

Research Article

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

Adolphe Lehavana^{1,2}, Julie A. Coetzee¹, Costas Zachariades^{3,4}, Christopher Birkinshaw² and Martin P. Hill¹

¹Centre for Biological Control, Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa

²Missouri Botanical Garden (MBG), Madagascar Research and Conservation Program, Antananarivo, Madagascar

³Plant Health and Protection, Agricultural Research Council, Cedara, South Africa

⁴School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

Corresponding author: Martin P. Hill (m.hill@ru.ac.za)

Citation: Lehavana A, Coetzee JA, Zachariades C, Birkinshaw C, Hill MP (2025) 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. *BioInvasions Records* 14(4): 883–898, <https://doi.org/10.3391/bir.2025.14.4.11>

Received: 29 October 2024

Accepted: 21 July 2025

Published: 26 September 2025

Handling editor: Tsungai Alfred Zengeya

Thematic editor: Karolina Bączal-Spychalska

Copyright: © Lehavana et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

Madagascar is a biodiversity hotspot with extensive freshwater ecosystems. It is also one of the world's least developed countries and relies on its wetland habitats for essential services such as rice production and fisheries. The floating aquatic weeds *Pontederia crassipes* Mart. (Pontederiaceae) (water hyacinth), *Salvinia molesta* D.S. Mitch. (Salviniaceae) (giant salvinia), *Pistia stratiotes* L. (Araceae) (water lettuce) and *Azolla filiculoides* Lam. (Salviniaceae) (red water fern) have been recorded from Madagascar, and some at least are known to have significant negative impacts. However, their identities and distribution have not been well documented. Here, we confirm identities and map distributions of the four species using field survey data, herbarium records and literature records. All species were widespread, each occurring in at least 13–16 of the 23 Administrative Regions (ARs) and in four of the five bioclimatic regions of Madagascar. In only four ARs were none of the four species recorded. *Pistia stratiotes* has the earliest collection records (1847) but there is some dispute as to whether it is an alien species or not. *Pontederia crassipes* was first collected in 1931, while *S. molesta* was first collected in 1995 and often confused with the native congener *S. hastata*. Finally, *A. filiculoides* had not previously been collected, and was often confused with the native congener *A. pinnata*. All four species occupied mainly lentic systems, including both rural and urban settings, and natural and agricultural (rice-growing) systems. *Salvinia molesta* is the most widespread species and causes the most problems, although both *P. crassipes* and *A. filiculoides* are also frequently problematic. *Pistia stratiotes* is the least aggressive of the species. An understanding of the distribution and frequency of occurrence of these weeds is essential in developing management programmes for them.

Key words: biodiversity impacts, plant distribution, floating aquatic weeds, giant salvinia, red water fern, water hyacinth, water lettuce

Introduction

Invasive Alien Aquatic Plants (IAAP) are globally recognized for their negative environmental and socio-economic impacts, especially for resource-poor communities where economic activities are dependent on waterways (Coetzee et al. 2019). These aquatic weeds, including *Pontederia*

crassipes Mart. (Pontederiaceae) (water hyacinth), *Salvinia molesta* D.S. Mitch. (Salviniaceae) (giant salvinia), *Pistia stratiotes* L. (Araceae) (water lettuce) and *Azolla filiculoides* Lam. (Salviniaceae) (red water fern), are of South American origin, but have been dispersed around the world due to the economic and ornamental value (Hill et al. 2020). These weeds escape cultivation and become highly invasive in slow-flowing and impounded aquatic ecosystems. The main drivers of invasion include changes in hydrological regimes through the damming of rivers which slows the flows and ensures constant water surface, eutrophication due to the runoff of nitrates and phosphates from point source and diffuse discharge, and the lack of co-evolved natural enemies (Hill and Coetzee 2017). Dense mats of these four weeds degrade aquatic ecosystems and limit their utilization (Hill 2003).

Madagascar is a global biodiversity hotspot, with high levels of endemism (Máiz-Tomé and Darwall 2018). Madagascar's wetlands are extensive and important for the provision of food, water, materials and services, but under high levels of threat from deforestation (leading to erosion and siltation) and conversion to agriculture (primarily rice production) (Máiz-Tomé and Darwall 2018). Invasive alien plants (IAPs) are recognised as a threat to aquatic ecosystems – in an assessment of the status of a number of taxonomic groupings (Máiz-Tomé and Darwall 2018), they were specifically listed as a threat to the indigenous aquatic flora (Phillipson et al. 2018) and molluscs (Van Damme et al. 2018). These IAPs also harbour disease-causing mosquitoes and snails (Van Damme et al. 2018), and control measures against both these pests and the IAPs themselves cause damage to the native biodiversity (Phillipson et al. 2018; Van Damme et al. 2018).

