



UNIVERSITÀ DEGLI STUDI DI SASSARI Corso di Dottorato di Ricerca in

SCIENZE AGRARIE

DIPARTIMENTO DI AGRARIA

CURRICULUM

Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo

XXX CICLO

"Invasive alien aquatic plants in South American inland waters: Inventory, prioritisation and distribution models"

Dott.ssa Vanessa Lucia Lozano Masellis

Coordinatore del corso: Prof. Antonello Cannas Referente di Curriculum: Prof. Alberto Satta Docente guida: Prof. Antonio Franceschini Docente tutor: Dott. Giuseppe A.D. Brundu

Anno accademico 2016 - 2017

DEDICATION

A MIS PADRES POR HABERME DADO TANTO AMOR, LOS MEJORES VALORES, POR DARME FUERZAS PARA CONTINUAR Y POR APOYARME A LO LARGO DE MI VIDA Y CARRERA.

A MI FEFI QUE AMO CON TODAS MIS FUERZAS

A CARLITOS QUE TANTO ME HA ENSEÑADO Y CON ESPECIAL CARIÑO A MINITA QUE SERÁ SIEMPRE MI ÁNGEL GUARDIÁN Y LA LUZ DE MIS OJOS.

USTEDES SON MI PILAR.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

DECLARATION

By submitting this thesis, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by the University of Sassari will not infringe any third-party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Chapters 2, 3, and 5 have been published in peer-reviewed journals. Chapters 1 and 4 are presented in the style of a journal manuscript. Work on Chapter 1, was started in 2015. Chapter 4 will be submitted to a peer-reviewed journal. More details on contributions to the thesis are provided at the start of each specific chapter. Figures and tables of the published chapters are inserted in the text near first referencing and are therefore not listed in the Table of Contents. This thesis contains a single bibliography to minimize duplication of referencing across the chapters.

Sassari, the 5th of November 2017

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

THESIS OUTLINE:

Name: Vanessa Lucia Lozano Masellis

Institution: University of Sassari

Major Field: Agriculture and Plant Science

Title of the study: INVASIVE ALIEN AQUATIC PLANTS IN SOUTH AMERICAN INLAND WATERS: INVENTORY, PRIORITISATION AND DISTRIBUTION MODELS.

Candidate for Ph Degree on Agricultural Science

I. Background

Biological invasions are a widespread process at the global level and can alter population dynamics, community structure and ecosystem services in the invaded range. Aquatic plants are very often particularly invasive, especially in areas that are modified by humans. Taking into consideration the little information available, it was considered essential to plan an inventory of South American native and non-native aquatic plant species, aiming to collect information on their status of invasion, identifying the major current and the potential future plant invaders. To this aim, all the available information was collected from literature, the GBIF database and according to expert opinion. To evaluate the invasiveness of a group of aquatic plant species in South America, a standard risk assessment scheme (USAqWRA) was applied. Finally, the inventory data was used to apply a model to assess the current potential distribution of South American invasive aquatic plants. As it can be expected, considering the large number of species and diverse habitats of the investigated Continent, despite the progress herewith presented, many fundamental questions in biological invasions in South American inland waters remain unresolved. However. For this reason, I think that the opportunity provided by establishing "Global Networks for Invasion Science" are a very powerful approach with plenty of benefits, increasing the capacity to identify and assess emerging invasion risks and global trends.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

II. Arguments

a. Inventory of the aquatic native and non-native plant species of South America (invasive status and main plant functional traits)

This inventory collects information on the invasive status and main plant functional traits for the native and non-native aquatic species in South America. It was planned and used to store data to support the knowledge, quantification and analysis of the major current and the potential aquatic plant invaders. This inventory poses the basis for further studies of biological invasions in aquatic environments in South America.

b. US Aquatic Weed Risk Assessment (USAqWRA)

To prioritize and classify the most invasive species, a standard risk assessment scheme for aquatic plants in South America was applied. The results of USAqWRA were compared with the existing a priori classification of the invasive status based on South American expert opinion.

c. Comparing and integrating GBIF records with literature data

GBIF (Global Biodiversity Information Facility) information reliability for South American aquatic plants was tested and compared with literature data, for a set of selected species. The integration of different information sources was proved to be the most reliable process.

d. Ecological niche dynamics across continents in aquatic plants native to South America and invasive elsewhere

Non-native species offer excellent model systems for examining niche conservatism associated with biological invasions. Part of the document is focused on the potential distribution and further niche shifts detected on invasive aquatic plants, that have major impacts in their introduced ranges. By applying rigorous modeling methods for aquatic environments, I aimed to assess the current potential distribution of South American invasive aquatic plants, across continents.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

e. Global networks for invasion science: benefits, challenges and guidelines

This paper remarks the need for 'Global networks' able to address research questions on biological invasions at the global scale and the primary data on model systems are collected to address specific global questions. In addition, it reviews how data collection is coordinated using standardized protocols and metrics that ensure comparability of data captured at different locations.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



III. Thesis conceptual Flow-Chart

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Contenuto della tesi

Le invasioni biologiche sono un processo diffuso a livello globale in grado di alterare le dinamiche di popolazione, la struttura della comunità e i servizi ecosistemici dell'area invasa. Le piante acquatiche sono spesso particolarmente invasive, specialmente nelle aree antropizzate. Considerate le poche informazioni disponibili è stato considerato essenziale porre le basi per la creazione di un inventario delle piante acquatiche native e non-native del Sud America, fornendo informazioni riguardo il loro stato di invasività e identificando le principali piante invasive presenti e potenzialmente future. Sono stati quindi raccolti e valutati i dati disponibili in letteratura e quelli presenti nel database GBIF. Il grado di invasività delle specie acquatiche del Sud America è stato valutato tramite un'analisi standard del rischio (USAqWRA). Infine, l'inventario ottenuto è stato utilizzato nell'elaborazione di un modello di distribuzione delle piante acquatiche nelle condizioni climatiche attuali. Nonostante i resultati ottenuti, molte delle domande riguardanti alcune questioni fondamentali sulle invasioni biologiche rimangono senza risposta. Comunque, le 'Global Networks for Invasion Science'sono uno strumento utile a migliorare la capacita di identificazione e valutazione dei rischi di invasione emergenti a livello gobale.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

ACKNOWLEDGEMENTS

I am sincerely grateful to Dr. Giuseppe Brundu for his advice, comments, encouragement and meticulousness during this study. His exceptional patience, guidance and dedication are noted. I would like to thank Professor Antonio Franceschini to guide my project. I would like to thank my committee members and reviewers for taking time from their busy schedules to guide me.

I gratefully acknowledge the University of Sassari to support the program "Visiting Professor" with the participation of Dr. Daniel Chapman and for creating the space that facilitated the work and the writing of this manuscript.

I acknowledge the funding received from the: 1) "COST-Action TD1209 Alien Challenge, in association with the Area Marina Protetta di Tavolara, University of Sassari and NEMO srl" for making the workshop possible, in Headquarters of the Area Marina Protetta di Tavolara, Via S. Giovanni 14 - 07026 Olbia, Sardinia; 2) "COST-Action TD1209" for making the Short Term Scientific Mission possible, in NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh, UK; 3) "COST-Action FP1403 "NNEXT" for making the workshop possible, in CIBIO/InBIO, Porto, Portugal; and 4) The project ALIEM "Action pour Limiter les risques de diffusion de espéces Introduites Envahissantes en Méditarrenée".

I gratefully thank Anibal Pauchard, Jonathan Urrutia and Valentina Escanilla (Laboratorio de Invasiones Biológicas, Facultad de Ciencias Forestales, Universidad de Concepción, Chile), Ramiro Bustamante (Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile), Sidinei Magela-Thomaz (Dep. Biologia, Universidade Estadual de Maringá, Brazil), Luis José Cumana Campos (Herbario Isidro Rafael Bermúdez R, UDO "IRBR", Venezuela), Heinke Jaeger (Charles Darwin Foundation Puerto Ayora, Galapagos, Ecuador), Rafaël Govaerts (Royal Botanic Gardens, Kew

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Richmond Herbarium, UK), Carlos Ramírez (Universidad Austral de Chile), Mark Hughes (Royal Botanical Garden of Edinburg), Thalia Morales (Jardín Botánico de la Universidad Central de Venezuela), Ernesto Brugnoli Olivera (Facultad de Ciencias, Universidad de la República Oriental del Uruguay), Michele Dechoum (Federal University of Santa Catarina Florianópolis, Santa Catarina, Brazil), Patricio Novoa (Depto. Horticultura Jardín Botánico Nacional, Chile) for providing useful information, literature and their kind help during the study.

I gratefully thank Pierfrancesco Deiana for his encouragement and companionship.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

TABLE OF CONTENTS

Dedication	ii
Declaration	iii
Thesis outline:	iv
I. Background	iv
II. Arguments	v
III. Thesis conceptual Flow-Chart	vii
Contenuto della tesi	viii
Acknowledgements	ix
Introduction to the field of biological invasions science	1
Chapter 1	
The database and inventory of the aquatic native and non-native plant species of	South America 3
Introduction and aims	
Methodology and main results	
Conclusions	
Chapter 2	
Prioritisation of aquatic invasive alien plants in South America with the US Aqua	atic Weed Risk
Assessment	
Introduction and aims	
Methodology and main results	
Conclusions	
Chapter 3	
Native and non-native aquatic plants of South America: comparing and integratin	ng GBIF records
with literature data	
Introduction and aims	
Methodology and main results	
Conclusions	
Chapter 4	
Ecological niche dynamics across continents in aquatic plants native to South Ar	merica and
invasive elsewhere	69

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Introduction and aims	69
Methodology and main results	69
Conclusions	
Chapter 5	
Global networks for invasion science: benefits, challenges and guidelines	
Introduction and aims	
Methodology and main results	
Conclusions	
General conclusions and recommendations	
Bibliography	
Appendix I	
A. The inventory for native and non-native aquatic plants of South America	
B. Records of aquatic plant species in the 16 regions of South America	
C. Relevant illustrative pictures (for information)	

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

INTRODUCTION TO THE FIELD OF BIOLOGICAL INVASIONS SCIENCE

Biological invasions are considered to be one of the greatest threats to biodiversity. Since the first generalization of biological invasion phenomena by Elton (1958), invasion by nonnative species (synonyms: alien, non-indigenous, exotic, introduced) (Pyšek et al. 2004) it has become renowned that invasive species can alter community structure and ecosystem functions and services, with significant impacts on biodiversity. Non-native species spread and their impacts have become an area of concern for scientists, managers, policy makers and members of the public and this in turn has led to global advice and, or, management by international organizations (e.g., FAO 1996; IUCN 1999). Invasions are a global phenomenon and comparison of geographically distant regions and their introduced biota is a crucially important methodological approach for describing observed patterns, and an essential step in the search for elucidation of the determinants of invasiveness and invasibility (Crawley et al. 1996; Goodwin et al. 1999).

Freshwater ecosystems are considerd the most endangered ecosystems in the world yet they represent major biodiversity hotspots (Murphy 2002) at global level (Strayer and Dudgeon 2010). Declines in biodiversity are far greater in freshwaters than in the most affected terrestrial ecosystems due to growth of the human population, rising consumption, pollution, and rapid globalization (Revenga et al. 2005), but efforts to set global conservation priorities have largely ignored freshwater diversity, thereby excluding some of the world's most species habitats, harboring threatened, and valuable taxa (Abell et al. 2011).

Invasive alien species (IAS) are considered to be one of the greatest threats to biodiversity, particularly through their interactions with other drivers of change (Vilà et al. 2011) and have negative impacts on ecosystem services. Aquatic invaders have strong negative impacts on native biodiversity and many different impacts from plants are reported in the literature for Europe and worldwide (e.g., Hussner 2012; Gallardo and Aldridge 2013).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Interactions between alien species and other contemporary stressors of freshwater ecosystems are strong and varied. Because disturbance is generally thought to favor invasions, stressed ecosystems may be especially susceptible to invasions, as are highly artificial ecosystems. In turn, alien species can strongly alter the hydrology, biogeochemical cycling, and biotic composition of invaded ecosystems, and thus modulate the effects of other stressors (Strayer 2010). However, do threats occur singly in freshwater ecosystems, with most risked species subjected to multiple interacting stresses, thus, biological invasions may be considered as one of a pattern of factors that characterize degraded aquatic ecosystems (Willby 2007).

Finally, aquatic habitats are in general very difficult to monitor. The high level of connectivity of freshwater systems means that fragmentation can have profound effects and threats such as pollution, invasive species, and disease are easily transported across watersheds (Dudgeon et al. 2006).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

CHAPTER 1

THE DATABASE AND INVENTORY OF THE AQUATIC NATIVE AND NON-NATIVE PLANT SPECIES OF SOUTH AMERICA

Introduction and aims

Invasive alien species (IAS) are identified as one of five major drivers of biodiversity loss in inland waters (MEA 2005). IAS grows rapidly, competing vigorously in the absence of their natural predators, out-competing native species and homogenizing ecosystems. In South America IAS have been documented only to a limited extent, due to the scarcity of regional inventories (Gardener et al. 2011) and because the invasion is a relatively recent phenomenon (Fuentes et al. 2008, 2010; Ugarte et al. 2010). The aim of the research was to assemble a comprehensive inventory of South American native and non-native aquatic plant species introduced into and within South American regions. Such a database would also be a basic tool for dedicated analysis on biological invasion in inland waters in South America.

Methodology and main results

This inventory is a collection of existing databases, checklists, floras and expert opinion already available for this macro-region, where the knowledge of the diversity of the aquatic alien flora is still limited indeed. The study project started in 2015 and this Chapter presents herewith the analysis of a sub-set of 250 (of the 1,463 native and non-native aquatic species so far recorded in the DB), belonging to 51 families, with 42 species ranked as invasive in at least one South American region. *Poaceae* and *Cyperaceae* were the families with the highest number of alien species. The majority of them are of South American origin (alien *in* South America), followed by those of African and Asian origin (alien *to* South America)

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Conclusions

The DB provides a baseline against which to compare future introductions, and a source for additional applied research in Biological Invasion Science in South America.

Abstract

Alien plant invasions in inland freshwaters can alter community structure, ecosystem functions and services with significant negative impacts on biodiversity and human activities. National inventories of aquatic alien plants are a fundamental basis for prioritization, risk analysis and management, and provide substantial insights to our understanding of general patterns of plant invasions in inland waters. This study built the basis for a comprehensive inventory of South American native and non-native aquatic plants, considering species that are alien *in* and *to* South America. This inventory is a collection of existing databases, checklist and expert opinion already available for this macro-region, where the knowledge of the diversity of the aquatic alien flora is still limited indeed. The study project started in 2015 and this Chapter presents herewith the analysis of a sub-set of 250 (of the 1,463 native and non-native aquatic species so far recorded in the DB), belonging to 51 families, with 42 species ranked as invasive in at least one South American region. *Poaceae* and *Cyperaceae* were the families with the highest number of alien species. The majority of them are of South American origin (alien *in* South America), followed by those of African and Asian origin (alien *to* South America). This study project is ongoing and open to further collaboration with other scientists working in this field.

Keywords: aquatic alien plants, native and non-native plants, inventory, South America, invasive alien species.

1.1 - Introduction

The globalization has a consequence in the increase of the introduction of alien species (Ugarte et al. 2010). When plants are introduced to new environments, some of them will naturalize, and of those some will become invasive (Richardson and Pyšek 2006). European colonization in South America has been associated to landscape modifications after a first wave of introductions of European plants, mostly in Chile (Mathei 1995; Arroyo et al. 2000). However, continents as South America has, overall, fewer naturalized alien species than temperate continents (e.g., North America, Europe and Australasia) (van Kleunen et al. 2015; Pyšek et al. 2017; Seebens et al. 2017). Many species from South America have

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

restricted ranges, reflecting high levels of regional endemism (Melo et al. 2016), as a consequence species are less likely to have been dispersed outside their native ranges (van Kleunen et al. 2015). As a result, inventories are a necessary prerequisite for conservation policies (Pressey and Adam 1995) after new introductions, pointing out the sites with the highest biological diversity.

Inventories of alien plants is a need to elucidate the causes and consequences of the invasion occurrence (Mack et al. 2000; Pimentel et al. 2005). Provide information about invasive plants distribution and provide new approaching of general patterns of plant invasions (Pyšek et al. 2004), allow the identification of future introductions, monitoring trends in invasive species spread and early detection for the potential elimination or control of invasive species through risk assessment protocols (Fuentes et al. 2010). In flora inventories, it seems to be important to considerer the study area as a whole, so that, a species that is native anywhere within this area is regarded as native (Preston et al. 2002). Ideally, native and non-native categories within a region should be identified, but such data sometimes are not available for large species sets.

Nonetheless, surveys of aquatic ["plant species that grow at least a part of their life history submerged or are closely bound to aquatic habitats" (Cook 1985)] and semi-aquatic plants [species that have the capacity to withstand a continuous or periodic submersion in water, at least of their roots, occupying environments that are at least periodically waterlogged (Amaral et al. 2008)] have been conducted in several types of ecosystems, including bays, sheltered river littoral zones, lakes and reservoirs. The most important plant communities occurring are the floating aquatic mats and associated emergent herbaceous-dominated communities. On the other side, floating and rooted plants typically develop around the margins of bays and lakes and along edges of slow-moving rivers (Fortney et al. 2004). These surveys provide ecological information, as well as, the presence of introduced species, increases or decreases in the frequency of native species and identify locations that have been colonized by species that could cause excessive threat (Mormul et al. 2012).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Although approximately 50% of the inventoried inland freshwater in South America are located in Brazil (França et al. 2003; Pompeo and Moschini-Carlos 2003; Neves et al. 2006; Amaral et al. 2008, Pivari et al. 2008; Cervi et al. 2009; Kufner et al. 2011; Lima et al. 2011; Meyer and Franceschinelli 2011; Pivari et al. 2011; Valadares et al. 2011; Araújo et al. 2012; Ferreira et al. 2014), specific information related to aquatic plant species is extremely scarce. Few works address aquatic plant biodiversity and updated list of the alien plant species as in the case of Argentina (Zuloaga et al. 2015), Brazil (Amaral et al. 2013; Moura-Júnior et al. 2013; Aona et al. 2015; Oliveira and Bove 2016), Chile (Ugarte et al. 2010; Ramirez et al. 2014; Alvarez and Deil 2015), Galapagos (Guézou et al. 2010; Diaz et al. 2017), the Guianas (Funk et al. 2007), Paraguay (De Egea et al. 2012, 2016), and Venezuela (Rial 2009).

In the published checklists and grey literature there is a lack of confidence in the distinction between native and naturalized or invasive alien species (e.g., Dubs 1998; Balick et al. 2000; Kress et al. 2003). This phenomenon is because the classification of categories (e.g., casual, naturalized or also invasive) depends on researcher's personal perception of the species. These discrepancies are accidentally carried over to analysis based on species numbers reported for particular countries (Pyšek et al. 2004).

Some studies have focused on the distribution and biological traits of problematic invasive aquatic plant species in South America (see Thomaz et al. 2011; Thomaz et al. 2015). However, comprehensive information on the status and ecological impact of invasive aquatic plants in South America is very limited. Since there is a lack of studies in this field, the greatest priority is to develop inventories of alien plants in order to first recognize threats, and then, develop programs to better control the invasive species.

The aim of the research was to assemble a comprehensive inventory of South American native and non-native aquatic plant species introduced into and within South American regions through a bibliographic survey based on checklists, floras, scientific papers and expert opinion, since this continent is floristically less documented than other ones. Such a

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

database would also be a basic tool for dedicated analysis on biological invasion in inland waters in South America.

1.2 - Methodology

1.2.1 -Study area

The study area the present inventory of aquatic native and non-native plant species was the whole South American continent. For the purposes of the study, South America was divided in 16 South American regions, and they were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela (Figure 1). All these South American regions, offer a great opportunity to study biological invasions because they hold a unique native flora with high levels of endemism, extraordinary richness and diverse climatic gradients, such as, for example, in the case of the Chilean region (Pauchard et al. 2004). In addition, they offer a large variety of water bodies and habitats for aquatic plant species with many large river systems across countries, representing clear examples of interconnecting transboundary water bodies like the Paraná River Floodplain, where freshwater wetlands cover 3,650 km². The Guiana Shield (Guyana, Suriname and French Guiana) constitutes a geological, hydrographical and biogeographic region in the Amazonian Basin that is considered a biodiversity hotspot (Delnatte and Meyer 2012) and the Galapagos island is another major hotspot particularly vulnerable to invasions by alien species, which now present the largest threat to terrestrial biodiversity (Trueman et al. 2010).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 1. The 16 South American regions considered in the study were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.

1.2.2 - The main life-forms of aquatic plants: helophytes and hydrophytes.

The life forms of the aquatic plants, have been recorded according to the Raunkiaer system (1934), modified by Govaerts et al. (2000). Following this, the helophytes are plants in which surviving buds are buried in water-saturated soil, or below water-level, but that have flowers and leaves that are fully emergent during the growing season, it includes emergent aquatic herbs. The hydrophytes are fully aquatic herbs in which surviving buds are submerged, or buried in soil beneath water, their stems and vegetative shoots growing entirely underwater with leaves submerged or floating, but only the flower-bearing parts emergent.

1.2.3 - Standardized terminology for alien plants

The classification of the native vs. non-native status followed the standard terminology for alien plants proposed by Richardson et al. (2000) and Pyšek et al. (2004). Following this, those aquatic plant species whose presence in South America is due to intentional or unintentional human involvement, or which have arrived in South America without the help of people from an area in which they are non-native, were considered alien. Those species with a South American origin but occurring as alien in other parts of the SA continent were

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

called *aliens in*, and those with a native range outside SA were *aliens to*, i.e. using a terminology in line with the EU project DAISIE (Pyšek et al. 2009). Due the lack of data on the date/period of the first introduction in South America there is no distinction, in this inventory, between archaeophytes and neophytes. The information on the status according to the "naturalization-invasion-continuum" (Blackburn et al. 2011) was also not always available. Status categories in the Data-Base were defined as follows (Table 1).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

	Status		_
Category	Sub-category code	Sub-category	Description
Native	IND	Native (indigenous)	Species originated in a given area without human involvement (adapted from Pyšek et al. 2004)
	ALNCULT	Alien cultivated	
	ALNCAS	Alien casual	Alien plant species that may flourish and even reproduce occasionally outside cultivation in South America, but that eventually die out because they do not form self-replacing populations in South Aerica (adapted from Pyšek et al. 2004)
	ALNNAT	Alien naturalized	Alien plant species that sustain self-replacing populations for at least 10 years without direct intervention by people, and do not necessarily invade natural, seminatural or human-made ecosystems (adapted from Richardson et al. 2000; Pyšek et al. 2004) Subset of naturalized plants that produce
Non-native	ALNINV	Alien invasive	reproductive offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over a large area (adapted from Richardson et al. 2000; Pyšek et al. 2004) with negative impacts on biodiversity, ecosystem services, economy and human health
	ALN IN	Alien in	Plant species with a South American origin but occurring as alien in other parts of the South American continent (adapted from EU project DAISIE, Pyšek et al. 2009)
	ALN TO	Alien to	Plant species with a native distribution area outside South America (adapted from EU project DAISIE in Pyšek et al. 2009)
	ALNNA	Alien not assessed	Alien plant whose invasive status has not been assessed
Cryptogenic	CRYP		Plant species that are neither clearly native nor alien to/in South America (adapted from Carlton 1996)
Present	RREF	Present in the region	Plant species for which at least one valid record for South America was found in the GBIF database, in the scientific literature and/or provided by expert opinion (personal communication)
Absent	ABS	Declared absent in the region (SA)	Explicitly mentioned as absent
Absent	RNA	Supposedly absent in the region (SA)	No presence data on the region

Table 1. The categories used for the native and alien plants recorded in the DB

1.2.4 - Data sources

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari. The available information on the native and non-native aquatic plants in South America was collected through a dedicated search in: Web of Science, Springerlink, Science Direct, Scopus and Google Scholar, using various combinations of the following words on the search field: 'non-native', 'non-indigenous', 'exotic', 'invader', 'alien', 'aquatic plants' and 'freshwater'. Reference lists were back-tracked from existing review papers and used relevant web sites and online databases (i.e., http://plants.jstor.org, http://www.ville-ge.ch/cjb, http://www.eppo.int, http://www.nobanis.org, http://www.issg.org, http://plants.usda.gov, and national or regional floras: http://www.floraargentina.edu.ar, http://floradobrasil.jbrj.gov.br, http://www.lib.udec.cl, http://www2.darwin.edu.ar) to assemble a comprehensive inventory of the native and non-native aquatic species of South America.

All available distributional data for selected aquatic species in South America was retrieved from the GBIF portal (http://www.gbif.org, accessed on 2015) and local experts where contacted by e-mail. They were asked to provide list of aquatic species for the region of their expertise, specifying the biogeographic status (alien/native) and the invasive status (invasive/non-invasive), as well as all the available scientific and grey literature. Some of the experts on biological invasions and botany contacted were: Laboratorio de Invasiones Biológicas (LIB, Chile); Universidad Austral de Chile Charles Darwin Foundation Puerto Ayora, Galapagos (Ecuador); Facultad de Ciencias, Universidad de la República Oriental del Uruguay and Dep. Biologia, Universidade Estadual de Maringá, Brazil. Botanical gardens were both contacted by e-mail and, in a few cases visited, to collect information from Herbarium samples (e.g., Jardín Botánico de la Universidad Central de Venezuela) and grey literature.

The main plant traits and descriptions of aquatic plant are reported in the Table below. For each species, taxonomy (APG III-IV); life forms (according to Raunkier 1934 and Sculthorpe 1967); life cycle, native range, status (*alien in* and *alien to*)] (Table S1), as well as, presence and status (alien vs. native; casual vs. naturalized vs. invasive) in their places of origin or occurrence within the 16 regions (Appendix IA) were recorded.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

1.2.5 - Taxonomic and nomenclatural validation

Due to the large number of species, there was the need to apply a fast method for taxonomic and nomenclature standardization. The synonyms used in the literature were handled in accordance to The Plant List portal (http://www.theplantlist.org/) and crosschecked using IPNI (International Plant Name Index, http://www.ipni.org/). The Plant List source was chosen as main reference because provides a single accepted taxonomic classification for each species that is represented. To facilitate this, "Taxonstand" was used (R package to standardize automatically the scientific names and remove orthographic errors).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Plant traits	Description / Source		
Biological information			
Plant names	IPNI, The Plant List (http://www.theplantlist.org) and "Taxonstand" R package		
Family names	Angiosperm Phylogeny Group (APG III-IV)		
Life forms (adapted from Raunkier 1934)	Hydrophytes and helophytes (rarely phreatophytes)		
Life form (according to Sculthorpe 1967)	Floating (plants rooted in the sediment with foliage extending into the air and floating-leaved), submerged (plants that grow completely submerged and are rooted into the sediment), and free-floating (plants that float on or under the water surface)		
Life cycle	Annual, biannual, perennial		
Distribution			
Native range (TDWG)	North America, Central America, South America, Europe, North Africa, South Africa, Asia, Eurasia, Australia, Cosmopolitan		
South American regions	Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Falklands Islands, French Guiana, Galapagos, Guyana, Paraguay, Peru, South Georgia and South Sandwich Islands, Suriname, Uruguay and Venezuela		
Status	Native, Alien		
Invasive Status	cultivated-only, casual, naturalized and invasive		
Initial introduction	Intentional / Unintentional		

Table 2. The main plant traits and descriptions of aquatic plant species recorded in the DB

TDWG: Taxonomic Databases Working Group

2. Results

2.1 - Data analysis on a sub-set of the species of the Inventory

So far, the inventory lists a total of 1,463 native and non-native aquatic plant species. The quantity of information received from all contributors for each species was quite different between regions. The Figure 1 (Appendix IB) can give the reader an idea of the reliability of the floristic list. The list of aquatic species, belongs to 131 families (Figure 2).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 2. Families name and number of native and non-native aquatic plants recorded for the 16 regions of South America recorded in the inventory list of 1,463 species.

The families, number of genera and species for the 250 South American aquatic plant species (native and non-native) are summarized in Figure 3.

The study project started in 2015 and by 2017 it was possible to collect very detailed and peer reviewed information only for a smaller data-set, i.e. for 250 native and non-native aquatic plants (Table S1, Appendix IA).

Was tested the significance of the difference between the native and non-native species in the 16 regions of South America applying a t-test. The evaluation of the floristic similarity between species on different regions was accomplished through a cluster analysis. For each pair of regions, the Jaccard index of similarity (Legendre and Legendre, 1998) was calculated, using the formula: J = a/(a+b+c), where J ranges from 0 (no similarity) to 1 (100% similarity), "a" is the number of species common to both regions, "b" is the number of species restricted to one region, and "c" is the number of species restricted to the other region. The Jaccard index was calculated based on the presence/absence of non-native aquatic species in each region, using "clusteval" package R (Ramey 2012).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 3. Families name, number of genera and species for 250 native and non-native aquatic plant species recorded for the 16 regions of South America.

2.2 - Taxonomic composition of the sub-set

The sub-set of 250 species of aquatic species, belongs to 51 families. The families with the highest number of species were *Poaceae* (55) and *Cyperaceae* (45). These two families contributed 40.4 % of the species recorded and together with *Araceae* (12) and *Hydrocharitaceae* (11) were the families with the highest number of species (Figure 3). The 13.2 % (33) of the listed species are exclusively *native to* South America (Table S1). The regions with a major presence of native species were Brazil (190), Bolivia (187), and Ecuador (178) (Table 3).

A total of 76 hydrophytes were found, where 32 were submerged (13 %), 25 floating (10 %), and 19 free-floating (8 %), and a higher quantity of helophytes (172) representing the 70 % (Table 4). Also, perennial was the most frequent life-cycle (181 species) (Table 5).

The difference between the total number of native and non-native species in the 16 regions of South America, was highly significant (t = 6.9203, df = 15, p-value = 2.446e-06).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Table 3. The number of the native and non-native aquatic plants for the sub-set of 250 species, are shown in each of the 16 regions of South America. SG and SSI = South Georgia and South Sandwich Islands.

Regions	Native	Non-native
Argentina	177	36
Bolivia	187	32
Brazil	190	73
Chile	72	62
Colombia	173	49
Ecuador	178	35
Falkland Islands	8	9
French Guiana	130	27
Galapagos	49	32
Guyana	134	22
Paraguay	149	23
Peru	168	36
SG and SSI	1	2
Suriname	134	20
Uruguay	129	24
Venezuela	177	58

Table 4. Life forms are shown for the sub-set of 250 native and non-native aquatic plants species in the 16 regions of South America.

LIFE FORM	SPECIES
Helophytes	172
Hydrophytes	
Floating	25
Free-Floating	19
Submerged	32
Hydrophytes/Helophytes	2

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

LIFE-CYCLE	SPECIES
Annual	27
Biannual	2
Perennial	182
Annual/Perennial	39

 Table 5. Life cycle are shown for the sub-set of 250 native and non-native aquatic plant species in the 16 regions of South America.

2.3 - Non-native status per region

As shown in table 6, was reported 39,2 % (98 species) of aquatic *aliens in* and 18,4 % (46 species) aquatic *aliens to* South America (i.e., reported as alien at least in one region). According to the results, the regions that holding the highest number of alien aquatic plant species were Brazil (73), Chile (62), and Venezuela (58) (Table 3). Most introduced species remain within the status "ALNNA" (i.e., alien species whose invasive status has not been assessed) (Table 6).

For regions as Bolivia, Falkland Islands and South Georgia and South Sandwich Islands no data about aquatic invasive alien plant species was found. Furthermore, Chile was the region with the highest number of invasive species (15) in our sub-set of aquatic species. Among the well-known alien categories, alien naturalized had the highest number of species (118).

In general, for South America, as a whole, a total of 139 species were considered alien (i.e., alien status at least in one region), although for most regions were dominant native species. Considering the worst status in South America, was found 42 alien invasive species, with 11 hydrophytes, 30 helophytes and two considered both (hy/he), 38 naturalized and 7 cultivated species, and other 52 species reported as non-native classified as ALNNA (Table S1).

The alien species reported in this inventory were represented by 31 families and the native species represented by 40 families. The sub-set of 250 South American native and non-

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

native aquatic plants share 20 families, of which *Cyperaceae* and *Poaceae* are the most represented in both.

Table 6. Number of non-native aquatic plants, for the sub-set of the 250 species, are shown in each of the 16 regions of South America. SG and SSI = South Georgia and South Sandwich Islands. ALNNA = alien not assessed, ALNCULT = alien cultivated, ALNNAT = alien naturalized and ALNINV = alien invasive.

Regions	ALNNA	ALNCULT	ALNNAT	ALNINV	ALNTOT
Argentina	21	-	10	5	36
Bolivia	20	3	9	-	32
Brazil	52	3	10	8	73
Chile	27	-	20	15	62
Colombia	30	3	6	10	49
Ecuador	25	5	3	2	35
Falkland Islands	_	-	9	-	9
French Guiana	13	3	10	1	27
Galapagos	22	3	4	3	32
Guyana	14	-	7	1	22
Paraguay	16	1	3	3	23
Peru	26	3	4	3	36
SG and SSI	_	_	2	_	2
Suriname	12	1	6	1	20
Uruguay	14	4	3	3	24
Venezuela	27	7	12	12	58

The dendrogram built using the Jaccard coefficient showed that South American regions are dissimilar among the different alien aquatic species. Four groups of regions can be roughly recognized: 1) Falkland Islands – South Georgia and South Sandwich Islands; 2) Chile – Uruguay; 3) Argentina – Bolivia – Brazil – Colombia – Ecuador – Paraguay –Peru –Venezuela; 4) French Guiana – Galapagos – Guyana – Suriname (Figure 4), where the similarity was based on the presence/absence of non-native aquatic species in each region and the results could be, in part, due to their geographical proximity. The distance similarities are shown in table S4.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

The results are partly in agreement with the hypothesis of Irgang and Gastal (1996) that, North Argentina, Paraguay and South Brazil form a phytogeographic unit, and therefore, the sampled number of species does not closely correlate with other evaluated areas.



Figure 4. Dendrogram of floristic similarity (Jaccard coefficient) based on 250 native and non-native aquatic plant species in the 16 regions of South America. FI = Falkland Islands, FG = French Guiana, SG and SS = South Georgia and South Sandwich Islands.

3. Discussion

Many aquatic plant species that have achieved nearly global distributions has been of phytogeographical interest for centuries (Höch 1893). Cosmopolitan species either possess widespread modern distributions because they are ancient and have existed since continents were more contiguous and dispersal was readily achieved or their global dispersal has occurred relatively recently (Les et al. 2003). Most of the (alien) aquatic plants has a cosmopolitan distribution and determine exactly the native range to distinguish wether a species is native or alien is still challenging (Chambers et al. 2008).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

According to Fuentes et al. (2013) alien plants have been less collected than native plants, which are reflected in a higher concentration. To elucidate which factor determines this relationship, it is necessary to work in a regional context, emphasizing on studies that requires comparable sampling efforts for both alien and native plant species.

According to Chambers et al. (2008), the Neotropical region has the highest number of vascular aquatic macrophyte species inventoried in the world (984 species), without considering introduced species. Nevertheless, compared to developed countries (Pyšek et al. 2008, van Kleunen et al. 2015), alien plant inventories are alarmingly scarce in developing countries (Gardener et al. 2011). One reason is that field observations and grey literature are geographical poor represented, and most of them has not been scientifically checked (Gardener et al. 2011).

In general, South American regions shows that *Poaceae* and *Cyperaceae* are the predominant families. *Poaceae* has been recognized as one of the most common family within alien floras of the world after *Compositae* (Pyšek 1998; Pyšek et al. 2017). The predominance of these families was also observed in several studies involving aquatic plants (França et al. 2003; Neves et al. 2006; Pivari et al. 2008; Cervi et al. 2009; Ferreira et al. 2014; Kufner et al. 2011; Lima et al. 2011; Meyer and Franceschinelli 2011; Pivari et al. 2011; Valadares et al. 2011; Araújo et al. 2012; Aona et al. 2015; Wang et al. 2016). According studies about species richness of *Cyperaceae* in aquatic environments in Brazil, their presence is an indicator of the anthropogenic influence on the native flora composition (Pivari et al. 2008, Bryson and Carter 2008). Since seasonal changes in the aquatic environments do not interfere with their establishment, their great richness will be justified (Aona et al. 2015). The hydrology is very likely one of the most important factor in the tropics, where there are a great number of large and medium-sized rivers with active floodplains experiencing relatively natural water level fluctuations (quite different from temperate regions where most large rivers are regulated), for example the Amazon river,

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Orinoco and Paraná-Paraguay and their populations are naturally controlled by water level fluctuations (Thomaz et al. 2011).

Thomaz et al. (2011) pointing out that in contrast to most temperate and tropical areas, where some non-native species are typically become trouble aquatic species, in South American reservoirs some native plants are the most troublesome species. For example, the submerged *Egeria densa*, *E. najas* and *Ceratophyllum demersum*, the emergent *Typha domingensis* and the free floating *Eichhornia crassipes* and *Pistia stratiotes* in the Jupiá Reservoir (Brazil).

