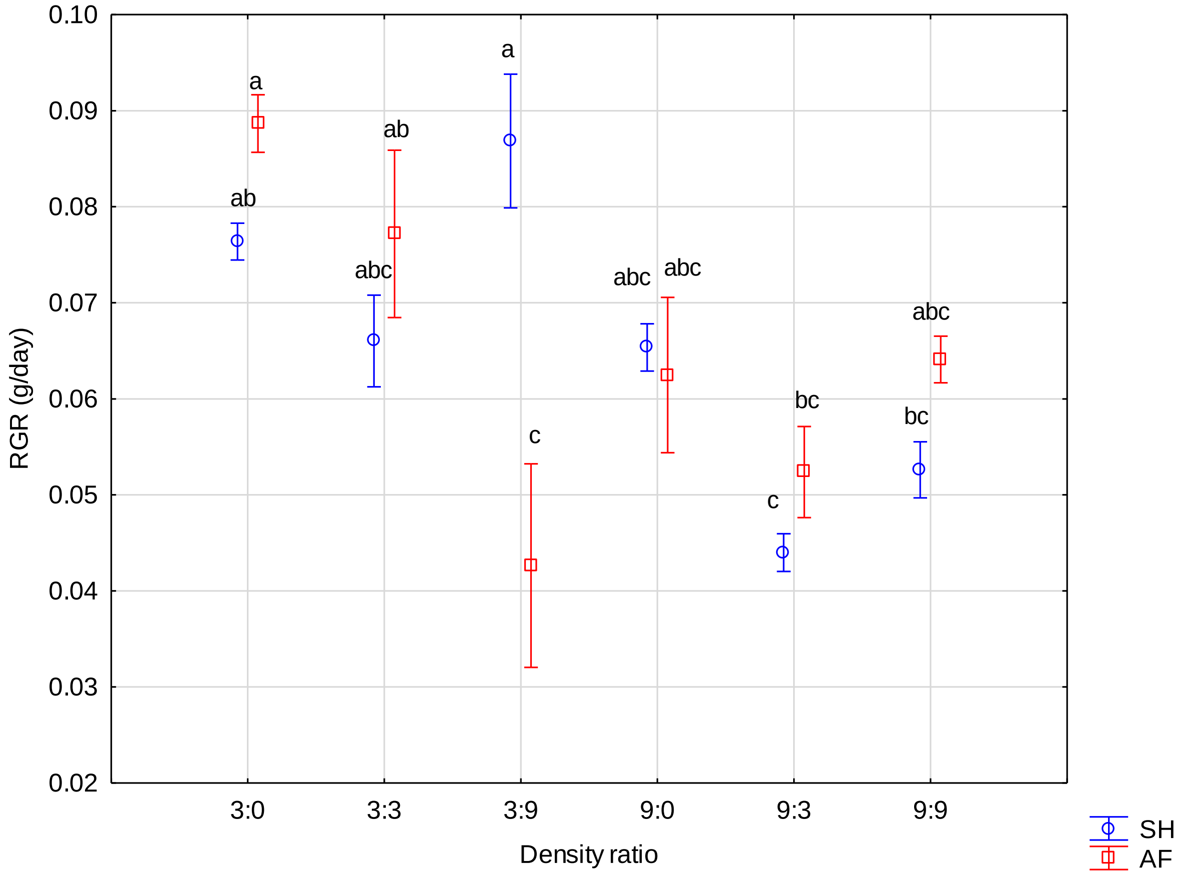

Figure 5.8.: Relative growth rate (RGR) of *Salvinia hastata* (SH) and *Azolla filiculoides* (AF) at select ratios of planting density. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, P<0.05).

Table 5.7.: Multiple regression analysis of relative growth rate (RGR) related to competition between *Salvinia hastata* and *Azolla filiculoides.*

Effect	**Degrees of Freedom**	**SS**	**MS**	**F**	***P***
Intercept	1	0.252613	0.252613	1578.493	0.000000
Density ratio	5	0.006786	0.001357	8.480	0.000008
Spp	1	0.000006	0.000006	0.037	0.847679
Density ratio*Spp	5	0.006094	0.001219	7.616	0.000025
Error	48	0.007682	0.000160		
Total	59	0.020567			

5.4.5 Comparison of the relative growth rates of *Salvinia hastata* in monoculture and in combination with the four invasive aquatic weeds

With the exception with *A. filiculoides* at density 3:9, the relative growth rates of *S. hastata* in association with the three other aquatic weeds were all significantly lower than in monoculture ($F_{(15,96)} = 8.12$, $P < 0.0001$) (Figure 5.9 and Table 5.8). At all planting densities, relative growth rates of *S. hastata* were higher with *A. filiculoides* compared with the other three invasive species. It is important to note that the relative growth rates of *S. hastata* were lowest in combination with *P. crassipes,* indicating that *P. crassipes* significantly reduced the relative growth rate of *S. hastata,* while growth rate increased in the presence of *A. filiculoides*.

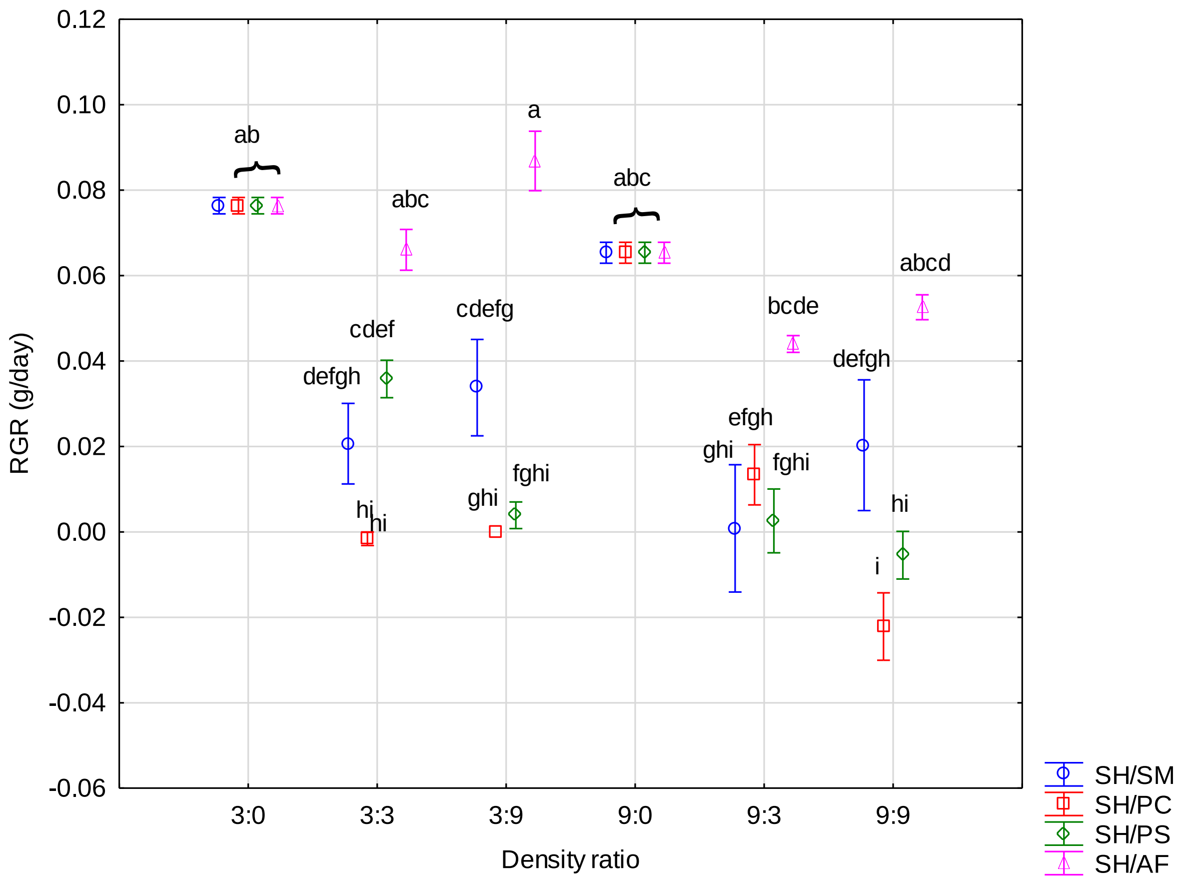

Figure 5.9.: Relative growth rates (RGR) of *Salvinia hastata* (SH) in combination with *Salvinia molesta* (SM), *Pontederia crassipes* (PC), *Pistia stratiotes* (PS) and *Azolla filiculoides* (AF) at select ratios of planting density. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, *P*<0.05).

Table 5.8.: Multiple regression analysis of the relative growth rates (RGR) of *Salvinia hastata* when grown in combination with four invasive alien aquatic species.

Effect	**Degrees of Freedom**	**SS**	**MS**	**F**	***P***
Intercept	1	0.175720	0.175720	822.8710	0.000000
Density ratio	5	0.071209	0.014242	66.6917	0.000000
Combo	3	0.032106	0.010702	50.1151	0.000000
Density ratio*Combo	15	0.026020	0.001735	8.1233	0.000000
Error	96	0.020500	0.000214		
Total	119	0.149835			

5.4.6 Comparison of relative growth rate of the competitors in monoculture and in association with *Salvinia hastata*

In all four invasive alien aquatic species treatments, the relative growth rates varied significantly from each other ($F_{(15,96)} = 5.54$, $P < 0.0001$) (Table 5.9). With the exception of planting combination 9:3, the relative growth rates of *A. filiculoides* were consistently higher than *P. crassipes*, *P. stratiotes* and *S. molesta* (Figure 5.10). However, at this planting density ratio, the relative growth rates of *S. molesta* were slightly higher than that of *A. filiculoides*. At all planting density ratios, except 9:9, the relative growth rates of *P. crassipes* were always the lowest.

Analysis of the relative growth rates of each species, combined or in monoculture, indicated that the values were slightly higher in combination with *S. hastata* than in monoculture, except for *P. stratiotes* and *P. crassipes* at planting density ratios of 3:9 and 9:9, and at all *A. filiculoides* planting density ratios. It is deduced that the association with *S. hastata* did not induce any remarkable reduction in the relative growth rates of the invasive aquatic aquatic weeds, except for *A. filiculoides*.