Pontederia crassipes (water hyacinth), *S. molesta* (giant salvinia), *P. stratiotes* (water lettuce) and *A. filiculoides* (red water fern) have all been recorded in Madagascar, and in some cases are known to be abundant, widespread and problematic. However, little has been quantified with respect to their distribution, socio-economic impacts, or effects on aquatic biodiversity in Madagascar. Regarding distribution, several gaps in the data were identified, in particular:

- (i) there are few voucher specimens lodged in herbaria, either nationally or internationally;
- (ii) if they exist, many of these formal records are over 50 years old, and lack georeferenced information;
- (iii) misidentification of specimens (e.g. confusion of invasive alien plant species with indigenous congeners) has occurred.

The aim of this study was thus to determine the current distribution of the four targeted aquatic weed species *P. crassipes*, *S. molesta*, *P. stratiotes* and *A. filiculoides* across Madagascar through field surveys, herbarium

records and the literature, to confirm species identities, and to provide a historical account of the introduction of the species.

Materials and methods

Herbarium records

The TAN herbarium, located in the *Parc Botanique et Zoologique de Tsimbazaza* (PBZT), is the only herbarium in Madagascar housing non-woody plant specimens. 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 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.

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 Catalog of the Plants of Madagascar (<http://legacy.tropicos.org/Name/26100027?projectid=17>) was consulted.

Field surveys

In order to manage IAPs, species- and site-specific studies are required to determine the weed's current distribution, and to allow predictions about its potential distribution and rate of spread (Wittenberg and Cock 2001; FAO 2006; Lizzio et al. 2009). Mapping of the extent of the IAP informs managers as to where the species is present or is likely to be found, as well as enabling prioritisation for early intervention (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 subsequent control interventions (Holcombe et al. 2007; FAO 2012; Rawlins et al. 2018; Rivas-Torres et al. 2018), and can also serve as an effective tool in efforts to educate the public about the species (IUCN Council 2000; FAO 2012; CBD 2014). In mapping IAPs, several methods can be used, depending on the objectives of the programme, the level of detail required, and the availability of technical, financial and human resources (Wittenberg and Cock 2001; FAO 2012).



Figure 1. Routes of the four trips undertaken for mapping distribution of the target aquatic species following national roads.

The mapping of the four target species was carried out across Madagascar. We gathered 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 species presence, was adopted because it is inexpensive and its simplicity also allowed data collected by colleagues to be integrated into the data set.

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 was undertaken in the south-east; and the fourth occurred around the central part of eastern Madagascar in the vicinity of Fenerive-Est (Figure 1).

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) (Rawlins et al. 2018).

The survey interval (distance) used between sampling points for roadside surveys in the literature is variable (Thapa et al. 2018). In East Africa, Wabuyele et al. (2014) used 25 km intervals for *Parthenium hysterophorus* L. (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 between survey points was 5–10 km. However, if the elevation changed dramatically within a short distance, the survey interval distance was reduced to as little as 1 km.

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 (BRs) subdivided into several bioclimatic zones, based on temperature, altitude, precipitation, water deficits and number of dry months. These different zones were later simplified by Schatz (2001) into five BRs, namely humid, sub-humid, dry, sub-arid and mountain. More recently, freshwater ecosystems in Madagascar have been grouped into five Madagascar Freshwater Ecoregions (Western Madagascar, North-Western Madagascar, the Eastern Highlands, Southern Madagascar and the Eastern Lowlands) (Máiz-Tomé and Darwall 2018). We superimposed Schatz' (2001) system onto our georeferenced distribution maps of the four target species in order to determine their distribution across bioclimatic regions.

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 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.

Results

Distribution of the four targeted invasive aquatic species in Madagascar

The data compilation from three sources discussed above (herbarium, online information, field trips) provided a general overview of the distribution of