The quantity of amateur naturalists provides an important source of information, e.g. in North America (Lodge et al. 2006). Nevertheless, in Galapagos, as in other locations of South America, was expect that botanists provide a best likelihood for detecting newly naturalizing species (Hoskins et al. 2004; Guézou et al. 2010). The importance of local inventories and databases for monitoring new introductions (e.g., Melo et al. 2016), is that this information should be linked with other local, regional, national, and international efforts (e.g., for the 16 regions of South America). This approach is important for rapid response and eradication, where it is imperative to know the existing range and potential distribution of the target species (Schnase et al. 2003). In Galapagos the inventory carried out by Guézou et al. (2010) focused on the new introductions. The species found during this survey were reviewed in terms of their potential for invasiveness. Therefore, invasiveness was assessed based on weed risk assessment developed for all known alien vascular plant species in the archipelago by C. Buddenhagen, A. Tye, P. Pheloung and J. Mader, which assigned an invasion-risk group for each species. This led to identification of key future invasive species that were included in eradication feasibility studies carried out by the Charles Darwin Foundation. Additionally, part of the inventory on non-native South American aquatic species were evaluated by Lozano and Brundu (2016) with the US Aquatic Weed Risk Assessment (USAqWRA).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

4. Conclusions and first applications of the Data-Base (DB)

As every floristic Data-Base, also the present inventory of the native and non-native aquatic plants of South America is a "never-ending" ongoing work. It provides a baseline against which to compare future introductions, and a source for additional applied research in Biological Invasion Science as described in other Chapters of the present Thesis.

In particular, the information stored in the DB has been used to: 1) apply a specific risk assessment scheme on a group of 40 aquatic plant species, across 16 South American regions. The results were presented in the second chapter as a scientific paper (Lozano and Brundu 2016); 2) evaluate the increase in reliability offered by the merging of information "manually" extracted from literature, for a set of native and non-native aquatic species of South America, with the information for the same species held in GBIF. The results were presented in the third chapter as a scientific paper (Lozano et al. 2017), and 3) assess the current potential distribution of South American invasive aquatic plants, using SDMs to compare, across continents the relative importance of the climatic, and spatial components of the niche space on each species distribution within a given region. The results were presented as a poster in the international conference EMAPi 2017 (Lozano, Chapman and Brundu 2017). This chapter will be submitted in a peer-review journal.

Most data on plant species are stored in different sources, including checklists, herbaria and floras. Although the present DB stored more than 1,000 species, at the moment it was possible to collect very detailed and peer reviewed information only for 250 aquatic species. This highlight that freshwater ecosystems are often difficult to survey, thus there might be a general scarcity of accurate information about the invasive alien aquatic plants in many part of the worlds, as is the case of South America (Lozano and Brundu 2016). However, as is reported in the next chapters, GIBF and literature datasets provided significantly different information and the combination of the two offered new information and a better coverage that would not exist in a single data source. Nevertheless, a careful quality evaluation of the primary biodiversity information, both in the case of literature and

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

GBIF should be conducted, before the data is used for further analyses in macroecological studies.

Importantly, a significant part of the native aquatic plants of SA is invasive elsewhere, as in the case of *Eichhornia crassipes*. This and other aquatic plants have been recently declared as invasive alien species of Union Concern according to the Reg. (EU) no. 1143/2014.

5. References

Alvarez M, Ulrich D (2015). Vascular plant assemblages of ephemeral wetland vegetation along the Mediterranean-temperate gradient in Chile. Ensambles de plantas vasculares asociadas a humedales temporales a lo largo del gradiente mediterráneo-templado en Chile. Gayana Botanica, 72(2): 177–191.

Amaral AG, Munhoz CBR, Eugênio CUO, Felfili JM (2013). Vascular flora in dry-shrub and wet grassland Cerrado seven years after a fire, Federal District, Brasil.

Amaral MCE, Bittrich V, Faria AD, Anderson LO, Aona LYS (2008). Guia de identificação de plantas aquáticas e palustres de São Paulo. Ribeirão Preto: Holos Editora. 452 pp.

Aona LYS, da Costa GM, Maria do Carmo E, de Faria AD, Duarte EF, Bittrich V (2015). Aquatic and marsh plants from the Recôncavo basin of Bahia state, Brazil: checklist and life forms. Check List, 11(6): 1806.

APG III (2009). An update of the angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society, 161: 105–121. doi: 10.1111/j.1095-8339.2009.00996.x

Araújo ES, Sabino JHF, Cotarelli VM, Siqueira-Filho JA, Campelo MJA (2012). Riqueza e diversidade de macrófitas aquáticas em mananciais da Caatinga. Diálogos & Ciência, 32: 229–234. doi: 10.7447/dc.2012.027

Arroyo MTK, Marticorena C, Matthei O, Cavieres L (2000). Plant invasions in Chile: present patterns and future predictions. Invasive species in a changing world, 385–421.

Balick MJ, Nee MH, Atha DE (2000). Checklist of the Vascular Plants of Belize. New York Botanical Garden Press, New York.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011). A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26: 333–339.

Bryson CT, Carter R (2008). The significance of Cyperaceae as weeds; pp: 15–101, in: R.F.C. Naczi and B.A. Ford (eds.). Sedges: uses, diversity, and systematics of the Cyperaceae. St. Louis: Missouri Botanical Garden Press.

Capinha C, Essl F, Seebens H, Moser D, Pereira HM (2015). The dispersal of alien species redefines biogeography in the Anthropocene. Science, 348: 1248–1251.

Cervi AC, Bona C, Moço MCC, Linsingen L (2009). Macrófitas aquáticas do Município de General Carneiro, Paraná, Brasil. Biota Neotropica 9(3): 215–222. doi: 10.1590/s1676-06032009000300022

Chambers PA, Lacoul P, Murphy KJ, Thomaz SM (2008). Global diversity of aquatic macrophytes in freshwater. Hydrobiologia, 595: 9–26.

Cook CDK (1985). Range extensions of aquatic vascular plant species. Journal of Aquatic Plant Management, 23: 1–6. http://www.apms.org/japm/vol23/v23p1.pdf

De Egea J, Mereles F, del Carmen Pena-Chocarro M, Céspedes G (2016). Checklist for the crop weeds of Paraguay. PhytoKeys, (73): 13.

De Egea J, Peña-Chocarro M, Espada C, Knapp S (2012). Checklist of vascular plants of the Department of Ñeembucú, Paraguay. PhytoKeys, 9: 15–179. doi: 10.3897/phytokeys.9.2279

Delnatte C, Meyer J-Y (2012). Plant introduction, naturalization, and invasion in French Guiana (South America). Biological Invasions, 14: 915–927. doi: 10.1007/s10530-011-0129-1

Jaramillo Díaz P, Guézou A, Mauchamp A, Tye A (2017). CDF Checklist of Galapagos Flowering Plants - FCD Lista de especies de Plantas con flores Galápagos. In: Bungartz, F., Herrera, H., Jaramillo, P., Tirado, N., Jiménez-Uzcátegui, G., Ruiz, D., Guézou, A. & Ziemmeck, F. (eds.). Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin. Charles Darwin Foundation. Fundación Charles Darwin, Puerto Ayora, Galapagos: http://darwinfoundation.org/datazone/checklists/vascular-plants/magnoliophyta/ Last updated: 20 Mar 2017

Dubs B (1998). Prodromus Florae Matogrossensis. Betronas Verlag, Küsnacht, Switzerland.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.
Ferreira FA, Pott A, Pott VJ (2014). Métodos de amostragem quali e quantitativos de macrófitas aquáticas; pp. 45–54, in: Silva TRS, Moura CWN, Lima LCL, Santos FAR (eds.). Botânica na América Latina: Conhecimento Interação e Difusão. Salvador: Eduneb.

França F, Melo E, Góes-Neto A, Araújo D, Bezerra MG, Ramos HM, Castro I, Gomes D (2003). Flora vascular de açudes de uma região do semi-árido da Bahia, Brasil. Acta Botanica Brasilica 17(4): 549–559. doi: 10.1590/s0102-33062003000400008

Fortney RH, Benedict M, Gottgens JF, Walters TL, Leady BS, Rentch J (2004). Aquatic plant community composition and distribution along an inundation gradient at two ecologically-distinct sites in the Pantanal region of Brazil. Wetlands Ecology and Management, 12(6): 575-585.

Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2013). A new comprehensive database of alien plant species in Chile based on herbarium records. Biological invasions, 15: 847–858.

Fuentes N, Ugarte E, Kühn I, Klotz S (2010). Alien plants in southern South America. A framework for evaluation and management of mutual risk of invasion between Chile and Argentina. Biological Invasions, 12: 3227–3236. doi: 10.1007/s10530-010-9716-9

Gardener M, Bustamante R, Herrera I, Durigan G, Pivello V, Moro M, Stoll A, Langdon B, Baruch Z, Rico A, Arredondo-Nunez A, Flores S (2011). Plant invasion in Latin America: fast track to a more focused agenda. Plant Ecology and Diversity, 0: 1–8

Guézou A, Trueman M, Buddenhagen CE, Chamorro S, Guerrero AM, Pozo P, Atkinson R (2010). An extensive alien plant inventory from the inhabited areas of Galapagos. PLoS One, 5(4): e10276.

Govaerts R, Frodin DG, Radcliffe-Smith A, Carter S (2000). World Checklist and Bibliography of Euphorbiaceae (with Pandaceae). Royal Botanic Gardens, Kew.

Höch F (1893) Kosmopolitische Pflanzen. Naturwiss Wochenschr, 8: 135–138.

Hoskins JR, Waterhouse BM, Williams PA (2004). Are we doing enough about early detection of weed species naturalising in Australia? In: Fourteenth Australian Weeds Conference. pp 68–71.

Irgang BE, Gastal Jr. CVS (1996). Macrófitas Aquáticas da planície costeira do RS. CPG - Botânica/UFRGS, Porto Alegre, Rio Grande do Sul, Brazil.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Kress WJ, DeFilipps RA, Farr E, Daw YYK (2003). A checklist of the trees, shrubs, herbs, and climbers of Myanmar. Contr. U.S. Natl. Herb. 45: 1–590.

Kufner DCL, Scremin-Dias E, Guglieri-Caporal A (2011). Composição florística e variação sazonal da biomassa de macrófitas aquáticas em lagoa de meandro do Pantanal. Rodriguésia 62(4): 803–812. http://rodriguesia-seer.jbrj.gov.br/index.php/rodriguesia/article/view/316

Les DH, Crawford DJ, Kimball RT, Moody ML, Landoltk E (2003). Biogeography of discontinuously distributed hydrophytes: a molecular appraisal of intercontinental disjunctions. International Journal of Plant Sciences, 164: 917–932.

Lima LF, Silva SSL, Zickel CS (2011). Composição florística e chave de identifica ção das macrófitas aquáticas ocorrentes em reservatórios do estado de Pernambuco. Rodriguésia 62(4): 771–783. http://rodriguesia-seer.jbrj.gov.br/index.php/rodriguesia/article/view/275

Lodge DM, Williams S, MacIsaac H, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT (2006). ESA Report: Biological Invasions: Recommendations for U.S. Policy and Management. In: Ecological Applications Ecological Society of America. pp 2035–2054.

Lozano V, Brundu G (2016). Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment. Hydrobiologia, 1-16.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications, 10: 689–710.

Meyer ST, Franceschinelli EV (2011). Influência de variáveis limnológicas sobre a comunidade das macrófitas aquáticas em rios e lagoas da Cadeia do Espinhaço, Minas Gerais, Brasil. Rodriguésia 62(4): 743–758. http://rodriguesia-seer.jbrj.gov.br/index.php/rodriguesia/article/view/293

Matthei O (1995). Manual de las malezas que crecen en Chile. Alfabeta Impresores, Chile.

Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis (World Resources Institute, Washington, DC, 2005).

Melo A, Amorim BS, Pessoa E, Maciel JR, Alves M (2016). Serra do Urubu, a biodiversity hot-spot for angiosperms in the northern Atlantic Forest (Pernambuco, Brazil). Check List, 12(1): 1842.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Mormul RP, Ahlgren J, Ekvall MK, Hansson L, Bronmark C (2012). Water brownification may increase the invasibility of a sub-merged non-native macrophyte. Biological Invasions, 14: 2091–2099.

Moura-Júnior EG, Lima LF, Silva SSL, Paiva RMS, Ferreira FA, Zickel CM, Pott A. (2013). Aquatic macrophytes of Northeastern Brazil: checklist, richness, distribution and life forms. Check List, 9(2): 298–312. doi: 10.15560/9.2.298

Neves EL, Leite KRB, França F, Melo E (2006). Plantas aquáticas vasculares em uma lagoa de planície costeira no município de Candeias, Bahia, Brasil. Sitientibus - Série Ciências Biológicas, 6(1): 24–29. http://www2.uefs.br/revistabiologia/pg6_n1.html

Oliveira A, Bove C (2016) Checklist of aquatic and marshy Monocotyledons from the Araguaia River basin, Brazilian Cerrado. Biodiversity Data Journal, 4: e7085. doi: 10.3897/BDJ.4. e7085

Pauchard A, Cavieres L, Bustamante R, Becerra P, Rapoport E (2004). Increasing the understanding of plant invasions in southern South America: first symposium on Alien Plant Invasions in Chile. Biological Invasions, 6: 255–257.

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Eno, 52: 273–288.

Pivari MO, Oliveira VB, Costa FM, Ferreira RM, Salino A (2011). Macrófitas aquáticas do sistema lacustre do Vale do Rio Doce, Minas Gerais, Brasil. Rodriguésia 62(4): 759–770. http://rodriguesia-seer.jbrj.gov.br/index.php/rodriguesia/article/view/322

Pivari MOD, Pott VJ, Pott A (2008). Macrófitas aquáticas de ilhas flutuantes (baceiros) nas subregiões do Abobral e Miranda, Pantanal, MS, Brasil. Acta Botanica Brasilica. 22(2): 563–571. http://www.scielo.br/scielo.php?pid=S0102-33062008000200023& script=sci arttext

Pompêo MLM, Moschini-Carlos V (2003). Macrófitas aquáticas e perifiton, aspectos ecológicos e metodológicos. 1st edition. São Carlos: Editora Rima. 134 pp.

Pressey RL, Adam P (1995). A review of wetland inventory and classification in Australia. Vegetatio, 118(1-2): 81-101.

Preston CD, Pearman DA, Dines T D (2002). New Atlas of the British and Irish flora. Oxford Univ. Press, Oxford.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Pyšek P, Pergl J, Essl F, Lenzner B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M, Antonova L.A, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castano N, Chacón E, Chatelain C, Dullinger S, Ebel AL, Figueiredo E, Fuentes N, Genovesi P, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Maurel N, Meerman J, Morozova O, Moser D, Nickrent D, Nowak PM, Pagad S, Patzelt A, Pelser PB, Seebens H, Shu W, Thomas J, Velayos M, Weber E, Wieringa JJ, Baptiste MP, van Kleunen M (2017). Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia, 89(3): 203–274.

Pyšek P, Lambdon PW, Arianoutsou M, Kuhn I, Pino J, Winter M (2009). Alien Vascular Plants of Europe. Handbook of Alien Species in Europe. Springer Series in Invasion Ecology, 43–61.

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008). Geographical and taxonomic biases in invasion ecology. Trends Ecology Evolution, 23: 237–244.

Pyšek P, Richardson D, Rejmánek M, Webster G, Williamson M, Kirschner J (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon, 53: 131–143.

Pyšek P (1998). Is there a taxonomic pattern to plant invasions? Oikos, 82: 282–294.

Ramey JA (2012). clusteval: Evaluation of Clustering Algorithms. R package version 0.1. https://CRAN.R-project.org/package=clusteval

Ramírez C, Fariña JM, Contreras D, Camaño A, San Martín C, Molina M, Moraga P, Vidal O, Pérez, Y. (2014). La diversidad florística del humedal. Ciénagas del Name (región del Maule) comparada con otros humedales costeros de Chile. Gayana Botánica, 71(1): 108-119.

Raunkiaer C (1934). The life forms of plants and statistical plant geography. London: Claredon Press Oxford. 632 pp.

Rial A (2009). Plantas acuáticas de los llanos inundables del Orinoco Venezuela. Fundación La Salle de Ciencias Naturales.

Richardson DM, Pyšek P (2006). Plant invasions: merging the concepts of species invasiveness and community invisibility. Progress in Physical Geography, 30(3): 409–431.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Schnase JL, Cushing J, Frame M, Frondorf A, E. Landis, D. Maier, and A. Silberschatz. (2003). Information technologychallenges of biodiversity and ecosystems informatics. Information Systems, 28: 339–345.

Sculthorpe CD (1967). The Biology of Aquatic Vascular Plants. Edward Arnold Publishers, London.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017). No saturation in the accumulation of alien species worldwide. Nature Communication, 8: 14435.

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilá M (2013). Impacts of biological invasions: what's what and the way forward. Trends in Ecology Evolution, 28(1): 58–66.

Thomaz SM, Kovalenko KE, Havel JE, Kats LB (2015). Aquatic invasive species: general trends in the literature and introduction to the special issue. Hydrobiologia, 746:1–12.

Thomaz SM, Michelan TS (2011). Associations between a highly invasive species and native macrophytes differ across spatial scales. Biological Invasions, 13: 1881–1891.

Trueman M, Atkinson R, Guézou A, Wurm P (2010). Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. Biological Invasions, 12: 3949–3960.

Ugarte E, Fuentes N, Klotz S (2010) European plants in southern South America unwanted visitors? In: Settele J, Penev L, Georgiev T, Grabaum R, Grobelnik V, Hammen V, Klotz S, Kotarac M, Kuhn I (eds) Atlas of biodiversity risk. Pensoft Sofia, Bulgaria, pp 148–149.

Valadares R, Souza FBC, Castro NGD, Peres ALSS, Schneider SZ, Martins MLL (2011). Levantamento florístico de um brejo-herbáceo localizado na restinga de Morada do Sol, município de Vila Velha, Espírito Santo, Brasil. Rodriguésia, 62(4): 827–834. http://rodriguesia-seer.jbrj.gov.br/index.php/rodriguesia/article/view/258

van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova L, Barcelona JF, Cabezas FJ, Cardenas D, Cardenas-Toro J, Castano N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Upriyanov A,

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelser PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu W, Thomas J, Velayos M, Wieringa JJ, Pyšek P (2015). Global exchange and accumulation of non-native plants. Nature, 525: 100–104.

Wang H, Wang Q, Bowler PA, Xiong W (2016). Invasive aquatic plants in China. Aquatic Invasions, 11(1).

Winter M, Schweiger O, Klotz S, Nentwig W, Andriopoulos P, Arianoutsou M, Basnoue C, Delipetrouf P, Didžiulis V, Hejda M, Hulme PE, Lambdon PW, Pergl J, Pyšek P, Roy DB, Kühna I (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proceedings of the National Academy of Sciences. Sci. USA, 106(51): 21721–21725.

Zuloaga FO, Belgrano MJ (2015). The Catalogue of Vascular Plants of the Southern Cone and the Flora of Argentina: their contribution to the World Flora. Rodriguésia, 66(4): 989-1024.

7. Supplementary material

 Table S1. The sub-set list of 250 native and non-native aquatic plant species, biological traits, native range and *alien in* vs. *alien to* status in the 16 regions of South America

Species	Family	Life form	Growth form	Life cycle	Native Range	Alien IN	Alien TO
Agrostis capillaris L.	Poaceae	He		Р	Es		х
Agrostis stolonifera L.	Poaceae	He		Р	Е		х
Alternanthera brasiliana (L.) Kuntze	Amaranthaceae	He		Р	CA/SA		
Alternanthera halimifolia (Lam.) Standl. ex Pittier	Amaranthaceae	He		Р	CA/SA		
Alternanthera philoxeroides (Mart.) Griseb.	Amaranthaceae	He		Р	NA/SA	х	
Andropogon bicornis L.	Poaceae	He		Р	CA/SA	х	
Aneilema umbrosum (Vahl) Kunth	Commelinaceae	He		A/P	Af/SA		
Arundo donax L.	Poaceae	He		Р	А		x
Astraea lobata (L.) Klotzsch	Euphorbiaceae	He		A/P	NA/SA		
Azolla caroliniana Willd.	Salviniaceae	Ну	FF	А	NA/SA	x	
Azolla filiculoides Lam.	Salviniaceae	Hy	FF	A/P	Am	х	
Azolla microphylla Kaulf.	Salviniaceae	Hy	FF	A/P	NA/SA		
Bidens laevis (L.) Britton, Sterns & Poggenb.	Compositae	He		A/P	SA	х	
Bidens pilosa L.	Compositae	He		А	CA/SA	х	
Blechnum cordatum (Desv.) Hieron.	Blechnaceae	He		Р	SA		
Bolboschoenus maritimus (L.) Palla	Cyperaceae	He		Р	Cosmopolitan	х	
Brachiaria arrecta (T. Durand & Schinz) Stent	Poaceae	He		Р	Af		x
Brachiaria brizantha (A.Rich.) Stapf	Poaceae	He		Р	Af		х
Brachiaria mutica (Forssk.) Stapf	Poaceae	He		Р	Af		х
Cabomba caroliniana A.Gray	Cabombaceae	Ну	S	Р	SA	х	
Cabomba furcata Schult. & Schult.f.	Cabombaceae	Hy	S	Р	CA/SA		
Cabomba warmingii Casp.	Cabombaceae	Ну	S	Р	SA	х	
Callitriche deflexa A.Braun ex Hegelm.	Plantaginaceae	Hy	F	А	SA/E	х	
Callitriche heterophylla Pursh	Plantaginaceae	Ну	F	A/P	Am		
Callitriche terrestris Raf.	Plantaginaceae	Ну	S	А	NA		

Canna indica L.	Cannaceae	He		Р	NA/SA	х	
Caperonia castaneifolia (L.) A.StHil.	Euphorbiaceae	He		Р	NA/SA		
Cardamine bonariensis Juss. ex Pers.	Brassicaceae	He		Р	NA/SA	х	
Carex aematorrhyncha Desv.	Cyperaceae	He		Р	SA		
Centella erecta (L.f.) Fernald	Apiaceae	He		Р	NA/SA		
Ceratophyllum demersum L.	Ceratophyllaceae	Hy	S	Р	A/Af/SA/E	х	
Ceratophyllum muricatum subsp. australe (Griseb.) Les	Ceratophyllaceae	Hy	S	Р	NA/SA		
Chamaecrista nictitans (L.) Moench	Leguminosae	He		А	NA/SA		
Chloris barbata Sw.	Poaceae	He		Р	A/Af/SA	х	
Coix lacryma-jobi L.	Poaceae	He		A/P	A/HM		х
Commelina diffusa Burm.f.	Commelinaceae	He		A/P	Trop./Sub-trop.	х	
Commelina obliqua Vahl	Commelinaceae	He		Р	CA/SA		
Conium maculatum L.	Apiaceae	He		В	Е		х
Cotula australis (Sieber ex Spreng.) Hook.f.	Compositae	He		A/P	Aus		х
Cotula coronopifolia L.	Compositae	He		A/P	Af		х
Crassula venezuelensis (Steyerm.) M.Bywater & Wickens	Crassulaceae	Hy	S	А	SA		
Crotalaria retusa L.	Leguminosae	He		Р	A/Af/AusA		х
Cuphea racemosa (L.f.) Spreng.	Lythraceae	He		Р	SA	х	
Cyperus alternifolius L.	Cyperaceae	He		Р	SAf/Arabian Pen.		х
Cyperus articulatus L.	Cyperaceae	He		P	NA/SA/SAf	x	
Cyperus difformis L	Cyperaceae	He		Р	E		x
Cyperus digitatus Roxh	Cyperaceae	He		P	Pantropical	x	
Cyperus eragrostis Lam	Cyperaceae	He		Р	CA/SA		
Cyperus esculentus L	Cyperaceae	He		A/P	Cosmonolitan	x	
Cyperus giganteus Vahl	Cyperaceae	He		P	CA/SA	л	
Cyperus dasnan I	Cyperaceae	He		Δ/Ρ	4/4f/C4/S4	v	
Cyperus iria I	Cyperaceae	He		Δ/Ρ	A/Af	~	v
Cyperus Ina E.	Cyperaceae	Не		P	E/SA	v	л
Cyperus licularis I	Cyperaceae	He		P	A f/N A/S A/F	л	
Cyperus luzulae (I) Retz	Cyperaceae	He		P	NA/SA	v	
Cyperus adoratus I	Cyperaceae	He		Δ/Ρ	A f/N A /S A	x	
Cyperus vallarus Vahl	Cyperaceae	Не		D	CA/SA	л	
Cyperus returdus I	Cyperaceae	Не		D	A/SA	v	
Cyperus roundus E.	Cyperaceae	Ца		1	Madagasaar	A V	
Cyperus squarosus E.	Cyperaceae	Не		A/P	NA/SA	A V	
Cyperus surmanhroditus (Joca) Standl	Cyperaceae	Не		D	NA/SA	A V	
Desmodium adscendens (Sw) DC	Leguminosae	Не		D	A/A f/N A/S A	Λ	
Desmodium dascenaens (Sw.) DC.	Leguminosae	Не		D	A/Af/NA/SA		
Desmodium incanum DC	Leguminosae	Не		D	CA/SA	v	
Digitaria ciliaria (Rota) Voolor	Baaaaaa	Ца		1 A /D		Λ	v
Digitaria citaris (Keiz.) Kocki	Loguminosoo	Ца		D		v	л
Dioteeu virgene (K.H.) Anishon	Baaaaaa	Ца		r D	Am	х	
Disticutis spicata (L.) Greene	Ameranthaaaaa	Ца		г л/D	Am	v	
Eshinochlog colong (L.) Hink	Reason	Ца		A	Alli CA	х	v
Echinochioa coiona (E.) Link	Poaceae	Пе		A	CA		X
Echinochioa crusgani (L.) F. Beauv.	Poaceae	Пе		A	CA		X
Echinochioa crus-pavonis (Kunth) Schutt.	Poaceae	Пе		A D	CA Arra		X
Echinochioa polystachya (Kuntii) Filtene.	Aliamataaaaa	Пе		P			
Echinodorus grandijiorus (Cham. & Schildi.) Michen	Aliamataceae	Пе	c	P	CA/SA	X	
Echinodorus norizontalis Kataj	Alismataceae	Ну	S	P A/D	SA	х	
Echinoaorus paniculatus Michell	Composite	ну	3	A/P	CA/SA		
Ecupia prostrata (L.) L.	Undreaharite	He	c	A/P	Am	X	
Egeria aensa Planch.	Hydrocharitaceae	Hy	5	P	SA	x	
Egeria najas Planch.	Hydrocharitaceae	Ну	S	P	SA	x	
Elennornia azurea (Sw.) Kunth	Pontederiaceae	Hy	FF	P	CA/SA	х	
Elennornia crassipes (Mart.) Solms	Pontederiaceae	Ну	FF	Р	SA	х	

Eichhornia paniculata (Spreng.) Solms	Pontederiaceae	He		А	NA/SA	х	
Eleocharis acicularis Roem et Schult.	Cyperaceae	Ну	S	Р	Nor. Hemis. /A/SA/E	х	
Eleocharis acutangula (Roxb.) Schult.	Cyperaceae	He		Р	Pantropical	х	
Eleocharis bonariensis Nees	Cyperaceae	He		Р	NA/SA		
Eleocharis elegans (Kunth) Roem. & Schult.	Cyperaceae	Hy	S	Р	A/Af/Am	х	
Eleocharis exigua (Kunth.) Roem. & Schult.	Cyperaceae	He		Р	Am		
Eleocharis geniculata (L.) Roem. & Schult.	Cyperaceae	He		Р	Pantropical	х	
Eleocharis interstincta (Vahl) Roem. & Schult.	Cyperaceae	He		Р	Am	х	
Eleocharis minima Kunth	Cyperaceae	He		А	Am		
Eleocharis montana (Kunth) Roem. & Schult.	Cyperaceae	He		Р	NA/SA		
Eleocharis mutata (L.) Roem. & Schult.	Cyperaceae	He		Р	Af/NA/SA		
Eleocharis sellowiana Kunth	Cyperaceae	He		Р	CA/SA	х	
Elodea canadensis Michx.	Hydrocharitaceae	Ну	S	Р	NA/SA	х	
Elodea granatensis Humb. & Bonpl.	Hydrocharitaceae	Ну	S	Р	SA	х	
Eragrostis ciliaris (L.) R.Br.	Poaceae	He		А	A/Af		х
Eragrostis hypnoides (Lam.) Britton, Stern & Poggenb.	Poaceae	He		А	Am		
Eragrostis pectinacea (Michx.) Nees	Poaceae	He		А	Am	х	
Euphorbia heterophylla L.	Euphorbiaceae	He		А	CA/SA		
Fimbristylis autumnalis (L.) Roem. & Schult.	Cyperaceae	He		А	Am	х	
Fimbristylis complanata (Retz.) Link	Cyperaceae	He		Р	Pantropical		
Fuirena umbellata Rottb.	Cyperaceae	He		Р	Cosmopolitan	х	
Glyceria fluitans (L.) R.Br.	Poaceae	He		Р	Af		х
Habenaria trifida Kunth.	Orchidaceae	He		Р	SA		
Hedychium coronarium J.Koenig	Zingiberaceae	He		Р	India/HM		х
Helanthium bolivianum (Rusby) Lehtonen & Myllys	Alismataceae	He		А	CA/SA		
Helanthium tenellum (Mart. ex Schult.f.) J.G.Sm.	Alismataceae	Hy	S	A/P	CA/SA		
Hippuris vulgaris L.	Plantaginaceae	Hy	S	Р	Е		х
Holcus lanatus L.	Poaceae	He		А	Е		х
Hydrilla verticillata (L.f.) Royle	Hydrocharitaceae	Hy	S	Р	A/Aus/NAf		х
Hydrocleys nymphoides (Humb. & Bonpl. ex Willd.) Buchenau	Alismataceae	Ну	F	Р	SA	х	
Hydrocotyle ranunculoides L.f.	Araliaceae	Hy/He	F/E	Р	Am	х	
Hydrocotyle umbellata L.	Araliaceae	Ну	F	Р	Am trop.	х	
Hydrolea spinosa L.	Hydroleaceae	He		Р	NA/SA	х	
Hymenachne amplexicaulis (Rudge) Nees	Poaceae	He		Р	Am	х	
Hymenachne donacifolia (Raddi) Chase	Poaceae	He		Р	CA/SA		
Hymenachne pernambucensis (Spreng.) Zuloaga	Poaceae	He		Р	CA/SA		
Hypoxis decumbens L.	Hypoxidaceae	He		Р	CA/SA		
Isachne polygonoides (Lam.) Döll	Poaceae	He		Р	CA/SA		
Isolepis cernua (Vahl) Roem. & Schult.	Cyperaceae	He		A/P	Cosmopolitan		
Juncus balticus Willd.	Juncaceae	He		Р	E/NA/SA	х	
Juncus bufonius L.	Juncaceae	He		A/P	Cosmopolitan	х	
Juncus capillaceus Lam.	Juncaceae	He		Р	SA		
Juncus cyperoides Laharpe	Juncaceae	He		Р	NA/SA		
Juncus effusus L.	Juncaceae	He		Р	Cosmopolitan	х	
Juncus imbricatus Laharpe	Juncaceae	He		Р	SA		
Juncus microcephalus Kunth	Juncaceae	He		Р	CA/SA		
Juncus pallescens Lam.	Juncaceae	He		Р	SA		
Juncus tenuis Willd.	Juncaceae	He		Р	NA		х
Justicia laevilinguis (Nees) Lindau	Acanthaceae	He		Р	Neotrop.		
Kyllinga brevifolia Rottb.	Cyperaceae	He		Р	Cosmopolitan	х	
Kyllinga vaginata Lam.	Cyperaceae	He		Р	Af/SA		
Lasthenia kunthii (Less.) Hook. & Arn.	Compositae	He		Р	Cosmopolitan		
Leersia hexandra Sw.	Poaceae	He		Р	Cosmopolitan	x	
Lemna aequinoctialis Welw.	Araceae	Hy	FF	Р	SA	х	

Lemna gibba L.	Araceae	Hy	FF	А	Cosmopolitan	х	
Lemna minor L.	Araceae	Hy	FF	Р	Cosmopolitan	х	
Lemna minuta Kunth	Araceae	Hy	FF	Р	Am		
Lemna valdiviana Phil.	Araceae	Hy	FF	Р	NA/SA		
Leptochloa virgata (L.) P.Beauv.	Poaceae	He		Р	Am	х	
Lilaeopsis macloviana (Gand.) A.W. Hill	Apiaceae	Hy	S	Р	SA		
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	Hydrocharitaceae	Hy	FF	A/P	SA	х	
Limnocharis flava (L.) Buchenau	Alismataceae	He		Р	CA/SA/India		
Limosella australis R.Br.	Scrophulariaceae	He		А	NA/SA	х	
Ludwigia grandiflora (Michx.) Greuter & Burdet	Onagraceae	He		Р	NA/SA		
Ludwigia hexapetala (Hook. & Arn.) Zardini, H.Y. Gu & P.H. Raven	Onagraceae	He		Р	Am/SA	x	
Ludwigia leptocarpa (Nutt.) H.Hara	Onagraceae	He		Р	Af/NA/SA	х	
Ludwigia octovalvis (Jacq.) P.H.Raven	Onagraceae	He		Р	Am	х	
Ludwigia peploides (Kunth) P.H.Raven	Onagraceae	He		Р	A/Aus/Am	х	
Ludwigia peruviana (L.) H.Hara	Onagraceae	He		Р	NA/SA		
Luziola bahiensis (Steud.) Hitchc.	Poaceae	He		Р	NA/SA		
Luziola subintegra Swallen	Poaceae	He		Р	CA/SA		
Mauritia flexuosa L.f.	Arecaceae	Не		Р	SA		
Mayaca fluviatilis Aubl	Mavacaceae	Hv	s	p	Am		
Mayaca madida (Vell) Stellfeld	Mayacaceae	Hy	S	A/P	SA		
Mayaca maanaa (Ven.) Stefficia Myrionhyllum aquaticum (Vell.) Verde	Haloragaceae	Hy	E/S	P	SA/NZ	v	
Myriophyllum autansa Kunth	Haloragaceae	Hy/He	173 S	D I	SA	Λ	
Najas guadalupansis (Sprang.) Magnus	Hydrocharitaceae	Hy	S	1	Am		
Najas marina I	Hydrocharitaceae	IIy Uv	5	A	Cosmonolitan		
Naturtium officing lo P. Pr	Prossionoono	Цо	3	A D	NA/Eq		v
Nasurium officiale K.Bl.	Nalumhanaaaaa	Пе	F	r	NA/ES		X
Neumbo nucijera Gaerin.	Neumbonaceae	Пу	Г	D	A/AI		
Nymphaea alba L.	Nymphaeaceae	Hy	F	P	AI/ES/E		х
Nymphaea amazonum Mart. & Zucc.	Nymphaeaceae	Hy	F	P	CA/SA	X	
Nymphaea ampia (Salisb.) DC.	Nymphaeaceae	Hy	F	P	CA/SA		
Nymphaea lotus L.	Nymphaeaceae	Ну	F	P	A/AI		х
Nymphaea mexicana Zucc.	Nymphaeaceae	Hy	F	P	CA/NA		x
Nymphaea micrantha Guill. & Perr.	Nymphaeaceae	Hy	F	P	At		Х
Nymphaea rubra Roxb. ex Andrews	Nymphaeaceae	Hy	F	Р	A trop.		х
Nymphoides fallax Orndutt	Menyanthaceae	Hy	F	A/P	NA		Х
Nymphoides indica (L.) Kuntze	Menyanthaceae	Hy	F	A/P	CA/SA		
Oryza grandiglumis (Döll) Prodoehl	Poaceae	He		A/P	SA		
<i>Oryza latifolia</i> Desv.	Poaceae	He		Р	CA/SA		
Oryza rufipogon Griff.	Poaceae	He		Р	A/Aus		Х
<i>Oryza sativa</i> L.	Poaceae	He		A/P	A/Af		х
Oxycaryum cubense (Poepp. & Kunth) Palla	Cyperaceae	He		Р	Af/Am	Х	
Panicum elephantipes Nees ex Trin.	Poaceae	Hy	F	Р	CA/SA		
Panicum grande Hitchc. & Chase	Poaceae	He		Р	CA/SA		
Panicum hylaeicum Mez	Poaceae	He		Р	CA/SA		
Panicum maximum Jacq.	Poaceae	He		A/P	A/Af		Х
Panicum repens L.	Poaceae	He		Р	A/Af/Aus/E		х
Paspalidium geminatum (Forssk.) Stapf	Poaceae	He		Р	A/Af/NA/SA		
Paspalum conjugatum P.J.Bergius	Poaceae	He		Р	Am	x	
Paspalum dilatatum Poir.	Poaceae	He		Р	SA	х	
Paspalum distichum L.	Poaceae	He		Р	NA/SA	х	
Paspalum fasciculatum Willd. ex Flüggé	Poaceae	He		Р	NA/SA	х	
Paspalum pallens Swallen	Poaceae	He		Р	CA/SA		
Paspalum paniculatum L.	Poaceae	He		Р	CA/SA	х	
Paspalum repens P.J.Bergius	Poaceae	Hy	F/S	Р	Am		
Paspalum vaginatum Sw.	Poaceae	He		Р	NA/SA	х	
Paspalum wrightii Hitchc. & Chase	Poaceae	He		Р	NA/SA	х	