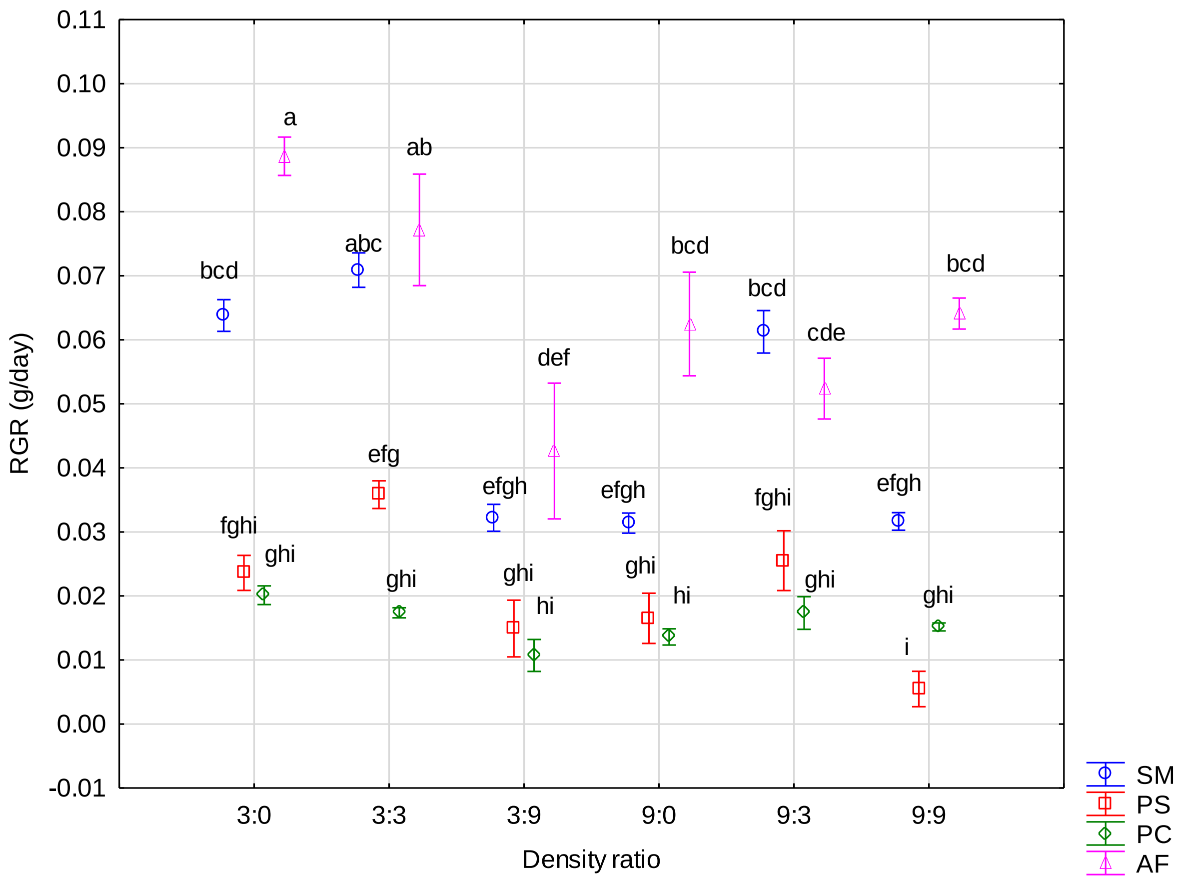

Figure 5.10.: Relative growth rates (RGR) of *Salvinia molesta* (SM), *Pontederia crassipes* (PC), *Pistia stratiotes* (PS) and *Azolla filiculoides* (AF) when grown in combination with *Salvinia hastata* (SH) at select ratios of planting density. Error bars represent S.E. Different letters represent significant differences (Tukey Post Hoc test, *P*<0.05).

Table 5.9: Multiple regression analysis of relative growth rates (RGR) of the four invasive alien aquatic species related to their competition with *Salvinia hastata.*

Effect	**Degrees of Freedom**	**SS**	**MS**	**F**	***P***
Intercept	1	0.166781	0.166781	1915.668	0.000000
Density ratio	5	0.011325	0.002265	26.017	0.000000
Spp	3	0.048735	0.016245	186.591	0.000000
Density ratio*Spp	15	0.007235	0.000482	5.540	0.000000
Error	96	0.008358	0.000087		
Total	119	0.075653			

5.5 Discussion

For all treatments in the current study, the invasive aquatic species were dominant competitors over *S. hastata*. *Pontederia crassipes* was 24 times more dominant, followed by *P. stratiotes* (12 times), then by *S. molesta* (8 times) and finally by *A. filiculoides* (1.2 times). The observation was made that when the level of competition, significantly influenced the biomass yield of *S. hastata*, interspecific competition was always more important compared to intraspecific competition. The nature of competition was trophic competition, i.e. competition for light, water and nutrients (Barbault, 1983; Nabors, 2008). Invasive species have a strong capacity for rapid nutrient acquisition, and efficient use of resources compared to native species (Fan *et al*. 2013; Zhou *et al.,* 2017). Joubert and Coetzee (unpublished data) measured competition between *S. molesta* and *S. minima* and showed that *S. molesta* was 65 times more competitive than *S. minima*. According to their analysis, the larger size of *S. molesta* gave it a dominance advantage over *S. minima* (Joubert and Coetzee, unpublished).

It was found in this study that the relative growth rates (RGR) of *S. hastata,* in association with *A. filiculoides,* were consistently higher compared to the other three invasive species. In addition, the influence of *A. filiculoides* was low in reducing the biomass yield of *S. hastata*. It is possible that the presence of *A. filiculoides* helped *S. hastata* through nitrogen fixation. According to the experiments conducted by Brouwer *et al.* (2017), *A. filiculoides* as well as *A. pinnata* can fix atmospheric nitrogen at rates up to 0.4 mg N/g of dry weight/h, increasing biomass by 0.33g/m^2/day. Although we didn't found the co-occurrence of *S. hastata* and *A. filiculoides* in the field, *S. hastata* does coexisted with *A. pinnata* in western Madagascar (Figure 5.11). Given the different climatic conditions and physico-chemical characteristics of the experimental area and native range of *S. hastata*, this could influence its competitive abilities with invasive species. In addition, the difference in nutrient content of water could also modify the performance of competing species. Research by Martin and Coetzee (2014) demonstrated that sediment nutrient levels significantly affected the competitive abilities of the South African native species *Lagarosiphon major* (Ridley) Moss (Hydrocharitaceae) and the invasive species *Myriophyllum specatum* Linnaeus (Haloragaceae). At high nutrient levels, *L. major* was 2.5 times more competitive that *M. spicatum* and produced more shoots, while in low nutrient concentrations, this competitive advantage disappeared.

During our field work, *S. hastata* and *P. crassipes* were found co-occurring in several places, for example at Lake Manompa (18°25′44.5″S 045°15′15.4″E), in the rural town of Ankijabe, Boeny region, and Lake Amparihely (16°07′25.2″S 047°36′48.7″E), in the municipality of Mampikony, Sofia region, at Lake Ravelobe, Ankarafantsika National Park (16°18'16.7″S 046°48'42.9″E), District of Marovoay, Boeny Region (Figure 5.12). These two species have been reported to co-occur at Lake Alaotra (Ranarijaona, 2007). So far, no other case have been reported where there was coexistence between *S. hastata* and *P. stratiotes, S. molesta* and *A. filiculoides*. However, these invasive alien aquatic species are highly mobile and we have shown that their distribution and abundance has increased over the last 10 years, and thus their potential impact on the indigenous *S. hastata* is high.

Recent research undertaken on aquatic biodiversity in Madagascar found that out of 489 aquatic macrophytes recorded from Madagascar, 114 species occurring in lentic habitats were threatened to the point of extinction due to competition for light and nutrients with invasive alien aquatic weeds (Manjato *et al.*, 2020, Manuscript in preparation).

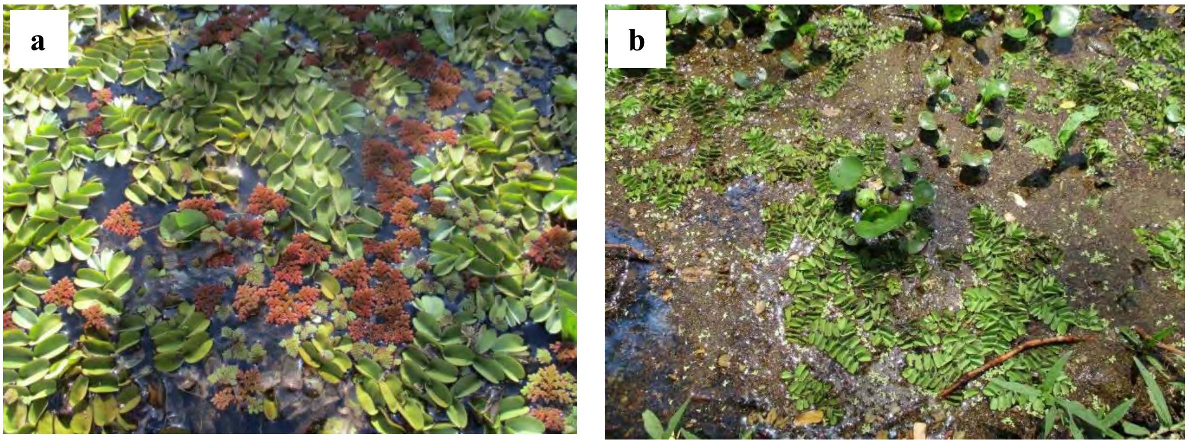

Figure 5.11.: Co-occurrence of species: (a) *Salvinia hastata* and *Azolla pinnata* at Ampombibe, rural commune of Tsiningia, District of Port-Bergé, Madagascar; (b) *Salvinia hastata* and *Pontederia crassipes* at Lake Ravelobe, Ankarafantsika National Park, Madagascar.

This research revealed that the four target aquatic weeds outcompeted *S. hastata* and all of them are well adapted to the different bioclimates of Madagascar (Chapter 2). Hence, their invasive potential remains an imminent threat to the aquatic biodiversity of Madagascar. To reduce the risk posed by aquatic weeds to the biodiversityof the systems that they invade, an area-wide integrated control strategy is required, which is described in Chapter 6. As part of the integrated management of aquatic weed infestations, research has demonstrated the benefit of using biological agents to reduce the competitiveness of aquatic weeds. For example, Joubert and Coetzee (unpublished data) found that without biological control, *S. molesta* was 65 times more competitive over *S. minima* and when using *Cyrtobogous salviniae* as biological control agent of *S. molesta*, this competitive ability was reduced to just 4.5 times. In the context of the present study, it would be interesting to engage in research which incorporates not only the competition between the four aquatic weeds and *S. hastata*, but also the integration of effective biological control agents (see Hill and Coetzee, 2017) following the same technical protocol developed by Spitters (1983).

Chapter 6: General Discussion

6.1 Introduction

In Madagascar, the framework document concerning the national strategy and action plans for the conservation of biodiversity considers issues relating to the impacts of biological invasions on all sectors of economic activity (Rabarison *et al.,* 2015). As aquatic weed invasions affect several sectors, including agriculture, continental fishing, and the environment, it is important to consider action plans aimed to mitigate them. All these issues are addressed in objective 9 of the national strategy (Rabarison *et al.,* 2015). For the agricultural sector, Madagascar's vision was defined by the Ministry of Agriculture, Livestock and Fisheries (MAEP) "*Towards food self-sufficiency and the emergence of a modern agricultural sector*", aiming among others, to achieve self-sufficiency in rice and protein (Ranarivelo, 2020).

The research presented in this thesis contributes to these sectorial action plans in the following ways:

1. The National Strategy and Action Plans for the conservation of biodiversity in Madagascar underlines the need for deeper knowledge on invasive species in Objective 9: "*By 2025, exotic and/or invasive species as well as the routes of introduction are identified and prioritized, priority species are controlled or eradicated; management measures are in place to prevent the introduction, manage entry routes and mitigate the establishment of these species and to enhance useful species*" (Rabarison *et al.,* 2015). This aligns with the Convention on Biological Diversity (CBD), Target 9 of the Aichi conference (Coates, 2016). More precisely, Madagascar's working document highlights the importance of research through an inventory program on invasive species in order to ensure full protection of natural ecosystems and to enhance utilisation of invasive species for socio-economic development (Rabarison *et al*., 2015).

2. For the agricultural sector (agriculture and fishery), the policy for implementing priority actions is based on the participation of partners, including research organizations to develop the sector (Ranarivelo, 2020).

In this general discussion, each part of the study is placed into a regional and global context. The results of the research presented in each chapter are used to contribute to a strategy for the long-term and effective management of invasive aquatic plant species in Madagascar.