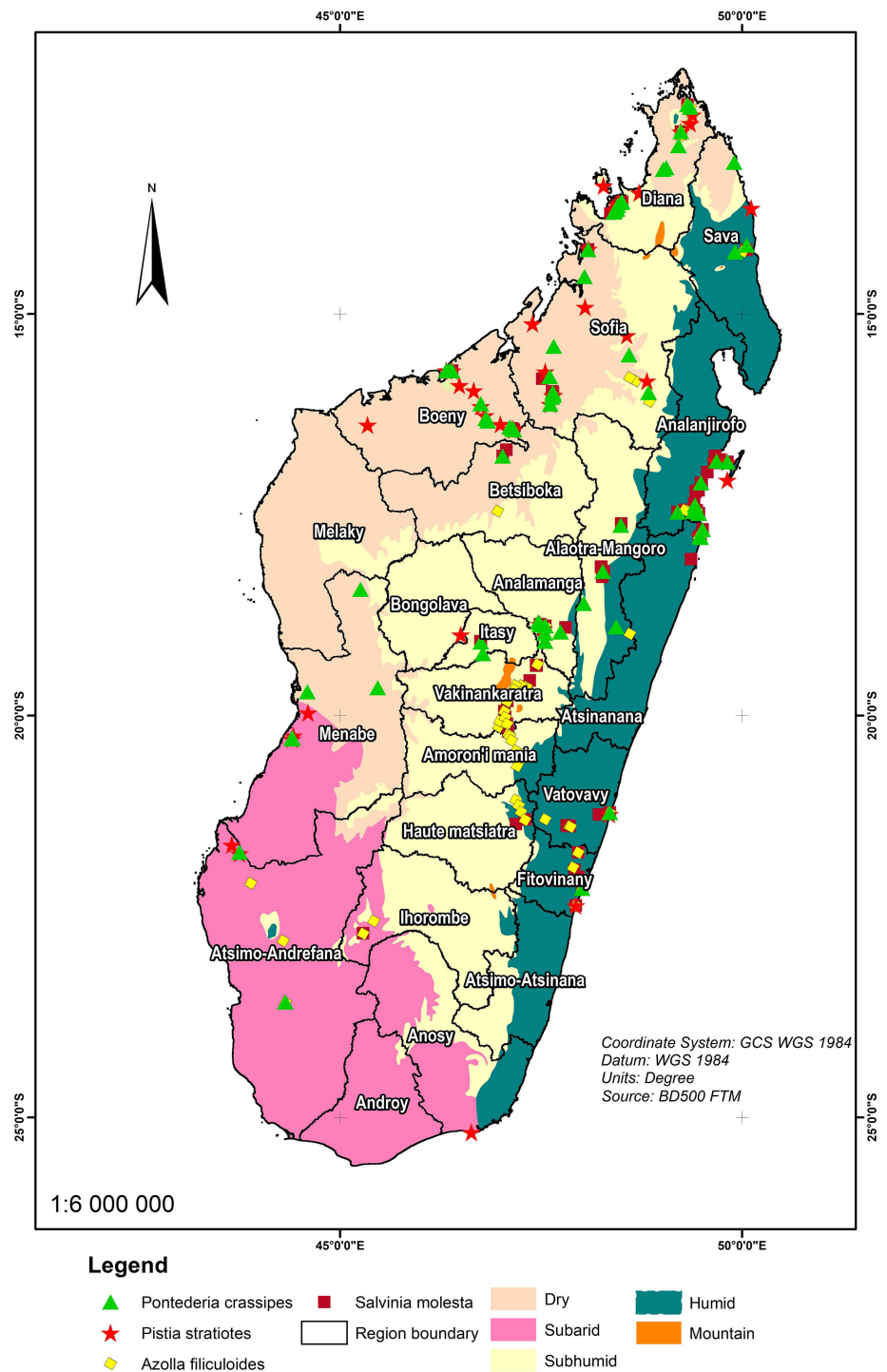


Figure 2. Distribution of the four invasive aquatic weeds according to the ARs and bioclimates of Madagascar. Names of the 23 Administrative Regions (ARs) indicated in *italics*. Simplified bioclimatic regions (BRs) (Cornet 1974; Schatz 2001) indicated using five colours.

the four targeted aquatic weed species in Madagascar (Figure 2). Madagascar is divided into 23 Administrative Regions (ARs). In total, 20 of the ARs in Madagascar were recorded as being infested with at least one of the target aquatic weed species. There were only three ARs, namely Melaky, Androy and Antsimo-Atsinanana, where the target species were not recorded. Of the 20 ARs, nine were invaded by all four species, three by three species, six by two species, and there were two ARs where only one species was



Figure 3. The different habitats infested by four aquatic weeds in Madagascar. A. *Azolla filiculoides* invading a rice field at Antatatra, Mandritsara, Sofia AR; B. *Pistia stratiotes* invading a pond in the town of Antonibe, Sofia AR; C. *Salvinia molesta* invading a rice field in Antananarivo town, Analamanga AR; D. *Pontederia crassipes* invading the sacred lake of Ambondromifehy, DIANA AR (2). Photo by Adolphe Lehavana.

recorded. No data were available for mountainous areas > 1800 m above sea level (asl), i.e. the Tsaratanana Massif (DIANA, SAVA and Sofia), Ankaratra Massif (Vakinankaratra and Itasy) and Andringitra (Haute-Matsiatra and Ihorombe) (Figure 2).