Passiflora foetida L.	Passifloraceae	He		A/P	A/SA		
Persicaria hydropiperoides (Michx.) Small	Polygonaceae	He		Р	SA	х	
Persicaria punctata (Elliott) Small	Polygonaceae	He		В	NA/SA	х	
Phalaris arundinacea L.	Poaceae	He		A/P	A/E/NA		х
Phragmites australis (Cav.) Trin. ex Steud.	Poaceae	He		Р	Cosmopolitan	х	
Pistia stratiotes L.	Araceae	Hy	FF	Р	SA	х	
Polypogon viridis (Gouan.) Breistr.	Poaceae	He		Р	Е		х
Pontederia cordata L.	Pontederiaceae	Hy	F	Р	NA/SA		
Pontederia rotundifolia L.f.	Pontederiaceae	Hy	F	Р	CA/SA		
Potamogeton illinoensis Morong	Potamogetonaceae	Hy	S	Р	Am		
Potamogeton lucens L.	Potamogetonaceae	Hy	S	Р	A/Af/E		х
Potamogeton natans L.	Potamogetonaceae	Hy	F	Р	A/NA/E		х
Potentilla anserina L.	Rosaceae	He		Р	Е		х
Pycreus polystachyos (Rottb.) P.Beauv.	Cyperaceae	He		Р	Cosmopolitan		
Pycreus unioloides (R.Br.) Urb.	Cyperaceae	He		Р	A/Af/CA/SA		
Ranunculus aquatilis L.	Ranunculaceae	Hy	S	A/P			
Rhabdadenia madida (Vell.) Miers	Apocynaceae	He		Р	CA/SA		
Rhynchospora holoschoenoides (Rich.) Herter	Cyperaceae	He		Р	Af/CA/SA		
Rhynchospora nervosa (Vahl) Boeckeler	Cyperaceae	He		Р	CA/SA		
Rhynchospora tenuis Link	Cyperaceae	He		Р	CA/SA		
Rumex acetosella L.	Polygonaceae	He		Р	E		x
Ruppia maritima L.	Ruppiaceae	Hv	S	P	Cosmopolitan		
Sagittaria guavanensis Kunth	Alismataceae	Hv	F	A/P	SA		
Sagittaria montevidensis Cham & Schltdl	Alismataceae	Не	-	A/P	NA/SA	x	
Sagittaria rhombifolia Cham	Alismataceae	He		Р	SA		
Sagittaria sagittifolia L	Alismataceae	Не		-	A/E		x
Salvinia auriculata Aubl	Salviniaceae	Hv	FF	А	Cosmonolitan	x	
Sawagesia erecta L	Ochnaceae	Не	••	Р	SA/Af		
Schoenonlectus californicus (C A Mey) Soják	Cyperaceae	He		A/P	Am	x	
Schrönig gaertneri Raddi	Cyperaceae	He		P	Af/CA/SA	x	
Setaria parviflora (Poir) M Kerspelen	Poaceae	He		P	Am	x	
Spermacoce verticillata L	Rubiaceae	He		P	CA/NA/SA	A	
Sphagneticola trilobata (L.) Pruski	Compositae	He		P	CA/SA		
Spirodela nunctata (G Mey) C H Thomps	Araceae	Hy	FF	P	SA		
Stachytarpheta indica (L.) Vahl	Verbenaceae	He		P	CA		
Steinchisma larum (Sw.) Zuloaga	Poaceae	He		A/P	CA/SA		
Stratiotes aloides I	Hydrocharitaceae	Hy	F	P	E		
Struckenia filiformis (Pers.) Börner	Potamogetonaceae	Hy	S	P	A/NA/SA/F		
Stuckenia nectinata (L.) Börner	Potamogetonaceae	Hy	S	P	Cosmonolitan		
Stuckenia striata (Ruiz & Pay.) Holub	Potamogetonaceae	Hv	S	P	NA/SA		
Syngonanthus caulescens (Poir) Ruhland	Eriocaulaceae	Не	5	Р	SA		
Thalia geniculata L	Marantaceae	Не		P	NA/SA		
Trana natans L	Lythraceae	Hv	F		A/E		x
Triglochin scilloides (Poir) Mering & Kadereit	Juncaginaceae	Не	-	А	NA/SA		
Typha angustifolia L	Typhaceae	He		Р	A/A f/E/NA		x
Typha domingensis Pers	Typhaceae	Не		P	SA	x	
Typha latifolia L	Typhaceae	He		Р	CA/SA/Holoartic	x	
Urena lobata L	Malvaceae	Не		P	Pantropical	x	
Utricularia foliosa L	Lentibulariaceae	Hv	F	Р	Af/NA/SA		
Utricularia gibba L	Lentibulariaceae	Hv	F	A/P	A/NA/CA		
Vallisneria americana Michx	Hydrocharitaceae	Hv	F		NA		x
Veronica anagallis-gauatica L	Plantaginaceae	He		A/P	Es/SA	x	A
Victoria amazonica (Poenn) J.C. Sowerby	Nymphaeaceae	Hv	F	A	SA	x	
Victoria cruziana A D. Orb	Nymphaeaceae	Hv	F	P	SA	x	
Vigna luteola (Jaca) Benth	Leguminosae	He		A/P	A/Af/Aus/SA	x	
	Deganniosue						

Wolffia brasiliensis Wedd.	Araceae	Hy	FF	Р	CA/SA	x
Wolffiella lingulata (Hegelm.) Hegelm.	Araceae	Hy	FF	Р	NA/SA	
Wolffiella oblonga (Phil.) Hegelm.	Araceae	Hy	FF	Р	NA/SA	
Wolffiella welwitschii (Hegelm.) Monod	Araceae	Hy	FF	Р	Am. Af Trop.	
Xyris laxifolia Mart.	Xyridaceae	He		Р	CA/SA	
Zannichellia palustris L.	Potamogetonaceae	Hy	S	A/P	Cosmopolitan	х

(Af Africa, Am America, Aus Australia, AusA Australasia, A Asia, CA Central America, E Europe, Es Eurasia, HM Himalayas, NA North America, NAf North Africa, NZ New Zealand, SA South America), and different life cycle and life forms (A annual, A/P annual/perennial, B Biannual, P perennial, He helophyte, Hy hydrophyte, F floating, FF free-floating, S submerged).

Table S2. List of families with the number of genera and species for the sub-set of 250 native and non-native aquatic plant species in the 16 regions of South America.

Family	Genera	Species
Acanthaceae	1	1
Alismataceae	5	9
Amaranthaceae	2	4
Apiaceae	3	3
Apocynaceae	1	1
Araceae	5	12
Araliaceae	1	2
Arecaceae	1	1
Blechnaceae	1	1
Brassicaceae	2	2
Cabombaceae	1	3
Cannaceae	1	1
Ceratophyllaceae	1	2
Commelinaceae	2	3
Compositae	5	7
Crassulaceae	1	1
Cyperaceae	14	45
Eriocaulaceae	1	1
Euphorbiaceae	3	3
Haloragaceae	1	2
Hydrocharitaceae	7	11
Hydroleaceae	1	1
Hypoxidaceae	1	1
Juncaceae	1	9
Juncaginaceae	1	1
Leguminosae	5	7
Lentibulariaceae	1	2
Lythraceae	1	1

Malvaceae	1	1
Marantaceae	1	1
Mayacaceae	1	2
Menyanthaceae	1	2
Nelumbonaceae	1	1
Nymphaeaceae	2	8
Ochnaceae	1	1
Onagraceae	1	6
Orchidaceae	1	1
Passifloraceae	1	1
Plantaginaceae	3	5
Poaceae	27	55
Polygonaceae	2	3
Pontederiaceae	2	5
Potamogetonaceae	3	8
Rubiaceae	1	1
Ruppiaceae	1	1
Salviniaceae	2	4
Scrophulariaceae	1	1
Typhaceae	1	3
Verbenaceae	1	1
Xyridaceae	1	1
Zingiberaceae	1	1

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Table S3. Distance matrix of floristic similarity (Jaccard coefficient) for the sub-set of 250 native and nonnative aquatic plant species in the 16 regions of South America. FI = Falkland Islands, FG = French Guiana, SG and SS = South Georgia and South Sandwich Islands.

	Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	FI	FG	Galapagos	Guyana	Paraguay	Peru	SG,SS	Suriname	Uruguay	Venezuela
Argentina	0.000	0.455	0.625	0.775	0.534	0.521	0.816	0.688	0.764	0.711	0.525	0.531	0.944	0.727	0.667	0.597
Bolivia	0.455	0.000	0.658	0.730	0.627	0.325	0.861	0.659	0.792	0.650	0.590	0.522	0.970	0.700	0.634	0.657
Brazil	0.625	0.658	0.000	0.729	0.663	0.671	0.922	0.738	0.767	0.753	0.724	0.675	0.973	0.795	0.775	0.653
Chile	0.775	0.730	0.729	0.000	0.679	0.689	0.855	0.873	0.854	0.909	0.867	0.759	0.968	0.907	0.716	0.763
Colombia	0.534	0.627	0.663	0.679	0.000	0.526	0.863	0.643	0.791	0.709	0.691	0.607	0.959	0.698	0.673	0.534
Ecuador	0.521	0.325	0.671	0.689	0.526	0.000	0.872	0.524	0.712	0.500	0.585	0.457	0.972	0.553	0.595	0.591
FI	0.816	0.861	0.922	0.855	0.863	0.872	0.000	0.971	0.975	1.000	0.968	0.875	0.778	1.000	0.821	0.919
FG	0.688	0.659	0.738	0.873	0.643	0.524	0.971	0.000	0.659	0.310	0.649	0.660	1.000	0.259	0.725	0.559
Galapagos	0.764	0.792	0.767	0.854	0.791	0.712	0.975	0.659	0.000	0.744	0.721	0.692	1.000	0.700	0.809	0.732
Guyana	0.711	0.650	0.753	0.909	0.709	0.500	1.000	0.310	0.744	0.000	0.594	0.682	1.000	0.250	0.789	0.644
Paraguay	0.525	0.590	0.724	0.867	0.691	0.585	0.968	0.649	0.721	0.594	0.000	0.628	1.000	0.656	0.795	0.714
Peru	0.531	0.522	0.675	0.759	0.607	0.457	0.875	0.660	0.692	0.682	0.628	0.000	0.973	0.727	0.667	0.657
SG,SS	0.944	0.970	0.973	0.968	0.959	0.972	0.778	1.000	1.000	1.000	1.000	0.973	0.000	1.000	0.960	0.966
Suriname	0.727	0.700	0.795	0.907	0.698	0.553	1.000	0.259	0.700	0.250	0.656	0.727	1.000	0.000	0.778	0.655
Uruguay	0.667	0.634	0.775	0.716	0.673	0.595	0.821	0.725	0.809	0.789	0.795	0.667	0.960	0.778	0.000	0.719
Venezuela	0.597	0.657	0.653	0.763	0.534	0.591	0.919	0.559	0.732	0.644	0.714	0.657	0.966	0.655	0.719	0.000

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

CHAPTER 2

PRIORITISATION OF AQUATIC INVASIVE ALIEN PLANTS IN SOUTH AMERICA WITH THE US AQUATIC WEED RISK ASSESSMENT

Introduction and aims

Many efforts have been directed to develop tools to predict and prevent future invasions, as after they became invasive their control is costly and might be inefficient. Reliable prioritization and risk assessment methods that could help in prevention and management of potentially harmful species and they are fundamental tools to tackle biological invasions. It is very important to predict which introduced species are able to establish viable populations and spread and possible to prevent their entry. In general, there are a number of risk analysis, impact assessment, ranking systems, decision trees, and prioritization, unfortunately the lack of a common framework for assessing risks posed by IAS on South American countries is seen as a key gap. The aim of this research was to prioritize and classify the most invasive species applying a standard risk assessment scheme for aquatic plants in South America

Methodology and main results

The USAqWRA (US Aquatic Weed Risk Assessment) was tested on a set of 40 native and non-native aquatic plants, retrieved from the South American DB of aquatic alien plants (*Cf.* Chapter 1). The USAqWRA addresses ecology, competitive ability, dispersal modes and reproductive capacity. The USAqWRA assigns a final score and defines categories of invasiveness indicating the risk associated with the introduction or invasion, establishing three levels of impacts: non-invader, minor and major invader. The USAqWRA distinguished between non-invaders and invaders with an overall accuracy of 84.9% in South America and 54.1% in the 16 regions.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Conclusions

The study highlights that the USAqWRA could represent a suitable screening protocol to prioritize aquatic species that have the potential to cause negative impacts, prevent attempts of introduction and to manage risky aquatic plants in South America.

Lozano, V., Brundu, G. (2016). Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment. Hydrobiologia 1-16, DOI: 10.1007/s10750-016-2858-8

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

PLANTS IN AQUATIC SYSTEMS



Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment

Vanessa Lozano · Giuseppe Brundu

Received: 25 March 2016/Revised: 2 June 2016/Accepted: 3 June 2016 © Springer International Publishing Switzerland 2016

Abstract Forty South American aquatic plant species were selected and categorised in four a priori status classes (alien naturalised, alien invasive, native and absent) according to expert opinion, for 16 South American regions (Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Falklands Islands, French Guiana, Galapagos, Guyana, Paraguay, Peru, South Georgia and South Sandwich Islands, Suriname, Uruguay and Venezuela). The 40 aquatic plant species were assessed using the US Aquatic Weed Risk Assessment (USAqWRA) scheme for each of the 16 South American regions, for a total number of 644 assessments and for South America (153 assessments). The method was benchmarked against expert opinion (invasive, non-invasive). We ranked 17 of them as naturalised, and 15 as invasive species in at least one South American region. The USAqWRA distinguished between non-invaders and invaders with an overall accuracy of 84.9% in South America and

Guest editors: M. T. O'Hare, F. C. Aguiar, E. S. Bakker & K. A. Wood / Plants in Aquatic Systems – a 21st Century Perspective

Electronic supplementary material The online version of this article (doi:10.1007/s10750-016-2858-8) contains supplementary material, which is available to authorized users.

V. Lozano (⊠) · G. Brundu Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy e-mail: vlozano@uniss.it

Published online: 20 June 2016

54.1% in the 16 regions, with areas under the curves equal to 0.893 and 0.853, at a threshold score of 51.5 and 43.5, respectively. The study highlights that the USAqWRA could represent a suitable screening protocol to prioritise aquatic species that have the potential to cause negative impacts, prevent attempts of introduction and to manage risky aquatic plants in South America.

Keywords Negative impacts · Non-native aquatic species · Aquatic plants · Risk assessment · Prioritisation

Introduction

Freshwater ecosystems, in particular lakes and reservoirs, have been identified to be both highly vulnerable to invasive species (Strayer, 2010; Simberloff, 2013; Boltovskoy & Correa, 2015) and the most endangered ecosystems in the world (e.g., Collen et al., 2014). Biological invasions in freshwaters can be dramatic because freshwater ecosystems have the greatest concentration of species per surface area in the planet (Thomaz et al., 2015) and they act as stepping stones for establishing invaders in new watersheds (Havel et al., 2015). At the same time, aquatic and semi-aquatic plants have a higher probability of becoming invasive than do species from terrestrial plant families (Daehler, 1998) and thus form

🖄 Springer

a significant proportion of potential invasive species (Andreu & Vilà, 2010; Azan et al., 2015).

The excessive growth of invasive alien macrophytes can produce negative impacts on the invaded freshwater ecosystem and substantially change the hydrology, sedimentation, water clarity and nutrient state of river and lakes (Gallardo et al., 2015; Havel et al., 2015). Aquatic invasion may, for example, reduce the habitat available for other species positioned higher in the trophic web such as invertebrates and fish (van Kleunen et al., 1999; Matsuzaki et al., 2009; Carniatto et al., 2014).

In order to effectively prioritise management options, stakeholders affected by biological invasions need to be able to identify those species, among different taxa, that are likely to cause the most damage (Hulme et al., 2012; Kumschick et al., 2015). Nonnative species are not uniformly invasive nor harmful (Santos et al., 2011), and may have a little or undetectable impact in the new region or produce negative impacts only after a certain period of time (Pyšek et al., 2012; Strayer, 2012) as "sleeping weeds" (Groves, 2006). These alien plants can behave as minor invaders for decades before they become serious invaders. Nevertheless, impacts may vary along time and among species and regions. In the framework of this research is essential not to understate the risk of potential impacts from species that may have delayed invasions.

The scarcity of studies on plant invasions both in terrestrial and aquatic ecosystems and the analogous paucity of supporting policy and investment in Latin America pose an opportunity to develop an invasive plant research agenda specifically focused on South America, to provide knowledge to help identify priorities for both decision makers and managers (Gardener et al., 2012). Impacts of invasive alien plants are not always perceived as such and they may differ throughout the South American region.

In South America, Chile, offers a unique opportunity to study biological invasions because it has a unique native flora with high levels of endemism, extraordinary richness and diverse climatic gradients (Pauchard et al., 2004). In addition, Chile and Brazil have been suggested as the very suitable regions to test invasion ecology generalities and hypotheses that have been tested in other parts of the world (Ormazabal, 1993; Arroyo et al., 2000; Myers et al., 2000). The Guiana Shield (Guyana, Suriname and French

2 Springer

Guiana) constitutes a geological, hydrographical and biogeographic region in the Amazonian Basin that is considered a biodiversity hotspot (Delnatte & Meyer, 2012) and the Galapagos island is another major hotspot particularly vulnerable to invasions by alien species, which now present the largest threat to terrestrial biodiversity (Trueman et al., 2010). South America offers a large variety of water bodies and habitats for macrophytes with many large river systems and streams cross many countries. Argentina, Brazil and Paraguay represent a clear example of interconnecting transboundary water bodies like the Paraná River Floodplain, where freshwater wetlands cover 3650 km². These networks provide opportunities of natural spread of aquatic plants in areas previously free of alien vegetation.

The accelerating worldwide movement of people and human activities are driving the increasing rate at which biological invasions are occurring (e.g., Essl et al., 2011; Seebens et al., 2013; Essl et al., 2015) and South America is not an exception to this trend (e.g., Almeida et al., 2015). Currently, introductions of nonnative plants caused by human-presence represent 45% of total plant species on Galapagos (Mauchamp, 1997; Guézou et al., 2010; Heleno et al., 2013). Trade and cross-border connections are, for example, constantly increasing between Brazil, French Guiana, Suriname, and Guyana. The cross-border cooperation program for the 2014-2020 period between the outermost region of French Guiana, Suriname and the states of Amapá and Amazonas in Brazil is expected to double the number of passengers (currently nearly 12,000) and triple the number of vehicles (currently 7800) crossing the Maroni by ferry each year (European Commission, 2015). Similarly, anthropogenic disturbances may contribute favouring naturalisation and invasion of intentionally or accidentally introduced alien plant species (Delnatte & Meyer, 2012). Bini & Thomaz (2005) reported a large number of aquatic weeds that were introduced in Paraná River, Brazil, affecting electric power generation. Fuentes et al. (2010) remarked how trade between Chile and Argentina may facilitate the transport of propagules, thus increasing the risk of new alien plant introductions.

Prioritisation, Risk Assessment and Risk Analysis are fundamental tools for managing non-native species and identifying those species that are likely to become invasive and cause significant negative

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

impacts (e.g., Brunel et al., 2010; Kumschick et al., 2012; Verbrugge et al., 2012). Among risk assessment schemes, the Australian Weed Risk Assessment (A-WRA, Pheloung et al., 1999) was shown to be effective in classifying plant invaders across several islands and continents (Gordon et al., 2008). The A-WRA is routinely used for regulatory purposes in Australia, New Zealand and Chile. The A-WRA has been adapted to other parts of the world including Hawaii (Daehler & Carino, 2000), Hawaii and Pacific Islands (Daehler et al., 2004), Czech Republic (Křivánek & Pyšek, 2006) and Bonin Islands (Kato et al., 2006). A-WRA has also been used to help manage quarantine issues between countries that share a land border, such as Chile and Argentina (Fuentes et al., 2010) and guidance questions could easily be modified to suit the needs in Latin America (Gardener et al., 2012).

However, many of the A-WRA questions are specific to terrestrial plant species, therefore, this scheme is considered less accurate in discriminating between aquatic invaders and non-invaders considered at least at the US scale (Gordon & Gantz, 2011). More recently, the Aquatic Weed Risk Assessment Model (AWRAM) was developed for New Zealand (NZAq-WRA) (Champion & Clayton, 2000, 2010) and subsequently it has been applied in Australia and Micronesia (Champion et al., 2008; Champion & Clayton, 2010). Gordon et al. (2012) developed a modified AWRAM scheme for USA called US Aquatic Weed Risk Assessment (USAqWRA).

As far as we know, our study is the first attempt to apply a specific risk assessment scheme (USAqWRA) for aquatic plants in South America. Therefore, the present research aims to benchmark the USAqWRA on a group of 40 aquatic plant species, across 16 South American regions, comparing its scoring and classification with the existing a priori classification of the invasive status based on South American expert opinion.

Methodology

Study area and species selection

The present research focuses on 40 aquatic plant species. Among them, four a priori status categories were defined according to expert opinion, classifying each of the forty species in one of the four following status categories for each of the 16 regions defined in the present study, or for part of the regions. The four status categories were as follows: alien naturalised (NNV),¹ alien invasive (INV),² native (IND) and absent (ABS) (e.g., Richardson et al., 2000; Pyšek et al., 2004, 2009). To perform data analysis, these four a priori status categories were grouped in an additional binary category: invasive and non-invasive, the latter including both alien naturalised (but not invasive) and native species. In addition, for each of the 40 species, we assigned a priori status for the entire region of South America, as a binary category: invasive and non-invasive. This South American status was based as well on expert opinion, taking into account the worst scenario, i.e. a species was categorised as invasive in South America whenever it was considered invasive in at least one of the 16 regions; otherwise it was considered as non-invasive in South America. Therefore, species only naturalised but non-invasive were included in this second category.

The invasive alien species are those reported as naturalised with negative ecological impacts on biodiversity, economy, and ecosystem services according to local experts' opinion. Local experts where contacted by e-mail. They were asked to provide list of aquatic species for the region of their expertise, specifying the biogeographic status (alien/native) and the invasive status (invasive/non-invasive), as well as all the available scientific and grey literature. Our data collection included both helophytes (plants in which surviving buds are buried in water-saturated soil, or below water-level, but that have flowers and leaves that are fully emergent during the growing season; it includes emergent aquatic herbs) and hydrophytes (fully aquatic herbs in which surviving buds are

Deringer

¹ Naturalised: alien plants that sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets capable of independent growth, and do not necessarily invade natural, seminatural or human-made ecosystems (Richardson et al., 2000; Pyšek et al., 2004; Blackburn et al., 2011).

² Invasive: subset of naturalised plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants (approximate scales: >100 m in <50 years for taxa spreading by seeds and other propagules; >6 m in 3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a large area. (Richardson et al., 2000; Pyšek et al., 2004; Blackburn et al., 2011).

submerged, or buried in soil beneath water; their stems and vegetative shoots growing entirely underwater with leaves submerged or floating, but only the flowerbearing parts emergent, see Raunkiaer 1934, as modified by Govaerts et al. 2000), and can be classified as free-floating, floating (rooted), emergent and submerged freshwater macrophytes (Table 1). We also cross-checked literature and databases on the status of the species reported in each region by experts (Table 1 of Appendix I—Supplementary Material).

The 16 South American regions (there after called "regions") are defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.

Risk assessment methodology

The USAqWRA scheme is a modified version by Gordon et al. (2012) of the original NZAqWRA scheme (New Zealand Aquatic Weed Risk Assessment). The USAqWRA addresses questions on ecology, competitive ability, dispersal modes, reproductive capacity and mode, potential for different types of impacts (e.g., hindrance to navigation, water quality), resistance to management, and history of invasion elsewhere. After answering the 38 questions, which are divided into 12 groups, the protocol assigns a final score as a sum of the values for each question. The final score can range between 3 and 91, with higher scores indicating species with a higher risk.

We calculated the USAqWRA total score for each of the 40 aquatic plants and for each South American region or part of region for a total number of 644 assessments (Table 2 of Appendix I—Supplementary Material). For example, *Catabrosa aquatica* (L.) P.Beauv., was assessed twice both for Argentina and Chile, as it is considered both as native in one part and non-native and non-invasive in another part of the region (Soreng & Fish, 2011). Similarly, *Egeria densa* Planch., is recorded both as native and alien invasive in different regions of Brazil (Rodrigues & Thomaz, 2010; Aona et al., 2015).

Among the 644 assessments, we selected a subset of 153 assessments, according to the following criteria: for each species we took into account the worst scenario for the whole 16 regions and selected all the assessments in accordance; i.e. if a species was invasive in one or more regions we selected one or more assessments accordingly, if a species was not invasive in any region we selected the assessments for the regions where it was considered at least naturalised.

The USAqWRA questions were answered using information from a variety of sources including online databases and factsheets (i.e. http://plants.jstor. org; http://www.ville-ge.ch/cjb; http://www.eppo.int; http://www.nobanis.org; http://www.issg.org; http:// plants.usda.gov; http://www.floraargentina.edu.ar; http://floradobrasil.jbrj.gov.br; http://www.tropicos. org). We collected all the available literature from Scopus, Web of Science, Google Scholar and Research Gate using specific key words and search term combinations: (invasive aquatic species OR aquatic invasion) AND (alien plant OR plant invasion OR exotic plant) AND (South American invasion OR South American macrophytes). Data about invasiveness from outside South America were used to answer questions about invasiveness. Nevertheless, when considering the questions 11, 27-29, 32 and 33-37 (noted in Results Table 3) in the USAqWRA scheme, we scored differently on a case by case basis, taking into account the native/alien status of the assessed species in that specific region.

In order to test the difference between the a priori binary status for the 16 regions and for South America (invasive vs. non-invasive), we used One-way Analysis of Variance (ANOVA).

Evaluation of the performance of USAqWRA scheme

The whole set of 644 assessments was considered for evaluating the performance of the USAqWRA scheme for each of the 16 regions, while the subset of 153 assessments was used to evaluated the scheme at South American level.

The performance of the USAqWRA was benchmarked using Receiver Operating Characteristic (ROC) curve analysis and compared to the expert opinion (invasive vs. non-invasive), respectively, for the 40 aquatic species for each region (644 assessments) and for South America (153 assessments). This method is widely used for assessing the performance of a screening test. A ROC curve represents test specificity (accuracy for correctly categorising non-

D Springer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Hydrobiologia

Species	Native origin	Life span	Life form	Pathy	way of duction	Expert opinion range	USAqWRA score range (min–max)
Alisma lanceolatum	E/NAf/A	Р	Hy/E	Y		ABS, NNV	32
Alisma plantago-aquatica	Aus/E/A	Р	Hy/S	Y		ABS, NNV	32
Alternanthera philoxeroides	SA	Р	He	Y	S/Ballast water	ABS, IND, NNV	51-63
Arundo donax	A/E	Р	He	Y		ABS, INV	66–69
Azolla filiculoides	SA/CA/NA	AP	Hy/FF	Y	S/Ballast water	ABS, IND, INV	39–54
Brachiaria subquadripara	Tropics	AP	Hy/E	Ν	C/Forage	ABS, INV	49-52
Catabrosa aquatica	Circumboreal/SA	Р	Hy	NA		ABS, IND, NNV	14–19
Ceratophyllum demersum	Cosmopolitan	Р	Hy/S	Y		ABS, IND, INV	28-39
Crassula peduncularis	Aus/NZ/SA	А	He	Y		ABS, IND	20-23
Cyperus difformis	E/Af/A	А	He	Ν	S/Machinery-equipment	ABS, INV	41-44
Echinodorus uruguayensis	SA	Р	Hy/S	NA		ABS, IND	25-28
Egeria densa	SA/E	Р	Hy/S	Y		ABS, IND, INV	54-66
Egeria najas	SA	Р	Hy/S	NA		ABS, IND, INV	36-51
Eichhornia azurea	SA	Р	Hy/F	NA		ABS, IND	49-61
Eichhornia crassipes	SA	Р	Hy/FF	Y		ABS, IND, INV	66–76
Elodea canadensis	NA	Р	Hy/S	Y		ABS, NNV	39
Hippuris vulgaris	E/NA/SA	Р	Hy/S	Y		ABS, IND, INV	38-46
Hydrilla verticillata	A/Af	Р	Hy/S	Y		ABS, INV	59-61
Hydrocleys nymphoides	SA	Р	Hy/F	Y		ABS, IND, NNV	30-37
Hydrocotyle leucocephala	SA	Р	Hy/F	NA		ABS, IND	34-47
Hydrocotyle ranunculoides	SA/CA/NA	Р	Hy/E	Y		ABS, IND, INV	47-62
Lemna gibba	NA/E/A/SA	AP	Hy/FF	NA		ABS, IND, NNV	36-46
Lemna minor	Cosmopolitan	Р	Hy/FF	Y		ABS, IND, NNV	40-49
Limnobium laevigatum	SA/CA	Р	Hy/FF	NA		ABS, IND, INV	45-60
Ludwigia grandiflora	NA/SA	Р	He	Y		ABS, IND	51-68
Ludwigia peploides	NA/CA/SA	Р	He	Y		ABS, IND, INV	49-64
Myriophyllum aquaticum	SA	Р	Hy/S	Y		ABS, IND, NNV	53-63
Myriophyllum quitense	SA	Р	Hy/S	NA		ABS, IND	28-45
Nymphaea alba	E/Es	Р	Hy/F	Y		ABS, INV	30-33
Nymphaea lotus	A/Af	Р	Hy/E	Y		ABS, NNV	39
Nymphoides indica	Subcosmopolitan	Р	Hy/F	Y		ABS, IND, NNV	23-28
Pistia stratiotes	SA	Р	Hy/FF	NA		ABS, IND, NNV	54-67
Potamogeton pusillus	Cosmopolitan	AB	Hy/S	NA		ABS, IND, NNV	28-30
Ranunculus aquatilis	E/A/Am/Aus/Af	AP	Hy/S	Y		ABS, IND, NNV	22–27
Sagittaria guayanensis	SA	Р	Hy/E	NA		ABS, IND	24-35
Salvinia auriculata	SA/CA	А	Hy/FF	NA		ABS, IND, NNV	44–55
Salvinia molesta	SA	Р	Hy/FF	Y		ABS, IND, NNV	49–64
Spirodela punctata	Aus/East A	Р	Hy/FF	Y	S/Ballast water	NNV	24
Typha angustifolia	Circumboreal	Р	Hy/E	Ν	S/Machinery-equipment	ABS, INV	39
Wolffia Braziliensis	SA	Р	Hy/FF	NA		ABS, IND	18-27

Table 1 List of the investigated 40 aquatic plant species varying for native origin

(Af Africa, Am America, Aus Australia, A Asia, E Europe, Es Eurasia, NA North America, NAf North Africa, SA South America), status according to expert opinion in South America (INV alien invasive, NNV alien non-invasive, IND native, ABS absent) and different life span and life forms (A annual, AB annual/biannual, AP annual/perennial, P perennial, He helophyte, Hy hydrophyte, E emergent, F floating rooted, FF free-floating, S submerged). Pathway of introduction is shown as a category and subcategory: Y Escape (the species was voluntary introduced as an ornamental), N pathway not related to the use as an ornamental species, NA information not available. Other pathway categories: C contaminant, S stowaway. The USAqWRA scores are shown as a range with minimum and maximum values

Deringer

Hydrobiologia

invasive plants as having low risk of invasiveness, i.e. true negatives) against the complement of sensitivity (accuracy for correctly categorising invasive plants as having high risk of invasiveness, i.e. true positives) over the range of potential cut-off levels (Conser et al., 2015).

The areas under the ROC curves (AUROC) were calculated using the software R (R Core Team, 2015) and the R package "pROC" (Carstensen et al., 2015). An AUC value closer to 1.0 would indicate that the scheme perfectly discriminates between invaders and non-invaders. On the contrary, values near 0.5 indicate an inability to discriminate (Conser et al., 2015). Threshold USAqWRA score was calculated by the point of the ROC curve closest to the point on the axes that maximises the true positives and minimises the false positives.

In addition, we used the R package "Ime4" (Bates et al., 2015) to perform a generalised linear mixed models (GLMM) analysis of the relationship between the USAqWRA scores (invasiveness risk) and the expert assessment status (alien invasive, alien non-invasive, native, absent), for each aquatic species and in each SA region (or part of region). The GLMM analysis was considered the most suitable method because the response variable of interest (USAqWRA scores) was not normally distributed (Shapiro-Wilk normality test, W = 0.97335, P value = 2.007e-09) and the Levene's test did not support the presence of equal variances. Furthermore, our USAqWRA scores were repeated measures (estimates) on the same set of species (40) and regions (16). Mixed models allow including both fixed and random variables, which is required in studies where individuals are repeatedly measured (Faraway, 2006; Bolker et al., 2009; Hamel et al., 2016). As fixed effects, we entered into the GLMM model the plant species (40) and the expert assessment of the status (4 categories), without interaction terms. As random effects, we had intercepts for species:status:regions. This model was selected among the other possible models (including the null model with no fixed effects and only species as random effect and a full model with three fixed effects), taking into account its lower AIC score (i.e. 118.55 vs. 453.98 for the null model).

Evaluation of the performance of the single questions of the USAqWRA scheme

To determine which questions of the USAqWRA scheme contributed to the predictability of invasiveness

versus non-invasiveness, we applied a logistic regression model, considering as a dependent binary variable the successful outcomes of the USAqWRA scores, i.e. the sum of true positive and true negatives versus the sum of false positives and false negatives (unsuccessful outcomes, over 644 assessments). Due to the large number of questions, to avoid convergence problems between parameters (for the maximum likelihood estimation, see Heinze & Ploner, 2003, 2004), Firth's bias reduced logistic regression was used as implemented in the R package "logistf" (Heinze et al., 2013). For each question, we calculated the percentage of times it was answered both for invasive and noninvasive aquatic species.

Results

Species status categories according to expert opinion

As a result, among the 40 investigated species, 17 are naturalised alien and 15 are invasive alien in at least one of the 16 South American regions considered in this study. Eight species are native to one or more regions, but are absent in the other regions and therefore they potentially could be introduced in the future. Using terminology in line with the EU project DAISIE (Pyšek et al., 2009), we can highlight that only 6 of the 15 invasive alien species and 5 of the 17 naturalised ones are alien to South America (i.e. with a native range outside SA), while the other 9 invasive and 12 naturalised species are alien in South America, i.e. with a SA origin but occurring as alien in other parts of the SA continent. While this sample size was relatively small, it included different categories of aquatic plant species which represent diversity in both taxonomic relationship, phenology, life form and level of risk according to expert opinion (Table 1 and Supplementary materials).

According to expert opinion, the regions with the larger numbers of alien invasive aquatic plant, among the forty species investigated in the present study, are as follows: Chile (9 species), Brazil (6) and Colombia (3) (Fig. 1). The regions with the larger numbers of alien non-invasive aquatic plants are as follows: Chile (16), Argentina (11) and Colombia (10). In two of the study regions, i.e. in Argentina and Bolivia, 21 of the 40 investigated species are considered native

Deringer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Fig. 1 Regional distribution of the four a priori status defined by expert opinion of the 40 South American aquatic plant species investigated (*ABS* absent, *IND* native, *INV* alien invasive, *NNV* alien naturalised and non-invasive)

according to expert opinion (Fig. 1). None of the 40 aquatic plant species investigated are present in the Falkland Islands, with the exception of *Myriophyllum quitense* Kunth which is considered native to the archipelago.

Noteworthy, *Eichhornia crassipes* (Mart.) Solms is considered invasive in 10 South American regions and native in 4 regions, while *Arundo donax* L., is considered invasive in 4 regions, *Cyperus difformis* L., and *E. densa* Planch., in 3 regions. All the other species are considered invasive in a lower number of regions, or they are considered alien but non-invasive or native (Table 1 and Supplementary materials).

USAqWRA scores and invasion categories

We assessed the 40 South American aquatic plant species in each of the 16 regions (or part of a region) for a total of 644 assessments. The information collected for each species allowed us to answer a mean of 37 questions (range 34–38 questions, ± 1.3 SD) out of 38 questions of the USAqWRA scheme, for each of the 644 assessments.

The scores obtained by the 15 species classified as invasive by expert opinion in at least one region (INV) ranged from 30 to 76 (33 assessments); the scores for the 17 species classified as non-invasive alien (NNV) ranged from 19 to 67 (82 assessments); the scores for the 8 species classified as native (IND) ranged from 14 to 66 (203 assessments). The other 326 assessments were done for those species not present in a region (ABS), therefore for all regions at potential risk of invasion, and scores ranged from 14 to 73.