6.2 Mapping invasive species

Mapping is one of the first stages in an integrated management plan for aquatic weeds as it is important to know what is there, where it is, and how much is there. The information provided from this study provides a starting point for site-specific actions for invasive aquatic species. The study describes the habitats, distribution and a brief description of the respective level of each infestation of the four target species *Pontederia crassipes* Mart. (Pontederiaceae), *Salvinia molesta* D.S. Mitch.) (Salviniaceae), *P. stratiotes* L. (Araceae) and *A. filiculoides* (Chapter 2). The study revealed that the four species grew in all bioclimates of Madagascar, except apparently in the montane bioclimate where there are no records for any of the species.

At the beginning of the 2000s, *S. molesta* was only present in a few lakes (Binggeli, 2003b), but this species has spread widely across the island causing significant negative socio-economic and environmental impacts (Chapter 3). Similarly, Raharinaivo (2012) classified *A. filiculoides* to be at Stage 2 of the invasiveness scale, i.e. "*moderately invasive species, spreading but still occur at low densities and are not considered an immediate problem*", but the weed is also now widespread and damaging. One of the reasons why these species appear to have spread very quickly, is that for several years they were not correctly identified being confused with look-a-like native relatives (*S. molesta* which was confused with *Salvinia hastata* Desv. (Salviniaceae) and *A. filiculoides* with *Azolla pinnata* R. Br. (Azollaceae). According to Wild (1961): "*One of the major problems in the fight against aquatic invasive plants in Africa, as in the rest of the world, is that infestations of particular species often spread alarmingly before the danger happens. This may be due to the fact that the botanical identity of the plant is not known soon enough, or because it is not recognised that the plant is a potential hazard as a pest*". On Lake Victoria, in Tanzania, *P. crassipes* was not identified properly for a long time, and people transferred the plant from one place to another before the dangers related to the species were later recognised (Mumma, 1999). Currently, the target species have not yet reached all suitable areas for their growth and they continue their expansion. Hence, it is important to reiterate that further study, based on modelling the suitable areas for invasion in the next twenty years, is essential to inform a proactive management approach for these species.

6.3 Socio-economic impacts

Quantifying the impacts of invasive alien species is important for decision making in various domains. A country must have reliable socio-economic, health and environmental impact information concerning invasive species to justify decisions to invest in the fight against biological invasions, and especially when addressing the social involvement of stakeholders in the management of invasive species (Reaser *et al.,* 2007; Binimelis *et al.,* 2014; Crowley *et al.,* 2017; Epanchin-Niell, 2017). Several sectors of activity are affected by these biological invasions, such as fisheries, agriculture, infrastructure, tourism, human health, ecosystem functioning and biodiversity (Born *et al.,* 2004; Reaser *et al.,* 2007). The socio-economic impacts of Invasive Alien Species (IAS), although difficult to assess, are crucial to understand how to adequately address the problems they cause (Reaser *et al.*, 2007).

For inland fisheries, the first action plan in the framework document of Madagascar's biodiversity conservation launches a call as "*carrying out studies and completing the information and data necessary to improve fisheries management*". Responding to this call, the present study found that aquatic weed invasions caused a significant (82%) reduction in fish caught (Chapter 3). *Salvinia molesta* was ranked as the most troublesome species, followed by *P. crassipes*, in terms of negative impacts on fishing performance, by blocking canoe access to fishing areas and mats preventing the use of nets. This information illustrates the degree of threat that could occur throughout Madagascar, and that the invasion of aquatic weeds constitutes an impediment to the inland fishing industry. The situation on Lake Itasy and Lake Alaotra is alarming. These two lakes are currently infested by *S. molesta* and *P. crassipes* (Chapter 2). Lake Itasy, with an area of 3500 ha on the high plateau of Madagascar, supports 20% of all freshwater fishermen in Madagascar, with an annual production of 173 tons (for the year 2007) (Thierry and Vialle-Guerin, 2008). More investigation is needed to evaluate the current trend in fish production, because *S. molesta* was collected for the first time in Madagascar from this lake in 1995.

Lake Alaotra, with an area of 20,000 ha, ensures an annual production of 2000 tons (for the year 2004) and some 560,000 people live along its shores, a large number of whom fishermen (Andrianandrasana *et al.,* 2005). The impacts evaluated through the present study at the two study sites (Foulpointe and Soanierana-Ivongo, on the east coast of Madagascar) showed that the invasions of *P. crassipes* and *S. molesta* are responsible for fish and freshwater shrimp production decreasing by 82%. When referring to these results, if no action is taken in the short- to medium-term, aquatic weed invasion could lead to a shortage of fish in Madagascar. On Lake Alaotra, the impacts of invasion were studied by Rakotoarisoa *et al*. (2015) who found a decrease in space for fishing due to the area occupied by the aquatic weeds, a reduction in fish catches due to waterway clogging and a destruction of fish nets by thick mats of water hyacinth. This has been confirmed at the two study sites (Foulpointe and Soanierana-Ivongo) where freshwater fish have become increasingly rare, difficult to find and prices have increased over time (Chapter 3). The consequence of a much-reduced fish industry would contribute to the poverty of a half-million rural Malagasy households whose livelihoods depend directly on this activity (MPRH, 2013).

Several cases are known from Africa that show the impacts of aquatic weeds on fisheries. For example, in Benin it was reported that during the height of its water hyacinth invasion, the annual income from fishing dropped from US$ 1984 to US$ 607 per person, a 69% decrease (De Groote *et al.* 2003). For the rice sector, it was found through this study that aquatic weeds generated a significant decrease in rice yield of 30% and an additional expense for cleaning rice plots of US$ 794/ha. The situation is worrying for Madagascar, given that self-sufficiency in rice production still remains a national priority (Ranarivelo, 2020), and the invasions of aquatic weeds could jeopardize the achievement of this goal. Currently, Lake Alaotra, which is the largest rice granary in Madagascar, is in a critical situation because *P. crassipes* and *S. molesta* have already invaded part of the lake (Ranarijaona, 2007; Rakotoarisoa *et al.,* 2015). Several rice growers in this region have complained about the invasion of rice fields by aquatic weeds (Rakotoarisoa *et al.,* 2015). *Pontederia crassipes* has also arrived on the plain of Marovoay, which is the second largest granary in Madagascar (Chapter 2). Lake Alaotra, with a rice-growing area of 82,000 ha, produces 180,000-210,000 tons/year of paddy with an average yield of 2.5 tons/ha, while the plain of Marovoay, with an area of 40,000 ha can produce 70,000-80,000 tons/year of paddy, with an average yield varying from 2-2.8 tons/ha (Droy, 1998). Considering the damage cost of 30% of the invasion of aquatic weeds for rice growing, and the additional expenses of control of US$ 794/ha, aquatic weed invasions will not only affect rice yield and but also increase production costs. On Lake Alaotra, Rakotoarisoa *et al.* (2015) reported that floating mats of water hyacinth moved around by winds, invaded rice fields, inhibiting germination of rice, interfering with rice harvest and suppressing the rice crop. In Bangladesh, a similar situation occurred where annually, rafts of water hyacinth weighing up to 300 tons/ha, stopped rice germinating after floods receded (NAS, 1976).

During the present study, the economic impacts caused by *A. filiculoides* were not studied. However, in South Africa, McConnachie *et al.* (2003) reported that the species caused a decrease in the quality of drinking water (bad odours, change of color, increase in water-borne diseases), obstruction of water pumps used for irrigation, slowing of water flow in irrigation canals, and reduction in leisure activities (fishing, swimming and water-skiing).

6.4 Environmental impacts

The environmental impacts of aquatic weed invasions are seldom quantified (Hill and Coetzee, 2017). Through this study, it was demonstrated that the invasion of these four aquatic species, in particular in Foulpointe where *S. molesta* and *P. crassipes*, significantly modified the functioning of the ecosystem and were partly responsible for the local disappearance of endemic species such as *Paratilapia* sp. (*zavaviantsohy* or *fony*), an unidentified species locally known as *laokalava*, and the reduction in the abundance of several other species of fish and shrimps (Chapter 3). A similar case was reported from Lake Ravelobe (Ankarafantsika National Park) where, following invasions of *P. crassipes*, some native species of fish (*Paratilapia polleni* Bleeker (Cichlidae), *Paretroplus kieneri* Arnoult (Cichlidae), and *Paretroplus maculatus* Kiener and Maugé (Cichlidae)), were no longer seen in the lake, while the introduced tilapia remained present (Sparks, 2011). In Lake Ravelobe, other species of fauna were also threatened by the invasion of *P. crassipes,* like the freshwater turtle *Erymnochelys madagascariensis* Grandidier (Podocnemididae), and the birds *Haliaetus vociferoides* Des Murs (Accipitridae), *Butorides striatus* L. (Ardeidae) and *Amaurornis olivaceus* Meyen (Rallidae) (Ranarijaona *et al*., 2013).

At Lake Alaotra, in a similar study, the waterfowl *Anas melleri* P.L. Sclater (Anatidae), *Anas hottentota* (Eyton) (Anatidae) and *Anas erythrorhyncha* Gmelin (Anatidae), and the critically endangered Alaoatran bamboo lemur, *Hapalemur alaotrensis* Rumpler (Lemuridae) were considered to be threatened by the invasion of water hyacinth (Andrianandrasana *et al.,* 2005; Ranarijaona, 2007). Although the impacts *A. filiculoides* were not well documented at invaded natural sites, compared to the three other species, FCBN (2012) considered this weed to cause significant negative impacts on biodiversity and on the functioning of the aquatic ecosystem. In Zimbabwe, *A. filiculoides* is responsible for reducing populations of Gastropoda, Odonata, Hemiptera, Coleoptera, Diptera, tadpoles and fish in invaded streams (Gratwicke and Marshall, 2001).

The competition trials between *S. hastata*, which is a native species in Madagascar, and the four aquatic invasive species showed that the latter were strong competitors. *Pontederia crassipes* was 24 times more competitive than *S. hastata*, followed by *P. stratiotes* (12 times), *S. molesta* (8 times) and *A. filiculoides* (1.2 times) (Chapter 5). These results demonstrated the degree to which native aquatic plant species are vulnerable to invasions by alien aquatic weeds.

In the present study, research concentrated on a few taxonomic groups of fauna (fish, shrimp) and a single plant species, namely *S. hastata*. It is strongly recommended that further studies be undertaken for other taxonomic groups. The freshwater Key Biodiversity Area (KBA) (Máiz-Tomé *et al.* 2018) and Ramsar sites (https://fr.wikipedia.org/wiki/Liste_des_sites_Ramsar_%C3%A0_Madagascar) might be proposed as a starting point to be considered where appropriate management of aquatic weeds should be focused. The results of this study will help in defining a strategic plan for the management of infestations at the local, regional and national levels.

6.5 Risk assessment analysis

Before proposing control strategies for invasive species, it is important to know the degree of invasiveness and to classify them to inform strategic planning at national and regional scales (Nel *et al.,* 2004). To achieve this objective, it is essential to have reliable information to be able to prioritise them and to consider a broad array of appropriate management actions simultaneously (Nel *et al.,* 2004). Achieving prioritization follows a long process to develop a Weed Risk Assessment (WRA) and conducting such analyses needs considerable information concerning the invasiveness, impacts, and potential distribution (Randall, 2000; Nel *et al.*, 2004; FAO, 2006; Fried, 2010; Branquart *et al.,* 2016). In addition to the information gathered by the investigator, the process should include workshops to access expert advice and leverage local knowledge for each of the species to be prioritised (Nel *et al.,* 2004).