Most of the data used for these maps came from the data collection trips along roads that were designated as part of this study. Remarkably few herbarium specimens for these species existed and thus few data were obtained from TAN and from online botanical databases. The aquatic weeds were found in a variety of freshwater habitats, including slow flowing streams, natural lakes and wetlands, man-made impoundments and most notably rice paddies (Figure 3).

Distribution and history of spread of Pontederia crassipes

Pontederia crassipes was recorded in 14 ARs of Madagascar, namely Alaotra-Mangoro, Analamanga, Analanjirofo, Antsinanana, Antsimo-Andrefana, Betsiboka, Boeny, DIANA, Itasy, Menabe, SAVA, Sofia, Vatovavy and Fitovinany. This species was found in all bioclimates, except in the mountain BR, extending over a range of elevations from 0 to 1429 m asl.

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), infestations were sometimes very large, even covering several hectares. Examples included (i) Lake Ambondromifehy, in the rural municipality of Anivorano, DIANA AR, where almost half of the lake (about 1.5 ha) was infested; (ii) Lake Manompa, in the rural town of Ankijabe, Boeny AR; and (iii) Lake Amparihely, in the municipality of Mampikony, Sofia AR, which each had an invaded area of more than 50 ha, 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 of 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.

The earliest collection of *P. crassipes* in Madagascar dates from 1931, when a specimen was collected by the agricultural service in the vicinity of Antananarivo. 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 programme, the surveys and collections were expanded beyond Antananarivo, gathering 10 additional records across different ARs 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.

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 16 ARs in Madagascar, namely Alaotra-Mangoro, Analamanga, Analanjirofo, Antsinanana, Betsiboka, Boeny, DIANA, Haute-Matsiatra, Ihorombe, Itasy, SAVA, Sofia, Vakinankaratra, Vatovavy and Fitovinany. These ARs included four bioclimates (humid, sub-humid, dry and sub-arid), over altitudes ranging from 0 to 1579 m asl (Figure 2). In all areas where *S. molesta* was present, it was observed that many different types of water bodies were invaded, especially lentic systems and rice fields. Here, it rapidly expanded to cover the entire body of water. As the fragments of the plant are readily dispersed, even by 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 the aquatic weeds.

In all the ecosystems conducive to its development (lakes, marshes, ponds, rice fields), the weed can cover several tens of hectares. Examples of colonised zones included (i) Lake Andramoma, the rural commune of Foulpointe, Antsinanana AR; (ii) Lake Sarondrano, in the rural commune of Ankiririky, District of Mampikony, Sofia AR; and (iii) Lake Antsokafina, Rural Municipality of Antanifotsy, District of Soanierana Ivongo, Analanjirofo AR. The carpets formed by the species also contributed to the plugging of the Pangalanes canal, making transport difficult or even impossible. Among the four targeted species in the present study, *S. molesta* was the most widespread in Madagascar.

Regarding the history records of its occurrence 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 (Curator NLH herbarium, Department of Botany and Nature Conservation, Agricultural University of Norway) and R. Solohery (Curator at Parc Botanique et Zoologique de Tsimbazaza, Madagascar) in shallow water at the western shore of Lake Itasy. 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 programme to create an inventory of aquatic plants in Madagascar, from 2010 to 2016, resulted in 12 additional collections. However, confusion regarding the identification of *S. molesta* and *S. hastata*, was not resolved until 2015, when this study was initiated. Fully developed leaves of *S. molesta* are characterised by leaf papillae 1.5–2 mm long with multicellular hairs bearing 2–4 branches joined at their tips on the upper surface. By contrast, fully developed leaves of *S. hastata* have leaf papillae up to 0.3 mm long, with multicellular hairs that are simple on the upper surface (Verdcourt 2000). The majority (68) of records for *S. molesta* 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.

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 13 ARs, namely Analamanga, Analanjirofo, Anosy, Antsinanana, Betsiboka, Boeny, DIANA, Ihorombe, Itasy, Menabe, Sofia, Vatovavy and Fitovinany. These invaded ARs encompassed all bioclimates, except the mountain BR, extending over an altitude ranging from 0 to 1255 m asl (Figure 2). The *P. stratiotes* collection made in January 1905 in Betsiboka AR, 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, *P. stratiotes* was observed as a primary invader of Lake Antsokafina.