The difference among invasion categories (invasive and non-invasive) were highly significant both in 16 regions (*P* value = 4.197e-16) and in South America (*P* value = 2.2e-16) (Fig. 2).

The four species with the highest scores were (76) E. crassipes; (69) A. donax; (68) Ludwigia grandiflora (Michx.) Greuter & Burdet, and (67) Pistia stratiotes L. (Table 1). The lowest USAqWRA scores were 14-19 and 18-27, respectively, for C. aquatica and Wolffia iensis Wedd. The lowest score for C. aquatica (14) refers to Argentina and Chile being considered native to part of these regions, and to the 14 regions where it is absent. On the contrary, the highest score for C. aquatica (19) refers to the parts of Argentina and Chile where this species is considered a naturalised alien. In the case of W. brasiliensis, the lowest score (18) was obtained for the 11 regions where the species is considered native, while the highest score (27) was obtained for the 5 regions where the species is presently absent (Table 2 Appendix I-Supplementary Material).

The results of the GLMM analysis for fixed effects are displayed in Table 2. These results clearly state that the USAqWRA scores are significantly correlated (positively or negatively) for 32 of the 40 aquatic species assessed (Table 2).



Fig. 2 Box and whisker plots showing USAqWRA scores of the 40 South American aquatic plant species. On the *left* the results for 16 regions (644 assessments), on the *right* for South America

as a single continental unit (153 assessments), for the two categories of invasion: alien invasive (INV) and alien naturalised (non-invasive), including native species (NNV)

Accuracy of the USAqWRA scheme

The USAqWRA distinguished between non-invaders and invaders with an overall accuracy of 54.1% and an AUC = 0.853, at a threshold score of 43.5 (point on the ROC curve that maximised the ability for classification of the test). The percentage of specificity (54.17%) was slightly lower than the sensitivity (54.54%).

In addition, on the subset of 153 assessments, we obtained for South America a higher overall accuracy of 84.9% and a larger AUC = 0.893, at a threshold score of 51.5 (Fig. 3). The percentage of specificity (87.50%) was higher than the sensitivity (75.75%).

Species with USAqWRA scores higher than the threshold are predicted as having a high risk of invasiveness while species with scores lower than the threshold are predicted as a non-invasive or at lower risk, respectively at region level and at South American level.

USAqWRA questions and their predictive power

To identify those questions having a significantly higher predictive power to separate invasive aquatic plants from non-invasive, we used a penalised likelihood based method called Firth logistic regression. A group of 8 questions (with a P < 0.05 over the 38 questions of the scheme) was delimited. These questions had a higher significant predictive power to separate invasive aquatic plants from non-invasive aquatic plants, although the percentage of time each

D Springer

question was answered was lower (for non-invasive species) (Table 3). These questions can be classified into three groups: (1) ecology and habitat of the species; (2) seeding ability; and (3) potential of impact and damage to natural areas. In Table 3, the percentages of times each of the 38 questions was answered are shown. The percentages for invasive plants ranged from 93 to 100% and for non-invasive plants ranged from 76 to 100%.

Discussion

As far as we know, this is the first application of the USAqWRA scheme to South America. Furthermore, only very few aquatic plant species have been risk assessed in South American countries using any other risk assessed with the Weed Risk Assessment for Chile and Argentina by Fuentes et al. (2010) (Supplementary materials). In the present research, we assessed 40 aquatic species using the USAqWRA concluding that the method can be conveniently applied to South American aquatic plant species, when there is enough available knowledge on the assessed species. At the same time, the USAqWRA score can be used to prioritise species according to their level of risk.

As remarked in the methodology section, the available expert opinion allowed the identification of only four a priori status categories that were subsequently grouped in a binary invasion category (invasive and non-invasive). Therefore, we were in a

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Table 2Results of theGLMM analysis for thefixed effects considered inthe model

Fixed effects	Estimate	SE	Z value	Pr(> z)	Sign. code
(Intercept)	3.47E+00	4.42E-02	78.39	<2.00E-16	***
Alisma plantago-aquatica	3.60E-05	6.25E-02	0.00	0.99954	
Alternanthera philoxeroides	6.89E-01	5.64E-02	12.22	<2.00E-16	***
Arundo donax	7.19E-01	5.55E-02	12.94	<2.00E-16	***
Azolla filiculoides	4.46E-01	5.95E-02	7.49	6.68E-14	***
Brachiaria subquadripara	4.25E-01	5.69E-02	7.47	8.13E-14	***
Catabrosa aquatica	-7.65E-01	7.60E-02	-10.06	<2.00E-16	***
Ceratophyllum demersum	3.39E-02	6.30E-02	0.54	0.590222	
Crassula peduncularis	-3.00E-01	6.96E-02	-4.31	1.65E-05	***
Cyperus difformis	2.44E-01	5.95E-02	4.09	4.25E-05	***
Echinodorus uruguayensis	-1.01E-01	6.54E-02	-1.54	0.12356	
Egeria densa	6.56E-01	5.46E-02	12.03	<2.00E-16	***
Egeria najas	3.66E-01	5.83E-02	6.28	3.49E-10	***
Eichhornia azurea	6.54E-01	5.74E-02	11.4	<2.00E-16	***
Eichhornia crassipes	8.57E-01	5.62E-02	15.24	<2.00E-16	***
Elodea canadensis	1.98E-01	5.98E-02	3.31	0.000925	***
Hippuris vulgaris	3.04E-01	5.84E-02	5.2	1.96E-07	***
Hydrilla verticillata	6.09E-01	5.50E-02	11.07	<2.00E-16	***
Hydrocleys nymphoides	1.56E-01	6.26E-02	2.5	0.012461	*
Hydrocotyle leucocephala	3.39E-01	6.00E-02	5.65	1.60E-08	***
Hydrocotyle ranunculoides	6.15E-01	5.60E-02	10.98	<2.00E-16	***
Lemna gibba	3.59E-01	5.89E-02	6.09	1.12E-09	***
Lemna minor	4.32E-01	5.75E-02	7.52	5.46E-14	***
Limnobium laevigatum	5.79E-01	5.80E-02	9.97	<2.00E-16	***
Ludwigia grandiflora	7.26E-01	5.56E-02	13.05	<2.00E-16	***
Ludwigia peploides	6.48E-01	5.68E-02	11.42	<2.00E-16	***
Myriophyllum aquaticum	6.84E-01	5.53E-02	12.36	<2.00E-16	***
Myriophyllum quitense	2.10E-01	6.21E-02	3.38	0.000725	***
Nymphaea alba	-6.59E-02	6.36E-02	-1.04	0.300309	
Nymphaea lotus	1.98E-01	6.00E-02	3.3	0.000961	***
Nymphoides indica	-1.11E-01	6.79E-02	-1.63	0.102099	
Pistia stratiotes	7.50E-01	5.66E-02	13.27	<2.00E-16	***
Potamogeton pusillus	7.53E-04	6.44E-02	0.01	0.990667	
Ranunculus aquatilis	-1.67E-01	6.58E-02	-2.54	0.011059	*
Sagittaria guayanensis	-1.06E-02	6.66E-02	-0.16	0.873466	
Salvinia auriculata	5.47E-01	5.79E-02	9.44	<2.00E-16	***
Salvinia molesta	6.88E-01	5.46E-02	12.6	<2.00E-16	***
Spirodela punctata	-2.87E-01	6.83E-02	-4.21	2.57E-05	***
Typha angustifolia	1.97E-01	5.99E-02	3.28	0.001035	**
Wolffia iensis	-2.77E-01	7.12E-02	-3.89	0.000101	***
Native	-2.32E-01	1.70E-02	-13.63	<2.00E-16	***
Alien invasive	2.27E-02	2.83E-02	0.8	0.423226	
Alien non-invasive	-5.77E-04	2.05E-02	-0.03	0.977564	

The significant *P* values are reported and graphically coded in the last column (0 '**' 0.001 '**' 0.01 '*' 0.05 '.'). The Species:Status:Country Intercept values (random factor) equal to 2.566e-18 and 1.602e-09

Deringer



Fig. 3 Receiver operating characteristic (ROC) curves graph of the performance of the USAqWRA scheme to predict whether species are invasive or non-invasive, as determined by expert opinion for 40 South American aquatic plants in each of 16 regions (*black line*) and for South America as a single continental unit (*red line*). Bootstrapping was used to calculate

the confidence intervals. *Upper* and *lower* bands representing 95% level of confidence and the horizontal light grey shape corresponds to the pAUC region. The *diagonal line* represents an area of 0.5 (i.e. complete inability to distinguish between invasive and non-invasive species)

different position to that of Gordon et al. (2012) who used three a priori status, i.e. non-invasive, minor invasive and major invasive. Our results indicate that the USAqWRA scheme is a reliable method to distinguish between non-invasive and invasive aquatic plant species in South America both at region level and at continental scale. The areas under the ROC curves for the 40 South American aquatic plant species assessed were, respectively, equal to 0.853 for the 16 regions (644 assessments) and to 0.893 for South America (153 assessments). Similarly, Conser et al. (2015) tested the Plant Risk Evaluation (PRE) tool by screening 56 known invasive plants and 36 known non-invasive plants and they found a high degree of accuracy for correctly categorising plant species as either high or low risk of invasiveness. On the other hand, Nishida et al. (2009) and McClay et al. (2010) evaluated the Australian Weed Risk Assessment (A-WRA), respectively, for Japan and Canada. Area under the ROC curve was 0.88 for Japan. Areas under the ROC curves for Canada were 0.867 when minor weeds were included as positives (minor weeds were counted as weeds), and 0.845 when only major weeds were counted as positives (only major weeds were

Deringer

considered weeds). Gordon et al. (2012) reported an AUC = 0.96 (when minor invaders were grouped with non-invaders) and AUC = 0.88 (when minor invaders were grouped with major invaders).

The A-WRA scheme is considered effective for different regions across the globe (Pheloung et al., 1999; Gordon et al., 2008; Nishida et al., 2009). However, the cut-off levels have to be selected case by case (Nishida et al., 2009). Gordon et al. (2012) tested USAqWRA for USA using adequate cut-off levels for that region. As remarked by Nishida et al. (2009), different cut-off levels might be required for different study areas. Accordingly, we used different cut-off levels to evaluate the performance of USAqWRA, respectively, for the group of 16 regions (644 assessments) and for South America (153 assessments) as a single continental unit.

The binary classification deriving from USAqWRA is in line with local expert opinion about invasion categories, but it highlights potential invasive species or emergent invaders that are not yet perceived as such by local expert and stakeholders. This could certainly help improve both prevention and early warning strategies. For example, there were 11 species that are not currently

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Hydrobiologia

Question (Q)#	Q–USAqWRA	FLR	% Q was answered for invasive plants	% Q was answered for non-invasive plants
1	Temperature tolerance	P = 0.427	100	100
2	Range of habitat	$P = 0.0005^{**}$	100	100
3	Water/substrate type tolerance	P = 1.000	100	100
4	Water clarity tolerance	<i>P</i> = 0.014*	100	100
5	Salinity tolerance	P = 0.066	93	100
6	pH tolerance	<i>P</i> = 0.046 *	100	96
7	Water level fluctuation-Tolerates periodic flooding/drying	P = 0.668	100	100
8	Lentic—rivers, streams, drains, or other flowing waters, including their margins	P = 0.126	100	100
9	Ponds, lakes and other standing waters, including their margins	P = 1.000	100	100
10	Swamp, marsh, bog	P = 0.249	100	100
11	Establishment-into existing vegetation	P = 0.074	93	100
12	Establishment-into disturbed vegetation	P = 0.167	100	100
13	Competition-between growth form	P = 0.082	100	96
14	Dispersal outside catchment by natural agents (e.g., birds, wind)	P = 0.170	100	100
15	Dispersal outside catchment by accidental human activity	P = 0.379	93	88
16	Dispersal outside catchment by deliberate introduction	P = 0.127	100	96
17	Effective spread within water body/catchment	P = 0.477	100	96
18	Generation time (time between germination of an individual and the production of living offspring, not seeds or other dormant structures)	P = 0.060	100	100
19	Seeding ability—Quantity	P = 0.154	100	100
20	Seeding ability-Viability/persistence	<i>P</i> = 0.045*	100	92
21	Vegetative reproduction (Cloning ability)	P = 0.343	100	100
22	Obstruction-Physical-water use, recreation	P = 0.387	93	100
23	Obstruction-Physical—access	P = 0.435	100	100
24	Obstruction- Physical-water flow, power generation	P = 0.025*	100	96
25	Obstruction-Physical-irrigation, flood control	$P = 0.0002^{**}$	93	100
26	Aesthetic-visual, olfactory	<i>P</i> = 0.014 *	100	100
27	Damage to natural areas-Reduces biodiversity	P = 0.690	93	96
28	Damage to natural areas-Reduces water quality	P = 1.000	100	100
29	Damage to natural areas—Negatively affect physical processes	<i>P</i> = 0.050	93	100
30	Human health impairment (e.g., drowning, poisonous, mosquito habitat)	P = 0.250	100	100
31	Weed of agriculture, including crops, livestock and aquaculture	P = 0.075	100	100
32	Resistance to management—Management—Ease of management implementation	P = 0.109	100	96
33	Resistance to management—Management—Recognition of management problem	P = 0.055	100	96
34	Resistance to management—Management—Scope of control methods	P = 0.063	93	88

Table 3 The thirty-eight questions of the USAqWRA scheme and their statistical predictability in separating known invasive and non-invasive alien species

D Springer

Table 3 continued				
Question (Q)#	Q–USAqWRA	FLR	% Q was answered for invasive plants	% Q was answered for non-invasive plants
35	Resistance to management—Management—Control method suitability	P = 0.068	93	76
36	Resistance to management—Management—Effectiveness of control	P = 0.158	93	84
37	Resistance to management—Management—Duration of control	P = 1.000	93	76
38	Problem in other countries	P = 1.000	100	96

Firth's bias reduced logistic regression (FLR) was used to compare invasive aquatic species with non-invasive aquatic species for each question of the scheme. The significant P values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.') are in **bold** letters. The percentage of time each question (% Q) was effectively answered is also reported

considered invasive by the expert opinion, but were scored as invasive by the USAqWRA, having scores higher than the threshold in at least one region of South America. This disagreement could be related to a general lack of information for South America or awareness of the negative impacts of those species or on their alien status as in the cases of M. quitense Kunth (28-45), Hydrocotyle leucocephala Cham. & Schltdl., (34-47), Lemna gibba L., (36-46), Lemna minor L., (40-49), Salvinia auriculata Aubl., (44-55), Eichhornia azurea (Sw.) Kunth (49-61), Salvinia molesta D.S. Mitch., (49-64), Alternanthera philoxeroides (Mart.) Griseb., (51-63), Ludwigia grandiflora (51-68), Myriophyllum aquaticum (Vell.) Verdc. (53-63) and Pistia stratiotes (54-67). These species may become invasive in the future, as forecasted by their USAqWRA scores, and also as they are very well known invaders worldwide, as in the case of Salvinia molesta and Pistia stratiotes. In addition, in many cases, the climatic similarity between the native range and the introduced range might successfully predict establishment and invasiveness risk (Hayes & Barry, 2008; Kumschick & Richardson, 2013).

Importantly, one of these 11 species, i.e. *Ludwigia* grandiflora, is recorded as an invasive alien in many countries outside its native range (Gordon & Gantz, 2011; EPPO, 2015) and it may require proactive management preventing its introduction in the 7 South American regions where it is considered absent.

On the contrary, *Ceratophyllum demersum* (28–39), *Nymphaea alba* (30) and *Typha angustifolia* (39) were considered invasive by the expert opinion, but scored lower with USAqWRA, which suggests that their actual invasive potential requires further attention.

We can highlight that species such as *Spirodela punctata* (G.Mey.) Les & D.J.Crawford (24), *Alisma plantago-aquatica* L. (32), and *Hydrocleys nymphoides* (Humb. & Bonpl. ex Willd.) Buchenau (30–37) (non-invasive according to expert opinion), with scores close to the threshold, may become invasive in the future. In fact, they are ranked as invasive according to Gordon & Gantz (2011) and Gordon et al., 2012 in North America. Those alien species could be considered "sleeping weeds" (Groves, 2006), and they may behave as minor invaders for decades before they become serious invaders.

When evaluating the predictive power of the 56 questions of the final PRE tool, Conser et al. (2015) detected that only 11 of them showed statistical significance in separating invasive from non-invasive species. Four were the result of merging two similar questions, where both were significant or near significant (e.g., different methods of vegetative reproduction, various biotic and abiotic propagule dispersal mechanisms). Similarly to Conser et al. (2015), we evaluated the predictive power of the 38 questions of the USAqWRA scheme for each region and for each species, demonstrating that 8 of them are the most powerful in separating invasive from non-invasive species. These questions were classified into groups because was the result of merging similar questions: (1) Ecology and habitat of the species (questions 2, 4, 6); (2) seeding ability (question 20) and (3) potential of impact and damage to natural areas (questions 24-26, 29).

2 Springer

Hydrobiologia

The application of the USAqWRA to South America resulted in having a specificity equal to 87.5% and higher than the sensitivity (75.75%), with an overall accuracy of 84.9%. This means that the method performs slightly better in identifying non-invasive species than invasive ones; therefore, some invasive species may be undetected (false negatives) while those scored as non-invasive could be considered relatively safe, with lower uncertainty. The application of the method to that investigated 40 species would result in rejecting 37.5% and accepting 62.5% of them if used a pre-border assessment.

Finally, the USAqWRA does not have questions that could specifically take into account the possible modification of the risk assessment outcomes in relation to global change, although several questions do consider the plasticity of the species to varying environmental and site conditions (e.g., temperature).

An increasing number of studies have documented evolutionary changes in invasive populations, typically over ecological timescales (Chown et al., 2015). Additionally, it is generally agreed that over the past century, the potential for aquatic species to expand their ranges at the global level has been enhanced both as a result of the construction of new canals and because of increased international trade (Seebens et al., 2015) and as results of global change and modified socio-economic frameworks (e.g., van Kleunen et al., 2015). Further, the USAgWRA does not include all the modules of a full standard Pest Risk Analysis scheme such as the IPPC/EPPO PRA and does not fulfil many of the minimum criteria for risk assessment of the European Regulation n. 1143/2014 (Roy et al., 2014).

Conclusions

We assessed 40 South American aquatic plant species using the USAqWRA scheme, ranking 17 of them as alien naturalised, and 15 as alien invasive species in at least one region. It is well known that the accuracy of any risk assessment and risk analysis schemes would be benchmarked and compared using test data from very well known species that have been satisfactorily investigated for their biological traits and impacts on biodiversity and related ecosystem services. However, such comprehensive data do not exist for South America. Furthermore, comprehensive risk estimates are difficult due to various sources of uncertainty (e.g., Dahlstrom et al., 2012). This uncertainty is an inherent component and can stem from a variety of factors, including knowledge gaps and systematic and random measurement error. While expert opinion is often the most appropriate method to make risk estimates under conditions of uncertainty (Halpern et al., 2007) and in a relatively short amount of time, this judgment should be preferably combined with empirical evidence (Dahlstrom et al., 2012) and standard protocols. The available risk classifications from other countries or regions can also be used to help in predicting whether or not a non-native species may become invasive (Verbrugge et al., 2012).

Due the continuously increasing number of nonnative species introduction in South America, there is urgent need to adopt and apply prioritisation and express risk assessment schemes which can help identify which new species to the region(s) have the higher potential to become invasive and list those risky aquatic species that can cause ecological negative impacts in South America to prevent attempts of introduction. We consider that our results support the use of the USAqWRA as a screening protocol for South American alien aquatic plant species, providing a rapid assessment scheme that may help reduce the costs of control in the future, and the prioritisation of the species according to their USAqWRA scores,

Acknowledgments We gratefully thank A. Pauchard, J. Urrutia, R. Bustamante, S. Magela-Thomaz and L. J. Cumana Campos for providing useful information and literature. We also wish to thank the two anonymous reviewers whose recommendations greatly helped in improving the manuscript.

References

- Almeida, W. R., A. V. Lopes, M. Tabarelli & I. R. Leal, 2015. The alien flora of Brazilian Caatinga: deliberate introductions expand the contingent of potential invaders. Biological Invasions 17: 51–56.
- Andreu, J. & M. Vilà, 2010. Risk analysis of potential invasive plants in Spain. Journal for Nature Conservation 18: 34–44.
- Aona, L. Y. S., G. M. da Costa, E. M. do Carmo, A. D. de Faria, E. F. Duarte & V. Bittrich, 2015. Aquatic and marsh plants from the Recôncavo basin of Bahia state, Brazil: checklist and life forms. Check List 11: 1806.
- Arroyo, M. T. K., C. Marticorena, O. Matthei, & L. Cavieres, 2000. Plant invasions in Chile: present patterns and future

Deringer

predictions. Invasive species in a changing world: 385-421.

- Azan, S., M. Bardecki & A. Laursen, 2015. Invasive aquatic plants in the aquarium and ornamental pond industries: a risk assessment for southern Ontario (Canada). Weed Research 55: 249–259.
- Bates, D., M. Maechler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.
- Bini, L. M. & S. M. Thomaz, 2005. Prediction of *Egeria najas* and *Egeria densa* occurrence in a large subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay). Aquatic Botany 83: 227–238.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson & D. M. Richardson, 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26: 333–339.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. Poulsen, M. Henry, H. Stevens & J. S. White, 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24: 127–135.
- Boltovskoy, D. & N. Correa, 2015. Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America. Hydrobiologia 746: 81–95.
- Brunel, S., E. Branquart, G. Fried, J. Van Valkenburg, G. Brundu, U. Starfinger, S. Buholzer, A. Uludag, M. Joseffson & R. Baker, 2010. The EPPO prioritization process for invasive alien plants. EPPO bulletin 40: 407–422.
- Carniatto, N., R. Fugia, S. M. Thomaz & E. R. Cunha, 2014. The invasive submerged macrophyte *Hydrilla verticillata* as a foraging habitat for small-sized fish. Natureza & Conservação 12: 30–35.
- Carstensen, B., L. Gurrin, C. Ekstrom & M. Figurski, 2015. MethComp: functions for analysis of agreement in method comparison studies. R package version 1.22.2. http:// CRAN.R-project.org/package=MethComp.
- Champion, P. D., & J. S. Clayton, 2000. Border control for potential aquatic weeds. Stage 1. Weed risk model. Department of Conservation.
- Champion, P. D. & J. Clayton, 2010. Assessing the Risk Posed to Micronesia by Invasive Aquatic Weeds. NIWA Client Report, Hamilton.
- Champion, P., D. Burnett & A. Petroeschevsky, 2008. Risk Assessment of Tradable Aquatic Plant Species in Australia. NIWA, Western Australia, O'Connor.
- Chown, S. L., K. A. Hodgins, P. C. Griffin, J. G. Oakeshott, M. Byrne & A. A. Hoffmann, 2015. Biological invasions, climate change and genomics. Evolutionary Applications 8: 23–46.
- Collen, B., F. Whitton, E. E. Dyer, J. E. Baillie, N. Cumberlidge, W. R. Darwall, C. Pollock, N. I. Richman, A. Soulsby & M. Böhm, 2014. Global patterns of freshwater species diversity, threat and endemism. Global Ecology and Biogeography 23: 40–51.
- Conser, C., L. Seebacher, D. W. Fujino, S. Reichard & J. M. DiTomaso, 2015. The development of a plant risk evaluation (PRE) tool for assessing the invasive potential of ornamental plants. PLoS One 10: e0121053.
- Daehler, C. C., 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biological Conservation 84: 167–180.

- Daehler, C. C. & D. A. Carino, 2000. Predicting invasive plants: prospects for a general screening system based on current regional models. Biological Invasions 2: 92–103.
- Daehler, C. C., J. S. Denslow, S. Ansari & H. Kuo, 2004. A risk assessment system for screening out invasive pest plants from Hawai'i and other Pacific Islands. Conservation Biology 18: 360–368.
- Dahlstrom, A., M. Campbell & C. Hewitt, 2012. Mitigating uncertainty using alternative information sources and expert judgement in aquatic non-indigenous species risk assessment. Aquatic Invasions 7: 567–575.
- Delnatte, C. & J. Y. Meyer, 2012. Plant introduction, naturalization, and invasion in French Guiana (South America). Biological Invasions 14: 915–927.
- Essl, F., S. Dullinger, W. Rabitsch, P. E. Hulme, K. Hülber, V. Jarošík, I. Kleinbauerc, F. Rausmanng, I. Kühnh, W. Nentwigi, M. Vilà, P. Genovesik, F. Gherardil, M. Desprez-Loustaum, A. Roquesn & P. Pyšek, 2011. Socioeconomic legacy yields an invasion debt. Proceedings of the National Academy of Sciences 108: 203–207.
- Essl, F., S. Bacher, T. M. Blackburn, O. Booy, G.Brundu, S. Brunel, A. C. Cardoso, R. Eschen, B. Gallardo, B. Galil, E. García-Berthou, P. Genovesi, Q. Groom, C. Harrower, P. E. Hulme, S. Katsanevakis, M. Kenis, I. Kühn, S. Kumschick, A. F. Martinou, W. Nentwig, C. O'flynn, S. Pagad, J. Pergl, P. Pyšek, W. Rabitsch, D. M. Richardson, A. Roques, H. E. Roy, R. Scalera, S. Schindler, H. Seebens, S. Vanderhoeven, M. Vilà, J. R. U. Wilson, A. Zenetos, & J. M. Jeschke, 2015. Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769.
- EPPO, 2015. Pest risk analysis for Alternanthera philoxeroides. EPPO, Paris. http://www.eppo.int/QUARANTINE/Pest_ Risk_Analysis/PRA_intro.htm.
- European Commission, 2015. EUR 19 million in European funds to step up cross-border co-operation between French Guiana and neighbouring countries in the Amazon. Regional Policy. Web Site (http://ec.europa.eu/regional_policy/en/newsroom/ news/2015/12/12-01-2015-eur-19-million-in-european-fundsto-step-up-cross-border-co-operation-between-french-guianaand-neighbouring-countries-in-the-amazon).
- Faraway, J. J., 2006. Extending the Linear Model with R: generalized Linear, Mixed Effects and Nonparametric Regression Models. Chapman and Hall, Boca Raton.
- Fuentes, N., E. Ugarte, I. Kühn & S. Klotz, 2010. Alien plants in southern South America. A framework for evaluation and management of mutual risk of invasion between Chile and Argentina. Biological Invasions 12: 3227–3236.
- Gallardo, B., M. Clavero, M. I. Sánchez & M. Vilà, 2015. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22: 151–163.
- Gardener, M. R., R. O. Bustamante, I. Herrera, G. Durigan, V. R. Pivello, M. F. Moro, A. Stoll, B. Langdon, Z. Baruch, A. Rico, A. Arredondo-Nuñez & S. Flores, 2012. Plant invasions research in Latin America: fast track to a more focused agenda. Plant Ecology & Diversity 5: 225–232.
- Gordon, D. R. & C. A. Gantz, 2011. Risk assessment for invasiveness differs for aquatic and terrestrial plant species. Biological Invasions 13: 1829–1842.
- Gordon, D. R., D. A. Onderdonk, A. M. Fox & R. K. Stocker, 2008. Consistent accuracy of the Australian weed risk

2 Springer

assessment system across varied geographies. Diversity and Distributions 14: 234–242.

- Gordon, D. R., C. A. Gantz, C. L. Jerde, W. L. Chadderton, R. P. Keller & P. D. Champion, 2012. Weed risk assessment for aquatic plants: modification of a New Zealand system for the United States. PLoS One 7: e40031.
- Govaerts, R., D. G. Frodin, A. Radcliffe-Smith & S. Carter, 2000. World Checklist and Bibliography of Euphorbiaceae (with Pandaceae). Royal Botanic Gardens, Kew.
- Groves, R. H., 2006. Are some weeds sleeping? Some concepts and reasons. Euphytica 148: 111–120.
- Guézou, A., M. Trueman, C. E. Buddenhagen, S. Chamorro, A. M. Guerrero, P. Pozo & R. Atkinson, 2010. An extensive alien plant inventory from the inhabited areas of Galapagos. PLoS One 5: e10276.
- Hamel, S., N. G. Yoccoz, & J. M. Gaillard, 2016. Assessing variation in life-history tactics within a population using mixture regression models: a practical guide for evolutionary ecologists. Biological Reviews. doi:10.1111/brv. 12254.
- Havel, J. E., K. E. Kovalenko, S. M. Thomaz, S. Amalfitano & L. B. Kats, 2015. Aquatic invasive species: challenges for the future. Hydrobiologia 750: 147–170.
- Hayes, K. R. & S. C. Barry, 2008. Are there any consistent predictors of invasion success? Biological Invasions 10: 483–506.
- Heinze, G. & M. Ploner, 2003. Fixing the nonconvergence bug in logistic regression with SPLUS and SAS. Computer Methods and Programs in Biomedicine 71: 181–187.
- Heinze, G., & M. Ploner, 2004. Technical Report 2/2004: A SAS-macro, S-PLUS library and R package to perform logistic regression without convergence problems. Section of Clinical Biometrics, Department of Medical Computer Sciences, Medical University of Vienna, Vienna.
- Heinze, G., M. Ploner, D. Dunkler & H. Southworth, 2013. Logistf: Firth's bias reduced logistic regression. R package version 1.21. http://CRAN.R-project.org/package=logistf.
- Heleno, R. H., J. M. Olesen, M. Nogales, P. Vargas & A. Traveset, 2013. Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. Proceedings of the Royal Society of London B: Biological Sciences 280: 17–50.
- Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner & M. Vila, 2012. Bias and error in current knowledge of plant invasions impacts. Trends Ecology Evolution 28: 212–218.
- Kato, H., K. Hata, H. Yamamoto, & T. Yoshioka, 2006. Effectiveness of the weed risk assessment system for the Bonin Islands. In: Koike, F., M. N. Clout, M. Kawamichi, M. De Poorter, K. Iwatsuki, (eds) Assessment and Control of Biological Invasion Risk. Shoukadoh Book Sellers and IUCN, Kyoto, Gland: 65–72.
- Křivánek, M. & P. Pyšek, 2006. Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic. Diversity and Distributions 12: 319–327.
- Kumschick, S. & D. M. Richardson, 2013. Species-based risk assessments for biological invasions: advances and challenges. Diversity and Distributions 19: 1095–1105.
- Kumschick, S., S. Bacher, W. Dawson, J. Heikkilä, A. Sendek, T. Pluess, T. B. Robinson & I. Kühn, 2012. A conceptual

framework for prioritization of invasive alien species for management according to their impact. NeoBiota 15: 69.

- Kumschick, S., S. Bacher, T. Evans, Z. Marková, J. Pergl, P. Pyšek, S. Vaes-Petignat, G. van der Veer, M. Vilà & W. Nentwig, 2015. Comparing impacts of alien plants and animals in Europe using a standard scoring system. Journal of Applied Ecology 52: 552–561.
- Mack, R. N., 2005. Predicting the identity of plant invaders: future contributions from horticulture. HortScience 40: 1168–1174.
- Matsuzaki, S-i S, N. Usio, N. Takamura & I. Washitani, 2009. Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. Oecologia 158: 673–686.
- Mauchamp, A., 1997. Threats from alien plant species in the Galápagos Islands. Conservation Biology 11: 260–263.
- McClay, A., A. Sissons, C. Wilson & S. Davis, 2010. Evaluation of the Australian weed risk assessment system for the prediction of plant invasiveness in Canada. Biological Invasions 12: 4085–4098.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca & J. Kent, 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
- Nishida, T., N. Yamashita, M. Asai, S. Kurokawa, T. Enomoto, P. C. Pheloung & R. H. Groves, 2009. Developing a preentry weed risk assessment system for use in Japan. Biological Invasions 11: 1319–1333.
- Ormazabal, C., 1993. The conservation of biodiversity in Chile. Revista Chilena de Historia Natural 66: 383–402.
- Pauchard, A., L. Cavieres, R. Bustamante, P. Becerra & E. Rapoport, 2004. Increasing the understanding of plant invasions in southern South America: first symposium on Alien Plant Invasions in Chile. Biological Invasions 6: 255–257.
- Pheloung, P. C., P. A. Williams & S. R. Halloy, 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57: 239–251.
- Pyšek, P., D. Richardson, M. Rejmánek, G. Webster, M. Williamson & J. Kirschner, 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53: 131–143.
- Pyšek, P., P. W. Lambdon, M. Arianoutsou, I. Kühn, J. Pino, & M. Winter, 2009. Alien Vascular Plants of Europe. Handbook of Alien Species in Europe. Springer Series in Invasion Ecology: 43–61.
- Pyšek, P., V. Jarošík, P. E. Hulme, J. Pergl & M. Hejda, 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species traits and environment. Global Change Biology 18: 1725–1737.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta & C. J. West, 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity Distribution 6: 93–107.
- Rodriguez, L. F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8: 927–939.
- Rodrigues, R. B. & S. M. Thomaz, 2010. Photosynthetic and growth responses of *Egeria densa* to photosynthetic active radiation. Aquatic Botany 92: 281–284.

Deringer

- Roy, H., K. Schonrogge, H. Dean, J. Peyton, E. Branquart, S. Vanderhoeven, G. Copp, P. Stebbing, M. Kenis, & W. Rabitsch, 2014. Invasive alien species: framework for the identification of invasive alien species of EU concern. Report to the EC, project ENV. B. 298.
- R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.
- Rybicki, N. B. & J. M. Landwehr, 2007. Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. Limnology and Oceanography 52: 1195–1207.
- Santos, M. J., L. W. Anderson & S. L. Ustin, 2011. Effects of invasive species on plant communities: an example using submersed aquatic plants at the regional scale. Biological Invasions 13: 443–457.
- Seebens, H., M. T. Gastner & B. Blasius, 2013. The risk of marine bioinvasion caused by global shipping. Ecology Letters 16: 782–790.
- Seebens, H., F. Essl, W. Dawson, N. Fuentes, D. Moser, J. Pergl, P. Pyšek, M. van Kleunen, E. Weber, M. Winter & B. Blasius, 2015. Global trade will accelerate plant invasions in emerging economies under climate change. Global Change Biology 21: 4128–4140.
- Simberloff, D., 2013. Invasive Species: what Everyone Needs to Know. Oxford University Press, Oxford.
- Strayer, D. L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174.
- Strayer, D. L., 2012. Eight questions about invasions and ecosystem functioning. Ecology Letters 15: 1199–1210.
- Soreng, R. J. & L. Fish, 2011. Catabrosa versus Colpodium (Poaceae: Poeae) in southern Africa, with a key to these genera and their species in Africa. Kew Bulletin 66: 101–110.
- Thomaz, S. M., K. E. Kovalenko, J. E. Havel & L. B. Kats, 2015. Aquatic invasive species: general trends in the literature

and introduction to the special issue. Hydrobiologia 746: 1-12.

- Trueman, M., R. Atkinson, A. Guézou & P. Wurm, 2010. Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. Biological Invasions 12: 3949–3960.
- van Kleunen, M., W. Dawson, F. Essl, J. Pergl, M. Winter, E. Weber, H. Kreft, P. Weigelt, J. Kartesz, M. Nishino, L. A. Antonova, J. F. Barcelona, F. J. Cabezas, D. Cárdenas, J. Cárdenas-Toro, N. Castaño, E. Chacón, C. Chatelain, A. L. Ebel, E. Figueiredo, N. Fuentes, Q. J. Groom, L. Henderson, Inderjit, A. Kupriyanov, S. Masciadri, J. Meerman, O. Morozova, D. Moser, D. L. Nickrent, A. Patzelt, P. B. Pelser, M. P. Baptiste, M. Poopath, M. Schulze, H. Seebens, W. Shu, J. Thomas, M. Velayos, J. J. Wieringa, M. J. VanderZanden, J. M. Casselman & J. B. Rasmussen, 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464–467.
- van Kleunen, M., W. Dawson, F. Essl, J. Pergl, M. Winter, E. Weber, H. Kreft, P. Weigelt, J. Kartesz, M. Nishino, L. Antonova, J. F. Barcelona, F. J. Cabezas, D. Cardenas, J. Cardenas-Toro, N. Castano, E. Chacón, C. Chatelain, A. L. Ebel, E. Figueiredo, N. Fuentes, Q. J. Groom, L. Henderson, A. Upriyanov, S. Masciadri, J. Meerman, O. Morozova, D. Moser, D. L. Nickrent, A. Patzelt, P. B. Pelser, M. P. Baptiste, M. Poopath, M. Schulze, H. Seebens, W. Shu, J. Thomas, M. Velayos, J. J. Wieringa & Petr Pyšek, 2015. Global exchange and accumulation of non-native plants. Nature 525: 100–104.
- Verbrugge, L., G. van der Velde, J. Hendriks, H. Verreycken & R. Leuven, 2012. Risk classifications of aquatic non-native species: application of contemporary European assessment protocols in different biogeographical settings. Aquatic Invasions 7: 49–58.