Several methods can be used to assess the risks of an introduced species into a given territory, by scoring the species using well-defined criteria, with the approach proposed by Phelloung (1995) being the most widely used throughout the world (Gordon *et al.,* 2008). For such evaluation, most attention has been given to screening species for their invasive potential before their introduction to a given region in order to minimize the risk beforehand (Navarantham and Catley, 1986; Daehler and Carino, 1999). For post-border weed risk assessment, as in the case of four target species of this study, the recommended method should be based on the available quantitative data on ecosystem, socio-economic and health impacts as well as updated information on population dynamics for defining the potential spread (Batianoff and Butler, 2002, 2003; FAO, 2006; Holt *et al.,* 2006; Stohlgren and Jarnevich, 2009). In this case, classifying the invasive species to help in formulating a national plan for management is acceptable (Nel *et al*., 2004). Thorp and Lynch (2000) suggested that, for most species, rankings in such exercises should be seen as approximate rather than absolute.

In Reunion and Mayotte, Lavergne (2010, 2016) applied a simple assessment method by classifying invasive species into six categories according to their coefficient of invasiveness ranging from the most invasive species (coefficient 5), potentially invasive species (coefficient 2), up to species not yet documented (coefficient 0). In South Africa, Nel *et al.* (2004) used a much simpler approach by categorizing species *a priori* into two classes: "major invaders" (invasive alien species that are well-established, and which already have a substantial impact on natural and semi-natural ecosystems) and the "emerging invaders" (locally common/scarce and largely confined to human-modified habitats or disturbed areas (road, railside, habitation, plantation, arable, pastoral, wasteland and transformed).

Based on the weed risk-assessment criteria proposed by Nel *et al.* (2004), although no extensive calculation was carried out, rapid assessments based on available data on distribution (Chapter 2), impacts (Chapter 3), and invasiveness (Chapter 4), we classified three of the target species of this study as major invaders (*P. crassipes, S. molesta* and *A. filiculoides*). Since the classification criteria were mainly based on the degree of impacts on natural or semi-natural environments, *P. crassipes* is considered as having higher impacts than *S. molesta.* The latter was dominant in anthropized environments such as rice fields and aquatic transportation routes, although it does cause significant impacts in some natural lakes. Although *A. filiculoides* occupies a wide distribution throughout the island, its impacts on natural aquatic ecosystems were assessed as much lower compared to those of *P. crassipes* and *S. molesta*, as it is more prevalent in rice paddies with rare cases in natural aquatic ecosystems. *Pistia stratiotes* is classified as an "emerging invader" (localised & common/scarce) because its presence is very localised, especially on the high plateau, but it is sometimes abundant in bodies of water influenced by human activities, for example in transport canals, in lakes under the influence of agricultural activities (rice growing or other crops), and in water bodies close to habitations. In South Africa, all four species were classified as major invaders, with *A. filiculoides* and *P. crassipes* being classified as more invasive (widespread – abundant) compared to *P. stratiotes* and *S. molesta*, which were in the localised – abundant category (Nel *et al.,* 2004).

By applying the classification method proposed by Lavergne (2016), also based on the impacts on natural environments, we propose to attribute a coefficient of invasiveness of 3+ for *P. crassipes* and *S. molesta*, where invasive in anthropized environments which are disturbed by human activities (wasteland, secondary vegetation, crop lands, pastures, forest plantations, gardens, roadsides), but also present in certain natural environments (species qualified as emerging or potentially invasive in a natural environment); while *A. filiculoides* and *P. stratiotes* merit a coefficient of invasiveness 3 (invasive only in anthropised environments, with a moderate distribution and density, without direct threat to natural environments). In Reunion, by applying this method, *P. crassipes* and *P. stratiotes* were classified as category 5, with *S. molesta* as category 4 (Lavergne, 2010).

In Madagascar, Raharinaivo (2012) assigned three categories for the coefficient of invasiveness, where he assigned a level 3 for *P. crassipes "highly invasive species"*, 2 for *A. filiculoides "moderately invasive species"*, and a 1 for *S. molesta "potentially invasive species"*. Referring to this method of classification, our results agreed well with the class of *P. crassipes,* while *S. molesta* and *A. filiculoides* are considered more invasive than the levels proposed by Raharinaivo (2012). This is due to the rapid expansion of their populations over the past 10 years, i.e since Raharinaivo's publication. With respect to the Raharinaivo (2012) classification, we propose that the status of *S. molesta* should be changed from level 1 to level 3, to match the level as *P. crassipes,* while *A. filiculoides* should be kept at level 2.

6. 6 Utilisation of invasive species

Several types of uses have been found for the four weeds during the present research and they will be discussed. NAS (1976) argued that in developing countries, where access to resources to apply other control methods (chemical, mechanical, biological control) seems difficult, the use of biomass should be considered, allowing for the control of infestations and acting as a source of valuable finished products (fodder, fertilizer, biogas, handicrafts).

As livestock fodder, water hyacinth is commonly used on the highlands to feed zebus, pigs, ducks and geese. Fresh biomass is given to the animals without prior treatment. According to livestock farmers in this area, the plant is less palatable and less nutritious compared to other types of forage but due to the insufficient food for the animals, from May to November (the Malagasy dry season), it is estimated that 70 to 80% of the forage of the animals comes from water hyacinth. The scarcity of forage of other species is largely due to the invasion of aquatic weeds which occupy the spaces to the detriment of other species. On Lake Alaotra, *P. crassipes* is also valued as feed for pigs and geese, but the use is very limited (Rakotoarisoa *et al.,* 2015). Ranarijaona *et al.* (2013) also reported the use of water hyacinth for livestock feed at Lake Ravelobe (Ankarafantsika National Park).

Worldwide, water hyacinth is widely used as food for domestic animals and even wild animals (NAS, 1976; Edwards, 1980; Heuzé *et al*., 2015). The mineral content of water hyacinth is very high in all parts of the plant: 12% to 25% of dry matter for aerial parts, and up to 30% or more for the whole plant (Heuzé *et al*., 2015). According to Brocard *et al*. (2015), the protein levels of water hyacinth are comparable to those for concentrated for animal feed, such as soybean meal. The leaves of water hyacinth are particularly rich in protein when young (more than 20% of dry matter, occasionally over 30%) but the protein content decreases with age (Boyd, 1970). However, the stems are poorer in protein and as a result the whole plant (roots included) has a protein content in the 10-20% range (Heuzé *et al*., 2015).

The presence of calcium oxalate in water hyacinth can damage the digestive tract and decreases the nutritional value of the plant as livestock food (NAS, 1976; Edwards, 1980; Bolenz *et al*., 1990). The use of fresh biomass could lead to diarrhoea in animals (Hossain, 1959). However, a preliminary treatment of the plant makes it possible to improve its taste and nutritional quality. This treatment includes a process of pressing and ensiling the residue which is then washed with sorbic acid to eliminate the calcium oxalate crystals that cause irritation in the mouth and are responsible for the low palatability (NAS, 1976; Franceschi and Horner, 1980; Göhl, 1982; Bolenz *et al*., 1990). The silage can be mixed with carbohydrate and protein sources such as molasses, maize grain, rice straw, urea and soybean meal to give a good quality product (Heuzé *et al*., 2015). In remote areas, especially in developing countries, the technique of dewatering undertaken through the use of a simple pressing machine which can process up to 4 tons of chopped water hyacinth per hour, or using a solar drying system capable of dewatering 16-18 tons of water hyacinth in 36-120 hours (NAS, 1976). It is also recommended to mix water hyacinth biomass with other feeds (Chatterjee and Hye, 1938).

Azolla filiculoides offers a good prospect as an animal feed in Madagascar. An experiment carried out by Raoelina (1995) in Madagascar showed that chicken feed with 5% *Azolla* incorporation gave better yields for chicken growth, and a similar result was obtained by Basak *et al.* (2002) in Bangladesh. *Azolla* is rich in nutrients including protein, which constitutes 23-30% of dry matter (Lumpkin and Plucknett, 1982). Chemical analysis of *A. pinnata*, dried in the sun for 3 days, showed that it contained 88.80% dry matter, of which 21.4% was crude protein, 12.7% crude fibre, 2.7% ether extract, 16.2% ash and 47.0%

carbohydrate (Alalade and Iyayi, 2006). Thus, *Azolla* feed can be a valuable protein supplement for many animals such as ruminants, poultry, pigs, fish, rabbits and pigs (Hasan and Chakrabarti, 2009; Heuzé *et al*., 2015). However, the recommended incorporation rates depended on the animal: 5% for chickens, 10% for chicks, 10-15% for pigs and even up to 40% of the diet for pond-reared tilapia (Abou *et al.,* 2007; Alalade and Iyayi, 2006; Raja *et al.,* 2012; Hêdji *et al.,* 2014).

During our study we discovered two rice growers, one in Antananarivo and one in Foulpointe, who had already experimented with composting *S. molesta*, but after a simple trial, they decided to stop because of the low production yield. Apart from this, no information relating to the composting of the four target species was collected during the study. Rakotoarisoa *et al.* (2015) reported that at Lake Alaotra, 2% of farmers used *S. molesta* to make compost to improve rice fields. The use of fertilizers is much less in Madagascar compared to some of its neighbours, with usage rates of 5.2kg/ha of arable land in Madagascar, compared to 58.5kg/ha in South Africa and 235.3kg/ha in Mauritius (FAO, 2016; MAEP, 2019). To fertilize their plots, Malagasy farmers use different kinds of fertilizers such as chemical fertilizers (NPK, urea), farm manure, crop residues, green manure like *Azolla*, household waste, TAROKA (an organic fertilizer made from agricultural by-products and waste, mixed with a powerful bacterial concentrate), natural phosphates from the Barren Isles (hyper Barren), and guano from bats (Guanomad) (MAEP, 2006). Madagascar is not self-sufficient in fertilizer and to supplement the island's needs, around 25,000 tons of fertilizer are imported annually (MAEP, 2019). The price of these products continue to increase, for example, the price of NPK increased from Ar 1500 (US$ 0.88)[19] in 2008 to Ar2,600 (US$ 1.24) in 2010 (Renaud *et al.,* 2011). This is far from affordable for poor farmers with low agricultural incomes, restricting the use of fertilizers and the development of agriculture in general, resulting in a low yield of agricultural production (MAEP, 2019).

Composting using aquatic weeds has the potential to improve agricultural yields in Madagascar. The chemical analyses carried out by Guiral and Etien (1991) showed that *P. crassipes* exhibits high concentrations of nitrogen and, to a lesser degree, of phosphorus (mainly at the level of its leaf system). The potassium and calcium concentrations are substantial in *P. stratiotes*, more particularly associated with its root system. In *S. molesta*, the nutrient composition of the aerial and submerged fronds are very similar, and compared to the three

[19] Exchange rate taken from https://perspective.usherbrooke.ca/bilan/tend/MDG/fr/PA.NUS.FCRF.html

species included in this study, *S. molesta* has the lowest nutrient concentrations. Overall, Guiral and Etien (1991) found that dried plants of *P. crassipes,* compared to *P. stratiotes* and *S. molesta,* presented 1.5 and 1.7 times more carbon, 2.2 and 6.0 times more nitrogen and 2.1 and 4.3 times more phosphorus respectively. According to Almoustapha *et al*. (2008), water hyacinth contains, among other things, 9.93kg of total phosphorus, 6.27kg of Kjeldahl nitrogen per ton of compost. Composts from aquatic weeds improves soils for crops by providing plants with nutrients, modifying the soil's physical structure and increasing the microbiological activity of the soil. This offers good prospects for future exploitation of aquatic weeds to improve crop productivity, both on a small and large scale, especially in developing countries (NAS, 1976). The main barrier to developing this potential benefit is the very high water content of the aquatic weeds (*ca.*90%) which makes transportation to compost heaps very expensive and also tends to lead to anaerobic decomposition.