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 on Sainte-Marie Island (Nosy Boraha). The second collection was in September 1879 by J.M. Hildebrandt 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 the Natural History Museum 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 the inventory of aquatic plants in Madagascar undertaken 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.

Distribution and history of spread of Azolla filiculoides

Azolla filiculoides was recorded in 15 ARs of Madagascar, namely Alaotra-Mangoro, Amoron'i Mania, Analamanga, Analanjirofo, Antsimo-Andrefana, Antsinanana, Betsiboka, DIANA, Haute-Matsiatra, Ihorombe, Sofia, Vakinankaratra, Vatovavy and Fitovinany. This species grows in four bioclimates (humid, sub-humid, dry and sub-arid) ranging in altitude from 0 to 1663 m asl (Figure 2). 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, close to the road to Mahajanga, in the rural commune of Antanimbarinandriana, District of Maevatanana, Betsiboka AR. In the ARs of Vakinankaratra, Amoron'i Mania, Vatovavy and 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 AR, *A. filiculoides* covered more than 60% of the rice fields starting from Andranomena and Ampasindava to Beronona, District of Ambositra, Amoron'i Mania AR.

With respect to the history of introduction of *A. filiculoides*, prior to 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. (Salviniaceae). 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 ARs 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 database) and 56 records from fieldtrips of the current study.

Discussion

The current study provides preliminary distribution of four invasive alien aquatic species in Madagascar. A total of 260 records were assimilated (72 for *P. crassipes*, 81 for *S. molesta*, 44 for *P. stratiotes* and 62 for *A. filiculoides*, of which 82% were collected during these fieldtrips). Prior to 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. 2022). Between 2010 and 2016, the number of collections of aquatic plant species increased due to the aquatic species inventory programme led by the Missouri Botanical Garden team, resulting in an additional 31 confirmed records for the four invasive aquatic species that form the subject of this study. For the current study, it is recognized that there is a lack of quantitative data on these four species from the Melaky, Bongolava, Androy and Atsimo-Atsinanana ARs, where no surveys have yet been made.

Despite their tropical origins, all species were present in all bioclimates of Madagascar, with the exception of the mountain bioclimate. 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 low temperatures (Janes 1998). 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). *Azolla filiculoides* 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. 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 ARs of Fitovinany and Analanjirofo.

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 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 (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 BRs, *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). In the laboratory, the growth rate is higher for *S. molesta* than *P. crassipes*, with leaf doubling time from about 2 to 4 days (Mitchell 1979), and from about one to eight days under field conditions (Room 1986b), while that of *P. crassipes* is estimated at 11 to 18 days under field conditions (Penfound and Earle 1948). Results from an experiment in Lake Antsokafina, Soanierana Ivongo, with a humid bioclimate (Cornet 1974), confirmed the higher growth rate of *S. molesta* compared to *P. crassipes*. Under field conditions, after one year, *S. molesta* covered 92.1% of the experimental surfaces whereas *P. crassipes* covered only 1.3%. *Pistia stratiotes* is 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 be 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*. This observation merits further investigation to better understand the bioclimatic conditions or physicochemical parameters of a water body that allow *P. stratiotes* to become highly competitive and aggressively invasive.

The current distribution of the four aquatic weed 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 scenarios. 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).

The effects of climate change manifest differently in southern and northern Madagascar. The southern part of the country, with an arid and sub-arid bioclimate, the average temperature increased by approximately 0.2 °C between 1970 and 2000, while in the north, with a humid and dry bioclimate, the average temperature increased by less than 0.1 °C (Rabefitia et al. 2008). Future climate projections (2046 to 2065) for Madagascar as a whole, averaged over 20 years, from the same study estimate 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 predicted 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). These changes in climate are likely to result in extreme events such as drought and frequent flooding, and to alter the future distribution of aquatic invasive species. For aquatic weeds, temperature is the most important parameter in predicting potential distribution (FAO 2006), while Heneidy et al. (2019) found that in addition to temperature, precipitation is a critical variable in models used to predict the distribution of *Hydrocotyle umbellata* L. (Araliaceae) and *Salvinia auriculata* Aubl. (Salviniaceae).

Carrying out a study based on climate-change information in Madagascar is essential to enable effective and proactive management of these four target species, currently in the saturation phase of invasion. Although currently these aquatic weeds are already widespread in Madagascar and only mountainous ecosystems above 1800 m asl are not infested, 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 (Mooney and Hofgaard 1999; Sciama 2010; 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 100–2100 m asl to 100–2300 m 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 (Martin et al. 2020).