Dispringer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

CHAPTER 3

NATIVE AND NON-NATIVE AQUATIC PLANTS OF SOUTH AMERICA: COMPARING AND INTEGRATING GBIF RECORDS WITH LITERATURE DATA

Introduction and aims

Open access to primary biodiversity data is essential for enabling effective decision making in the conservation of biodiversity. In the scientific and conservation communities, there is wide emerging consensus that data should be freely, openly available in a sustained, persistent and secure way. This adversely affects the optimal utility of the biodiversity data. The main goal of this study was to assess the state of data availability and reliability for aquatic plant species in South America.

Methodology and main results

A set of 40 native and 40 non-native aquatic species was selected from the South American DB (*Cf.* Chapter 1). These 80 species included a sub-set of 40 alien species previously evaluated with the USAqWRA scheme (US Aquatic Weed Risk Assessment) (*Cf.* Chapter 2). Species with non-reliable identification, duplicates of the same collection, records poorly georeferenced were removed from the dataset. New records were manually compiled through classical literature research. All the georeferenced records (GBIF + literature) were used for the mapping and the comparative analysis.

Conclusions

The two datasets provide quite significantly different information and the combination of the two offers new information that would not exist in a single data source. Nevertheless, a careful quality evaluation of the primary information, both in the case of literature and GBIF should be conducted, before the data is used for further analyses.

Lozano V, Chapman DS, Brundu G (2017). Native and non-native aquatic plants of South America: comparing and integrating GBIF records with literature data. Management of Biological Invasions, 8, 443-454.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Management of Biological Invasions (2017) Volume 8, Issue 3: 443–454 DOI: https://doi.org/10.3391/mbi.2017.8.3.18 © 2017 The Author(s). Journal compilation © 2017 REABIC



Special Issue: Management of Invasive Species in Inland Waters

Information Management

Native and non-native aquatic plants of South America: comparing and integrating GBIF records with literature data

Vanessa Lozano^{1,*}, Daniel S. Chapman² and Giuseppe Brundu¹

¹Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy ²NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK Author e-mails: vlozano@uniss.it (VL); dcha@ceh.ac.uk (DSC); gbrundu@uniss.it (GB) *Corresponding author

*Corresponding author

Received: 27 December 2016 / Accepted: 28 June 2017 / Published online: 14 July 2017

Handling editor: Elena Tricarico

Editor's note:

This study was first presented at the special session on aquatic invasive species at the 33rd Congress of the International Society of Limnology (SIL) (31 July - 5 August 2016, Torino, Italy) (http://limnology.org/meetings/past-sil-congress/). This special session has provided a venue for the exchange of information on ecological impacts of non-native species in inland waters.

Abstract

The Global Biodiversity Information Facility (GBIF) is at the moment one of the largest and most widely used biodiversity databases. Nevertheless, there are still some limitations, e.g. in terms of plant species status (native vs. non-native) and geographic resolution of records. At the same time, it is well known that alien plant invasions in inland freshwaters can alter community structure, ecosystem functions and services with significant negative impacts on biodiversity and human activities. We assessed if the GBIF database has a geospatial homogeneous information for native and non-native aquatic plant species for South America and whether or not literature resources not yet digitalized (floras, checklists and other papers) could provide additional information. We selected a set of 40 native and 40 non-native aquatic species. These 80 species included a sub-set of 40 alien species previously evaluated with the USAqWRA scheme (US Aquatic Weed Risk Assessment). Species with non-reliable identification, duplicates of the same collection, records poorly georeferenced records (GBIF + literature) were used for the mapping and the comparative analysis. As a result, we can conclude that the two datasets provide quite significantly different information and the combination of the two offers new information that would not exist in a single data source. Nevertheless, a careful quality evaluation of the primary information, both in the case of literature and GBIF should be conducted, before the data is used for further analyses.

Key words: alien aquatic plants, biodiversity occurrence data, Global Biodiversity Information Facility, ModestR software, risk assessment

Introduction

The Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) is one of the largest and most widely used biodiversity database (Jetz et al. 2012; Beck et al. 2014), and it offers freely and universally primary biodiversity data (Roberts and Moritz 2011). This kind of information, together with tools to analyze it (e.g. Geographic Information Systems software, and statistical analysis packages), has facilitated large-scale analyses and interpretation of biodiversity and distribution data (García-Roselló et al. 2015; Maldonado et al. 2015) for both native and non-native plant species.

Most data on plant species distribution are stored in different sources, including checklists, herbaria, floras and field observations, and are based on point occurrence records, representing what is generally

443

referred as the primary distribution data, i.e., the occurrence of a particular plant species at a particular location at a particular point in time (Soberón and Peterson 2004). Millions of these records from herbaria and other sources have been mobilised via international data-sharing networks and databases (Edwards et al. 2000) although there might be constraints to a generalised use of this occurrence data due to its coverage (or thematic resolution) and level of accuracy.

Coverage has several components and subcomponents, but three main aspects are most commonly considered. The first one is the "taxonomic coverage", i.e., how many of the existing species and valid lower taxa are well documented (Funk et al. 1999; Hortal et al. 2007; Brummitt et al. 2015) and how frequently the taxonomic and nomenclature resolution and precision of the database is updated and cross-checked. The second is the "geographical coverage", i.e., how precisely and completely species locations and resulting ranges are documented within records (Feeley and Silman 2011). Finally, the "temporal coverage", i.e., the time resolution of the database, based, e.g. on more or less continuous recording of species through time (Brummitt et al. 2015) and on the verification of the persistency along time of a given species in one historical locality (Troia et al. 2016). However, gaps and biases usually exist in the available biodiversity information (Boakes et al. 2010; Feeley and Silman 2011: Sousa-Baena et al. 2014: García-Roselló et al. 2015) and data limitations may occur as a result of an inadequate financial and institutional support (Vollmar et al. 2010; Amano and Sutherland 2013) or of different sampling efforts focusing more on regions with certain appeal like endemism, species richness or protected areas (Petřík et al. 2010; Yang et al. 2014). Petřík et al. (2010), showed that the bias in grid mapping of flora seems to be dependent on spatial scale. In addition, the number of botanists involved and duration of the study are associated with some level of bias in estimates of species richness.

GIBF records are widely used in ecology, evolution and conservation (Meyer et al. 2015) and have been used for many different purposes, e.g. to identify native ranges of invasive alien species or species climatic and environmental requirements (Peterson 2003; Suarez and Tsutsui 2004; Chapman 2005; García-Roselló et al. 2015).

In addition to these well-known problems, specific limitations in the GBIF database become evident when one wants to use it as a tool for the analysis of plant invasions, e.g. concerning the plant species status (alien vs. native; casual vs. naturalized vs. invasive; archaeophyte vs. neophyte), because the invasive status and residence time cannot be inferred for most of the records. GBIF created a dedicated working group to address the enhancement of the system to be used in the field of biological invasions (McGeoch et al. 2016). In fact, it has been remarked that the information available in GBIF has been in some cases used to rapidly assess patterns of diversity and allodiversity, without much attention being paid to the quality and reliability of the data (García-Roselló et al. 2015; Maldonado et al. 2015).

However, GBIF distribution data for alien plants, after expert review, may help in identifying not only highly invaded areas, but also the overall distribution, in predicting locations susceptible to further establishment (Duursma et al. 2013) and in identifying areas that are at greatest risk from future invasions. The knowledge of the spatial distribution of invasive species and invaded habitats is one of the pillars supporting an effective strategy for their management and control (Thuiller et al. 2005). In this concern, the identification of invasive species risk hotspots is a useful tool to prioritize management of plant invasions at large scale (Liang et al. 2014; Adhikari et al. 2015).

Among invaded ecosystems, freshwater ecosystems and habitats, especially lakes and streams are particularly vulnerable (Strayer 2010; Simberloff 2013; Boltovskoy and Correa 2015; Brundu 2015) and prone to dramatic biodiversity loss (Ricciardi and Rasmussen 1999) because of their high concentration of species per surface area (Thomaz et al. 2015). Nutrients in suspension and in sediments are also important determinants of aquatic plants invasion (Engelhardt 2011). While in some continents, intracontinental propagule pressure can be assumed to have been larger, because of the shorter distances, South America have species with restricted ranges, and as the consequence they are less likely to have been dispersed outside their native ranges (van Kleunen et al. 2015). In addition, freshwater ecosystems are often difficult to survey and monitor, so there might be a general scarcity of information about the distribution of invasive alien aquatic plants in many part of the worlds, as is the case of South America (Lozano and Brundu 2016). In particular, Chile, Brazil (Brazil's Atlantic Forest), Ecuador and Tropical Andes, where biodiversity hotspots are mainly represented, offers a unique opportunity to study biological invasions because they hold a unique native flora with high levels of endemism, extraordinary richness and diverse climatic gradients (Myers et al. 2000; Pauchard et al. 2004). In Brazil, for example, the Guiana Shield constitutes a geological, hydrographical and biogeographic region in the Amazonian

444

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Alien aquatic plants of South America

Basin that is considered a very important biodiversity hotspot (Delnatte and Meyer 2012). However, the degree of susceptibility of ecosystems to invasion in these regions is poorly understood and investigated (Thomaz et al. 2015).

The main goal of this study was to assess the state of data availability for aquatic plant species in South America. Therefore, the present research aimed to: (1) evaluate the increase in reliability offered by the merging of information "manually" extracted from literature, for a set of native and non-native aquatic species of South America, with the information for the same species held in GBIF, and (2) evaluate the relationship between the density of non-native aquatic species and large-scale expected predictors such as the Human Influence Index (HII) and the distribution of protected areas in 16 regions of South America.

Methods

Species selection and study area

For the purposes of the present research, we selected a set of 80 species composed by 40 native and 40 non-native aquatic plant species thriving in South America (Supplementary material Table S1). The set included both helophytes (growing in anaerobic saturated soils) and hydrophytes, free-floating, floating (rooted) and submerged freshwater vascular plants. The selection of these 80 species was based on the availability of reliable information found in the literature concerning taxonomical, geographical and biological traits data, which are a fundamental prerequisite for any reliable modelling and risk assessment.

The 16 South American regions (there after called "regions") considered in the study were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.

Collection of distribution records

We first created two distribution datasets for the selected 80 species, using two different methodologies. The first dataset (hereafter called literature dataset) included the geographical coordinates (Lat/Long WGS84) of species records that were collected through classical literature research (national or regional floras: http://www.floraargentina.edu.ar, http://floradobrasil.jbrj.gov.br, http://www.lib.udec.cl, http://www2.darwin.edu.ar, flora checklists and papers) for the 16 regions of South America. The second dataset (hereafter called GBIF dataset) was created using the ModestR software (freely available at the website http://www.ipez.es/ModestR, accessed on 2016) (Pelayo-Villamil et al. 2012; García-Roselló et al. 2013). We retrieved all available distributional data for the 80 selected aquatic species in South America from the GBIF portal (http://www.gbif.org, accessed on 2016). Acknowledgments for all the sources of the downloaded records from GBIF are shown in the supplementary materials (Table S4). Finally, we merged the two datasets in a new "integrated dataset", including new information (e.g. status of invasion and the risk level for non-native species using the USAqWRA scheme).

Taxonomical and geographical validation of distribution records

The synonyms used in the literature were handled in accordance to The Plant List portal (http://www. theplantlist.org/) and crosschecked using IPNI (International Plant Name Index, http://www.ipni.org/), to ensure that all records were assigned to an accepted valid name in agreement with GBIF taxonomic treatment. For species reported in the literature without georeferenced localities, but with an accurate description of the collection locality, geographical coordinates were assigned using Google Earth. On the other hand, the GBIF data were checked and cleaned using the menu facility of ModestR (García-Roselló et al. 2014). Species with non-reliable identification, duplicates of the same collection (discriminating between real duplicates and records of the same specimen sent to different collections), records without (georeferenced) locations or with latitude/longitude equal to 0° and records on the sea (i.e., coordinates that did not project onto land) were removed from the dataset. In addition, the software automatically classified valid and invalid samples depending on whether records were within or outside the inland freshwater. In addition, the software allowed retrieval for all species at the same time by including a file with the species names following a simple taxonomic classification, correcting wrong or invalid synonyms. Once the taxonomic data was introduced, distribution maps for each species was stored in the ModestR database.

Invasive status and distribution maps

Four a priori status categories were defined according to expert opinion, classifying each species in one of the following status categories for each of the 16 regions defined in the present study, or for part of the regions. The four status categories were as

445

follows: alien non-invasive (NNV), alien invasive (INV), native (IND) and absent (ABS). We used the scores of the 35 non-native species previous evaluated by Lozano and Brundu (2016) with the US Aquatic Weed Risk Assessment (USAqWRA). We assessed the five additional alien aquatic species with the USAqWRA scheme (originally shaped by Gordon et al. 2012), i.e., Agrostis stolonifera L., Aponogeton distachyos L.f., Eleocharis acicularis (L.) Roem. & Schult., Nasturtium officinale R.Br., and Nymphaea micrantha Guill. & Perr. (Supplementary material Table S1, S5 and S6). The USAqWRA scores and invasion status, per species/region, improved the information downloaded from GBIF, that at the moment does provide only limited features related to biological invasions. This information allowed to correlate the invasive species risk in South America (i.e., the scores derived from the USAqWRA scheme) with large-scale expected predictors such as the Human Influence Index (HII) and the location of the protected areas (PAs).

The whole set of cleaned records, for alien invasive and alien non-invasive species obtained from the "integrated dataset", was used to map species distribution in each of the 16 regions or part of regions in South America. Distribution maps were created with: 1) GBIF presence records with the addition of records retrieved from literature and 2) GBIF presence records with the invasion status according to expert opinion (see Table S5 and S7). We also produced choropleth maps, based on the number of records, to highlight species density at regional level. Finally, we mapped the allodiversity of the 16 investigated regions.

GIS & statistical data analysis

We tested the difference between the raw and cleaned records within the two datasets for the 80 species, respectively for GBIF and literature. We also tested the difference between the native and non-native records downloaded from the GBIF and literature dataset applying a t-test (see Table 1). Additionally, we evaluated whether the information collected by literature did improve the information obtained through GBIF.

We downloaded the data set at continental-level (grid format, 1×1 km cell size) for the Human Influence Index (HII) available at the Socioeconomic Data and Applications Center [Wildlife Conservation Society - WCS; Center for International Earth Science Information Network - CIESIN - Columbia University 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). http://dx.doi.

org/10.7927/H4M61H5F), accessed on December 2016]. Afterward, we extracted the HII values for each pairs of coordinates, corresponding to each species records, in the 16 regions of South America. After projecting the set of cleaned records from GBIF and literature dataset into the HII layer, we used the Pearson's correlation to evaluate the relationship between the non-native species HII scores and their USAqWRA scores, at each geographical location. A Wilcoxon test was performed to check differences between the HII scores at individual points where native species were recorded vs. the points where non-native species were recorded. We addressed the possible bias due to spatial autocorrelation treating HII data with Generalized Least Square Models. GLS was fitted using the function gls, with "nlme" R package (Dormann et al. 2007; see Table S10). On the other side, polygon layers of nature reserves or protected areas (PAs) data sets for South America, were obtained from the World Database on Protected Areas (WDPA, http://www.wdpa.org, accessed on December 2016). We assessed the relationship between the non-native species proportion of records inside and outside the protected areas and their USAqWRA scores, using a generalized linear model (logistic regression). The risk of invasion was evaluated when the records of the non-native species were within or outside the PAs and in accordance with USAqWRA scores, using the software R (R Core Team 2015). Chi-square test on the contingency table between native/non-native records and inside/outside PAs was also performed. We addressed the spatial autocorrelation treating PAs data with autocovariate regression. The regression was conceived for binary data (as autologistic regression). We used the function autocov_dist, with "spdep" R package (Dormann et al. 2007; see Table S10).

Results

Number of records and distribution in the 16 South American regions

The GBIF database held valid georeferenced distribution records for 79 of the 80 aquatic plant species investigated in the present study. Importantly, there were no GBIF records for the alien species *Aponogeton distachyos* L.f. (cape pondweed), in South America. On the other hand, the distribution records downloaded from GBIF covered only 15 of the 16 regions, i.e., excluding South Georgia and South Sandwich Islands. The data downloaded from GBIF contained 10,735 raw records (Table 1). Overall, cleaning and validation led to an exclusion of 1,825 records.

446
Table 1. Difference of the main descriptors of primary biodiversity information. Studies were performed comparing between GBIF and literature datasets: the total number and total records of native, non-invasive and invasive species, and the total records found in the 16 regions of South America, after the cleaning process with the software ModestR.

Feature	GBIF	Literature	p value
No. native species	40	40	_
No. non-invasive alien species	17	18	0.839
No. invasive alien species	22	22	_
Total no. of species	79	80	0.977
Total no. of raw records	10,735	452	< 0.001
Total no. of cleaned records	8,910 (82.99%)	427 (94.46%)	< 0.001
No. of records native species	4,536	126	0.001
No. of records non-invasive alien species	1,565	78	< 0.001
No. of records invasive alien species	2,809	223	< 0.001
No. of regions with records	15	16	0.895
No. sources (GBIF) and manuscripts (Literature)	559	210	0.356

The GBIF data were supplemented with records collected from literature sources. This resulted in the addition of 427 records, obtaining a final total number of 9,337 records (integrated dataset). The difference between the total number of records provided by GBIF and those obtained from the literature dataset, for the 80 species, were highly significant (p value < 0.001) (Table 1, Figure 1). The average records for species found in the GBIF dataset was 111.3 while for the literature dataset was 5.33. The literature dataset provided information lacking in the GBIF dataset, as it was possible to add records in regions not documented by GBIF such as South Georgia and South Sandwich Islands (Table S2). Although the additional number of records (4.79%) provided by the literature dataset was relatively low, we had an increase in terms of new/different species coverage of 1.26% and of 6.66% coverage for regions: the overall bias rate was considerably lower (5.53%). In addition, literature search provided information such as life form, plant traits and invasion status according to expert opinion.

Native and non-native status

The records available in the GBIF dataset for the selected 40 native and 40 non-native (alien non-invasive + alien invasive) aquatic plant species were in almost equal proportions: 4,536 for native and 4,374 for non-native species (Table 1). The literature dataset provided 126 records for native species, and 301 for non-native species (Table 1). The choropleth maps highlight areas differing in the number of records for native, non-invasive and invasive alien species (Figure 2). Noteworthy, the regions with the higher occurrence of non-native aquatic species records were Brazil (2,182), Colombia (454) and Argentina (444) (Supplementary material Figure S1). In both



Figure 1. Map showing the distribution of records downloaded from GBIF (grey circle) and collected from literature sources (red triangle), for South America.

datasets, the total records for alien invasive species were higher than the records for alien non-invasive species (Table 1, Figure 2B, C). The country with the higher density of native and non-native species was Brazil. Regions like French Guiana, Guyana, Suriname and Venezuela, had the tendency to hold more native species than the non-native (Figure 2), and those with the higher density of native and nonnative species per square kilometers were Ecuador and Paraguay (Figure S2).

The data downloaded from GBIF showed a massive tendency towards denser species concentration of native and non-native species in Brazil (53), Argentina (52)

447



Figure 2. Choropleth maps showing the density of records of aquatic species in each of the 16 regions of South America, downloaded from GBIF dataset, cleaned and increased through the addition of records from literature. (A) Records of native species; (B) Records of non-invasive alien species per region; (C) Records of invasive alien species per region. The 16 South American regions considered in the study were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.

and Colombia (50). In the data collected manually from the literature the denser concentrations were found in Brazil (38), Chile (30) and Argentina (28) (Table S3).

According to GBIF Eichhornia azurea (Sw.) Kunth, E. crassipes (Mart.) Solms, Ludwigia octovalvis (Jacq.) P.H.Raven, Nymphoides indica (L.) Kuntze, Pistia stratiotes L., Salvinia auriculata Aubl. and Utricularia foliosa L. were the species with the highest numbers of records across the 16 regions of South America. Importantly, among these species, E. crassipes (76) and P. stratiotes (67) were classified as invasive alien as they reached the highest scores with the USAqWRA, meaning that they represent a major risk (Table S1 and S2). In the literature dataset, the most commonly cited species were: E. crassipes, Hydrocotyle ranunculoides L.f., P. stratiotes, and U. foliosa. The literature dataset improved the results adding new records and new species not present in the GBIF dataset, such as Alisma lanceolatum With., Alisma plantago-aquatica L., A. distachyos, H. ranunculoides, Lemna minor L., Potamogeton nodosus Poir. and Ranunculus aquatilis L. (Table S2).

The reliability of GBIF and literature datasets, after cleaning process using ModestR, was 47% and 59% respectively (Table S2). This means that the literature dataset considered in the present study contained a higher proportion of species with reliable information in comparison to GBIF.

The allodiversity of the 16 investigated regions (i.e., the number of alien species present in a specific area, *sensu* Barthlott et al. 1999) is shown in Figure

3A. According to our results, the regions holding the highest number of different alien aquatic plant species were Argentina and Brazil. The ordinary Kriging map of Figure 3B shows with a better spatial resolution those parts of the regions holding the highest numbers and densities of alien invasive and alien non-invasive species.

When the Human Influence Index was considered, the alien invasive and alien non-invasive species with a high level of risk according to the USAqWRA scheme were positively correlated (t = 3.5851, df =4421, p value < 0.001) with those locations with the higher level of anthropisation (Figure 4 and S3). In addition, we observed that in Brazil, Colombia, Ecuador, Uruguay and Venezuela the records were mostly found along the cost, probably close to the main ports, and this could be related to the pathway of introduction (intentional, e.g. ornamental, Table S1) or secondary release. We predicted a significantly higher HII for non-native occurrences (p value < 0.001). We did not found spatial autocorrelation with the HII scores and the USAqWRA scores (p value = 0.0014).

The correlation between the distribution of the most invasive species according to the USAqWRA scheme and the PAs in South America was found significant (p value = 0.034) and with a negative correlation coefficient, meaning that there is a higher probability of founding the most risky alien species outside the PAs (Figure 4). The chi-square test was significant (p value < 0.001), meaning that there is a higher number of records of non-native species outside the PAs in comparison to native species records.

448

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 3. Number of different invasive alien and non-invasive alien species present in each of the 16 regions of South America, downloaded from GBIF dataset, cleaned and increased through the addition of records from literature. A) Choropleth map of the number of non-native species. B) Kriging of estimated non-native species density according the number of different species in the 16 regions of South America. The 16 South American regions considered in the study were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galagagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.



Figure 4. Human Influence Index (HII) map on the left side and the Protected Areas (PAs) map on the right side. The records of the invasive alien and non-invasive alien species downloaded from GBIF dataset and integrated through the addition of records compiled manually are shown in both maps (dots). The HII grid layer was downloaded from the Wildlife Conservation Society [WCS; Center for International Earth Science Information Network – CIESIN – Columbia University 2005] and the PAs map was downloaded from the World Database of Protected Areas (WDPA).

449

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Discussion

Globalization facilitates the spread of aquatic invasive plants as international commerce develops (Perrings et al. 2005; Donaldson et al. 2014; Seebens et al. 2015, 2017), and most of the aquatic alien species have been deliberately introduced as ornamental or for other commercial uses. After being introduced they might escape into the environment and also South America is unfortunately negatively affected by this process (Table S1). For example, Arundo donax L., was introduced in the Galapagos as an ornamental (Guézou et al. 2014). Hippuris vulgaris L., was introduced in Chile from Europe as ornamental (Ramírez and San Martin 2006). In Chile, 21% of the aquatic and riparian flora has been introduced. It is likely, that this percentage will increase as the country develops and together with it the water bodies are subjected to greater disturbances and prone to accidental escapes or even to intentional releases (Urrutia et al. 2016). To this concern, ports can be one of the main entrance points for aquatic alien species from other countries arriving as stowaways (e.g. ship hull fouling or transport with ballast water, Hulme 2009). Although GBIF and literature data may be biased and have limits in the coverage, especially in poorly investigated regions, we can expect that part of the difference in allodiversity detected in South America using a sample of 80 aquatic species, might be due to the distribution of ports acting as points of entry, and to the intense trade of ornamental plants. The native species considered in the present research could be considered as a "control group" whose distribution pattern reflects the sampling biases in the data when the effects of introduction dynamics and pathways are not important. Therefore, we can assume that differences between native and non-native records (e.g. non-natives in higher HII) could be a result of introduction and secondary release pathways.

In our study, similarly to other studies where the primary biodiversity information is used (Sousa-Baena et al. 2014; García-Roselló et al. 2015; Maldonado et al. 2015; Meyer et al. 2015), a critical point that decreased the data reliability was the inaccurate georeferencing (17.0% of wrong/missing locations). Hijmans et al. (1999) suggested that a relatively large proportion of all available records are not correctly georeferenced. Feeley and Silman (2011), reported the extreme lack of collections data in GBIF (and a similar database for Brazil named SpeciesLink; http://splink.cria.org.br/) for tropical plant species. They estimated that about 65% of tropical plants lack available geo-referenced collections. This lack of reliable spatial information over

V. Lozano et al.

vast extents demonstrates that for many regions with large conservation opportunities there are not sufficient occurrence data to support even the most sophisticated modeling approaches (Meyer et al. 2015). Feeley and Silman (2011) termed this lack of knowledge as the "data void". They pointed out the importance of investigating species responses to climate change through species distribution modeling to predict rates of habitat loss and the associated extinction risks. Nevertheless, Collen et al. (2008), found for the tropical South America that species distributions and their responses to climate change is potentially crippled by a lack of basic data. Using 'presence-only" data, a minimum of 20-50 collections per taxa are generally required to produce accurate species distribution models. Due to the paucity of digitized collections, very few tropical species meet this criterion (Feeley and Silman 2011).

Sousa-Baena et al. (2014), pointed out that incompleteness not only is due to the lack of collection effort, but may also correspond to existing knowledge that is not digital or not accessible. In accordance with Maldonado et al. 2015, we would like to emphasize that the sources of information should be always accompanied by good metadata, including specific details on how the coordinates were obtained, and on whether the coordinate assignment was done manually (e.g. literature sources) or automatically (GBIF data). Periodically, researchers will need to re-evaluate coverage and completeness, and this information will need to incorporate additional coverage information. An advantage of enhancing GBIF dataset with occurrence records collected manually is that they might increase information about local patterns of occurrence, species abundances or community composition.

Feeley (2015) quantified the amount of occurrence data available through GBIF for plant species in tropical South America and examined how data availability had changed through time. He found that most of this increase was due to the inclusion of additional pre-existing records rather than new collections. This increase was driven in large part by the incorporation of SpeciesLink data into GBIF. The greatest density of collections comes from the Northern Andean Paramo and Andean ecoregion, consistently with part of our data occurrence. In tropical South America, more than 10% is still represented by no collection and the reason is that the vast majority of species are sterile, therefore many collections are not identified to species or are identified incorrectly.

The importance and advantage of increasing the digitized records (e.g. in South America) is due to the fact that many ecoregions are very poorly

450

Alien aquatic plants of South America

represented in the GBIF collections database. Our results suggested that literature records can improve the coverage of the GBIF dataset, e.g. in Argentina, Brazil and Chile. For example, the Cerrado is one of the South America's largest, most diverse, and most threatened ecoregions but it is not well-represented (Feeley and Silman 2009). In contrast, the Andean ecoregion are well-represented, maybe their collection intensities were higher and there is not a lack of access (due to physical or bureaucratic impediments) (Feeley 2015). Major rivers, such as the Tocantins and Tapajós in Pará State, and the Rio Negro and Rio Madeira in Amazonas State, are sometimes associated with higher information content. Nevertheless, for our dataset the information in this wellknown place is still lacking.

Importantly, in contrast with the general trend, the biodiversity hotspot regions in Brazil (Myers et al. 2000) have the highest concentration of the invasive alien plants and include a large number of protected areas (World Conservation Union and UNEP-World Conservation Monitoring Centre 2007). Protected areas are usually characterised by high levels of biodiversity, unique habitats, pristine ecosystems or protected or endangered species (Yang et al. 2014; Kumschick et al. 2015). The Andes biodiversity hotspot is one of the most diverse regions and supports many endemic species of high conservation priority (Myers et al. 2000), yet the lack of usable data interferes in conservation efforts. Immediate efforts are needed to increase the quality and number of data available from this and other underrepresented systems (Feeley and Silman 2010).

In accordance with our results, Feeley and Silman (2011) reported that in Ecuador a relatively large number of collections are available online, thanks to the efforts of local herbaria, including the Museo de Historia Natural (QCNE), the Pontificia Universidad Católica del Ecuador (QCA), and the Universidad Central del Ecuador (QAP).

There is a clear need for more frequent and intensive collection campaigns, not just for our set of aquatic species but in general, and research efforts in the structure and dynamic across the Amazon and Tropical South America (Feeley 2015).

The fact that Protected areas are holding a low quantity of invasive species (Foxcroft et al. 2017), could be related to a lower sampling effort (Figure S4). Nevertheless, in the past years, there have been attempts to standardize inventory data (i.e., plot data) in the Amazon forest (e.g. the Amazon Tree Diversity Network (ATDN, http://web.science.uu.nl/ Amazon/atdn/) and the RAINFOR Amazon Forest Inventory Network (http://www.rainfor.org/) (Feeley 2015) and this information would be useful to reduce the artefact of sampling bias. Schulman et al. (2007), showed that much of the Amazonian Basin shows little or no evidence of botanical exploration. Therefore, geographical gaps and the small number of herbarium collections available impede accurate mapping of plant distributions and mapping biodiversity (Hopkins 2007).

Among the 59 alien plant species that are reported as invaders from 135 protected areas from around the world (in Foxcroft et al. 2013) there are many aquatic plants such as *Arundo donax*, *Hydrilla verticillata*, *Pistia stratiotes* and *Salvinia molesta*. According to our results and in combination with the USAqWRA scores, those species were the most invasive species in South America, prone to causes biodiversity loss in PAs.

The Human Influence Index could be considered a useful proxy to detect areas where the alien species could arrive and establish. Our results reflected that alien species were favoured in locations with a high effect of anthropisation. According to Gallardo et al. (2015) transport networks are at the moment one of the most important driver for the entry and the distribution of invasive plants (e.g. port proximity determined the presence of freshwater invaders) and directly linked to the vectors and pathways of introduction and secondary release for invasive species. These findings confirm that the relationship between invasive species and the human influence are quite important to explain highest risk values in areas where propagule pressure can be presumed high (i.e., close to transport networks and densely populated areas).

In accordance with García-Roselló et al. (2015), the inclusion of species in localities from which they had not been recorded by the use of predicted maps generally involves an increase in species richness. Extrapolations of individual species ranges, alternatively, do not appear to affect the geographical position of hotspots or patterns of global species richness.

Conclusion

The GIBF and literature datasets provided significantly different information and the combination of the two offered new information and a better coverage that would not exist in a single data source. Nevertheless, a careful quality evaluation of the primary biodiversity information, both in the case of literature and GBIF should be conducted, before the data is used for further analyses in macroecological studies.

The identification of invasive species risk hotspots for aquatic invasive plant species could promote the development of prevention and control strategies. Particularly, the biodiversity hotspots and the protected areas should be efficiently prevented and

451

monitored. The human influence amplifying the potential for invasion could be translated into highest cumulative risk scores in close relation to the location of commercial ports, dense populated areas and intensely used landscapes. The methodology used in the present research, if applied on a larger dataset including all non-native species, could facilitate prevention and monitoring, at least for some regions of South America.

Finally, we would like to stress that GBIF data and tools are very valuable and important. However constant efforts at increasing sample sizes through the generation of new data and the publishing of existing datasets are particularly required of native and alien aquatic plants in South America.

Acknowledgements

We gratefully thank A. Pauchard, J. Urrutia, R. Bustamante, S. Magela-Thomaz and L.J. Cumana Campos for providing useful information and literature. The University of Sassari Visiting Professor programme supported DC.