The use of aquatic weeds as green manure is another form of valorization with the aim of improving agricultural yields. In the highlands of Madagascar, some rice growers spread *A. filiculoides* in non-infested rice fields in order to restore soil fertility. In general, farmers recognise the role of aquatic weeds as a green manure. However, rice growers in the city of Antananarivo said if the plots are fully infested with aquatic weeds, especially *S. molesta*, the rice leaves grow too abundantly and few seeds are produced. Aquatic weed biomass can be used as green manure through simple process, the green plants are either applied to the soil as a surface mulch or they are ploughed under or buried by hand in shallow troughs (NAS, 1976). Since many Malagasy farmers are accustomed to fertilising rice plots with *A. pinnata* (Ranarijaona *et al*., 2010), the closely related *A. filiculoides* offers the highest agronomic potential and is likely to be valued by rice growers. The use of *Azolla* as a green manure has been shown to provide a superior nitrogen boost compared to that of nitrogen supplied in the form of urea (Schramm and Rakotonaivo, 1987). Worldwide, *Azolla* species including *A. filiculoides* are well known for their agronomic values as a source of nutrients while helping to improve soil structure (Lumpkin and Plucknett, 1980; 1982; Cagauan, 1999).

In Madagascar aquatic weeds are rarely used as raw materials for handicrafts, and during the study we discovered only a single group of women (of around ten members in Anjambamaho, Foulpointe) who valued water hyacinth for different craft products. The products were of a good quality and strength due to the characteristics of the hard and flexible water hyacinth fibre, and the resulting products could last 3-5 years (Keawmanee, 2015). Technically, after several months of use, we noticed that products finished with a varnish coat were more durable than those not protected in this way (see also Keawmanee, 2015). However, hand-weaving with water hyacinth (collection of raw materials, drying, weaving) requires a high investment of time. The high water content (around 90%) makes it difficult to transport the plant from harvesting areas to the site of production (Okoye *et al.,* 2000; Su *et al*., 2018). In addition to the difficulty of production, the market is very small, as the city of Toamasina is the only place where they sell their products. Finally, weavers are forced to set high selling prices compared to other products made from other raw materials. For example, a basket made from water hyacinth costs Ar40,000 (US$ 11.40), while the same product made from grey sedge, *Lepironia articulata* (Retz.) Domin (Cyperaceae) costs a quarter of the price, Ar10,000 (US$ 2.85). In a similar case on Lake Alaotra, Rakotoarisoa *et al.* (2016) reported that, despite greater investment in work to select, transport and dry water hyacinth compared to papyrus (*Cyperus madagascariensis* (Willd.) Roem. & Schult. (Cyperaceae)) (seven days vs three days) and the additional costs for the decoration of objects (23% more), there are some advantages of the former compared to the latter; the handicrafts are easier to assemble (33% less time), more robust products, higher quality, and have a sales price three times higher (US$ 2.25 vs. US$ 0.75). These authors also underlined the importance of substituting raw materials from water hyacinth for those of papyrus because the latter provides habitat and food for *H. alaotrensis*, a locally endemic and critically endangered lemur.

The market for products derived from water hyacinth is far too small to imagine that promoting exploitation could contribute to reducing infestations (UNEP, 2013), yet it could provide socio-economic benefits especially for the creation of employment. The products are innovative and potentially open to further improvement, thereby contributing to product diversification, especially for the tourism industry. For example, in Thailand, thousands of villagers rely on handicrafts made from water hyacinth for their livelihoods, and the weavers export 80% of what they make to Japan, USA, Hong Kong, Singapore, and Italy (Keawmanee, 2015). Similarly, in Nigeria, an entrepreneur makes handicrafts from water hyacinth and employs more than 300 women (https://www.africanews.com/2019/03/13/nigerian-entrepreneur-makes-handcraft-products-from-water-hyacinth/). In Madagascar, this sector deserves to be supported by the government so that families in invaded areas may derive at least some benefits. According to Rakotomalala (2014, cited in Rakotoarisoa, 2015), a collaborative initiative has been launched between the Government of Madagascar and the Indonesian Embassy to promote water hyacinth as a source of materials for handicrafts. This initiative should be continued by supporting, organizationally and financially, appropriate associations to find and access both national and international markets (Andriantseheno, 2007). The handicraft sector occupies an important place in Madagascar's economy as it employs approximately 2,000,000 people, contributing 15% of the country's gross domestic product (Rakotovelo and Gachie, 2011).

In nature, wastewater is likely to be contaminated with toxic substances - dangerous for both human health and the environment (Ali *et al*., 2020). These hazardous wastes, especially heavy metals, come from different sources, domestic, industrial, and agricultural (Suess and Huismans, 1984; MIA, 2017; Andriamananjara, 2019; Ali *et al*., 2020). During the study, only one case of aquatic weeds being used for water purification was encountered. This was in the village of Andrangazaha, where *P. stratiotes* was used to treat water in a well. Among the species studied, both *P. stratiotes* and *P. crassipes* are known to contribute to water purification and the phytoremediation of metals, with both these species being considered to be effective, aesthetically pleasing, low cost and an environmentally friendly technology for the remediation of potentially toxic metals from the environment (Ingole and Bhole, 2002; Ogunlade, 2002; Gupta *et al.,* 2012; Ali *et al.,* 2020).

In Madagascar, research has been undertaken to study the feasibility of wastewater treatment using *P. crassipes* (Mandimbinirina, 2013; Rajaonarivelo, 2013; MEEMF, 2017), however this has yet to be adopted. With the support of the GALANA Company in Toamasina, a laboratory experiment conducted by Mandimbinirina (2013) reported that after three weeks, water hyacinth, with a density of 190/m^3, eliminated the hydrocarbons. The experimental trials conducted by Tripathi *et al.* (2010) revealed high removal (> 90%) of different heavy metals (Fe, Zn, Cu, Cr, Cd, Hg), during a 15-day experiment using *P. crassipes* and *P. stratiotes,* with the former more effective than the latter. Similar results have been reported by Nayanathara and Bindu (2017) for the intensive purification of domestic sewage with high nitrogen concentrations. *Pontederia crassipes* and *P. stratiotes* can accumulate heavy metals in their tissues without the production of any toxicity or reduction in growth, and can be used for the large-scale removal of heavy metals from waste water (Mishra and Tripath, 2008). This same research study found that *P. crassipes* and *P. stratiotes* are well adapted to the different climates of Madagascar and therefore could contribute to purifying wastewater in large cities throughout the country. Several fields of application were possible, from small-scale (domestic wastewater and hydroponics) to large-scale (municipal and industrial wastewater) (Jafari, 2010; Nayanathara and Bindu, 2017; Ali *et al*., 2020).

Another use of aquatic weeds is for biogas production through anaerobic fermentation, with all four target species potentially being used in this way. According to a study conducted by WWF (2011), the first biogas projects began in Madagascar in the 1960s. Of 99 installation units, two-thirds were not operational until the date of publication in 2011. As part of the DIANA Biogas Project, 414 digesters were installed, most of which started in 2008 (Ferrer, 2018). So far, operators have only used household waste as the main inputs. For anaerobic digestion, whether based on household waste or biomass from invasive species, the technology remains the same. The difference can be observed in the biogas yield (a litre of biogas produced per kg of material), depending on the nature of the organic materials introduced. For example, rapeseed cake has a yield of 350 litres/kg and household organic waste a yield of 75 litres/kg (Ferrer, 2018). Almoustapha *et al.* (2008) found 392.3 litres/kg/dry material (DM) of water hyacinth. Hassen *et al.* (2004) concluded that the methane potential of the household waste was in the range of 200 to 500 litres/kg/dry material for a processing time that fluctuates between 10 and 50 days. However, it should be noted that on average globally 10 kg of water weeds are required to make 1 kg of dry matter (Su *et al.,* 2018).

Biogas from aquatic weed biomass, although not yet exploited in Madagascar, deserves to be researched further and trialled in a model demonstration. Analyses from household waste have shown positive economic (macro- and micro-economic), social and environmental impacts for both the country and households, especially in rural areas (Ferrer, 2018). The same author estimated a cost of Ar3,000,000 (US\$ 763) (exchange rate 1US\$ = 3,930 in October 2020) for a digester of 8 m^3, a fairly large price especially for the majority of Malagasy whose annual income per capita is in the order of US\$ 390 (INSTAT, 2013). Knowing the potential public interest related to projects on biogas production from aquatic weeds (reduction of socio-economic, environmental and health impacts related to biological invasions; reduction of risks associated with the use of toxic chemical fertilizers for humans), such projects should be supported by subsidising operations and by providing technical supervision until the operators are financially and technically autonomous. Loans from micro-credit institutions are another option for individual projects, where after an initial investment, the loan will be repaid after five years (Ferrer, 2018). Gas stoves and piping must be changed every eight years for Ar130,000. After 15 years, the household would potentially benefit by Ar7,300,000 from this investment (Ferrer, 2018).

The use of the digestant from the biodigesters constitutes a special advantage as a fertilizer for rice cultivation because while the production of biogas removes carbon from the fermentation process, there is little loss of the other elements (NAS, 1976; Edwards, 1980). According to Ferrer (2018), the application of 40t/ha/year of digestant would increase rice yields by 23%. All three target species are recognised as having potential for biogas production, yielding 370 litres/kg/DM for *P. crassipes* (Ruskin and Shipley, 1976; Cathryn *et al*., 2010); 58.16 litres/kg for *S. molesta* (Kawaroe *et al.,* 2019); and 21–28 litres/kg of fresh weight for *P. stratiotes* (Tripathi *et al.,* 2010; Pantawong *et al*., 2015).

6.7 Conflicts of interest

Many alien species globally have been introduced to specific areas to provide socio-economic benefits and social wellbeing, with some of these becoming invasive and causing adverse ecological and socio-economic impacts (De Wit *et al.,* 2001; van Wilgen *et al.,* 2011; Ellender *et al.,* 2014). Conflicts of interest arise when an individual (or groups of individuals) oppose the management of one or more species, called "conflict-generating species", providing benefits but also having negative impacts (Stanley and Fowler, 2004; Zengeya *et al.* 2017). The benefits and negative impacts linked to invasive species can be assessed using a scoring approach, the results of which allow species to be classified in a decision support matrix with four levels (negligible, low, medium and high) for positive and negative impacts, giving 16 possible configurations (Johnson, 2007). The classification system was simplified by Zengeya et *al.* (2017) who suggested just four classes (inconsequential species, destructive species, beneficial species and conflict-generating species). For better illustration of the cases of each of the target species, we adopted the classification method proposed by Johnson (2007). The scoring system considers information relating to the actual utility of the species in Madagascar (benefits) and the risks, based on socio-economic and environmental impacts (Chapter 3), distribution (Chapter 2), invasive capacity (Chapter 4) and competitive dominance over native species (Chapter 5) (negative impacts on native species) (Table 6.1).