Knowledge of current distributions of the invasive alien plant species in question gives an appreciation of their status as important weeds in Madagascar, their ecological tolerances, and data that can be extrapolated using models to predict where else they may currently be found, and where they may spread to under both current and future climate scenarios. Further, it may leverage funding for further research on control and management methods for these weeds, and the implementation of management plans.

Authors' contribution

The authors have accepted responsibility for the entire content of this manuscript and approved its submission. AL – research conceptualization; sample design and methodology; investigation and data collection; data analysis and interpretation; wrote the original draft. JC – sample design and methodology; data analysis and interpretation; review and editing of drafts of the manuscript. CZ – research conceptualization; sample design and methodology; data analysis and interpretation; review and editing of drafts of the manuscript. CB – review and editing of drafts of the manuscript. MH – research conceptualization; sample design and methodology; data analysis and interpretation; funding provision; review and editing of drafts of the manuscript.

Authors' ORCIDs

Martin Hill: [0000-0003-0579-5298](https://orcid.org/0000-0003-0579-5298); Costas Zachariades: [0000-0002-5855-9558](https://orcid.org/0000-0002-5855-9558); Julie Coetzee: [0000-0002-0364-3349](https://orcid.org/0000-0002-0364-3349).

Acknowledgements

AL thanks the Missouri Botanical Garden's Madagascar Program for permission to undertake this study as part of his doctoral dissertation. The authors thank the anonymous reviewers of previous drafts of this manuscript. Their comments considerably improved quality of the manuscript.

Funding declaration

Funding for this work was provided by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation of South Africa (grant number 84643) to MH. Any opinion, finding, conclusion or recommendation expressed in this material is that of the authors and the NRF does not accept any liability in this regard. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Ethics and permits

Rhodes University Animal Research Ethics Committee (RU-AREC) Numbers 2015-3842-8102; 2016-3842-8102; 2017-3842-8102; 2018-3842-8102; 2019-3842-8102 and 2020-3842-8102.

References

- CBD (2014) Convention on Biological Diversity. A toolkit to facilitate Parties to achieve Aichi Biodiversity Target 9 on invasive alien species (Prototype). Global Invasive Alien Species Information Partnership, 80 pp
- Coetzee JA, Hill MP, Hussner A, Nunes AL, Weyl OLF (2019) Chapter 16. Invasive aquatic species. In: Hughes JMR (ed), *Freshwater Ecology and Conservation: Approaches and Techniques*: Oxford University Press, pp 338–358, <https://doi.org/10.1093/oso/9780198766384.003.0016>
- Cornet A (1974) Essai de cartographie Bioclimatique à Madagascar. Note explicative n°55, Office de la Recherche Scientifique et technique outre-mer. OROSTOM, Paris, 41 pp
- Engel K, Tollrian R, Jeschke J (2011) Integrating biological invasions, climate change and phenotypic plasticity. *Communicative & Integrative Biology* 4: 247–250, <https://doi.org/10.4161/cib.4.3.14885>
- FAO (2006) Procedures for post-border weed risk management. Plant Production and Protection Division, Food and Agriculture Organization of the United Nations, Rome, 21 pp