References

- Adhikari D, Tiwary R, Barik SK (2015) Modelling Hotspots for Invasive Alien Plants in India. *PloS ONE* 10: e0134665, https://doi.org/10.1371/journal.ponc.0134665
 Amano T, Sutherland WJ (2013) Four barriers to the global
- Amano T, Sutherland WJ (2013) Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. *Proceedings of the Royal* Society B 280: 20122649, https://doi.org/10.1098/rspb.2012.2649
- Barthlott W, Biedinger N, Braun G, Feig F, Kier G, Mutke J (1999) Terminological and methodological aspects of the mapping and analysis of the global biodiversity. *Acta Botanica Fennica* 162: 103–110
- Beck J, Böller M, Erhardt A, Schwanghart W (2014) Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics* 19: 10–15, https://doi.org/10.1016/j.ecoinf.2013.11.002
- Boakes EH, McGowan PJ, Fuller RA, Chang-qing D, Clark NE, O'Connor K, Mace GM (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biol* 8: e1000385, https://doi.org/10.1371/journal.pbio.1000385
- Boltovskoy D, Correa N (2015) Ecosystem impacts of the invasive bivalve Limnoperna fortunei (golden mussel) in South America. Hydrobiologia 746: 81–95, https://doi.org/10.1007/s10750-014-1882-9
- Brummitt N, Bachman SP, Aletrari E, Chadburn H, Griffiths-Lee J, Lutz M, Moat J, Rivers MC, Syfert MM, Lughadha EMN (2015) The Sampled Red List Index for Plants, phase II: groundtruthing specimen-based conservation assessments. *Philosophical Transactions of the Royal Society B* 370: 20140015, https://doi.org/10.1098/rstb.2014.0015
- Brundu G (2015) Plant invaders in European and Mediterranean inland waters: profiles, distribution, and threats. *Hydrobiologia* 746: 61–79, https://doi.org/10.1007/s10750-014-1910-9
- Chapman AD (2005) Uses of primary species-occurrence data, version 1.0. Report for the Global Biodiversity Information Facility, Copenhagen
- Collen B, Ram M, Zamin T, McRae L (2008) The tropical biodiversity data gap: addressing disparity in global monitoring. *Tropical Conservation Science* 1: 75–88, https://doi.org/10.1177/ 194008290800100202

- Delnatte C, Meyer JY (2012) Plant introduction, naturalization, and invasion in French Guiana (South America). *Biological Invasions* 14: 915–927, https://doi.org/10.1007/s10530-011-0129-1
- Donaldson JE, Hui C, Richardson DM, Robertson MP, Webber BL, Wilson JR (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. *Global Change Biology* 20: 1527–1537, https://doi.org/10.1111/gcb.12486
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kuhn I, Ohlemuller R, Peres-Neto PR, Reineking B, Schroder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 606–628, https://doi.org/10.1111/j.2007.0906-7590.05171.x
- Duursma DE, Gallagher RV, Roger E, Hughes L, Downey PO, Leishman MR (2013) Next-generation invaders? Hotspots for naturalised sleeper weeds in Australia under future climates. *PloS ONE* 8: e84222, https://doi.org/10.1371/journal.pone.0084222
- Edwards JL, Lane MA, Nielsen ES (2000) Interoperability of biodiversity databases: biodiversity information on every desktop. *Science* 289: 2312–2314, https://doi.org/10.1126/science. 289.5488.2312
- Engelhardt KAM (2011) Eutrophication, aquatic. In: Simberloff D, Rejmánek M (eds), Encyclopedia of Biological Invasions. University of California Press, Berkeley, pp 209–213
- Feeley KJ, Silman MR (2009) Extinction risks of Amazonian plant species. Proceedings of the National Academy of Sciences 106: 12382–12387, https://doi.org/10.1073/pnas.0900698106
- Feeley KJ, Silman MR (2010) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *Journal of Biogeography* 37: 733–740, https://doi.org/10.1111/j. 1365-2699.2009.02240.x
- Feeley KJ, Silman MR (2011) The data void in modeling current and future distributions of tropical species. *Global Change Biology* 17: 626–630, https://doi.org/10.1111/j.1365-2486.2010.02239.x
- Feeley KJ (2015) Are We Filling the Data Void? An Assessment of the Amount and Extent of Plant Collection Records and Census Data Available for Tropical South America. *PLoS ONE* 10: e0125629, https://doi.org/10.1371/journal.pone.0125629
- Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (eds) (2013) Plant invasions in protected areas: patterns, problems and challenges. Springer, Dordrecht, pp 656, https://doi.org/10.1007/978-94-007-7750-7
- Foxcroft LC, Pyšek P, Richardson DM, Genovesi P, MacFadyen S (2017) Plant invasion science in protected areas: Progress and priorities. *Biological Invasions* 19: 1353–1378, https://doi.org/10. 1007/s10530-016-1367-z
- Funk V, Zermoglio MF, Nasir N (1999) Testing the use of specimen collection data and GIS in biodiversity exploration and conservation decision making in Guyana. *Biodiversity & Conservation* 8: 727–751, https://doi.org/10.1023/A:1008877222842
- Gallardo B, Zieritz A, Aldridge DC (2015) The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. *PloS ONE* 10, e0125801, https://doi.org/10.1371/journal.pone.0125801
- García-Roselló E, Guisande C, González-Dacosta J, Heine J, Pelayo-Villamil P, Manjarrás-Hernández A, Vaamonde A, Granado-Lorencio C (2013) ModestR: a software tool for managing and analyzing species distribution map databases. *Ecography* 36: 1202–1207, https://doi.org/10.1111/j.1600-0587.2013.00374.x
- García-Roselló E, Guisande C, Heine J, Pelayo-Villamil P, Manjarrés-Hernández A, González Vilas L, González-Dacosta J, Vaamonde A, Granado-Lorencio C (2014) Using ModestR to download, import and clean species distribution records. *Methods in Ecology and Evolution* 5: 708–713, https://doi.org/ 10.1111/2041-210X.12209
- García-Roselló E, Guisande C, Manjarrés-Hernández A, González-Dacosta J, Heine J, Pelayo-Villamil P, González-Vilas L, Vari

452

Alien aquatic plants of South America

RP, Vaamonde A, Granado-Lorencio C (2015) Can we derive macroecological patterns from primary Global Biodiversity Information Facility data? *Global Ecology and Biogeography* 24: 335–347, https://doi.org/10.1111/geb.12260

- Gordon DR, Gantz CA, Jerde CL, Chadderton WL, Keller RP, Champion PD (2012) Weed risk assessment for aquatic plants: modification of a New Zealand system for the United States. *PloS ONE* 7: e40031, https://doi.org/10.1371/journal.pone.0040031
- Guézou A, Chamorro S, Pozo P, Guerrero AM, Atkinson R, Buddenhagen C, Jaramillo Díaz P, Gardener M (2014) CDF Checklist of Galapagos Introduced Plants - FCD Lista de especies de Plantas introducidas Galápagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado, N, Jiménez-Uzcátegui G, Ruiz D, Guézou A, Ziemmeck F (eds), Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin. Charles Darwin Foundation / Fundación Charles Darwin, Puerto Ayora, Galapagos: http://www.darwinfoundation.org/datazone/checklists/introduced-pecies/ introduced-plants/ (last updated: 21 January 2014)
- Hijmans RJ, Schreuder M, De la Cruz J, Guarino L (1999) Using GIS to check co-ordinates of genebank accessions. *Genetic Resources and Crop Evolution* 46: 291–296, https://doi.org/10. 1023/A:1008628005016
- Hopkins MJ (2007) Modelling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography* 34: 1400–1411, https://doi.org/10.1111/j.1365-2699.2007.01737.x
- Hortal J, Lobo JM, Jiménez-Valverde A (2007) Limitations of Biodiversity Databases: Case Study on Seed-Plant Diversity in Tenerife, Canary Islands. *Conservation Biology* 21: 853–863, https://doi.org/10.1111/j.1523-1739.2007.00686.x
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, https://doi.org/10.1111/j.1365-2664.2008.01600.x
- Jetz W, McPherson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution* 27: 151–159, https://doi.org/ 10.1016/j.tree.2011.09.007
- Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: quantification, scope, caveats and recommendations. *Bioscience* 65: 55–63, https://doi.org/10.1093/biosci/biu193
- Liang L, Clark JT, Kong N, Rieske LK, Fei S (2014) Spatial analysis facilitates invasive species risk assessment. *Forest Ecology and Management* 315: 22–29, https://doi.org/10.1016/j.foreco.2013.12.019
- Lozano V, Brundu G (2016) Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment. *Hydrobiologia* 1–16, https://doi.org/10.1007/s10750-016-2858-8
- Maldonado C, Molina CI, Zizka A, Persson C, Taylor CM, Albán J, Chilquillo E, Ronsted N, Antonelli A (2015) Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? *Global Ecology and Biogeography* 24: 973–984, https://doi.org/10.1111/geb.12326
- Meyer C, Kreft H, Guralnick R, Jetz W (2015) Global priorities for an effective information basis of biodiversity distributions. *Nature Communications* 6, https://doi.org/10.1038/ncomms9221
- McGeoch MA, Groom QJ, Pagad S, Petrosyan V, Ruiz G, Wilson J (2016) Data fitness for use in research on alien and invasive species. Copenhagen: GBIF Secretariat. http://www.gbif.org/resou rcc/82958 (accessed on 5 January 2017)
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858, https://doi.org/10.1038/35002501
- Pauchard A, Cavieres L, Bustamante R, Becerra P, Rapoport E (2004) Increasing the understanding of plant invasions in southern South America: first symposium on Alien Plant Invasions in

Chile. Biological Invasions 6: 255–257, https://doi.org/10.1023/B: BINV.0000022137.61633.09

- Pelayo-Villamil P, Guisande C, González-Vilas L, Carvajal-Quintero JD, Jiménez-Segura LF, García-Roselló E, Heine J, González-Dacosta J, Manjarrés-Hernández A, Vaamonde A (2012) ModestR: Una herramienta infromática para el estudio de los ecosistemas acuáticos de Colombia. Actualidades Biológicas 34(97): 225–239
- Perrings C, Dehnen-Schmutz K, Touza J, Williamson M (2005) How to manage biological invasions under globalization. *Trends in Ecology & Evolution* 20: 212–215, https://doi.org/10.1016/j.tree. 2005.02.011
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78: 419–433, https://doi.org/10.1086/378926
- Petřík P, Pergl J, Wild J (2010) Recording effort biases the species richness cited in plant distribution atlases. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 57–65, https://doi.org/ 10.1016/j.ppecs.2009.06.004
- Ramírez C, San Martín C (2006) Diversidad de macrófitos chilenos. In: Vila I, Veloso A, Schlatter R, Ramírez C (eds), Macrófitas y vertebrados de los sistemas límnicos de Chile. Editorial Universitaria, Santiago, Chile, pp 358–363
- Ricciardi A, Rasmussen JB (1999) Extinction rates of North American freshwater fauna. *Conservation Biology* 13: 1220– 1222, https://doi.org/10.1046/j.1523-1739.1999.98380.x
- Roberts T, Moritz A (2011) A framework for publishing primary biodiversity data. *BMC Bioinformatics* 12: 11, http://www.biomed central.com/1471-2105/12/S15/11
- Schulman L, Toivonen T, Ruokolainen K (2007) Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography* 34: 1388– 1399, https://doi.org/10.1111/j.1365-2699.2007.01716.x
- Seebens H, Essl F, Dawson W, Fuentes N, Moser D, Pergl J, Pyšek P, Kleunen M van, Weber E, Winter M, Blasius B (2015) Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology* 21: 4128–4140, https://doi.org/10.1111/geb.13021
- Seebens H, Blackburn T, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435, https://doi.org/10.1038/ncomms14435
- Simberloff D (2013) Invasive species: What everyone needs to know. Oxford University Press, New York, 352 pp
- Soberón J, Peterson T (2004) Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions* of the Royal Society of London B: Biological Sciences 359: 689– 698, https://doi.org/10.1098/rstb.2003.1439
- Sousa-Baena MS, Garcia LC, Peterson AT (2014) Completeness of digital accessible knowledge of the plants of Brazil and priorities for survey and inventory. *Diversity and Distributions* 20: 369– 381, https://doi.org/10.1111/ddi.12136
- Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174, https://doi.org/10.1111/j.1365-2427.2009.02380.x
- Suarez AV, Tsutsui ND (2004) The value of museum collections for research and society. *BioScience* 54: 66–74, https://doi.org/10. 1641/0006-3568(2004)054[0066:TVOMCF]2.0.CO;2
- R Core Team (2015) R: A language and environment for statistical computing. Vienna, Austria. http://www.R-project.org/

453

- Thomaz SM, Kovalenko KE, Havel JE, Kats LB (2015) Aquatic invasive species: general trends in the literature and introduction to the special issue. *Hydrobiologia* 746: 1–12, https://doi.org/10. 1007/s10750-014-2150-8
- Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234–2250, http://dx.doi.org/10.1111/j.1365-2486.2005. 001018.x
- Troia MJ, McManamay RA (2016) Filling in the GAPS: evaluating completeness and coverage of open-access biodiversity databases in the United States. *Ecology and Evolution* 6(14): 4654–4669, http://dx.doi.org/10.1002/ecc3.2225
- Urrutia EJ, Sánchez González P, Pauchard Cortés A (2016) Flora acuática y palustre introducida en Chile. Laboratorio de Invasiones Biológicas LIB, 87 pp
- van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cardenas D, Cardenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelser PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu WS, Thomas J, Velayos M, Wieringa JJ, Pyšek P (2015) Global exchange and accumulation of non-native plants. *Nature* 525: 100–103, https://doi.org/10.1038/nature14910

- Vollmar A, Macklin JA, Ford L (2010) Natural history specimen digitization: challenges and concerns. *Biodiversity Informatics* 7, https://doi.org/10.17161/bi.v7i2.3992
- Wildlife Conservation Society WCS; Center for International Earth Science Information Network - CIESIN - Columbia University (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC), http://dx.doi.org/10.7927/H4M61H5F
- World Conservation Union and UNEP-World Conservation Monitoring Centre (2007) World Database on Protected Areas, Version 2007, WCMC, Cambridge, UK, 2007, https://www.unepwemc.org
- Yang W, Ma K, Kreft H (2014) Environmental and socio-economic factors shaping the geography of floristic collections in China. *Global Ecology and Biogeography* 23: 1284–1292, https://doi.org/ 10.1111/geb.12225

Supplementary material

The following supplementary material is available for this article:

 Table S1. List of the investigated 80 aquatic plant species varying for native origin.

- Table S2. List of the investigated 40 native and 40 non-native aquatic plant species according to GBIF and literature records.
- Table S3. The 16 regions of South America considered in the present study and the taxonomic diversity of the 80 native and non-native aquatic plant species according to GBIF database and literature sources.

Table S4. Species data downloaded from GBIF dataset with the software ModestR.

Table S5. Qualitative a priori categorization for the 40 South American alien aquatic species evaluated with the US Aquatic Weed Risk Assessment scheme.

Table S6. Total scores for the 40 South American alien aquatic species evaluated with the US Aquatic Weed Risk Assessment scheme.

Table S7. Qualitative a priori categorization for the 40 South American native aquatic species for each region.

Table S8. GBIF and Literature records for South American regions (data clean).

Table S9. Contingency table between native/non-native records and inside/outside protected area.

Table S10. Script and output of Generalized Least Squares to evaluate the spatial autocorrelation in Human Influence Index data.

Table S11. Kriging parameters of estimated non-native species density according the number of different species in the 16 regions of South America.

Figure S1. Distribution of species records, downloaded from GBIF.

Figure S2. Choropleth maps on the density of aquatic species in each of the 16 regions of South America.

Figure S3. Box plots of the Human Influence Index (HII) for invasive alien and non-invasive alien species.

Figure S4. Box plots of the number of records in the protected areas for invasive alien and non-invasive alien species.

This material is available as part of online article from:

http://www.reabic.net/journals/mbi/2017/Supplements/MBI_2017_Lozano_etal_Supplementary_Tables.xlsx http://www.reabic.net/journals/mbi/2017/Supplements/MBI_2017_Lozano_etal_Supplementary_Figures.pdf

454

CHAPTER 4

ECOLOGICAL NICHE DYNAMICS ACROSS CONTINENTS IN AQUATIC PLANTS NATIVE TO SOUTH AMERICA AND INVASIVE ELSEWHERE

Introduction and aims

Understanding possible niche shifts between the native and invaded ranges of invasive aquatic plants is challenging. Most studies address terrestrial species, due to the lack of freshwater-specific environmental information at sufficiently fine spatial resolution. On the assumption that niche is conserved during the invasion process, I investigated the extent to which niches of aquatic plants are conserved comparing their native niches in South America with invaded niches in Africa, Australia, Europe and North America.

Methodology and main results

The estimated niche for the native region was projected onto each invaded region to generate potential distributions there. Freshwater-specific climate and environmental variables were collected from a standardized 1x1-km grid. Species occurrences were obtained from different world-databases. PCA-env analyses was used to assess the similarity between niches with the ecospat R package. Niche dynamics analysis was performed using three approximations to compare invaded niches with native niche: 1) niche overlap (D); 2) niche equivalence and 3) the niche similarity. Additionally, niche zones within the environmental space were identified by overlapping the native and invasive niches: unfilled; overlap and expansion. While the overlap values measured the proportion of niche conserved, the expansion values estimated the proportion niche expanded. It was found, that when analog climate niches are compared between species distribution ranges, some are conserved, while others expand their ranges. The results can be useful to demonstrate that while species occupied subsets of its original native niche, in some continents can occupy new environments, meaning that the niche is shifted.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Conclusions

These findings can be used to identify areas at risk of recently introduced alien plants, and develop future monitoring programs for aquatic ecosystems, prioritizing control efforts, which enables the effective use of ecological niche models to forecast aquatic invasion in other geographic regions.

Ecological niche dynamics across continents in aquatic plants native to South America and invasive elsewhere

Niche shift during invasion

Vanessa Lozano¹, Giuseppe Brundu¹ and Daniel S. Chapman²

¹ Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy

² NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK

E-mail: vlozano@uniss.it; gbrundu@uniss.it; dcha@ceh.ac.uk

Abstract

Niche shifts between the native and invaded ranges of invasive aquatic plants have been challenged. Most studies address terrestrial species, due to the lack of freshwater-specific environmental information at sufficiently fine spatial resolution. On the assumption that niche is conserved during the invasion process, we investigated the extent to which niches of aquatic plants are conserved comparing their native niches in South America with invaded niches in Africa, Asia, Australia, Europe and North America. The estimated niche for the native region was projected onto each invaded region to generate potential distributions there. Niche dynamics analysis was performed using three approximations to compare invaded niches with native niche: niche overlap; niche equivalence and the niche similarity. Additionally, we indentified niche zones within the environmental space by overlapping the native and invasive niches: unfilled; overlap and expansion. While the overlap values measured the proportion of niche conserved, the expansion values estimated the proportion niche expanded. We found, that when analog climate niches are compared between species distribution ranges, some are conserved, while others expand their ranges. Our results are useful to demonstrate that while occupied subsets of its original native niche, in some continents its niche shifted. These findings can be used to identify areas at risk of recently introduction of neophytes, and develop future monitoring programs for aquatic ecosystems, prioritizing control efforts, which enables the effective use of ecological niche models to forecast aquatic invasion in other geographic regions.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Keywords climate change, hydroclimatic variables, invasive aquatic plants, niche dynamics, niche shift, species distribution models (SDMs)

1. Introduction

Freshwater ecosystems, are vulnerable to both climate change and biological invasion at broad spatial scales (Dudgeon et al. 2006). In future years, water temperature is expected to increase, and the modification of precipitation events may alter flow regimes (Whitehead et al. 2009; Watts et al. 2015). Compared to terrestrial plants, aquatic plants are shown to have a higher probability of becoming invasive in new environments (see Andreu and Vilà, 2010). For example, Egeria densa Planch. (Hydrocharitaceae); Eichhornia crassipes (Mart.) Solms (Pontederiaceae); Myriophyllum aquaticum (Vell.) Verdc. (Haloragaceae); Pistia stratiotes L. (Araceae) and Salvinia molesta D.S. Mitch. (Salviniaceae) are five aquatic plant species native to South America and highly invasive elsewhere. They have been introduced into Europe, North America, Australia and New Zealand, where they increasingly expand their range (Yarrow et al. 2009; Hussner 2012; Thouvenot et al. 2013a) and have been reported as the most damaging alien plants in South Africa's freshwater systems (Henderson and Cilliers, 2002; Hoveka et al. 2016). In both, terrestrial and freshwater ecosystems species distribution models (SDMs) can be used as tools for assessing the suitability for establishment if introduced outside the native range (e.g., Ficetola et al 2007; Broennimann and Guisan; 2008; Hulme 2012; Petitpierre et al.; 2012; Guisan et al. 2013). Through SDMs predictions is also possible identify the factors that contribute to niche shifts between native and invaded ranges (Li et al. 2014). SDMs have generally been proven to reflect the correct response to climate change (Stephens et al. 2016). Species distributions are correlated with climatic conditions more strongly than with other factors, at least at coarse spatial resolutions (Thuiller et al., 2004; Luoto et al., 2007; Hortal et al., 2010). Such models identify sets of variables associated with the presence of invasive species to project their requirements onto the geographic space (Guisan and Thuiller 2005).

One assumption underlying SDMs is the principle of niche conservatism. This concept assumes that species tend to preserve their ancestral niches requirements over time and

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

space (Wiens et al. 2010) or change only slowly over hundreds to millions of years (Wiens and Graham 2005, Pearman et al. 2008). Assuming niche conservatism, then invasive ranges can be predicted with models fitted with data from the native range (Peterson and Vieglais 2001). For example, the reliability of predictions provided by SDMs is questionable if niche shifts have truly taken place in different areas (Bennett et al. 2010, Wiens and Graham 2005, Wiens et al. 2010). Chapman et al. (2017) demonstrated how can be simulate a potential niche shift of Ambrosia artemisiifolia L. using forward-mechanistic species distribution model. They provide a relationship between changes to functional traits of the species and their consequences for niche and distributional shifts (i.e., established population triggers a niche shift toward cooler climates), probably occuring by rapid evolution process during invasion. Guisan et al. (2014) built a review on empirical invasion studies, reporting 36 studies comparing the niche of exotic species between their native and exotic ranges. Therefore, they concluded niche shifts probably depend on the organism, methods and data used. Petitpierre et al. (2012) concluded, in a study on 50 Holarctic plant invaders, that climatic niche shift are rare between the native and the invasive ranges, consequently the models can usefully predict invasion in the non-native range.

Many studies have investigated invasive plant species distribution through projection by SDMs (Kriticos et al. 2003; Peterson et al. 2008; Qin et al. 2014; Thalmann et al. 2015) and climatic niche shifts (Early and Sax 2014; Guisan et al. 2014), but only few of them have used non-native aquatic plant species (Heikkinen et al. 2009; Alahuhta et al. 2011; Hoveka et al. 2016; Lopes et al. 2017). Although few studies have investigated whether or not the niches of aquatic plant species are conserved at broad spatial extents (see Alahuhta et al. 2017), Chambers et al. (2008) suggest that the ecological niches of aquatic macrophytes remain unchanged in space. Based on the general assumption of conserved niches for aquatic plant species (Chambers et al. 2008), the expectation is that species niche remain relatively similar in the native and invaded range and that niche extent are moderately wide for all species in all study areas. Nevertheless, recent studies have suggested that niche conservatism does not occur in all invasive species (Broennimann et al. 2010; Petitpierre et al. 2012).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Non-native species offer excellent model systems for examining niche conservatism associated with biological invasions (Sax et al. 2007; Peterson 2011; Schulte et al. 2012). In particular the five aquatic species chosen for this study, in both ranges (native and nonnative), occurs in disturbed and natural freshwater ecosystems, but it rarely reaches densities in the native range as high as observed in the invaded range. In this study, we focused on the potential distribution and further niche shifts detected on five South American invasive aquatic plants, that have major impacts in their introduced ranges. Previous studies considered the distribution of some of these species, but so far they have only been made at a country scale or based on a limited set of algorithms or bioclimatic variables useful mostly for terrestrial plants (Gallardo and Aldridge 2013; Kelly et al. 2014). By applying rigorous modelling methods and selected hydroclimatic variables specific for aquatic environments, we aimed 1) to assess the current potential distribution of five South American invasive aquatic plants, using SDMs to compare, across continents the relative importance of the climatic, and spatial components of the niche space on each species distribution within a given region and 2) quantified the dynamics of climatic niches in analogous climates (i.e., the climates that are available in both native and invaded extents) between the native and the invaded ranges for five South American aquatic plant species at large-scale.

2. Methodology

2.1 - Study species and occurrence data

We selected five well-known aquatic plant species native from South America and invasive elsewhere (i.e., *Eichhornia crassipes* (Mart.) Solms, *Egeria densa* Planch., *Myriophyllum aquaticum* (Vell.) Verdc., *Pistia stratiotes* L. and *Salvinia molesta* D.S. Mitch.), to carried out the distribution models and ecological niche shift. We selected this five species based on the high level of invasiveness reported by Lozano and Brundu (2016) in the risk assessment for aquatic species in South America. In addition to the native distribution, we distinguish locations where the species has become invasive within South America but outside the historic native range (classified as *alien in*).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Species occurrences from their native and introduced ranges were obtained using the "Spoce" R package (Chamberlain 2017). The package allowed us download data occurrence from Global Biodiversity Information Facility (www.gbif.org), Atlas of Living (www.ala.org.au/), Biodiversity Information Serving Australia Our Nation (www.bison.usgs.gov), iNaturalist (www.inaturalist.org), Ecoengine Interface (www.github.com/ropensci/ecoengine), iDigBio (www.idigbio.org) and Ocean Biographic Information System (www.iobis.org) (accessed February, 2017). Occurrence data were supplemented with information from the literature and from an expert working group. Occurrence records with insufficient spatial precision, potential errors (e.g., taxonomic misunderstand, duplicates of the same sample), or that were outside of the coverage of the predictor layers (e.g., sea points, small islands) were excluded. We also excluded records collected before 1950. After an evaluation of casual records, e.g. those where winter frosts are known to kill the species or populations known to occupy climatically anomalous micro-habitats, were also removed. We decided to remove these records based mostly on: mean temperature of the warmest quarter < 10 - 15 °C (below the minimum growth temperature); mean minimum temperature of the coldest month < -3 - 0 °C (prolonged exposure to lethal frosts) and precipitation of the warmest quarter < 4 - 5 mm (only small and seasonally dry habitat is available, which is expected to be of low suitability). Table 1 shows the requirements for each hydroclimatic variable used in the model.

		Hydroclimatic variables		
Species	Tolerances range	Hydro 6	Hydro 10	Hydro 18
Egeria densa	stop growth at < 6 degree, but can survive at 1 degree under 15 cm of ice	> -2	> 15	> 4,09
Eichhornia crassipes	limiting temperature for germination is 5-10 C°	> -3	> 10	> 4,09
Myriophyllum aquaticum	tolerate freezing temperatures in California's Bay		> 10	> 4,09
Pistia stratiotes	prolonged exposure to lethal frosts		> 10	> 5
Salvinia molesta	prolonged exposure to lethal frosts	> 0	> 10	> 6

Table 1. Tolerances range for each species in the hydroclimatic variables used in the model.

After removing duplicate records or doubtful point data, we created the models with a total geographic records of 652 for *E. densa*, 3,210 for *E. crassipes*, 1,485 for *M. aquaticum*, 1,688 for *P. stratiotes*, and 704 for *S. molesta* (Figure S1). The remaining records were gridded at a 0.25 degree resolution.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

2.2 - Climate and freshwater system data

Freshwater-specific climate data were collected from "Near-global environmental information for freshwater ecosystems" (www.earthenv.org/streams). The dataset consists of near-global, spatially continuous, and freshwater-specific environmental variables in a standardized 1km grid. Domisch et al. (2015) "delineated the sub-catchment for each grid cell along the HydroSHEDS river network and summarized the upstream environment (climate, topography, land cover, surface geology and soil) to each grid cell using various metrics (average, minimum, maximum, range, sum, inverse distance-weighted average and sum). All variables were subsequently averaged across single lakes and reservoirs of the Global lakes and Wetlands Database that are connected to the river network". We found useful and novel for our specific aquatic research that monthly climate variables were summarized into 19 long-term climatic variables following the "bioclim" framework, there after called "hydroclimatic variables". Based on natural history data of each aquatic species, the following hydroclimatic and environmental variables that we chose to model the species were: Hydro 06 = Minimum Upstream Temperature of Coldest Month (reflecting exposure to frost); Hydro 10 = Mean Upstream Temperature of Warmest Quarter (reflecting the growing season thermal regime) and Hydro 18 (log10 (1+ hydro 18 transformed mm) = Upstream Precipitation of Warmest Quarter (seasonal drying out of waterbodies may reduce suitability). Since our model have aquatic habitat requirements, we filtered our projected suitability maps to only include cells containing aquatic ecosystems adapted to our species. We downloaded land use datasets from the Global lakes and wetlands cover (GLWD) (Lehner and Döll 2004).

2.3 - Species distribution models (SDMs)

We used species distribution models (SDMs) to predict potential suitable areas for the invasion on aquatic species, employing "biomod2" R package (Thuiller et al. 2016). We generated potential distributions of the species in their native and invaded regions. For assembling the model, we used presence-background data (presence-only). The background (called "pseudo-absences"), contrast the environment at the species occurrence locations

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

against a random sample of the global background environmental conditions. The background region comprised the native range, accessible parts of the invaded range and highly unsuitable regions. To control for spatial biases in recording effort, the background was weighted in proportion to the Tracheophyte record density on GBIF. To sample as much of the background environment as possible, twenty background sub-samples and 10,000 randomly generated points (i.e., pseudo-absences) were used to estimate the density of available environments, in each cell of the environmental space, which is sufficiently large to ensure model convergence (Figure S2).

Each dataset (i.e., combination of the presences and the individual background samples) was randomly split into 80% for model training and 20% for model evaluation. Then, nine statistical algorithms were fitted with the default biomod2, including: three regression methods 1) Generalised linear model (GLM), 2) Generalised additive model (GAM) and 3) Multivariate adaptive regression splines (MARS); two classification methods 4) Classification tree algorithm (CTA) and 5) Flexible discriminant analysis (FDA); and four machine learning methods 6) Artificial neural network (ANN), 7) Generalised boosting model (GBM), 8) maximum entropy (MaxEnt) and 9) Random forest (RF).

Variable importance was obtained and variable response functions were produced using biomod2 (Figure S3). Model predictive performance was assessed by calculating the Area Under the Receiver-Operator Curve (AUC) for model predictions on the evaluation data, that were reserved from model fitting. AUC can be interpreted as the probability that a randomly selected presence has a higher model-predicted suitability than a randomly selected absence. This information was used to combine the predictions of the different algorithms to produce ensemble projections of the model. For this, the three algorithms with the lowest AUC were first rejected and then predictions of the remaining algorithms were averaged, weighted by their AUC (Table S1).

2.4 - Niche analysis

2.4.1 - Niche overlap and test of niche shift

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

We used PCA-env analyses (see Broennimann et al. 2012) to assess the similarity between niches, depicting a multivariate climatic space calculated with the climatic variables. This procedure allowed us to evaluate the hypothesis of niche conservatism between native and invaded ranges. For each PCA, performed to compare the native niche with its niches estimated for each invaded region, we used the first two axes to define the environmental space (i.e., each cell corresponds to a unique set of climate conditions) divided into 100 x 100 cells. We used three approximations to compare invaded niches with native niche: 1) niche overlap (the zone shared between native and invasive niches) - measuring of the D metric, indicates the overall match between two niches over the whole climatic space and varies between 0 (no overlap) and 1 (complete overlap) - (Schoener, 1970; reviewed in Warren et al. 2008); 2) test of niche equivalency (NE) and 3) test of niche similarity (NS) (methodology described in Warren et al. 2008). NE determines whether niches in two geographical ranges are equivalent (i.e., whether the niche overlap is constant when randomly reallocating the occurrences among the two ranges) and NS addresses whether the environmental niche occupied in one range is more similar to the one occupied in the other range than would be expected by chance. Rejection of NE means that the niches of native and non-native populations are not statistically equivalent, while a rejection of NS indicates that niches are more similar than expected at random.

2.4.2 - Niche unfilling and expansion

Additionally, we indentified niche zones within the environmental space by overlapping the native and invasive niches (see Petitpierre et al. 2012): 1) unfilled (U), the zone on the native niche not shared with the invaded niche; 2) stable (S), the zone where species occurs in both ranges; and 3) expansion (E), the zone on the invaded niche not shared with the native niche. While the S values measured the proportion of niche conserved, the E values estimated the proportion niche expanded (i.e., characterize true niche shifts). The unfilled zone (U) assesses the fraction of niche not yet occupied by the species in the invaded range. These indices were measured in the climatic space shared between the native and invaded ranges in order to avoid detecting niche shifts due to climatic non-availability in the native

range.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

3. Results

3.1 - Model evaluation

In total, there were 645 grid cells with recorded occurrence for *E. densa*, 1077 for *E. crassipes*, 637 for *M. aquaticum*, 817 for *P. stratiotes* and 237 for *S. molesta* available for the modeling.

Across the modelled, the discrimination ability (AUC) between aquatic species records and grid cells without records ('absences') was shown in table S1. The minimum and maximum AUC values from model outputs generated by ensemble model for the species ranged from 0.867 to 0.970. These results indicate a relatively high performance of our species distribution models. The variable importance of the fitted model algorithms and the ensemble suggested that suitability was most strongly determined by the minimum upstream temperature of coldest month ranged between 53.3% and 85% among the five species (Table S1).

The response plots show that the ensemble model estimated biologically reasonable curves, with suitability limited by harsh frosts, low growing season temperatures particularly in the case of *E. crassipes*, low cover of large wetlands and low precipitation in the growing season (Figure S3). The function also indicated that suitability was reduced if minimum temperatures were too high.

3.2 - Current potential distribution

The areas estimated to be climatically suitable for the invasive aquatic species under current climatic conditions were illustrated for the world (Figure 1). The projection of *E. densa, E. crassipes* and *S. molesta* models indicated high suitability throughout the tropical and subtropical parts of the world (areas in yellow; Figure 1). In addition, areas suitable for the distribution of *M. aquaticum* and *P. stratiotes* were found in subtropical parts of the world. Non-native occurrences of the species were largely consistent with this projection. Among the five species the potential geographical range for *E. crassipes* and *S. molesta* was predicted to be extremely broad. In general terms, its region extent is restricted by cold stress. The model predictions were based on natural water temperatures. Nevertheless,

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

wherever the water temperature is warm enough (e.g., warming associated with industrial outflows), the species might established. No climatically suitable areas for the species were identified in the Andean cordillera in Chile (some high altitude areas are too cold for persistence), but a high suitability in southeast North America, possible causing an invasion threat where there are sources of standing water.



Figure 1. Global projected suitability for: *Egeria densa*, *Eichhornia crassipes*, *Myriophyllum aquaticum*, *Pistia stratiotes and Salvinia molesta*. Establishment in the current climate. For visualization, the projection has been aggregated to a 0.25 x 0.25 degree resolution, by taking the maximum suitability of constituent higher resolution grid cells. The white areas have climatic conditions outside the range of the training data so were excluded from the projection.

3.3 - Niche analysis

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

We report the results of niche dynamics quantified by PCA calibrated on climate availability within the native range extents at fine resolution, due to the larger sample size of invaded ranges. The PCA-env analyses of native and invaded regions showed changes in the size of the niches and in the position of the areas (i.e. highest density of occurrences). In general, the correlation circle, the arrow directions show that the niche moved towards colder (BIO6) and driest (BIO 18) climates in all continents except in North America (Figure S4). The importance of climate and environmental variables on the studied species' distributions varied strongly across study across the areas. Of the climate proxy variables, minimum temperature of the coldest month had the highest effect on the studied species.

The level of niche overlap among species vary between 3 and 49%. In general M. aquaticum had the highest average in the overlap index (D = 0.33) and S. molesta the lowest (D = 0.14). North America was the continent with the higher values of overlap area (E. densa D = 0.39; E. crassipes D = 0.36; M. aquaticum D = 0.43; P. stratiotes D = 0.43; S. molesta D = 0.10, around 40% of the predicted distribution is occupied by the species (Figure 2, S5; Table S2). On the contrary, Africa was one of the continent with the highest unfilled areas (i.e., zone on the native niche not shared with the invaded niche) of the predicted distribution. Niche expansion beyond native climate conditions varied widely among species. Expansion areas were big for North America compared with other continents (Table S2; Figure S5). The highest expansion values were reported for S. molesta in Europe (0.95), Africa (0.86) and North America (0.75), followed by E. densa (0.33) in North America. In all cases, the native region had a greater niche breadth than any of the invaded regions and the shift occurs within the limits of the native niche (Figure S5). In Amazonian E. densa and S. molesta occupy areas not predicted by its distribution in the native range (see Figure 1). When the South American model was projected onto Africa, Asia and (modified-niche-to-invaded), the unfilled area in both continents (i.e., new potential distribution areas) increased in 88% and 77% respectively for *E. densa*. The same for *M. aquaticum* in Africa (71%) and Asia (62%) and for *S. molesta* in Europe with 69% (Table S2; Figure S5). In all cases, the native region had a greater niche breadth than any of the invaded regions.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 2. Example of climatic niche dynamics between native and invaded ranges of *Eichhornia crassipes*. The contour lines delineate the available niche in its native range (green) and in its invaded range (red). The solid and dashed contour lines illustrate, respectively, 100% and 75% of the available (background) environment. The colored areas correspond to the expansion zone (red), unfilled zone (green) and the overlap zone (blue), resulting from overlaying the native niche with the invaded niche. The solid arrows represent the change in the centre of the species niche (climatic space) between the native and invaded ranges. The colored numbers represent the niche unfilling (green), expansion (red) and overlap (blue) index.

In North America, the shift on the highest density of occurrences surpasses the limits of the native niche for *E. densa*, *E. crassipes* and *M. aquaticum*, while for the other continents, this shift occurs within these limits (Figure S5).

The niche equivalency tests confirmed that invasive niches for the five species are not identical to the native niche. The niche similarity test across the world were not significant for all species (i.e., similarity test with a significance level ≤ 0.05) (Table S3, Figure S6). This indicates that the occupation of the species does not follow a pattern expected by native niche requirements and seems to be random. Nevertheless, this pattern can be explained by several factors as: 1) the distribution observed could be mostly human induced, 2) the database is biased or 3) the environmental data are too broad scaled. This indicates that the species not remain in South America climates and are rarely found in new climates, and not only occupies areas with similar climatic condition to those found in its native range (i.e., the niche of the species in invasive ranges is less similar to the niche of the native region than would be expected by chance). In accordance with this, when the climate niches in the invaded region and the native region are not more similar than expected by chance, indicates that in the invaded range the occupation of the species does not follow a pattern expected by native niche requirements and seems to be random (i.e.,

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

some of which are similar to the climatic condition in its native range, while others are different).

4. Discussion

In this study, we predicted the global changes in climate suitability for five invasive aquatic plants which have massive economic and ecological impacts, highlighting that large portions of aquatic ecosystems are predicted to be suitable for these species in most regions of the world. Our predictions illustrate the potential climatic range of species based on their modeled environmental niches, and the occurrence of species within their suitable climatic range, but the models did not consider local factors such as water body size, water depth, or water quality (pH, nutrients and turbidity) which can greatly influence the suitability of aquatic environments for the aquatic plants (Feijoó et al. 2002; Hussner et al. 2009; Hussner et al. 2010; Bornette and Puijalon 2010).

The predictions on the current climate ranges, of the invasive aquatic species presented in this study, reflect their current distribution, especially outside their native range, but in some cases, have not yet been introduced into every continent. According to Gillar et al. (2017), one reason is, the time since introduction into their invasive range has not always allowed them to be in equilibrium with the environment, and probably have not reached all of their suitable environments yet. Since in many cases the species are not at equilibrium, model performance is not accurate during the invasion process, and false-presences may be misleading if they represent areas that have yet to be colonized (Peterson et al., 2008) and are treated as pseudo-absences in model building.

On the other hand, in marginal habitat quality, these species would be unable to reproduce, and this may lead to an overestimation of the potential impact of invasive species (Bradley, 2013).

In the native range of *E. densa*, *E. crassipes*, *P. stratiotes* and *S. molesta* the climatic potential range appears to extend into cooler areas of Argentina than it has been reported. The northern potential distribution for *E. crassipes* in Europe is defined by cold stress, with climatically suitable habitat encircling the Pyrenees in southern France. All of the countries

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

of the Mediterranean basin and North Africa are at significant risk, in terms of degree of climate suitability. Nonetheless, the standing water resources throughout the Mediterranean basin are critical to human survival as a means of surviving the summer drought period that typifies the Mediterranean climate (Kriticos and Brunel 2016). The climatic potential range for *M. aquaticum* and *E. densa* appears to extend into cooler areas of north Europe.

The native potential distribution showed the highest probabilities of presence across in Amazonian for *E. densa*, *P. stratiotes* and *S. molesta*, also in the lower slopes of the Andean cordillera in Colombia – except for *P. startiotes* and *S. molesta* –, and some evergreen forests in southern Venezuela, except for *M. aquaticum* – all characterized by dry and warm climates – showed the highest presence probabilities.

The predicted range of *M. aquaticum* shows that this species has suitable climatic areas at latitudes which are further north than those suitable the others aquatic plants, this result is consistent with models by Kelly et al. (2014) in Ireland and Gillar et al. (2017) at global scale, where could expand their distribution. In accordance with Gillard et al. (2017) *M. aquaticum* generally having the lowest habitat suitability throughout the world.

In general, at global scale climate is most strongly driver associated with the distribution changes but is the least important factor associated with the regional distribution of aquatic invasive species, e.g. in Ireland (Kelly et al. 2014). The global ranges climatic tolerances set by mean annual temperature and minimum temperature of coldest month. According to Kelly et al. (2014) is possible that a stronger association with climatic variables would emerge if variables specific to freshwater habitats will used (e.g., max, min and mean water surface temperatures). In our study we used specific hydroclimatic variables associated with freshwater environments. Additionally, the GLWD used in this study to limit the potential presence of the species to aquatic environments, represents current locations of water bodies and wetlands.