Table 6.1.: Decision support matrix based on actual risk and utility determining legislative and management responses to conflict-of-interest species (UPPERCASE). Cases of each target weed have been outlined (in lowercase) (modified from Johnson, 2007)

Weed Risk of species (Negative impact)	**Utility of species (Positive impact)**			
	Negligible	**Low**	**Medium**	**High**
Negligible	NO ACTION	NO ACTION	NO ACTION	NO ACTION

Low	PROTECT SITES	MONITOR/MANAGE SITES Water lettuce (*Pistia stratiotes*)	MONITOR/ MANAGE SITES	NO ACTION/ MANAGE SITES
Medium	DESTROY INFESTATIONS	CONTAIN SPREAD Red water fern (*Azolla filiculoides*)	MANAGE SITES	MANAGE SITES
High	ERADICATE/ PREVENT FURTHER INTRODUCTIONS	DESTROY INFESTATIONS Giant salvinia (*Salvinia molesta)* and Water hyacinth (*Pontederia crassipes*)	CONTAIN SPREAD	PROTECT SITES/ MANAGE SPECIES

6.7.1. *Pistia stratiotes*

This species is listed as one that would pose a "*low weed risk*" (Table 6.1). Across the country, infestations are localised and the impacts are low. The species can be classified as a beneficial species using the classification proposed by Zengeya *et al.* (2017). Active management is not necessary or should only be performed in particular cases such as along the Pangalanes Canal or in certain sites of conservation interest. As the species is considered by some to be native to Madagascar, there is not much concern of the invasion in natural habitats (Renner and Zhang, 2004; http://www.tropicos.org/Name/2103622?projectid=17). However, it may be appropriate to identify key sites in natural areas which need to be protected from invasions and which need to have general integrated weed management techniques promoted. Monitoring of species spread is suggested. The species can be used for water purification, phytoremediation of metals, biogas production and compost production as fertilizer. However, the actual value is still low, as it is practiced by few people. In some parts of Madagascar, especially the north-west, the species has significant cultural value for treating spiritual illnesses through the ancestral practice of "tromba" (Chapter 3). As this practice is widespread among the different ethnicities of Sakalava, Tsimihety and Antakarana, the species has acquired an important cultural value within society. An attempt to eradicate the species is not recommended given the strong links to local cultures and the preservation of ancestral cultures. A similar case can be cited for the tree *Entada chrysostachys* (Benth.) Drake (Fabaceae) which is a native species in Madagascar and traditionally used by soothsayers-healers of "sikidy" (Rabedimy, 1976; Ramamonjisoa, 2009). In South Africa, there was huge public resistance to the removal of and to the regulations preventing replanting *Jacaranda mimosifolia* D. Don (Bignoniaceae) as well as several species of *Eucalyptus* and *Pinus* because they are labelled as iconic tree species, champion trees, and regarded as part of the identity and 'sense of place' in several locations in the country (DAFF, 2013; Dickie *et al.,* 2014). In Madagascar, the utility of *P. stratiotes* is assessed as low and the species is classified as an "inconsequential species".

6.7.2 *Azolla filiculoides*

Azolla filiculoides is classified as a species that poses "*medium weed risk*". Competition trials in outdoor conditions with *S. hastata* showed that *A. filiculoides* has a slight dominance over *S. hastata*. During the present study, we could not measure the impacts of the species on aquatic biodiversity from the functioning of the ecosystem in general under natural conditions. A particular concern, above all, is to know its competitive capacity over the closely related *A. pinnata* which is native to Madagascar. Currently, the species is expanding rapidly, covering a wide range across Madagascar. Research from other countries such as in South Africa and in Zimbabwe, have proven its adverse impacts both environmentally and socio-economically (McConnachie *et al.,* 2003).

In terms of utility, the species is valuable as a green manure. This species has been well valued by farmers in the high plateau of Madagascar to correct soil fertility and fertilize crop plots. Given that the actual valorisation is restricted to the highlands of Madagascar, and with a limited number of users, the species is still considered as an "inconsequential species". But, referring to its potential impacts from other countries and its potential utilisation, this status could change to "*conflict-generating species*". (Without effective control measures, this may happen in the near future). Limiting the use of a species is not a good option, given that it is useful. The management strategy for *A. filiculoides* should begin with identification and management of key sites to prevent further weed invasion. This should then be accompanied by effective awareness among stakeholders who value it, to not spread it outside crop-production areas. As the species is easily spread by water currents, birds, small mammals, amphibians, cattle, and humans, containment requires effective actions to prevent infestation at the key natural sites.

6.7.3 *Salvinia molesta*

Salvinia molesta is classified as a " *high weed risk*" species. Thus far no viable utilisation of the species has been found in Madagascar. A few rice growers tried composting it, but the yield was not encouraging. However, it remains an interesting prospect in terms of composting and in the production of biogas, although the utilisation of the species is far from being the first choice over other species such as *A. filiculoides* and *P. crassipes*. Looking at its negative impacts, in relation to the other aquatic species covered in this thesis, it is the most impactful with respect to the socio-economy and the environment. For these reasons, the species is classified as a *"destructive species"* (Zengeya *et al.,* 2017). The destruction of all individuals, and the prevention of sale and movement is desirable to achieve eradication, at least locally. This will require monitoring and mapping to locate any infestations (Johnson, 2007). As the spread of the species is very rapid and the impacts are high, both for individuals and for the countryas a whole, the fight against this species must be a government priority. Biogas production is strongly advocated as a source of motivation for people to collect biomass and clean up infested areas.

6.7.4 *Pontederia crassipes*

Pontederia crassipes is also classified as a *"high weed risk"* species. The difference between it and *S. molesta* lies in the fact that *P. crassipes* is already valued by the Malagasy, and that national experimental trials have shown that this species has high economic potential (albeit not widely realised until recently). Concerning its socio-economic impact, a similar case to *S. molesta* was observed, although to a lesser degree for *P. crassipes*. However, specifically regarding natural sites with biodiversity importance, *P. crassipes* has greater environmental impact.

Pontederia crassipes is somewhat valued in Madagascar for animal feed, raw material handicrafts, and offers future prospects for use as compost and for biogas production. Although the species is widely valued to feed animals especially in the region of Antananarivo, breeders do not foresee a conflict of interest related to the control of the species as they argued that once the spread of *P. crassipes* is managed, other forage species will become available. Since the negative impacts of the species outweigh its benefits, *P. crassipes* is classified as a "*destructive species*". If the infestations of the species are managed at an acceptable level, there will be other available alternatives to users, i.e. other abundant sources of basketwork raw materials and other types of fodder to feed the animals.

6.7.5 Global situation of conflicts of interest

It was observed through this analysis that none of the target species were classified as "conflict-generating species". This category includes species with high utility and high impact (Zengeya *et al.,* 2017). Several types of values are included in the process of evaluating benefits, among others, intrinsic values which represent some form of emotional relationship between society and nature, and utilitarian values for species that are economically important because they provide food and raw materials for industry and local communities (Zengeya *et al.,* 2017). In India, *P. crassipes* has been listed as a "conflict-of-interest" species because some industry groups working on paper production, mulch, biogas production, and sewage purification were opposed to its control, and this has caused a delay in the implementation of a biological control programme (Stanley and Fowler, 2004). In South Africa, out of 552 alien species assessed, only 6% were classified as conflict-generating species (Zengeya *et al.,* 2017). This included species associated with utilitarian benefits, including *Opuntia ficus-indica* (L.) Mill. (Cactaceae) and *Opuntia robusta* H.L. Wendl. (Cactaceae) (Zengeya *et al.,* 2017).

The controversial story of the attempted control of the thorny cactus *Opuntia monacantha* (Cactaceae) in southern Madagascar by the cochineal insect, *Dactylopius coccus* Costa (Hemiptera: Dactylopiidae) serves as a good example of how conflicts can arise over endeavours to control alien, naturalised species. This story has spanned almost 100 years, from 1924, when the insect was introduced to control the population of cactus (Decary, 1929/1930; Binggeli, 2003c; Allorge & Matile-Ferrero, 2011). In 1924, the cochineal was introduced to Antananarivo from Reunion, and over the next four years, the cochineal spread rapidly, ravaging the populations of cactus on the highlands where they served as enclosures for dwellings (Decary, 1929/1930). In southern Madagascar, the cochineal completely wiped out the population of *O. monacantha* (Frappa, 1932; Bingelli, 2003c). Following this event, opinions were divided about the balance of positive and negative impacts from this introduction, even among the leaders of the colonial administration. One group (composed mostly by researchers) supported the value of the operations purporting that: 1) the destruction of thorny *Opuntia* allowed fertile land to be reclaimed for agricultural development that previously had been unusable due to the abundance of *O. monacantha*, thereby alleviating the famines that frequently affected the region; 2) the flower and spiny fruit are causes of bovine tuberculosis; 3) the fruits had a low nutritional value and should not be used for human subsistence; 4) there are other thornless species, such as *O. inermis,* that more preferentially fed on by zebus; 5) cochineal produces a popular dye that could provide additional income for local populations; and 6) the destruction of the *Opuntia* eliminated the refugia of cattle rustlers (Perrie de la Bathie, 1928; Decary, 1929/1930; Allorge and Matile-Ferrero, 2011). Another group (french administrator and Antandroy communities in the Southern of Madagascar) opposed the biological control, argued that: 1) *O. monacantha* was very important for the economic and social well-being of the people of southern Madagascar; 2) *O. monacantha* played an important role as a fence to protect livestock from rustlers and to provide food and moisture for cattle and humans, especially during the dry seasons, leading to the proverb ″the Antandroy and the prickly pear are relatives″ (Decary, 1929/1930). As a consequence of destruction of the population of *O. monacantha* by *D. coccus,* it was estimated that there was 20% reduction in cattle during the 1930s, leading to a major famine and human migration (Decary, 1933; Allorge and Matile-Ferrero, 2011). Other examples of invasive species, both plants and animals, presenting a risk of conflicts of interest, are provided in a non-exhaustive list by Lehavana (2012).

6.8 Global management strategies for the four target species

As discussed in Chapter 3, with the current infestation levels of the four aquatic weeds, control is globally recommended as the most feasible management approach, with a few exceptions for *P. stratiotes* and *A. filiculoides,* where containment may still be possible. Several control methods can be applied depending on the species and the nature of the infestations (Chapter 1). The control strategy for each species should consider their invasion status. Overall, infestations are often concentrated in anthropic zones, with a few exceptions in areas with less human influence, i.e. natural or semi-natural ecosystems. Being aware of this situation, management strategies should consider the characteristics of the invader (Stohlgren and Jarnevich, 2009).

In natural or semi-natural ecosystems with high biodiversity values, the management strategy has to limit the spread of aquatic weeds by applying containment or control measures. However, this requires knowledge of the species (distribution, abundance, biology, ecology, dispersal mechanism) and feasibility of actions as well as long-term continuing commitment (Grice, 2009; Sarat *et al.,* 2015a). The control measures can initially be manual, such as the case of actions undertaken by Durrell Wildlife Conservation Trust at Lake Ravelobe from 2016 to 2019 (i.e. removing biomass in collaboration with local communities), but should eventually followed by permanent monitoring and an expectation of additional control measures (Velosoa, 2019).

Once infestations have been reduced to a low enough level that has little impact, and the population of the species behaves as an emergent weed whose range or abundance is "localised and common/scarce", then as a long-term perspective, infestations could potentially be managed by biological control (Nel *et al.,* 2004; Olckers, 2004). It is important to note that the use of biological control agents reduces the competitive ability of some invasive species and is both environmentally sound and economically cost-effective (Pantone *et al.,* 1989; Center *et al.,* 2001, 2005; Coetzee *et al.,* 2005; Mony *et al.,* 2007; Ajuonu *et al*., 2009; Tipping *et al*., 2009; Bownes *et al.,* 2010; van Wilgen and de Lange, 2011; Martin and Coetzee, 2014; Strange *et al.,* 2019).