- FAO (2012) Invasive species survey techniques: Plant survey. FISNA Workshop: Forest invasive species, forest health technologies and phytosanitary standards. Seeta, Uganda – 1–4 February 2012, Food and Agriculture Organization (FAO), pp 1–17
- Forno IW (1983) Native distribution of the *Salvinia auriculata* complex and keys to species identification. *Aquatic Botany* 17: 71–83, [https://doi.org/10.1016/0304-3770\(83\)90019-0](https://doi.org/10.1016/0304-3770(83)90019-0)
- Gautier L, Tahinarivony JA, Ranirison P, Wohlhauser S (2018) Vegetation. In: Goodman M, Raherilalao MJ, Wohlhauser S (eds), The terrestrial protected areas of Madagascar: their history, description, and biota. Association Vahatra, Antananarivo, Madagascar, pp 207–242
- Heneidy SZ, Halmy MWA, Fakhry AM, El-Makawy AM (2019) The status and potential distribution of *Hydrocotyle umbellata* L. and *Salvinia auriculata* Aubl. under climate change scenarios. *Aquatic Ecology* 53: 509–528, <https://doi.org/10.1007/s10452-019-09705-4>
- Hill MP (2003) The impact and control of alien aquatic vegetation in South African aquatic ecosystems. *African Journal of Aquatic Science* 28: 19–24, <https://doi.org/10.2989/16085914.2003.9626595>
- Hill MP, Coetzee J (2017) The biological control of aquatic weeds in South Africa: Current status and future challenges. *Bothalia* 47: a2152, <https://doi.org/10.4102/abc.v47i2.2152>
- Hill MP, Coetzee JA, Martin GD, Smith R, Strange EF (2020) Invasive alien aquatic plants in freshwater ecosystems. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA (eds), Biological Invasions in South Africa. Invading Nature - Springer Series in Invasion Ecology. Springer International Publishing, Cham, pp 97–114, https://doi.org/10.1007/978-3-030-32394-3_4
- Holcombe T, Stohlgren TJ, Jarnevich C (2007) Invasive species management and research using GIS. In: Witmer GW, Pitt WC, Fagerstone KA (eds), Managing Vertebrate Invasive Species: Proceedings of an International Symposium. USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, CO, pp 108–114
- IUCN Council (2000) Guidelines for the prevention of biodiversity loss caused by alien invasive species. *Invasive species specialist group (ISSG)* 1: 12–25
- Janes R (1998) Growth and survival of *Azolla filiculoides* in Britain. *New Phytologist* 138: 367, <https://doi.org/10.1046/j.1469-8137.1998.00114.x>
- Jiménez-Valverde A, Peterson AT, Soberon J, Overton JM, Aragon P, Lobo JM (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785–2797, <https://doi.org/10.1007/s10530-011-9963-4>
- Kelly R, Leach K, Cameron A, Christine AM, Reid N (2014) Combining global climate and regional landscape models to improve prediction of invasion risk. *Diversity and Distributions* 20: 884–894, <https://doi.org/10.1111/ddi.12194>
- Kosaka Y, Saikia B, Mingki T, Tag H, Riba T, Ando K (2010) Roadside distribution patterns of invasive alien plants along an altitudinal gradient in Arunachal Himalaya, India. *Mountain Research and Development* 30: 252–258, <https://doi.org/10.1659/MRD-JOURNAL-D-10-00036.1>
- Lizzio J, Richmond L, Mewett O, Hennecke B, Baker J, Raphael B (2009) Methodology to prioritise Weeds of National Significance (WoNS) candidates. Bureau of Rural Sciences, Canberra, 58 pp
- Máiz-Tomé L, Darwall W (2018) Background: Madagascar and the Indian Ocean islands biodiversity hotspot. In: Máiz-Tomé L, Sayer C, Darwall W (eds), The status and distribution of freshwater biodiversity in Madagascar and the Indian Ocean islands hotspot. IUCN, Gland, Switzerland, pp 1–5, <https://doi.org/10.2305/IUCN.CH.2018.RA.1.en>
- Manjato NV, Ranarijaona HL, Randriamiarisoa BA, Maharombaka C, Lowry PP, Phillipson PB (2022) Vascular plants of Malagasy freshwater wetlands. In: Goodman, SM (ed), The new natural history of Madagascar 1, Princeton University Press, USA, pp 470–492, <https://doi.org/10.1515/9780691229409>
- Martin GD, Magengelele NL, Paterson ID, Sutton GF (2020) Climate modelling suggests a review of the legal status of Brazilian pepper *Schinus terebinthifolia* in South Africa is required. *South African Journal of Botany* 132: 95–102, <https://doi.org/10.1016/j.sajb.2020.04.019>
- Mitchell DS (1979) The incidence and management of *Salvinia molesta* in Papua New Guinea. Office of Environmental and Conservation, and Department of Primary Industry, Konedobu, Papua New Guinea, 62 pp
- Mooney HA, Hofgaard A (1999) Biological invasions and global change. In: Sandlund OT, Schei PJ, Viken Å (eds), Invasive species and biodiversity management. Based on a selection of papers presented at the Norway/UN Conference on Alien Species, Trondheim, Norway. Population and Community Biology Series, 24, Kluwer Academic Publishers, pp 139–148, https://doi.org/10.1007/978-94-011-4523-7_9
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful. *Global Ecology and Biogeography* 12: 361–371, <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Penfound WMT, Earle TT (1948) The biology of the waterhyacinth. *Ecological Monographs* 18: 448–473, <https://doi.org/10.2307/1948585>
- Phillipson P, Andriambololonera S, Letsara R, Maharombaka C, Ramiandrisoa BA, Manjato N, Ranarijaona HL, Darwall W, Máiz-Tomé L (2018) The status and distribution of aquatic