Niche shift has been documented in several invasive plant species (Chapman et al. 2017; Goncalves et al. 2014; Li et al. 2014) and there is still, considerable debate on the climatic niche conservatism of species (Losos 2008; Wiens et al. 2010; Peterson 2011; Pearman et

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

al. 2014). As far as we are aware, our study is one of the first approach to identify the realized climatic niche shifts between invaded and native ranges for invasive aquatic species. It is well known that realized niche shifts can result from 1) changes in dispersal limitations and biotic interactions between native and invaded ranges and 2) introduction history and rapid evolution (Pearman et al. 2008; Alexander and Edwards 2010). Our results demonstrate that even though the niches occupied by the five aquatic species across the world are subsets of its native niche in South America, mostly in North America these species' niche shifted towards colder climates, with temperatures that frequently exceed the maxima recorded in its native region. The presence of the aquatic species in novel climatic conditions indicates that its niche has not been conserved in some continents (e.g., North America and Africa) throughout the process of invasion, therefore suggesting a greater capacity to invade new regions than previously thought.

The proportion of realized niche shifts in the invaded range implies that many non-native aquatic species only occupy, in the native and invaded range, a part of the environment that is potentially suitable, because of dispersal limitations and changes in biological interactions.

In addition, for widespread species as *E. crassipes* or *M. aquaticum* multiple introductions across continents from different source populations in the native range, could facilitate the mixture of previously native populations and increase the genetic variation in invading populations (Kolbe et al. 2004). Such event may promote the capacity of the species to respond to selection in new environments, favoring the occurrence of fundamental niche shifts (Pearman et al. 2008; Alexander and Edwards, 2010).

According to Li et al. (2014) larger native range sizes may, however, explain the lower niche shifts in plants, compared with other species. In contrast, Alahuhta et al. (2017), found little evidence for niche conservatism in the distributions of the 11 macrophyte species among Finland, Sweden, Minnesota and Wisconsin. They found that species were mostly affected by same climate variables, as well as in our study. Nevertheless, their main finding that niches of lake for some aquatic plants (mostly hydrophytes) may not be conserved over space and time has various ecological implications. Modelling the distributions of invasive species and those of species assumed to respond to climate change

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

is based on the idea that niches are conserved (Wiens and Graham 2005, Wiens et al. 2010). Soberón and Peterson (2011) demonstrated even in the absence of competitors and evolutionary processes, diverse environmental conditions will produce different existing fundamental niches, and therefore, different realized niches. Then Alahuhta et al. (2017), discussed that the potential lack of niche conservatism in aquatic plants could be due: 1) an unsuitable or incomplete set of explanatory variables; 2) genetic variation; or 3) phenotypic plasticity within species. According to Ackerly (2003), genetic variation may explain niche shift between continents, whereas phenotypic plasticity may be a more important factor in within-continent comparisons. On the other hand, high levels of phenotypic plasticity have been reported for aquatic plant species (Eller and Brix 2012).

5. Conclusion

Our models predicted future northward shifts in the bioclimatic ranges of the species in their invasive ranges (e.g., North America). The increase in bioclimatic suitability may accelerate the rate of expansion of their northernmost invasion front.

The results provided insights into the climatic niche dynamics for both native and invaded ranges on aquatic plants. Based on our results, ordinations seem to be more appropriate than SDMs for investigating niche overlap. However, SDMs are able to select and rank variables according to their importance in delimiting the niche. This understanding may facilitate better that biological invasion predictions are a global problem and, thus, a global-scale approach is necessary to test the underlying mechanisms involved in this process.

The aquatic species we studied have global ranges (Chambers et al. 2008), and probably lack of climatic control on the distributions of these species, even at broad geographical extents. We suggest in further analysis (e.g., case of weak climatic effects), study the importance of local habitat conditions. In this case we agree with Alahuhta et al. (2017), that the climate niches of aquatic plants are more or less conserved, whereas the local niches of those species are more likely to be driven by variations in local environmental conditions (i.e., investigating local niches).

6. Acknowledgments

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

The project was funded by the COST-Action TD1209 Short Term Scientific Mission, NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK.

7. References

Ackerly DD (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Science, 164: S165–S184.

Alahuhta J, Virtala A, Hjort J, Ecke F, Johnson LB, Sass L, Heino J (2017). Average niche breadths of species in lake macrophyte communities respond to ecological gradients variably in four regions on two continents. Oecologia,184: 219–235.

Alahuhta J, Heino J, Luoto M (2011). Climate change and the future distributions of aquatic macrophytes across boreal catchments. Journal of Biogeography, 38: 383–393.

Alexander JM, Edwards PJ (2010). Limits to the niche and range margins of alien species. Oikos, 119: 1377–1386.

Andreu J, Vilà M, (2010). Risk analysis of potential invasive plants in Spain. Journal of Nature Conservation, 18: 34–44.

Bennett JR, Cumming BF, Ginn BK, Smol JP (2010). Broad-scale environmental response and niche conservatism in lacustrine diatom communities. Global Ecology and Biogeography, 19: 724–732.

Bornette G, Puijalon S (2011). Response of aquatic plants to abiotic factors: a review. Aquatic Sciences, 73(1): 1–14.

Bradley BA (2013). Distribution models of invasive plants over-estimate potential impact. Biological Invasions, 15: 1417–1429.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH, Guisan A (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography, 21(4): 481–497.

Broennimann O, Guisan A (2008). Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters, 4: 585–589.

Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007). Evidence of climatic niche shift during biological invasion. Ecology Letters, 10:701–9.

Chambers PA, Lacoul P, Murphy KJ, Thomaz SM, (2008). Global diversity of aquatic macrophytes in freshwater. Hydrobiologia, 595: 9–26.

Chapman DS, Scalone R, Štefanić E, Bullock JM (2017). Mechanistic species distribution modeling reveals a niche shift during invasion. Ecology, 98: 1671–1680.

Chamberlain S (2017). spoce: Interface to Species Occurrence Data Sources. R package version 0.7.0. https://CRAN.R-project.org/package=spoce

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Domisch S, Amatulli G, Jetz W (2015). Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. Scientific data, 2: 150073.

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A, Soto D, Stiassny MLJ, Sullivan CA (2006). Freshwater biodiversity: importance, threats, status and conservationchallenges. Biological Reviews, 81: 163–182.

Early R, Sax DF, (2014). Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Global Ecology and Biogeography, 23: 1356–1365.

Eller F, Brix H (2012). Different genotypes of Phragmites australis show distinct phenotypic plasticity in response to nutrient availability and temperature. Aquatic Botany, 103: 89–97.

Ficetola GF, Thuiller W, Miaud C (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Diversity and Distribution, 13: 476–485.

Feijoó C, García ME, Momo F, Toja J (2002). Nutrient absorption by the submerged macrophyte *Egeria densa* Planch.: Effect of ammonium and phosphorus availability in the water colum on growth and nutrient uptake. Limnetica, 21: 93–104.

Gallardo B, Aldridge DC (2013). The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. Journal of Applied Ecology, 50: 757–766.

Gillard M, Grewell BJ, Deleu C, Thiébaut G (2017). Climate warming and water primroses: Germination responses of populations from two invaded ranges. Aquatic Botany, 136: 155–163.

Goncalves E, Herrera I, Duarte M, Bustamante RO, Lampo M, Velasquez G, Sharma GP, García-Rangel S (2014). Global invasion of Lantana camara: has the climatic niche been conserved across continents? PloS one, 9(10): e111468.

Guisan A, Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. Ecology letters, 8: 993–1009.

Guisan A, Tingley R, Baumgartner JB, et al (2013). Predicting species distributions for conservation decisions. Ecology Letters, 16: 1424–1435.

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014). Unifying niche shift studies: Insights from biological invasions. Trends in Ecology & Evolution, 29: 260–269.

Heikkinen R, Leikola N, Fronzek S, Lampinen R, Toivonen H (2009). Predicting distribution patterns and recent northward range shift of an invasive aquatic plant: Elodea canadensis in Europe. BioRisk, 2: 1–32.

Henderson L, Cilliers CJ (2002). Invasive aquatic plants: a guide to the identification of the most important and potentially dangerous invasive aquatic and wetland plants in South Africa. PPRI Handbook No. 16. Agricultural Research Council, Pretoria.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Hoveka LN, Bezeng BS, Yessoufou K, Boatwright JS, Van der Bank M (2016). Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa. South African Journal of Botany, 102: 33–38.

Hulme PE, (2012). Weed risk assessment: a way forward or a waste of time? Journal of Applied Ecology, 49: 10–19.

Hussner A (2012). Alien aquatic plant species in European countries. Weed Research, 52: 297-306.

Hussner A, van de Weyer K, Gross EM, Hilt S (2010). Comments on increasing number and abundance of non-indigenous aquatic macrophyte species in Germany. Weed Research, 50(6): 519-526.

Hussner A, Meyer C, Busch J (2009a). Influence of water level on growth and root system development of *Myriophyllum aquaticum* (Vell.) Verdcourt. Weed Research, 49: 73–80.

Kelly R, Leach K, Cameron A, Maggs CA, Reid N (2014). Combining global climate and regional landscape models to improve prediction of invasion risk. Diversity and Distributions, 20: 884–894.

Kriticos DJ, Brunel S (2016). Assessing and managing the current and future pest risk from water hyacinth, (*Eichhornia crassipes*), an invasive aquatic plant threatening the environment and water security. PloS one, 11(8): e0120054.

Kriticos DJ, Sutherst RW, Brown JR, Adkins SA, Maywald GF (2003). Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. Journal of Applied Ecology, 40: 111–124.

Lehner B, Döll P (2004). Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology, 296: 1–22.

Li Y, Liu X, Li X, Petitpierre B, Guisan A (2014). Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species. Global ecology and biogeography, 23: 1094–1104.

Lopes A, Wittmann F, Schöngart J, Householder JE, Piedade MTF (2017). Modeling of regionaland local-scale distribution of the genus Montrichardia Crueg.(Araceae). Hydrobiologia, 789: 45– 57.

Losos JB (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology letters, 11: 995–1003.

Lozano V, Brundu G (2016). Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment. Hydrobiologia, 1–16.

Luoto M, Virkkala R, Heikkinen RK (2007). The role of land cover in bioclimatic models depends on spatial resolution. Global Ecology and Biogeography, 16: 34–42.

Pearman PB, Lavergne S, Roquet C, Wüest R, Zimmermann NE, Thuiller W (2014) Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. Global Ecology and Biogeography, 23: 414–424.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Pearman PB, Guisan A, Broennimann O, Randin CF (2008). Niche dynamics in space and time. Trends in Ecology Evolution, 23: 149–158.

Peterson AT (2011). Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography, 38: 817–827.

Peterson AT, Vieglais DA (2001). Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. Bioscience, 51: 363–371.

Peterson AT, Papers M, Soberón J (2008). Rethingking receiver operating characteristics analysis applications in ecological niche modeling. Ecological Modelling, 213: 63–72.

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012). Climatic niche shifts are rare among terrestrial plant invaders. Science, 335: 1344–1348.

Qin Z, DiTommaso A, Wu RS, Huang HY (2014). Potential distribution of two Ambrosia species in China under projected climate change. Weed Research, 54:520–531.

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007). Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution, 22: 465–471.

Schoener TW (1968). Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology, 49:704–726.

Schulte U, Hochkirch A, Lötters S, Rödder D, Schweiger S, Weimann T, Veith M (2012). Cryptic niche conservatism among evolutionary lineages of an invasive lizard. Global Ecology and Biogeography, 21: 198–211.

Soberón J, Peterson AT (2011). Ecological niche shifts and environmental space anisotropy: a cautionary note. Revista Mexicana de Biodiversidad, 82: 1348–1353.

Stephens PA, Mason LR, Green RE, et al (2016). Consistent response of bird populations to climate change on two continents. Science, 352: 84–87.

Thalmann DJK, Kikodze D, Khutsishvili M, Kharazishvili D, Guisan A, Broennimann O, Müller-Schärer H (2015). Areas of high conservation value in Georgia: present and future threats by invasive alien plants. Biological Invasions, 17: 1041–1054.

Thouvenot L, Haury J, Thiebaut G (2013a). A success story: water primroses, aquatic plant pests. Aquatic Conservation: Marine and Freshwater Ecosystems, 23:790–803.

Thuiller W, Georges D, Engler R, Breiner F (2016). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 3.3-7. https://CRAN.R-project.org/package=biomod2

Yarrow M, Marin VH, Finlayson M, Tironi A, Delgado LE, Fischer F (2009). The ecology of *Egeria densa* Planchon (Liliopsida: Alismatales): A wetland ecosystem engineer? Revista Chilena de Historia Natural, 82: 299–530 313.

Warren DL, Glor RE, Turelli M (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution, 62: 2868–2883.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Watts G, Battarbee RW, Bloomfield JP et al (2015). Climate change and water in the UK-past changes and future prospects. Progress in Physical Geography, 39: 6–28.

Whitehead PG, Wilby RL, Battarbee RW, Kernan M, Wade AJ (2009). A review of the potential impacts of climate change on surface water quality. Hydrological Sciences Journal, 54: 101–123.

Wiens JJ, Graham CH (2005). Niche conservatism: integrating evolution, ecology and conservation biology. Annual Review of Ecology Evolution and Systematic, 36: 519–539.

Wiens JJ, Ackerly DD, Allen AP et al. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters, 13: 1310–1324.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

8. Supplementary materials



Figure S1. Map with geographic points showing the occurrence records obtained for *Egeria densa*, *Eichhornia crassipes*, *Myriophyllum aquaticum*, *Pistia stratiotes* and *Salvinia molesta*.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure S2. Randomly selected background grid cells used in the modelling of *Egeria densa*, *Eichhornia crassipes*, *Myriophyllum aquaticum*, *Pistia stratiotes and Salvinia molesta*.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure S3. Partial response plots from the fitted models. Thin coloured lines show responses from the seven algorithms, while the thick black line is the response of their ensemble. In each plot, other model variables are held at their median value in the training data.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Australia

North America









 $x_{131} = 51.57 / 6 a_{x_{132}} = 25.55$

Europe



axis1 = 51.15 % axis2 = 2

Asia



Figure S4. The last line shows the correlation circles, which indicate the weight of each bioclimatic variable on the niche space defined by the first two principal component axes. The predictor climatic variables are Hydro 06 (Minimum Upstream Temperature of Coldest Month), Hydro 10 (Mean Upstream Temperature of Warmest Quarter), Hydro 18 (Upstream Precipitation of Warmest Quarter) and the Global lakes and wetlands cover (GLWD).

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure S5. Niche dynamics between native and invaded ranges of five South American aquatic species. The contour lines delineate the available niche in its native range (green) and in its invaded range (red). The solid and dashed contour lines illustrate, respectively, 100% and 75% of the available (background) environment. The colored areas correspond to the expansion zone (red), unfilled zone (green) and the overlap zone (blue), resulting from overlaying the native niche with the invaded niche. The solid arrows represent the change in the centre of the species niche (climatic space) between the native and invaded ranges. The colored numbers represent the niche unfilling (green), expansion (red) and overlap (blue) index.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.


Figure S6. Statistical tests for niche comparisons between native and invaded regions. Observed frequencies for the niche overlap index (D) in relation to the expected D for p = 0.05. The columns compare niches between the native range and invasive ranges.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Table S1. Summary of the cross-validation predictive performance (AUC) and variable importance of the fitted model algorithms and the ensemble (AUC-weighted average of the best performing seven algorithms). Results are the average from models fitted to five different background samples of the data.

Species	Algorithm	Predictive AUC	Minimum upstream temperature of coldest month (%)	Mean upstream temperature of warmest quarter (%)	Upstream precipitation of warmest quarter (%)	Global lakes and wetlands (%)
	GLM	0.785	64.1	11.2	10.9	13.8
	GBM	0.869	57.2	25.4	8.4	9.1
	GAM	0.837	52.5	25.8	8.9	12.8
	CTA	0.820	51.2	28.0	8.8	12.0
F · /	ANN	0.854	51.2	30.4	6.9	11.5
Egeria densa	FDA	0.818	56.9	14.0	6.4	22.6
	MARS	0.852	53.9	23.7	9.8	12.6
	RF	0.797	42.7	31.2	9.4	16.7
	MAXENT	0.861	50.4	25.8	10.1	13.6
	Ensemble	0.867	53.3	24.8	8.5	13.4
	GLM	0.933	72.1	19.4	6.6	2.0
	GBM	0.936	64.9	23.0	10.4	1.7
	GAM	0.935	64.8	23.9	10.1	1.2
	СТА	0.920	65.4	21.9	10.6	2.1
Eichhornia	ANN	0.937	59.0	27.9	9.8	3.3
crassipes	FDA	0.928	78.9	13.8	6.1	1.2
	MARS	0.936	63.6	23.3	11.7	1.4
	RF	0.886	54.4	24.7	14.7	6.2
	MAXENT	0.936	59.6	26.9	12.2	1.3
	Ensemble	0.939	66.1	22.6	9.6	1.7
	GLM	0.890	91.5	0.3	5.7	2.6
	GBM	0.920	86.1	3.5	9.4	0.9
	GAM	0.914	85.8	2.9	8.8	2.5
	СТА	0.879	81.2	6.9	11.1	0.8
Myrionhyllum	ANN	0.916	72.7	16.0	10.0	1.3
aquaticum	FDA	0.892	91.5	0.9	5.2	2.4
	MARS	0.915	86.0	1.3	10.4	2.2
	RF	0.859	57.6	21.9	12.0	8.5
	MAXENT	0.9197	81.6	4.4	11.1	3.0
	Ensemble	0.917	85.0	4.2	8.7	2.1
	GLM	0.886	82.7	10.7	5.8	0.9
	GBM	0.910	84.2	4.3	10.5	1.0
	GAM	0.900	73.7	15.2	10.3	0.7
	СТА	0.861	87.3	2.1	9.2	1.4
	ANN	0.909	75.7	12.5	10.5	1.3
Pistia stratiotes	FDA	0.891	30.6	63.8	47	0.9
	MARS	0.901	84.2	4 4	10.3	11
	RF	0.863	52.7	23.7	15.2	8.4
	MAXENT	0.005	59.1	24.6	14.2	21
	Ensemble	0.909	70.1	19.3	9.5	11
	GLM	0.955	88.6	4 4	5.7	12
	GBM	0.973	69.9	9.5	20.4	0.1
	GAM	0.973	78.8	10.2	10.6	0.4
	СТА	0.949	83.8	0.5	15.7	0.0
	ANN	0.974	66 1	15.2	17.8	0.9
Salvinia molesta	FDA	0.965	82.5	8 1	9.4	0.0
	MARS	0.966	83.3	0.0	16.7	0.0
	RF	0.959	57.9	16.3	22.1	3.6
	MAXENT	0.9750	63 7	11.8	23.5	11
	Ensemble	0.970	71 7	10.2	17.2	0.9
	Ensemble	0.270	/ 1./	10.2	1/.4	0.7

Table S2. Niche change indices for five invasive aquatic plants species across the world. D: Schoener's D index, a measure of the overlap between native and invaded range; niche expansion; stable niche (overlap) and unfilling niche in the climate space of a species' native range characterized by the three climate variables.

Species	Continent	D overlap %	Expansion	Stability	Unfilling
	Australia	14.06	0.00	1.00	0.61
	North America	39.00	0.33	0.67	0.19
Egeria densa	Africa	3.12	0.00	1.00	0.88
	Europe	7.27	0.02	0.98	0.54
	Asia	3.84	0.00	1.00	0.77
	Australia	22.25	0.05	0.95	0.26
	North America	36.41	0.08	0.92	0.04
Eichhornia crassipes	Africa	34.45	0.10	0.90	0.01
	Europe	5.14	0.00	1.00	0.42
	Asia	16.27	0.05	0.92	0.01
	Australia	48.71	0.01	0.99	0.23
	North America	42.75	0.14	0.86	0.06
Myriophyllum aquaticum	Africa	15.27	0.00	1.00	0.71
	Europe	42.82	0.04	0.96	0.38
	Asia	17.69	0.00	1.00	0.62
	Australia	12.08	0.00	1.00	0.31
	North America	43.09	0.07	0.93	0.01
Pistia stratiotes	Africa	34.69	0.01	0.99	0.11
	Europe	31.36	0.12	0.88	0.21
	Asia	19.42	0.00	1.00	0.30
	Australia	25.61	0.67	0.33	0.02
	North America	9.57	0.75	0.25	0.00
Salvinia molesta	Africa	2.56	0.86	0.14	0.31
	Europe	1.95	0.95	0.05	0.69
	Asia	28.27	0.58	0.42	0.30

Table S3. Shows the observed niche overlap D between the two ranges and simulated niche overlaps on which tests of niche equivalency and niche similarity of native range (South America) to invasive ranges (Australia, North America, Africa, Europe and Asia).

	Equivalency p-value												
Continent	Egeria densa	Eichhornia crassipes	Myriophyllum aquaticum	Pistia stratiotes	Salvinia molesta								
Australia	0.01	0.02	0.13	0.01	0.56								
North America	1	1	0.99	1	0.12								
Africa	0.01	0.13	0.05	0.05	0.01								
Europe	0.01	0.07	1	-	-								
Asia	0.01	0.01	0.01	0.07	0.73								
			Similarity p-value										
Australia	0.57	0.80	0.96	0.92	0.97								
North America	1	1	0.98	1	0.98								
Africa	0.73	0.95	0.94	0.97	0.49								
Europe	0.79	0.99	0.99	-	-								
Asia	0.75	0.70	0.85	0.79	0.95								

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

CHAPTER 5

GLOBAL NETWORKS FOR INVASION SCIENCE: BENEFITS, CHALLENGES AND GUIDELINES

Introduction and aims

"Global Networks for Invasion Science" are defined through their primary purpose of collecting new primary data to answer specific questions about patterns, mechanisms and impacts of biological invasions at the global scale. To be eligible as 'global', the networks needs to cover gradients as latitudinal and longitudinal, or from natural to human-dominated ecosystem, with nodes (network partners) across biogeographic zones over both hemispheres and including at least three continents. This paper proposes a framework for the development of Global Networks for Invasion Science to help generate approaches to address these critical and fundamentally biogeographic questions.

Methodology and main results

In April 2016, the University of Sassari, Italy, host a group of researchers from different countries around the world, to attend a dedicated workshop the "PhragNet 2016". After a hard work and brain storming on 'challenges of biological invasions' the result was the consolidation of a transdisciplinary network on *Phragmites* species and the published paper 'Global networks for invasion science: benefits, challenges and guidelines'.

Conclusions

Despite the urgent need, to answer the most important biological invasion questions, only a few large-scale collaborations have been established within invasion science, and none have focused on these fundamental global or high impact applied questions. Global Networks for Invasion Science are a powerful approach to address fundamental questions and transform this knowledge into appropriate policy and management recommendations. The network is to work in an interdisciplinary platform to increase our understanding of the effects of global environmental change on species distributions.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Packer JG, Meyerson LA, Richardson DM, Brundu G, Allen W, Bhattarai GP, Brix H, Canavan S, Castiglione S, Cicatelli A, Čuda J, Cronin JT, Eller F, Guarino F, Guo W-H, Guo WY, Guo X, Hierro J, Lambertini C, Liu J, Lozano V, Mozdzer TJ, Skálová H, Villarreal D, Wang RQ, Pyšek P (2017) Global network for invasion science: benefits, challenges and guidelines. Biological Invasions 19. doi:10.1007/s10530-016-1302-3

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

PERSPECTIVES AND PARADIGMS



Global networks for invasion science: benefits, challenges and guidelines

Jasmin G. Packer · Laura A. Meyerson · David M. Richardson · Giuseppe Brundu · Warwick J. Allen · Ganesh P. Bhattarai · Hans Brix · Susan Canavan · Stefano Castiglione · Angela Cicatelli · Jan Čuda · James T. Cronin · Franziska Eller · Francesco Guarino · Wei-Hua Guo · Wen-Yong Guo · Xiao Guo · José L. Hierro · Carla Lambertini · Jian Liu · Vanessa Lozano · Thomas J. Mozdzer · Hana Skálová · Diego Villarreal · Ren-Qing Wang · Petr Pyšek

Received: 13 July 2016/Accepted: 26 October 2016 © Springer International Publishing Switzerland 2016

Abstract Much has been done to address the challenges of biological invasions, but fundamental questions (e.g., which species invade? Which habitats are invaded? How can invasions be effectively managed?) still need to be answered before the spread and impact of alien taxa can be effectively managed. Questions on the role of biogeography (e.g., how does biogeography influence ecosystem susceptibility,

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1302-3) contains supplementary material, which is available to authorized users.

J. G. Packer (⊠) Environment Institute, The University of Adelaide, Adelaide, SA 5005, Australia e-mail: j.packer@adelaide.edu.au

J. G. Packer School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

J. G. Packer Department of Environmental Systems Science, Institute of Integrative Biology, Swiss Federal Institute of Technology (ETH), 8092 Zurich, Switzerland

L. A. Meyerson Department of Natural Resources Science, The University of Rhode Island, Kingston, RI 02881, USA

D. M. Richardson · S. Canavan Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Matieland 7602, South Africa

and the second second

resistance and resilience against invasion?) have the greatest potential to address this goal by increasing our capacity to understand and accurately predict invasions at local, continental and global scales. This paper proposes a framework for the development of 'Global Networks for Invasion Science' to help generate approaches to address these critical and fundamentally biogeographic questions. We define global networks on the basis of their focus on research questions at the global scale, collection of primary data, use of standardized protocols and metrics, and commitment to long-term global data. Global networks are critical for the future of invasion science because of their

G. Brundu · V. Lozano Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy

W. J. Allen · J. T. Cronin Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

G. P. Bhattarai Indian River Research and Education Center, University of Florida, Fort Pierce, FL 34945, USA

H. Brix · F. Eller · C. Lambertini Department of Bioscience, Aarhus University, 8000 Århus C, Denmark

S. Canavan Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735, South Africa

D Springer

£,

ana aistribution models – resi di Dottorato in Scienze Agrarie – Curriculum Montioraggio e controtto aegii ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari. potential to extend beyond the capacity of individual partners to identify global priorities for research agendas and coordinate data collection over space and time, assess risks and emerging trends, understand the complex influences of biogeography on mechanisms of invasion, predict the future of invasion dynamics, and use these new insights to improve the efficiency and effectiveness of evidence-based management techniques. While the pace and scale of global change continues to escalate, strategic and collaborative global networks offer a powerful approach to inform responses to the threats posed by biological invasions.

Keywords Biogeographic · Biological invasions · Collaboration · Global change · Global research network · Multitrophic · Transdisciplinary

Introduction

Considerable progress has been made on multiple fronts in understanding the many dimensions of invasion science (as defined by Richardson 2011). Despite such advances, the three fundamental questions that have driven most research on biological invasions since the 1980s have not been fully answered (Drake et al. 1989; Mooney et al. 2005): Which species invade? Which habitats are invaded? How can invasions be effectively managed? Plant

S. Castiglione · A. Cicatelli · F. Guarino Department of Chemistry and Biology "A. Zambelli", University of Salerno, 84084 Fisciano, SA, Italy

J. Čuda · W.-Y. Guo · H. Skálová · P. Pyšek Institute of Botany, The Czech Academy of Sciences, Zámek 1, 252 43 Průhonice, Czech Republic

J. Čuda · P. Pyšek Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 44 Prague 2, Czech Republic

W.-H. Guo · X. Guo · R.-Q. Wang Institute of Ecology and Biodiversity, School of Life Sciences, Shandong University, Jinan 250100, People's Republic of China

W.-H. Guo · X. Guo · R.-Q. Wang Shandong Provincial Engineering and Technology Research Center for Vegetation Ecology, Shandong University, Jinan 250100, People's Republic of China J. G. Packer et al.

invasions have been more intensively studied than any other major group of alien organisms (Pyšek et al. 2006, 2008) and have contributed most to our theoretical understanding of organism-focused (what determines invasiveness of particular taxa?) and ecosystem-centered (what makes a community, ecosystem or region susceptible to invasion?) questions in invasion science. Observations of invasions and associated biotic and abiotic processes have historically been important in informing invasion science (e.g., Richardson et al. 2004). More recently, manipulative experiments (garden and field-based), predictive modeling, and conceptual/theoretical approaches have helped to integrate our understanding of species invasiveness with that of community invasibility (Catford et al. 2009). Research areas contributing substantially to invasion science include the characteristics that predispose taxa to become invasive (van Kleunen et al. 2010; Guo et al. 2014; Suda et al. 2015) and interactions between biological invasions and environmental change at multiple scales (Walther et al. 2007; Pyšek et al. 2010; Kueffer et al. 2013). There is increasing realization that solutions to problems associated with invasions must be sought by placing the phenomenon firmly within the domain of social-ecological systems (Meyerson and Mooney 2007; Hui and Richardson 2017). Despite the progress, many fundamental questions in invasion science remain unresolved. Answers to the four research questions below are among those that hold the greatest potential to deepen our understanding of biological

X. Guo

College of Landscape Architecture and Forestry, Qingdao Agricultural University, Qingdao 266109, People's Republic of China

J. L. Hierro Instituto de Ciencias de la Tierra y Ambientales (CONICET-UNLPam), 6300 Santa Rosa, Argentina

J. L. Hierro · D. Villarreal Universidad Nacional de La Pampa, Ave Uruguay 151, RA-6300 Santa Rosa, Argentina

J. Liu

Institute of Environmental Research, Shandong University, Jinan 250100, People's Republic of China

T. J. Mozdzer Department of Biology, Bryn Mawr College, Bryn Mawr, PA 19010, USA

Description Springer

and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

invasions and improve our capacity to manage invasion dynamics (see also Richardson 2011):

- 1. How does biogeography influence ecosystem susceptibility, resistance and resilience against invasion?
- 2. How does biogeography influence the ecological (e.g., enemy release and invasional meltdown) and socio-economic (e.g., dynamic travel and trade routes) mechanisms and impacts of biolog-ical invasions?
- 3. Are 'space for time' substitutions effective to predict the likelihood of an invasion, and the vulnerability of ecosystems to potential impacts, as the global environment continues to change?
- 4. What is the role of adaptation and evolution in determining invasion success, specifically:
 - a. evolutionary history within the native range prior to invasion?
 - b. adaptation to environments, and evolution, in the invaded range?

To facilitate progress on these global priorities for invasion science, researchers must consider which critical questions can realistically be answered (Strayer 2012; Kueffer et al. 2013) and then strategically collect and analyze data to address them. The vast spatial scale and breadth of experience required to address these big-picture questions presents a logistical challenge for research groups working in isolation. In this paper we focus on plant invasions to explore the benefits and challenges of addressing these otherwise intractable questions with global-scale research via transdisciplinary networks (sensu Wickson et al. 2006; see also Meyerson and Mooney 2007; Fraser et al. 2013) and provide a road map to encourage new, and more effective, international collaborations.

Global networks for invasion science: a delimitation

We define 'Global Networks for Invasion Science' through their primary purpose of collecting new primary data to answer specific questions about patterns, mechanisms and impacts of biological invasions at the global scale (e.g., the effect of sea level rise on the distribution of cosmopolitan littoral taxa) or finer resolutions that are best addressed by multiple regions contributing to a global synthesis (e.g., the effects of rising temperatures on the invasion of grasslands in arid biomes). Although most existing large-scale collaborations focus on a particular taxon (e.g., *Ambrosia artemisiifolia*, www.ragweed. eu) or specific invasion issues (e.g., effectiveness of sentinel plants as an early warning system; Roques et al. 2015), networks could also use model systems (e.g. *Phragmites australis*; Meyerson et al. 2016b) to accelerate deeper understanding of the patterns (e.g., changing spatial distributions; Dietz et al. 2006) and processes (e.g., the mechanisms by which invasive plants disrupt pollination networks; Lopezaraiza-Mikel et al. 2007) of invasion dynamics.

To qualify as 'global', we suggest that networks cover gradients (e.g., latitudinal and longitudinal, and from natural to human-dominated ecosystem) with nodes (network partners and/or sites) spanning biogeographic zones over both hemispheres and including at least three continents. This suggestion is motivated by the need for a practical operational definition of networks for international-and potentially transdisciplinary-research teams that aim to study invasion dynamics at a representative set of locations and regions (Kueffer et al. 2013). Transdisciplinary refers to the generation of new knowledge and solutions to real-world problems through shared, standardized and iterative methodologies drawn from two or more disciplines (adapted from Wickson et al. 2006). The current distribution of most invasive organisms, in both their native and introduced ranges, spans two or more continents but rarely covers the entire globe (cf. Rejmánek and Richardson 2013). Limiting the selection of focal taxa to those that have a large global range would focus research efforts on a manageable set of cosmopolitan, model systems that are well-represented spatially and with good coverage in the literature (Table 1).

The objectives of Global Networks for Invasion Science can be summarized by four defining characteristics. (1) Global networks address research questions on biological invasions at the global scale (as defined above) through a biogeographic synthesis of insights from multiple localities across large regions (Hierro et al. 2005; Colautti et al. 2014b; Cronin et al. 2015). (2) Primary data on model systems are collected to address specific global questions, for example through common gardens, field experiments and/or field observations. Collaborations that use existing

Deringer

valessa Lucia Lozano Mascins – invasive anen aquanc pianis in Soum American Iniana walers, inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Model organism (Family)	Model system category	Distribution	Key characteristics
Acacia spp.	Intensively studied	Native: Australia	Multiple invasive and native species
(Fabaceae)	species	Introduced: Africa,	Global distribution
	Specialized research	Asia, EU, New	Known invasion history
		Zealand, NA, SA	Habitat generalists
			Vegetative reproduction (stem cuttings)
			Interspecific hybridization
			Major economic and environmental impacts (displacement of native vegetation, disruption to water flow leading to streambank erosion and changed nutrient cycling patterns)
Alternanthera philoxeroides	Intensively studied species	Native: SA Introduced: Asia, EU,	Intraspecific genetic and phenotypic variability Global distribution
Alligator weed		NA, Oceania	Known invasion history
(Amaranthaceae)			Habitat generalist
			Vegetative reproduction (stem cuttings)
			Fast growing
			Major economic and environmental impacts (deleterious effects on other plants and animals, water quality, aesthetics, hydrology; degrades pasture, turf and crop production in terrestrial ecosystems)
Ambrosia Intensively studied		Native: NA	Pre-existing research network
artemisiifolia	species	Introduced: Africa,	Global distribution
Common	Specialized research	Asia, EU, Oceania,	Known invasion history
ragweed		SA	Habitat generalist
(Asteraceae)			Fast growing
			Major economic, environmental and social impacts (decreases crop yield, displaces native species, allergenic pollen)
Arundo donax	Understudied species	Native: Asia	Global distribution
Giant reed		Introduced: Africa,	Known invasion history
(Poaceae)		Asia, EU, NA,	Habitat generalist
		Oceania, SA	Vegetative reproduction (rhizomes or plant fragments)
			Fast growing
			Major economic, environmental and social impacts (outcompetes native species, alters hydrology and fire regimes)
Colocasia spp.	Understudied species	Native: Asia	Multiple invasive and native species
Elephant ear/taro	Genera/families with an	Introduced: Africa,	Global distribution
(Araceae)	underrepresentation of	Asia, EU, NA,	Known invasion history
	invasive species	Oceania, SA	Habitat generalists
			Vegetative reproduction (corm)
			Fast growing
			Interspecific hybridization
			Major economic, environmental, and social impacts (displacement of native vegetation, altered hydrology and aesthetic qualities, agricultural crop)

Table 1 Examples of species/genera which may make useful model organisms, their native and introduced distributions, and key characteristics which make them suitable candidate species for global network studies

Deringer

į.