In South Africa, biological control of weed programmes have proven very successful - in particular for three of the target species (*P. stratiotes, A. filiculoides* and *S. molesta*). The control of infestations of these weeds has been so effective that no other control options are needed (Coetzee *et al.,* 2011; Hill *et al.,* 2020). The control of *A. filiculoides* was the most spectacular, since, within the space of a year, the frond-feeding weevil *Stenopelmus rufinasus* Gyllenhal (Coleoptera: Curculionidae), caused a dramatic reduction in the populations of this fern and the species no longer poses a threat to aquatic ecosystems (Hill *et al*., 2008). For *P. crassipes*, while the biological agents have contributed significantly to a reduction in invasion, an integrated control program which includes the use of chemicals is required to reduce the weed to below a damage threshold (Coetzee *et al.,* 2011; Hill *et al.,* 2020). Taking into account the high cost associated with the use of manual control, and the environmental and health risks related to chemical control, Ranarijaona *et al.* (2013) considered biological control as a good option for *P. crassipes*, but on condition that rigorous scientific study first be undertaken to evaluate the potential negative impacts before introducing biological control agents. While the cost of herbicidal control of *P. crassipes* was evaluated as US$ 250/ha, biological control was much less expensive at US$ 44/ha (Hill *et al.,* 2020). For classical biological control, once the initial expensive research has completed (exploration, host-range testing) and the agents have been released and have established, they are in the system permanently, being self-sustaining and essentially requiring no or little further input from humans. Therefore, the benefit:cost ratio increases year-on-year. In South Africa, the biological control of *A. filiculoides* showed the evolution of the benefit–cost ratio of 2.5:1 for the year 2000, increasing to 13:1 in 2005, and 15:1 in 2010 (McConnachie *et al.,* 2003). Given the economic and environmental advantages of biological control, it is strongly recommended that Madagascar should collaborate with neighbouring countries such as South Africa to enhance technical capacity for such interventions. In addition, biological control sometimes also requires special infrastructure such as glasshouses and quarantine facilities to safely contain and conduct tests on potential agents, while ensuring they do not escape until fully approved for use. These are future investments that will have to be made in Madagascar.

Best practice for biological control requires a long and technically rigorous process (see Chapter 1; Charudattan *et al.,* 1996). For instance, in the case of French Polynesia, it took a decade for biological control to be socially accepted and scientifically recognised as an efficient and safe tool (Meyer, 2014). However, it is fortunate that the biological control of floating invasive aquatic plants has already been proven extremely successful, safe, and has been a critical factor in the long-term, sustainable and cost-effective control of these species (Coetzee and Hill, 2009; Coetzee *et al.,* 2011; van Wilgen and De Lange, 2011).

In anthropized ecosystems, the control strategy must also consider the management of nutrient inputs such as phosphorus and nitrogen. Discharge from sewerage and agricultural runoff are the main preventable forms of nutrient input (Osmond and Petroeschevsky, 2013). Management of infestations should include actions such as reducing nutrient loads in wastewater including "habitat manipulation" (Sarat *et al.,* 2015a). Coetzee *et al.* (2011) reported that below a concentration of 0.06mg of phosphorus per litre, biological control was effective at suppressing infestations of *P. crassipes* whereas at higher concentrations (from 0.1mg to 1.06 mg P/litre), the plants were able to survive and grow actively despite the presence of the biological control agent.

All recommended actions cited above must be coupled under a coordinated umbrella plan. A concrete example, although on a small scale, which can serve as a model, occurred in the west of the Digue Plain in Antananarivo. Here rice growers coordinated the removal of *S. molesta*, resulting in a greater impact, compared to each working independently following different time tables. Since 2015, the level of infestation has dramatically reduced. It should be noted that this area is sheltered from sewage discharges from the main part of Antananarivo (Chapter 3).

6.9 Legal instruments and governance for management of invasive alien species

Invasive alien species often range across national boundaries, and in such cases they can only be tackled effectively through international cooperation. While the management of biological invasions is mainly implemented at the national level, international agreements and collaborative endeavours may be required for these efforts to be effective. International collaboration includes sharing information and expertise on the ecology of invasive species, their impacts, control and management experiences. The application of international conventions and laws helps to ensure the framing and operation of appropriate national legislation and regulations to address current and potential problems related to invasive alien species. There are now over 40 binding international agreements that refer either directly or indirectly to such species and of these, less than a dozen are specifically related to aquatic environments (Moore, 2005).

Madagascar has ratified 22 international conventions, agreements and treaties with the shared objective of sustainable development and the conservation of biodiversity (https://www.environnement.mg/wp-content/uploads/2019/04/Annex-1.-Conventions internationales_ratifi% c3% a9es_Madagascar.pdf). Those relevant to invasive aquatic species include:

● Convention on Biological Diversity (CBD), adopted in 1992 and in force from 1993, is the most comprehensive instrument that provides the basis for measures to protect all components of biodiversity from the impacts of invasive alien species. Article 8 (h) of this convention urges parties, as part of a suite of *in situ* conservation measures and as far as possible and as appropriate, "*to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species*"(CBD, 2005) (Ratification in Madagascar: decree n°95-695 of 03 November 1995).

● Convention on Wetlands, adopted in 1971 and in force from 1975, also known as the Ramsar Convention, provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources (Article 3.1). A resolution was taken regarding invasive species and wetlands in 1999 during the 7th Meeting, Resolution VII.14 that urged Contracting Parties to: *"address the environmental, economic and social impact of the movement and transport of alien species; inventory alien species in wetlands in their jurisdictions; target invasive alien species for eradication or control; adopt legislation to prevent the introduction and spread of invasive alien species; and build capacity to identify alien species and enforce legislation"* (Ramsar Convention, 1999) (Date of ratification by the Malagasy State: March 24, 1998)

● Implementation plan of the World Summit on Sustainable Development (WSSD) solicited country members to *"Strengthen national, regional and international efforts to control invasive alien species, which are one of the main causes of biodiversity loss, and encourage the development of effective work program on invasive alien species at all levels"* (Paragraph 44 (i)) (Kiss and Doumbe-bille, 1992; WSSD, 2002) (Ratified by the Malagasy State in 1995).

Bilateral or regional cooperation is a necessary element of management strategies, especially in the case where alien invasive species move across national boundaries (Shine *et* *al.,* 2000). Madagascar is an island, and the risk of introduction is relatively low compared to countries with shared land borders. However, gathering and sharing information on invasive species management practices from other countries is essential to improve overall management effectiveness. To do this, Madagascar has joined regional cooperation platforms (Rabarison *et al.,* 2015). In terms of information sharing, Madagascar, mainly researchers and proponents of biological invasions, have benefited from information sharing in the regional platform the Western Indian Ocean Network on Invasive Species (WIO-IAS). (https://list.auckland.ac.nz/sympa/info/wio-ias). This network, created in 2012, is one of the largest platforms exchanging up-to-date information (data, news, alerts, advice, expertise, technical assistance, training, funding) on invasive species in the Indian Ocean region.

At the national level, Madagascar has a strategy and a framework plan for the application of various international and regional agreements, developed by the previous Ministry of the Environment, Ecology, Sea and Forest (now with a modified remit and renamed as the Ministry of the Environment and Sustainable Development). Nevertheless, this strategy must be transformed into a concrete action plan with a clear focus on the management of invasive alien species. The analyses made by Shine *et al.* (2000), in the context of the application of international/regional instruments at the national level, revealed a number of common weaknesses. These include, among others: a) fragmented legal and institutional frameworks; b) low levels of coordination and/or familiarity between agencies responsible for sectors such as development and biodiversity conservation, with regard both to international standard setting and to legislative development and implementation; c) dispersed character of existing provisions and inconsistent legislative treatment, reflected in different institutions, definitions, criteria, standards and procedures; d) weak connectivity between different levels of government, particularly in decentralized regions; e) low enforcement (low levels of compliance, poor accountability) because conventional criminal and civil law procedures are difficult to apply in the context of alien species. Following these findings, they formulated several strategic orientations that are proposed here to be used as recommendations forming the basis for the effective and efficient management of aquatic weedaquatic weeds in Madagascar while taking into account the realities of the country. These observations have been emphasised by IUCN (2020) when launching more concrete recommendations in terms of law enforcement and regulations.

1. Given the importance of negative impacts of aquatic weed throughout the country, affecting multiple sectors related to both development and biodiversity, Madagascar should develop a realistic strategic plan dedicated specifically to aquatic aquatic weeds. As mentioned above, there is little concern regarding conflicts of interest relative to the four target species. However, if the strategic plan is extended to other species, then attention should be paid to evaluating current negative impacts and benefits of these, while addressing and openly balancig any positive and negative aspects of each species. This plan should be integrated into diverse sectorial objectives, especially those of the Environment and Sustainable Development sector, the Agriculture, Livestock and Fisheries sector, and the transport sector. At the regional level, Reunion could serve as an example (national strategy, structure and action plan), although requiring adaptation to the Malagasy context (Baret *et al.,* 2010). The plan should include a framework to evaluate and rationalise regulatory components of alien species control, management and monitoring across the sectors.

2. At the national level, a lead government agency should be created, formed by staff from the administrative services (e.g. representatives of relevant Ministries), tasked and legally empowered, whose role is specifically to tackle invasive species and biosecurity issues (IUCN, 2020). This structure must be mirrored within the Regions.

3. Identify all relevant institutions and sectors to be grouped within a cross-sectorial invasive species advisory committee, at both national and regional levels (government, university researchers and experts from public and private sectors and non-governmental organizations), mandated to support the lead agency (IUCN, 2020). At a regional level, the committee should include all stakeholder representatives concerned by invasive alien species, particularly the local communities, so that possible conflicts and concerns can be quickly recognised.

4. Constitute a country-wide program to counter the growing threat from invasive alien species (IUCN, 2020), to review the existing national invasive species strategy and to state clear objectives and an implementation plan.

5. The Government should financially support the programme albeit perhaps with the help of international donors. The lead agency will need to act with good governance to ensure that resources are used in line with validated strategies.

6. Reviewing existing laws. Currently, each sector has its own legislation. As the invasions of aquatic weeds affect several sectors, it is more strategic to harmonize relevant sectorial laws and regulations to ensure the absence of conflicting provisions and to promote more uniform and consistent practice throughout the country (Shine *et al.,* 2000). This can be extended to other invasive species, as needed, to avoid repetitive revision. The regulatory tools related to alien species should be pragmatic and realistic, thereby enhancing acceptance and compliance. The example of the regulations used in South Africa can serve as a model (Molewa, 2014). These regulatory tools must be accompanied by criteria (e.g. categorization of species based on scientific studies concerning weed risk assessment, permit systems, periodic review, operational standards for transport and containment, etc.). They must prohibit, or strictly regulate, the use and release of alien species in or near closed or vulnerable ecosystems and protected areas. According to Decary (1965), in February 1928 a decree was issued prohibiting the sale of water hyacinth in Madagascar, yet there was a lack of enforcement and oversight.

7. The planning process should also support the development or expansion of a knowledge base, at national or regional level. IUCN (2020) proposed the establishment of a national database of invasive alien species and a first draft of this tool is now available. However, a review of this information reveals how very little is known about the current status, the invasive potential and the diverse impact of the many exotic species of animals and plants that currently occur in Madagascar. Given the pace of change in scientific information, criteria for control of introductions, transport and other activities need to be capable of amendment, probably on a regular basis. Implementation programs related to alien species control and management need instead to be designed for easy adjustment as updated information becomes available.

8. Provide for the establishment of cost-effective preventive and mitigation measures tailored to national conditions and capacity, building where possible on the contributions that local communities and other stakeholders can provide.

9. The planning process should provide for monitoring, public participation in management, and early warning and emergency planning systems to support rapid responses when biological invasions are detected around or within protected areas or vulnerable ecosystems. This implies the need for support of research, training, education and public awareness. Regulatory frameworks alone cannot solve problems related to invasive alien species and rather they need to be complemented by efforts to promote information, education and awareness-raising campaigns. A well-designed planning process with enforced regulatory regimes that is supported by a well-educated public, is the combination most likely to yield a successful outcome. National planning processes should therefore recognise the responsibility to improve public awareness of invasive alien species problems and ultimately provide the means whereby this can be achieved.