- plants. In: Máiz-Tomé L, Sayer C, Darwall W (eds), The status and distribution of freshwater biodiversity in Madagascar and the Indian Ocean islands hotspot. IUCN, Gland, Switzerland, pp 59–74
- Rabefitia Z, Randriamarolaza LYA, Rakotondrafara ML, Tadross M, Ki Yip Z (2008) Le changement climatique à Madagascar. Direction Generale de la Meteorologie, 32 pp
- Raholijao N, Arivelo TA, Rakotomavo ZAPH, Voahangin-dRakotoson D, Srinivasan G, Shanmugasundaram J, Dash I, Qiu J (2019) Les tendances climatiques et les futurs changements climatiques à Madagascar - 2019. MTTM, CPGU, Meteo Madagascar, Banque Mondiale, RIMES, 20 pp
- Rajeriarison C, Faramalala H (1999) Nomenclature des formations végétales de Madagascar. Association Nationale pour la Gestion des Aires Protégées (ANGAP) et WWF, 43 pp
- Rawlins KA, Wallace RD, Moorhead DJ, Bargerion CT, Swain SJ (2018) EDDMapS: Identifying and Mapping Invasives. The University of Georgia. Center for Invasive Species and Ecosystem Health, Tifton GA. BW-2018-01, 32 pp
- Rivas-Torres GF, Benitez FL, Rueda D, Sevilla C, Mena CF (2018) A methodology for mapping native and invasive vegetation coverage in archipelagos: An example from the Galápagos Islands. *Progress in Physical Geography* 42: 83–111, <https://doi.org/10.1177/0309133317752278>
- Room PM (1986a) Equations relating growth and uptake of nitrogen by *Salvinia molesta* to temperature and the availability of nitrogen. *Aquatic Botany* 24: 43–59, [https://doi.org/10.1016/0304-3770\(86\)90116-6](https://doi.org/10.1016/0304-3770(86)90116-6)
- Room M (1986b) *Salvinia molesta* - a floating weed and its biological control. In: Kitching RL (ed), The ecology of exotic animals and plants. John Wiley, Brisbane, Queensland, Australia, pp 164–186
- Schatz GE (2001) Generic tree flora of Madagascar. Royal Botanic Gardens, Kew & Missouri Botanical Garden, Great Britain, 477 pp
- Sciama Y (2010) Le changement climatique, une nouvelle ère sur la Terre. Petite Encyclopedie Larousse, 128 pp
- Shrestha UB, Sharma KP, Devkota A, Siwakoti M (2018) Potential impact of climate change on the distribution of six invasive alien plants in Nepal. *Ecological Indicators* 95: 99–107, <https://doi.org/10.1016/j.ecolind.2018.07.009>
- Thapa S, Chitale V, Rijal SJ, Bisht N, Shrestha BB (2018) Understanding the dynamics in distribution of invasive alien plant species under predicted climate change in Western Himalaya. *PLoS ONE* 13: e0195752, <https://doi.org/10.1371/journal.pone.0195752>
- Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasion at global scale. *Global Change Biology* 11: 2234–2250, <https://doi.org/10.1111/j.1365-2486.2005.001018.x>
- Van Damme D, Köhler F, Andriamaro L, Darwall W, Máiz-Tomé L, Sayer C, Darwall W (eds), The status and distribution of freshwater molluscs. In: Máiz-Tomé L, Sayer C, Darwall W (eds), The status and distribution of freshwater biodiversity in Madagascar and the Indian Ocean islands hotspot. IUCN, Gland, Switzerland, pp 29–41
- Verdcourt B (2000) Salviniaceae. Flora of Tropical East Africa, 194, CRC Press, pp 1–3
- Wabuyele E, Lusweti A, Bisikwa J, Kyenune G, Clark K, Lotter WD, McConnachie AJ, Wondi M (2014) Roadside survey of invasive weed *Parthenium hysterophorus* (Asteraceae) in East Africa. *Journal of East African Natural History* 103: 49–57, <https://doi.org/10.2982/028.103.0105>
- Whiteman JB, Room PM (1991) Temperatures lethal to *Salvinia molesta* Mitchell. *Aquatic Botany* 40: 27–35, [https://doi.org/10.1016/0304-3770\(91\)90071-C](https://doi.org/10.1016/0304-3770(91)90071-C)
- Wittenberg R, Cock MJW (eds) (2001) Invasive Alien Species: A Toolkit of Best Prevention and Management Practices. CAB International, Wallingford, Oxon, UK, 228 pp, <https://doi.org/10.1079/9780851995694.0000>