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Survey questionnaire

Name of investigator:_Adolphe Lehavana____

Assistant (s) : ____

Date : ____

Village : _______________.Fkt :___________________.Commune :__________________

GPS : ____

A. Questions related to the respondents

Name of respondent:____

Age: [ ]<15 years [ ]15-20 years [ ]20-30 years [ ]30-40 years [ ]40-50 years [ ]50-60 years [ ]>60 years

Gender: [ ]Male [ ]Female

Academic level: [ ]Uneducated [ ]Primary education [ ]Secondary education [ ]High school [ ]University

Marital status: [ ]Married [ ]Single

a. How many children do you have: [ ] 0-2 [ ]2-4 [ ]4-6[ ]6-8 [ ]>8

b. How many other dependents do you have: [ ] 0-2 [ ]2-4 [ ]4-6

Ranking the activities according to their importance (1,2,3, …)[ ]Agricultural activities [ ]Fishing [ ]Livestock [ ]Transportation [ ]Timber selling [ ]Charcoal selling

B. Questions related to the presence of invasive aquatic plants

1. Are you aware of the existence of any invasive aquatic species in the river/lake/canal in this area? [ ]Yes [ ]No

2. If, yes, what species do you know? [ ]Water hyacinth [ ]Giant Salvinia [ ]Water lettuce [ ]Red water fern [ ]Others:

3. Which between them is the most troublesome invasive aquatic species? [ ]Water hyacinth [ ]Giant Salvinia [ ]Water lettuce [ ]Red water fern [ ]Others:

4. Are they prevalent in any specific locations in this area? [ ]Yes [ ] No

5. If yes, name any three specific locations:1)___________________________ 2)______________________________ 3)____

6.How long have you stayed in this village? [ ]<5year [ ]5-10 years [ ] 10-15 years [ ] 15-20 years [ ]20-55 years [ ]25-30 years [ ]30-35 years [ ] 35-40 years [ ]>40 years

7. When did you notice the first presence of invasive aquatic plant species in this lake and canal Antsokafina? [ ]Less than 5 years [ ]10 years ago [ ]15 years ago [ ]20 years ago [ ]30 years ago [ ]40 years ago [ ]more than 40 years

8. When did you notice that the canal was completely clogged up? [ ]Less than 5 years [ ]10 years ago [ ]15 years ago [ ]20 years ago [ ]30 years ago [ ]40 years ago [ ]more than 40 years

9. Do you know, where did these species come from before invading the lake and canal? [ ]Yes [ ]No

10. If yes, are there any specific locations:____________________________________

11. Do you know, how did they arrive there? [ ] by animals [ ]Human [ ]birds [ ]water flow [ ] [ ] hook of canoe [ ] other (specify)

12. In your time here, have you noticed any major differences in terms of the amount of invasive aquatic plants on the lake? How has it changed? [ ] There is no difference [ ]There is generally more invasive aquatic plant now [ ]There is generally less invasive aquatic plant now [ ] it varies

13. Do you value them positively? [ ] Yes [ ]No

14. If yes, which species and how? [ ]Fodder [ ] compost [ ]Medicinal plants [ ]Mulch [ ]Handicraft [ ] Other (specify)

15. How often do you use it/them and how much (in kilograms)? [ ] every day [ ] 4 times a week [ ] 3 times a week [ ] 2 times a week [ ] per week [ ] every 2 weeks [ ] once a month

C. Questions related to the impacts of invasive aquatic plants to fishing

16. How many fishermen were there in the village before the invasion of the invasive aquatic plants? [ ]0-20 [ ]20-40 [ ]40-60 [ ]60-80 [ ]80-100 [ ]100-120 [ ]120-140 [ ]140-160 [ ]>160

17. And how many there now? [ ]0-20 [ ]20-40 [ ]40-60 [ ]60-80 [ ]80-100 [ ]100-120 [ ]120-140 [ ]140-160 [ ]>160

18. Do you fish for commercial purpose or for consumption? (Please indicate percentage if both) [ ] Commercial (1/10 ; 1/5; 1/3; ½; 1) [ ] Consumption (1/10 ; 1/5; 1/3; ½; 1)

19. How many kilograms (kg) of fish did you catch daily before the presence of invasive aquatic plants in the lake? (*if the invasion period of IAS a was long time ago, perhaps, it would be important to take a timescale, example 16 years before now, i.e. comparison between 2000 and 2016*) [ ] 0-20 [ ] 20-40 [ ]40-60 [ ]60-80 [ ]80-100 [ ]>100

20. And now, with the invasion of invasive aquatic plants, how many kg can you catch? [ ] 0-10 [ ] 10-20 [ ]20-30 [ ]30-40 [ ]40-60 [ ]50-60 [ ]>60

21. How many kilograms (kg) of shrimp did you catch daily before the presence of invasive aquatic plants in the lake? [ ] 0-20 [ ] 20-40 [ ]40-60 [ ]60-80 [ ]80-100 [ ]>100

22. And now, with the invasion of invasive aquatic plants, how many kg can you make? [ ] 0-10 [ ] 10-20 [ ]20-30 [ ]30-40 [ ]40-60 [ ]50-60 [ ]>60

23. Before the presence of invasive aquatic plants, at what price (per kg) was fish sold (in Ariary)? [ ] 0-1000 [ ] 1000-2000 [ ]2000-3000 [ ]3000-4000 [ ]4000-5000 [ ]5000-6000 [ ]6000-7000 [ ]>7000

24. And now, with the presence of invasive aquatic weeds, at what price (per kg) is fish sold (in Ariary)? [ ] 0-4000 [ ] 4000-5000 [ ]5000-6000 [ ]6000-7000 [ ]7000-8000 [ ]8000-9000 [ ]9000-10000 [ ]>10000

25. Before the presence of invasive aquatic plants, at what price (per kg) was shrimp sold (in Ariary)? [ ] 0-1000 [ ] 1000-2000 [ ]2000-3000 [ ]3000-4000 [ ]4000-5000 [ ]5000-6000 [ ]6000-7000 [ ]>7000

26.And now, with the presence of invasive aquatic weeds, at what price (per kg) is shrimp sold (in Ariary)? [ ] 0-4000 [ ] 4000-5000 [ ]5000-6000 [ ]6000-7000 [ ]7000-8000 [ ]8000-9000 [ ]9000-10000 [ ]>10000

27. Where do you sell your fish and shrimps to? [ ] local market [ ] regional market [ ] mix of local and regional markets

28. How many days a week did you go for fishing before the lake was invaded? [ ]0-2 [ ]3-4 [ ]5-6 [ ] whole week

29. How many days a week do you go for fishing now? [ ]0-2 [ ]3-4 [ ]5-6 [ ] whole week

30. Do you have a period of the year when you do not fish? [ ]Yes [ ]No

31. If yes, when?...

32. If you do not fish, what activities do you perform? [ ] Agriculture [ ]Trade [ ]timber selling [ ]charcoal selling [ ]other:

33. What techniques of fishing did you usually use before the invasion of invasive aquatic plants? [ ] Gill net [ ]Cast net [ ]trap [ ]chemical products [ ]fishing line [ ]other technique

34. What techniques of fishing do you usually use after the invasion of invasive aquatic plants?

[ ] Gill net [ ]Cast net [ ]trap [ ]chemical products [ ]Fishing line [ ]other technique

35. In the case of decline of fish harvest, what do you do to compensate the family's needs?

[ ]Reduce the family consumption [ ]Fishing in other zones [ ]Fish farming

[ ]Buying [ ]Others……………..

36. How do invasive aquatic plants affect your fishing activities? [ ] Clog fishing gear [ ]Block water ways [ ]Block navigation [ ]prevalence of crocodile [ ]reduce fish species [ ]reduce the size of fish caught

D. Questions related to the impacts of invasive aquatic plants to transport activities

37. How long have you been involved in transport? [ ]less than a year [ ]1-2 years [ ]3-5 years [ ] 5-10 years [ ]more than 10 years

38. How many times do you use to cross the canal or lake for transportation? [ ] Every day [ ] 1-2 times a week [ ]3-4 times a week [ ]>5 times

39. What do you transport across the canal or lake? [ ] Goods [ ] People [ ] Fish [ ] other

40. Do you have a period of the year, when you do not do transportation? [ ] Yes [ ] No

41. If yes, when?---

42. How much money (in Ariary) do you make as benefit from one trip when you transport?

[ ] 0-50.000 [ ] 50.000-80.000 [ ] 80.000-120.000 [ ] 120-150.000 [ ]150.000-200.000 [ ]>200.000

43. Do you have a period of year, where you make less benefits because of invasive aquatic plants? [ ] Yes [ ] No

44. If yes, when?..

45. Do you use paddling or engine boats? [ ] Paddling [ ] Engine boats

E. **Questions related to the impacts of invasive aquatic plants to biodiversity**

46. What kind of fish, shrimps, animals, and useful plants were present in the area before the invasion?

Animals: ____

Plants:____

Fish: ____

Shrimps:____

47. What kind of species have disappeared when invasive aquatic species invaded the area?

Animals: ____

Plants:____

Fish: ____

Shrimps:____

48. What kind of species do you notice to appear when the area is invaded by invasive aquatic plants?

Animals: ____

Plants:____

Fish: ____

Shrimps:____

49. What are the animals which feed on those invasive aquatic plants? [ ] Crocodile [ ]Fish[ ]Shrimps [ ] Insects [ ]Birds [ ]Snakes [ ] Other

50. Do you know other problems caused by invasive aquatic plants? (please explain)

Disease: …………………………………………………………………………………

Animals drowning:………………………………………………………………………

Floods:……………………………………………………………………………………

F. Control of invasive aquatic plants

51. Have you ever attempted to control the invasive aquatic plants in any way? [ ]Yes [ ] No

52. If yes, what techniques did you use? [ ] remove and burn [ ]remove and use [ ]remove and leave at the edge [ ] remove and leave with the water flow [ ] Apply herbicide [ ] other

53. Are the practices adopted successful? [ ] Yes [ ] No?

54. If no, why do you think the practices were not successful? [ ] The plant rejuvenates too fast [ ]seeds germinate and grow very fast [ ]the plant sprouts from cutting of all parts [ ] the plant is resistant to herbicide

55. What do you think of applying other techniques? [ ] natural enemies [ ] herbicide [ ]mechanical removal

56. Have you ever participated in community work for cleaning of Invasive alien plants on the lake and canal? [ ]Yes [ ]no. Why?

57. If yes, how often?

58. Now, the community is deciding to reinforce the control of aquatic weeds, what contribution will you want to bring**?** [ ]Yes [ ]No

59.If yes, [ ] financial: how much money (Ariary) …[ ] workforce: how often: [ ] 1 per week [ ] twice a week [ ]other:

60. With your experience how else do you intend to deal with the problems of the IAS?

[ ] Seek extension advice [ ] Report the situation to government [ ] seek assistance from NGOs [ ]Work harder to contain the situation [ ]Other

61. What would you propose if the entire lake would be covered with invasive aquatic plants?

[ ] Applying more herbicide at higher dose [ ] Introducing natural enemies [ ] Physical removal and burn regularly

62. Will you welcome the introduction of any new plants in your area? [ ] Yes [ ]No

63. If No, why not? [ ] They may pose health problems [ ] They may take over the environment and damage biodiversity [ ] They reduce fish populations and diversity [ ] They may reduce water quality [ ] They may impede water utilisation [ ] They may introduce pests and diseases [ ] Other (specify)……………….

64. If yes, Why? [ ] They may enhance fishing [ ] they provide herbs for medicines [ ] they are food for domestic animals and wild life [ ] they can be used as botanical pesticides [ ] they may possess aesthetic value [ ] Other (specify)_...._

65. What will you do to prevent the recurrence of the plant/IAS in your community?

[ ] Refrain from introduction of plants without the necessary quarantine certification and advice colleagues to do same: [ ] Report strange plants to extension officers, NGOs, government [ ] Physically remove and destroy strange plants before they spread [ ] Other (Specify)