Model organism (Family)	Model system category	Distribution	Key characteristics
Eucalyptus spp.	Understudied species	Native: Australia, Asia	Multiple invasive and native species
(Myrtaceae)	Genera/families with an	Introduced: Africa,	Global distribution
	underrepresentation of	Asia, EU, New	Known invasion history
	invasive species	Zealand, NA, SA, EU	Habitat generalists
			Vegetative reproduction (stem cuttings)
			Interspecific hybridization
			Major economic and environmental impacts (loss of native biodiversity, alteration of water and nutrient regimes)
Lythrum salicaria	Intensively studied	Native: Africa, Asia,	Intraspecific genetic and phenotypic variability
Purple loosestrife	species	Australia, EU	Global distribution
(Lythraceae)	Specialized research	Introduced: New	Known invasion history
		Zealand, NA, SA	Habitat generalist
			Vegetative reproduction (stem cuttings)
			Fast growing
			Interspecific hybridization
			Major economic and environmental impacts (harmful to livestock and crop production, alters hydrology and nutrient cycling, displaces native species)
Opuntia spp.	Genera/families with an	Native: NA, SA	Pre-existing research network
Prickly pear	underrepresentation of	Introduced: Africa,	Multiple invasive and native species
(Cactaceae)	invasive species	Asia, EU, NA,	Global distribution
		Oceania, SA	Known invasion history
			Habitat generalists
			Vegetative reproduction (cladodes)
			Interspecific hybridization
			Major economic, environmental and social impacts (harmful to livestock, native plant and arthropod community, hinders human use of recreational areas, cultivated crop)
Phragmites spp.	Intensively studied	Native: Africa, Asia,	Pre-existing research networks
Common reed	species	EU, NA, Oceania, SA	Multiple invasive and native species
(Poaceae)	Specialized research	Introduced: NA,	Intraspecific genetic and phenotypic variability
	Genera/families	Oceania	Global distribution
			Known invasion history
			Habitat generalists
			Vegetative reproduction (rhizomes or plant fragments)
			Fast growing
			Intraspecific and interspecific hybridization
			Major economic and environmental impacts (alters hydrology, ecosystem function and degrades habitat for native species)
Rumex spp.	Intensively studied	Native: Africa, Asia,	Multiple invasive and native species
Dock/sorrell	species	EU	Intraspecific genetic and phenotypic variability
(Polygonaceae)	Genera/families with an	Introduced: Africa,	Global distribution
	invasive species	Asia, INA, Oceania, SA	Habitat generalists

Global networks for invasion science: benefits, challenges and guidelines

D Springer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

ţ

Table 1 continue	d		
Model organism (Family)	Model system category	Distribution	Key characteristics
			Vegetative reproduction (roots)
			Fast growing
			Interspecific hybridization
			Major economic impacts (decreases crop quality)

The model system categories are based on Kueffer et al. (2013), and distributions include Europe (EU), North America (NA), and South America (SA). Genera/families with an under-representation of invasive species enable phylogenetically controlled contrasts between native and invasive taxa, furthering understanding of mechanisms underlying invasion success. As pointed out by Kueffer et al. (2013), groups of species with an underrepresentation of invasive species have attracted less research interest, but understanding why these groups have not become invasive may help to advance invasion science significantly



Fig. 1 Structure of a global network on invasive species. The core project (*in green*) involves all partners and addresses big picture research questions at the global scale through: collection of primary data; use of standardized protocols and metrics; and commitment to long-term global data. Knowledge, and iterative global research questions, are generated by the core project and are exchanged (*green arrows*) with all partners through mutual dialogue. Satellite projects (*in blue*) that are performed by

secondary information to answer global questions (e.g., GloNAF database of naturalized alien floras, van Kleunen et al. 2015, and international invasion monitoring, Latombe et al. 2016) are therefore not included in this definition. (3) Data collection is coordinated using standardized protocols and metrics (e.g., Wilson individual partners, or among partners, focus on questions that are biogeographically restricted to certain partner contexts or priorities (e.g., the competition of the focal taxa with a locally present congener, or addressing the effect of Mediterranean climates only). Satellite projects contribute (*blue line*) to the overall knowledge base within the core project; these inform the iteration of hypotheses and questions, some of which are addressed by other satellite projects

et al. 2014) that ensure comparability of data captured at different locations, and rigorous data analysis. (4) Global networks are enduring collaborations that collect long-term data over an agreed timeframe (e.g., 10 years) to address complex invasion dynamics. Ongoing networks may also initiate shorter-term

🖉 Springer

and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

"snapshot" satellite projects to address specific questions that relate to the main research direction of the respective network (see Fig. 1) (e.g., Richardson et al. 2011; Woodford et al. 2016).

Why global networks are critical for invasion science

Collaborative global networks are a powerful approach with many benefits for invasion science because they increase our collective capacity to: (1) set global priorities for research agendas (such as the strategic priorities we have outlined above); (2) identify and assess the risks that emerge from global trends; (3) unravel the mechanisms that mediate genetic diversity at multiple scales of space and time-the elucidation of such complexity cannot practically be achieved through experimental manipulation at a single site (Fig. 1); (4) understand biogeographic influences on the interactions between alien plants and other biota, both native and introduced, across different trophic levels; (5) build our collective capacity to predict future invasion dynamics; and (6) tap into the innovative approaches that diverse, transdisciplinary networks can generate to integrate new knowledge and evidence-based management of biological invasions.

Identifying and assessing the risk of emerging trends

Networks provide unparalleled opportunities to identify and assess emerging trends in the distribution patterns, ecology, genetics, and risk of the target taxa and their close relatives. Invasion processes are context-dependent and likely to evolve differently across biogeographic regions and environmental settings (Richardson and Bond 1991; Cronin et al. 2015; Packer et al. 2016). Some species or genotypes are therefore likely to vary in response to different environments (Meyerson et al. 2016a) suggesting that early warning signals of invasiveness could come from a single site rather than from multiple locations. For this reason, coordinated experiments that span bioclimatic zones on multiple continents can also utilize natural gradients to predict the influence of future climatic conditions.

Any emerging risks can be assessed rapidly through informal discussions (online and/or face-to-face) and more formal risk-assessment processes developed by the network or partner agencies. Active networks then have the opportunity to use the wider associations of members to notify the relevant policymakers, managers and broader community of the risk (nature and magnitude) and to present a clear, consistent plan on the appropriate priority actions, across multiple locations if necessary, to address the threat (e.g., Wilson et al. 2014 for Australian acacias).

Facilitating biogeographic insights into the genetics of invasion

A growing body of literature suggests that a biogeographical approach is fundamental to understanding the current and potential dynamics of invasions in their alien and native ranges (e.g., Hierro et al. 2005; Colautti et al. 2009; Hejda 2013; Parker et al. 2013; Cronin et al. 2015; Pyšek et al. 2015; van Kleunen et al. 2015). The distribution of genetic variation within taxa that have a broad geographic range (spanning several biogeographic regions and continents) is changing due to increased dispersal opportunities across continents and post-invasion evolution (e.g., Thompson et al. 2015 for Acacia saligna; see also Eriksen et al. 2014). Studies from single sites or regions cannot distinguish phenotypic variation in traits related to invasiveness (genotype × environment interactions) from post-invasion adaptation and evolution (Maron et al. 2004; Hierro et al. 2013). There is increasing evidence that global change factors (such as warming, drought, precipitation, and their spatiotemporal variation) can alter macroevolutionary patterns and, eventually, the genetic diversity and structure of plant populations within just a decade (Avolio et al. 2013; Ravenscroft et al. 2015). A lack of information on intraspecific genetic diversity currently hampers our ability to understand potential responses of species to these global changes (Pauls et al. 2013; Meyerson et al. 2016b). It is not possible to accurately predict such responses by individual invasive species from isolated studies of local populations (which may not necessarily be representative of the fitness of the species in total, or of the genus) (Meyerson et al. 2010). The cultivation of a common set of genotypes representing intraspecific

Deringer

vanessa Lucia Lozano Maseins – invasive anen aquaic pianis in souin American iniana waiers: inveniory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

phylogeographic variation (e.g., the global genetic structure of a species) in combination with field studies of natural populations and common garden studies can simultaneously identify lineages of high fitness and the interaction of biogeographic factors crucial for the success of these lineages at a specific location. Global networks can thereby help to predict and monitor invasion risk even before potentially invasive genotypes are introduced to new areas accidentally or on a larger scale intentionally.

Establishing collaborative common gardens on all continents through a global network also provides an opportunity to assess the role of environmentally influenced genetic traits such as epigenetics (e.g., DNA methylation status; Schrey et al. 2013) and phenotypic plasticity in the adaptation and spread of potentially invasive plants. For instance, Guarino et al. (2015) demonstrated that ramets of the same clone of white poplar (*Populus alba*) had a different methylation status, and thus potentially different gene expression regulation and invasion risk, in relation to their geographical provenance on the island of Sardinia.

Understanding biogeographic influences on trophic interactions

Global networks that focus on a model system can provide important insights into complex species interactions that limit or facilitate invasion processes. The geographic structuring of alien plant distributions (e.g., higher rate of invasions in temperate than tropical or polar regions; e.g., Lonsdale 1999; Fridley et al. 2007; van Kleunen et al. 2015) may intensify trophic interactions where alien species are more common (Iannone et al. 2016) and cause large-scale geographic shifts in species interactions and distributions (e.g., He et al. 2013; Lord and Whitlatch 2015). Invasional meltdowns may also be more common in regions where introductions are more likely. Long-term coordinated experiments across multiple biomes may help to identify anthropogenic drivers of change, including human-assisted introductions, and the mechanisms underpinning trophic interactions in response to these.

Herbivores and other natural enemies are widely recognized as having a strong influence on the establishment and subsequent spread of invasive plant species (Keane and Crawley 2002; Rogers and Siemann 2004; Jeschke et al. 2012). Controlled common garden experiments, one of the core approaches that can be used by global networks, are often performed to assess the importance of the Enemy Release Hypothesis at different localities (whether invasive species are more resistant to natural enemies than native species) and whether invasive species evolve in response to their natural enemies in their introduced range (e.g., Agrawal et al. 2005; Joshi and Vrieling 2005; Rapo et al. 2010). Coordinated research across multiple sites has also been influential in advancing our understanding of how climate change variables, plant genetics (genomic, ploidy and genotypic variation), epigenetics (e.g., variation in DNA methylation status), and geographic origins affect invasive/native plant-herbivore interactions (e.g., Lee and Kotanen 2015; Lu et al. 2015; Meyerson et al. 2016a).

Mutualisms play a key role in facilitating plant invasions (Richardson et al. 2000), but the roles of many symbionts in influencing progress at different stages along the introduction-naturalization-invasion continuum (sensu Richardson and Pyšek 2006) are poorly understood. Contrasting the levels of performance of the same species in different biogeographic regions is useful for understanding the roles of mutualisms in invasions. For example, cross-region comparisons have shed crucial light on the role of nitrogen-fixing bacteria in facilitating invasions of Australian *Acacia* species around the world and in determining the extent to which introduced legumes can form novel associations with resident bacteria (Rodríguez-Echeverría 2010; Ndlovu et al. 2013).

Predicting the future of invasion dynamics

Another incentive for globally coordinated research is the increased capacity to develop reliable predictions on invasive species responses to global change (incorporating both anthropogenic and climatic drivers) and future dynamics of their spread in general (Dukes and Mooney 1999; Guisan and Thuiller 2005). Predictive modelling could incorporate data from the network, including both data from natural invaded environments and responses from standardized common gardens. Identifying whether some characteristics predispose a species or genotype to naturalize or become invasive under projected future conditions would be particularly useful for biological security risk assessments and planning (Kolar and Lodge 2001; Meyerson and Reaser 2003; Pyšek and Richardson 2007; van Kleunen et al. 2010; Guo et al. 2014, 2016;

Description Springer

1

vanessa Lucia Lozano Maseins – invasive anen aquaic pianis in souin American iniana waiers: inveniory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Suda et al. 2015; Tho et al. 2016). The responses of plant functional traits across invasion stages differ (Pyšek et al. 2009, 2015) and can be used as predictors of response of an introduced species to multiple interacting global change factors (e.g., stages in the invasion process reached by the same species differ by region; Richardson and Pyšek 2012). The network approach offers the opportunity, by comparing the conditions under which the same alien taxa occur as casual, naturalized or invasive, to determine how the environmental context in a particular biogeographical setting interacts with functional traits in its invasion success.

Generating innovative solutions through diverse perspectives

A further benefit of global networks is their potential to overcome one of the greatest challenges within invasion science; translating new knowledge into action that will prevent or minimize biological invasions (Hulme 2003; Lindenmayer et al. 2008). The spread of invasive species globally is linked so closely to human influence that developing lasting, effective solutions to reverse this trend demands iterative and collaborative input from applied and fundamental perspectives (Wickson et al. 2006; see also Hulme 2006; Hui and Richardson 2017). Kueffer (2010) argues that transdisciplinary perspectives are not only desirable, but essential, because of the fundamentally socio-ecological aspects of plant invasions, including: (1) dynamic patterns of propagule pressure along evolving trade and transport routes; (2) the potential risk of novel organisms created through synthetic biology; and (3) variable human perceptions on the nature of invasions and the mechanisms underpinning them.

Better systems are needed to identify and assess these threats globally, to understand the underlying mechanisms, to develop and prioritize response actions, and communicate levels of threat and recommended interventions to policymakers and practitioners worldwide. The scale and breadth of these roles are clearly beyond the scope of a single research group, profession or discipline. Integrating theoretical and applied approaches can help to ensure that research questions address the most current and pertinent aspects of these global priorities, and that the management actions being implemented are the most effective and efficient.

To bridge the gap, where it exists, research scientists, policymakers and managers need to create new ways of exchanging knowledge and designing effective solutions together (Nassauer and Opdam 2008: Kueffer 2010: Ahern 2013: Richardson and Lefroy 2016). Global networks that span multiple approaches as well as continents have great potential to foster innovation by drawing on complementary expertise and experience on the focal issue or taxa (Max-Neef 2005; Pohl 2005; Wickson et al. 2006). The "virtual global acacia college" that was assembled in 2010-2011 to compile a collection of 20 papers on the invasion ecology of Australian acacias (Richardson et al. 2011) was a short-term demonstration of bringing together 104 researchers from 18 countries representing diverse subdisciplines in biology (e.g., genetics, invasion ecology, population ecology, plant pathology, plant physiology) and humanities (history, geography, philosophy) to develop a comprehensive overview of the many issues involved in acacia introductions and invasions. Although this initiative does not strictly correspond to our definition of a global network, it provides a tangible example of the benefits of invasion scientists working together across scientific disciplines.

Longer-term collaborations are needed to move from identification of issues to the implementation of effective solutions. The European Cooperation in Science and Technology (COST; www.cost.eu) Actions are bridging this gap with practical research outputs, such as the illustrated guide to invasive taxa and rapid assessments in the Mediterranean Sea (Zenetos 2015). The MIREN group (www. mountaininvasions.org) is well regarded for the innovative solutions it generates through long-term partnerships between scientists and practitioners across multiple continents. South African MIREN partners have contributed to developing an emerging global threats system to identify potential risks (e.g., pompom weed; Campuloclinium macrocephalum) and recommend management strategies to deal with outbreaks in KwaZulu-Natal Province (McDougall et al. 2011). More recently, MIREN has capitalized on long-term relationships and trust between network members to explore innovative ways to overcome the ecological and economic burden of international travel by reducing their face-to-face network meetings (Kueffer 2016). As it becomes increasingly difficult to access sufficient resources to cope with the growing

Description Springer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Network name	Focus and scale	Status	Outputs (Expected or achieved)	Key citations
COST Action FP1401— A global network of nurseries as an early warning system against alien tree pests	Consortium of over 40 countries. Europe, EU neighboring Countries and Extra EU Countries	2014–2018	Early warning system and common protocols for alien tree pests and diseases to be established for countries involved	Roques et al. (2015)
COST Action FA1203— Sustainable management of <i>Ambrosia artemisiifolia</i> in Europe "SMARTER"	Consortium of over 40 countries. Europe, EU neighboring Countries and Extra EU Countries	2013–2017	Long-term management and monitoring protocols, development of innovative management solutions	www.ragweed.eu
COST Action TD1209 European Information System for Alien Species "Alien Challenge".	Invasive Alien Species in Europe. Consortium of over 30 countries. Europe, EU neighboring Countries and Extra EU Countries	2012–2016	Knowledge gathering and sharing through a network of experts, support to a European IAS information system, implementation of EU 2020 Biodiversity Strategy targets	http://www.brc.ac. uk/alien-challenge/ home
European Information and Research Network on Aquatic Invasive Species (ERNAIS)	Online information system on aquatic invasive species with early warning functions and decision support	2002– current	International cooperation in research, scientific information exchange and management of aquatic invasive species in Europe and worldwide.	http://www.reabic. net/ERNAIS.aspx
Global Garlic Mustard Field Survey (GGMFS)	16 countries in North America and Europe. Standardized field measurements of performance traits	2008– current	Replicating the GGMFS approach with other invasive species	Colautti et al. (2014a)
Global Invader Impact Network	Impact of invaders on vegetation & soil	2013– current	Experimental framework for a standard methodology to identify the ecological impacts of invasive plants.	Barney et al. (2015)
Global Invasions Research Coordination Network	International network of scientists supported by the U.S. National Science Foundation addressing the ecological and evolutionary causes of biological invasions	Ongoing	Coordination of both theoretical and empirical research on biological invasions around the globe	http://invasionsren. si.edu/
International Plant Sentinel Network (IPSN)	Plant pest and pathogens	Ongoing	Early warning, standardized methodologies for monitoring and surveying of damaging plant pests and pathogens, risk analysis	https://www.bgci. org/plant- conservation/ipsn/
INVASIVESNET	International association for open knowledge and open data on invasive alien species and their management	2016– current	Developing a sustainable network of networks for effective knowledge exchange	Lucy et al. 2016
Mountain Invasions Research Network (MIREN)	Effects of global change on plant invasions and plant biodiversity in mountainous areas	2005– current	Database on invasive plant distribution in mountain environments	Dietz et al. 2006; McDougall et al. (2011); www. mountaininvasions. org
Phragmites Network (PhragNet)	Addressing global scale questions in ecology and biological invasions through a	2014– current	Experimental framework and standardized methodology across common gardens to	Meyerson et al. (2016b)

Table 2 Examples of existing multilateral collaborations within invasion science (see also Box 2 in Lucy et al. 2016)

D Springer

ţ

Global networks for invasion science: benefits, challenges and guidelines

Table 2 continued											
Network name	Focus and scale global network of common gardens in Asia, Australia, Europe, North America, and South America	Status	Outputs (Expected or achieved) identify the ecological impacts of invasive plants	Key citations							
Southern Hemisphere Network on Conifer Invasions	All aspects of conifer invasion in the southern hemisphere	2007– current	Promotes interaction and collaboration between researchers, managers and planners	Richardson et al. (2008); Simberloff et al. (2010)							

threat of invasive species globally, the imperative to find creative and collaborative ways to address this threat is also likely to grow.

Building on existing and previous collaborations: challenges and lessons learned

Good examples of multilateral research collaborations within invasion science exist already (McDougall et al. 2011; Colautti et al. 2014a). Some of the most extensive and important initiatives for both theoretical and applied research are summarized in Table 2. Past and current groups dealing with invasive species have mainly focused on plants rather than other organisms and have provided new tools for risk assessment and management, standardized protocols for data collection and management, and an avenue for different stakeholders to work together. Some of these global collaborations address the impact of invasive plants on a diverse range of taxa, such as the Global Invasions Research Coordination Network (www.invasionsrcn. si.edu), or The Global Invader Impact Network (https://weedeco.ppws.vt.edu/giin; Barney et al. 2015). Existing networks, focused on collecting primary data, are complemented by more technologybased collaborations. The Global Invasive Species Information Network (GISIN) was established to overcome the limitations of traditional approaches in responding to the growing demand for coordinated gathering, storing and disseminating information on introduced species (Ricciardi et al. 2000; Katsanevakis and Roy 2015). The GISIN has subsequently developed an online portal for standardized data (Jarnevich et al. 2015, http://www.gisin.org).

Establishing a productive and sustainable global research network presents many challenges, particularly in the areas of developing shared goals, expectations, coordination, communication, and funding (Gaziulusoy et al. 2016). Below we summarize the major stumbling blocks that can limit the long-term success of networks, and outline strategies to avoid or resolve these barriers (see Online Resource 1, Protocol Guidelines in Supplementary Material, for more information). Overcoming challenges requires shared learning and authentic collaboration amongst network members. One of the many potential strategies could be facilitating "progress reports" between invasion science networks to disseminate information about data protocols, governance, and preliminary outcomes from individual networks. This would enable data trends to be more readily detected, research priorities identified and promoted, and research approaches shared amongst the scientists involved. Ecology and Management of Alien Plant invasions (EMAPi; Richardson et al. 2010; Daehler et al. 2016), for example, has an international focus, holds conferences held every two years and could provide an accessible forum for invasion scientists to share and reflect on updates from other relevant networks. Another potential forum is the European Neobiota initiative (Kowarik and Starfinger 2009), which coordinates biennial conferences and the open-access journal NeoBiota which deals with biological invasions (Kühn et al. 2011).

Sustainability through communication and coordination

Successful global networks require active and continuing engagement of many collaborators (Petersen et al. 2014). Promoting long-term partnerships through collaborative, flexible governance can build trust and accommodate the various motivational levels and drivers over time of individuals members and the institutions they represent (Online Resource 1; see

2 Springer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

also Richardson and Lefroy 2016). Reaching agreement through collaborative processes for potentially divisive matters, such as data management (how to collect, store, integrate, analyze and use data) and authorship, is critical yet may be highly time-intensive for large global networks in particular. Failing to define and agree on a common research agenda and approach, and to communicate the importance of this to the scientific and broader community, are sure ingredients for failure in network initiatives.

Navigating the variability in biosecurity requirements across regions

Biosecurity legislation (international through to regional) and regulations of the donor (providing plant material) and host (receiving plant material for experiments and/or analysis) countries can strongly influence the feasibility and timeframes of initiatives. Hosting a garden with living, potentially weedy species or genotypes demands strict adherence to permit requirements, responsible husbandry practices, and countries may have vastly different standards and procedures to address biosecurity risks. Australia, New Zealand, South Africa and North America are renowned internationally for their strict biosecurity standards. Within China there are a range of biosecurity measures stipulated, such as the isolation buffer (natural or man-made to separate the garden from the surrounding area) and documentation of garden management that is required in some provinces but not necessarily in others. Networks that rely on sharing plant material need to resolve these biosecurity issues early in the planning process to allow adequate time for receiving and propagating material.

Informing policy

Biological invasions can only be reduced worldwide by engaging multinational support across all sectors of society. Global initiatives can help to bring these decision-making policies and processes into alignment with each other by improving the dialogue on complex scientific issues between researchers, policymakers, stakeholder networks and the broader public (Richardson and Lefroy 2016). The COST Action TD1209 "Alien Challenge" (www.brc.ac.uk/alien-challenge/ home) is one example of how a global collaboration within invasion biology can inform policy and

Springer

stakeholders. This initiative is improving knowledge gathering and sharing through a network of experts informing the European Alien Species Information System (EASIN), including assessing the pathways and gateways of alien species introductions within Europe (Katsanevakis and Roy 2015). The knowledge gained from this initiative can be used to inform policy decisions and develop shared formats for alien species information in line with the EU 2020 Biodiversity Strategy targets, Regulation EU no. 1143/2014. The Invasive Species Specialist Group (ISSG) is another global community which combines scientific and policy experts on invasive species under the auspices of the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN, see review by Pagad et al. 2015). While these initiatives demonstrate some effective relationships between science and policy at high levels in Europe particularly, stronger science-policy partnerships are needed in other biogeographic zones.

Funding global networks

Active, productive networks need to be resourced over at least several years. While some activities can occur with in-kind resources or minimal funding (e.g., developing shared goals, establishing a core collection of plant material, and communicating through electronic media), others demand substantial investment of time and funding (e.g., meeting face-to-face, establishing experimental infrastructure, and field surveys). Only a small proportion of funding, if any, is likely to come from grants allocated to the whole network. Multilateral funding could include regional sources such as the European Union's Horizon 2020 and COST Actions which support collaborations with non-European Union research groups. More realistically, each network location will need to source its own funding, for example by identifying the synergies between network activities, ongoing or related research projects, and capitalizing on existing research networks and international funding opportunities. Several national or regional centers or institutes that focus on invasion science are now well established (e.g., the Laboratorio de Invasiones Biológicas in Chile-http:// www.lib.udec.cl/home.html; Department of Invasion Ecology of the Institute of Botany, The Czech Academy of Science-http://www.ibot.cas.cz/invasions; or the Centre for Invasion Biology, Stellenbosch

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

University in South Africa—http://academic.sun.ac. za/cib/; van Wilgen et al. 2014). Such centers already function as hubs in global networks in invasion science, but there is scope for more focused global collaborations such as outlined in this paper.

Conclusions

The complexity and scale (spatial and temporal) of the most important biological invasion questions is well beyond the scope of individual biogeographic regions, disciplines, professions or local research groups. Despite the urgent need, only a few large-scale collaborations have been established within invasion science, and none have focused on these fundamental global (e.g., how does biogeography influence ecosystem resistance and resilience against invasion?) or highimpact applied (e.g., rapid responses to new threats) questions. Global Networks for Invasion Science are a powerful approach to address fundamental questions and transform this knowledge into appropriate policy and management recommendations. We encourage researchers, policymakers and practitioners to build global networks and generate the innovative solutions to minimize biological invasions that can only come from such a collaborative and global approach.

Acknowledgements We gratefully acknowledge the generosity of the University of Sassari, Italy, in hosting the PhragNet 2016 planning meetings and creating the space that facilitated this manuscript. DMR and SC acknowledge support from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative research project on 'Integrated management of invasive alien species in South Africa' and the National Research Foundation of South Africa (Grant 85417 to DMR). SC's work was supported by the South African National Department of Environment Affairs through its funding of the South African National Biodiversity Institute Invasive Species Programme. HB, CL and FE were supported by the Danish Council for Independent Research | Natural Sciences (Project DFF-4002-00333). JTC, WJA and GPB were supported by NSF grant DEB 1050084 to JTC. LAM was supported by NSF DEB 1049914 to LAM and by the University of Rhode Island, College of Environment and Life Sciences. PP, JC, WYG and HS were supported by long-term research development project RVO 67985939 (The Czech Academy of Sciences), and Project No. 14-15414S (Czech Science Foundation). PP acknowledges support by Praemium Academiae award from The Czech Academy of Sciences. JGP warmly thanks the Institute of Integrative Biology, ETH Zürich for welcoming hospitality and the Environment Institute and Faculty of Sciences, The University of Adelaide for support from Travel Grant 13116630.

References

- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989. doi:10.1890/05-0219
- Ahern J (2013) Urban landscape sustainability and resilience: the promise and challenges of integrating ecology with urban planning and design. Landscape Ecol 28:1203–1212. doi:10.1007/s10980-012-9799-z
- Avolio ML, Beaulieu JM, Smith MD (2013) Genetic diversity of a dominant C-4 grass is altered with increased precipitation variability. Oecologia 171:571–581. doi:10.1007/s00442-012-2427-4
- Barney JN, Tekiela DR, Barrios-Garcia MN, Dimarco RD, Hufbauer RA, Leipzig-Scott P, Nuñez MA, Pauchard A, Pyšek P, Vítková M, Maxwell BD (2015) Global Invader Impact Network (GIIN): toward standardized evaluation of the ecological impacts of invasive plants. Ecol Evol 5:2878–2889. doi:10.1002/ece3.1551
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15:22–40
- Colautti RI, Maron JL, Barrett SCH (2009) Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. Evol Appl 2:187–199. doi:10.1111/j.1752-4571.2008.00053.x
- Colautti RI, Franks SJ, Hufbauer RA, Kotanen P, Torchin M, Byers JE, Pyšek P, Bossdorf O (2014a) The Global Garlic Mustard Field Survey (GGMFS): challenges and opportunities of a unique, large-scale collaboration for invasion biology. NeoBiota 21:29–47. doi:10.3897/neobiota.21.5242
- Colautti RI, Parker JD, Cadotte MW, Pyšek P, Brown CS, Sax DF, Richardson DM (2014b) Quantifying the invasiveness of species. NeoBiota 21:7–27. doi:10.3897/neobiota.21. 5310
- Cronin JT, Bhattarai GP, Allen WJ, Meyerson LA (2015) Biogeography of a plant invasion: plant–herbivore interactions. Ecology 96:1115–1127. doi:10.1890/14-1091.1
- Daehler CD, van Kleunen M, Pyšek P, Richardson DM (2016) EMAPi 2015: highlighting links between science and management of alien plant invasions. NeoBiota 30:1–3. doi:10.3897/neobiota.30.9594
- Dietz H, Kueffer C, Parks CG (2006) MIREN: a new research network concerned with plant invasion into mountain areas. Mount Res Develop 26:80–81. doi:10.1659/0276-4741(2006)026[0080:MANRNC]2.0.CO;2
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds) (1989) Biological invasions: a global perspective. Wiley, Chichester
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends Ecol Evol 14:135–139. doi:10.1016/S0169-5347(98)01554-7
- Eriksen RL, Hierro JL, Eren Ö, Andonian K, Török K, Becerra PI, Montesinos D, Khetsuriani L, Diaconu A, Kesseli R (2014) Dispersal pathways and genetic differentiation among worldwide populations of the invasive weed *Centaurea solstitialis* L. (Asteraceae). PLOS ONE 9:e114786
- Fraser LH, Henry HAL, Carlyle CN, White SR, Beierkuhnlein C, Cahill JF Jr, Casper BB, Cleland E, Collins SL, Dukes

Deringer

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

JS, Knapp AK, Lind E, Long R, Luo Y, Reich PB, Smith MD, Sternberg M, Turkington R (2013) Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. Front Ecol Environ 11:147–155. doi:10.1890/110279

- Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. doi:10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2
- Gaziulusoy AI, Ryan C, McGrail S, Chandler P, Twomey P (2016) Identifying and addressing challenges faced by transdisciplinary research teams in climate change research. J Clean Prod 123:55–64. doi:10.1016/j.jclepro. 2015.08.049
- Guarino F, Cicatelli A, Brundu G, Heinze B, Castiglione S (2015) Epigenetic diversity of clonal white poplar (*Populus alba* L.) populations: could methylation support the success of vegetative reproduction strategy? PLoS ONE 10(7):e0131480. doi:10.1371/journal.pone. 0131480
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009. doi:10.1111/j.1461-0248.2005.00792.x
- Guo WY, Lambertini C, Nguyen LX, Li XZ, Brix H (2014) Preadaptation and post-introduction evolution facilitate the invasion of *Phragmites australis* in North America. Ecol Evol 4:4567–4577. doi:10.1002/ece3.1286
- Guo WY, Lambertini C, Guo X, Li XZ, Eller F, Brix H (2016) Phenotypic traits of the Mediterranean *Phragmites australis* M1 lineage: differences between the native and introduced ranges. Biol Invasions 18:2551. doi:10.1007/ s10530-016-1236-9
- He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett 16:695–706
- Hejda M (2013) Do species differ in their ability to coexist with the dominant alien *Lupinus polyphyllus*? A comparison between two distinct invaded ranges and a native range. NeoBiota 17:39–55
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15
- Hierro JL, Eren Ö, Villarreal D, Chiuffo MC (2013) Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation? Oikos 122:583–590
- Hui C, Richardson DM (2017) Invasion dynamics. Oxford University Press, Oxford
- Hulme PE (2003) Biological invasions: winning the science battles but losing the conservation war? Oryx 37:178–193
- Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. J Appl Ecol 43:835–847
- Iannone BV, Potter KM, Guo Q, Liebhold AM, Pijanowski BC, Oswalt CM, Fei S (2016) Biological invasion hotspots: a trait-based perspective reveals new sub-continental patterns. Ecography (in press, doi: 10.1111/ecog.01973)
- Jarnevich CS, Simpson A, Graham JJ, Newman GJ, Bargeron CT (2015) Running a network on a shoestring: the Global

Invasive Species Information Network. Manage Biol Invasions 6:137–146. doi:10.3391/mbi.2015.6.2.04

- Jeschke JM, Aparicio LG, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14:1–20. doi:10.3897/neobiota.14.3435
- Joshi J, Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecol Lett 8:704–714
- Katsanevakis S, Roy HE (2015) Alien species related information systems and information management. Manage Biol Invasions 6:115–117. doi:10.3391/mbi.2015.6.2.01
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170
- Kolar CS, Lodge TS (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204
- Kowarik I, Starfinger U (2009) Neobiota: a European approach. NeoBiota 8:21–28
- Kueffer C (2010) Transdisciplinary research is needed to predict plant invasions in an era of global change. Trends Ecol Evol 25:619–620
- Kueffer C (2016) A year without flying: the importance of virtual networking, The Mountain Blogs, Mountain Research Institute. Posted 22 January 2016. http://www.blogs-mri. org/a-year-without-flying/. Accessed 31 Aug 2016
- Kueffer C, Pyšek P, Richardson DM (2013) Integrative invasion science: model systems, multi-site studies, focused metaanalysis, and invasion syndromes. New Phytol 200:615–633. doi:10.1111/nph.12415
- Kühn I, Kowarik I, Kollmann J, Starfinger U, Bacher S, Blackburn TM, Bustamante RO, Celesti-Grapow L, Chytrý M, Colautti RI, Essl F, Foxcroft LC, García-Berthou E, Gollasch S, Hierro J, Hufbauer RA, Hulme PE, Jarošík V, Jeschke JM, Karrer G, Mack RN, Molofsky J, Murray BR, Nentwig W, Osborne B, Pyšek P, Rabitsch W, Rejmánek M, Roques A, Shaw R, Sol D, van Kleunen M, Vilà M, von der Lippe M, Wolfe LM, Penev L (2011) Open minded and open access: introducing NeoBiota, a new peer-reviewed journal of biological invasions. NeoBiota 9:1–12. doi:10. 3897/neobiota.9.1835
- Latombe G, Pyšek P, Jeschke JM, Blackburn TM, Bacher S, Capinha C, Costello MJ, Fernández M, Gregory RD, Hobern D, Hui C, Jetz W, Kumschick S, McGrannachan C, Pergl J, Roy HE, Scalera R, Squires ZE, Wilson JRU, Winter M, Genovesi P, McGeoch MA (2016) A vision for global monitoring of biological invasions. Biol Cons. doi:10.1016/j.biocon.2016.06.013
- Lee Y, Kotanen PM (2015) Differences in herbivore damage and performance among *Arctium minus* (burdock) genotypes sampled from a geographic gradient: a common garden experiment. Biol Invasions 17:397–408
- Lindenmayer D, Hobbs RJ, Montague-Drake R, Alexandra J, Bennett A, Burgman M, Cale P, Calhoun A, Cramer V, Cullen P, Driscoll D, Fahrig L, Fischer J, Franklin J, Haila Y, Hunter M, Gibbons P, Lake S, Luck G, MacGregor C, McIntyre S, Mac Nally R, Manning A, Miller J, Mooney H, Noss R, Possingham HP, Saunders D, Schmiegelow F, Scott M, Simberloff D, Sisk T, Tabor G, Walker B, Wiens J, Woinarski J, Zavaleta E (2008) A checklist for ecological

Deringer

management of landscapes for conservation. Ecol Lett 11:78-91

- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536
- Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J (2007) The impact of an alien plant on a native plantpollinator network: an experimental approach. Ecol Lett 10:539–550
- Lord J, Whitlatch R (2015) Predicting competitive shifts and responses to climate change based on latitudinal distributions of species assemblages. Ecology 96:1264–1274
- Lu XM, Siemann E, He MY, Wei H, Shao X, Ding J (2015) Climate warming increases biological control agent impact on a non-target species. Ecol Lett 18:48–56
- Lucy FE, Roy H, Simpson A, Carlton JT, Hanson JM, Magellan K, Campbell ML, Costello MJ, Pagad S, Hewitt CL, McDonald J, Cassey P, Thomaz SM, Katsanevakis S, Zenetos A, Tricarico E, Boggero E, Groom QJ, Adriaens T, Vanderhoeven S, Torchin M, Hufbauer R, Fuller P, Carman MR, Conn DB, Vitule JRS, Canning-Clode J, Galil BS, Ojaveer H, Bailey SA, Therriault TW, Claudi R, Gazda A, Dick JTA, Caffrey J, Witt A, Kenis M, Lehtiniemi M, Helmisaari H, Panov VE (2016) INVASIVESNET towards an international association for open knowledge on invasive alien species. Manage Biol Invasions 7:131–139
- Maron J, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. Ecol Monog 2:261-280. http://www.jstor.org/stable/4539056
- Max-Neef MA (2005) Foundations of transdisciplinarity. Ecol Econ 53:5–16
- McDougall K, Alexander J, Haider S, Pauchard A, Walsh N, Kueffer C (2011) Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. Divers Distrib 17:103–111
- Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Front Ecol Environ 5:199–208
- Meyerson LA, Reaser JK (2003) Biosecurity, bioterrorism, and invasive alien species. Front Ecol Environ 1:307–314
- Meyerson LA, Viola D, Brown R (2010) Hybridization of invasive *Phragmites australis* with a native subspecies in North America. Biol Invasions 12:103–111
- Meyerson LA, Cronin JT, Bhattarai GP, Brix H, Lambertini C, Lučanová M, Rinehart S, Suda J, Pyšek P (2016a) Do ploidy level and nuclear genome size and latitude of origin modify the expression of *Phragmites australis* traits and interaction with herbivores? Biol Invasions 2016:1–19. doi:10.1007/s10530-016-1200-8
- Meyerson LA, Cronin JT, Pyšek P (2016b) Phragmites australis as a model organism for studying plant invasions. Biol Invasions 2016:1–11. doi:10.1007/s10530-016-1132-3
- Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) (2005) Invasive alien species: a new synthesis. Island Press, Washington
- Nassauer JI, Opdam P (2008) Design in science: extending the landscape ecology paradigm. Landsc Ecol 23:633–644
- Ndlovu J, Richardson DM, Wilson JRU, Le Roux JJ (2013) Coinvasion of South African ecosystems by an Australian legume and its rhizobial symbionts. J Biogeogr 40:1240–1251
- Packer JG, Delean S, Kueffer C, Prider J, Abley K, Facelli JM, Carthew SM (2016) Native faunal communities depend on

habitat from non-native plants in novel but not in natural ecosystems. Biodiv Conserv 25:503–523

- Pagad S, Genovesi P, Carnevali L, Scalera R, Clout M (2015) IUCN SSC Invasive Species Specialist Group: invasive alien species information management supporting practitioners, policy makers and decision takers. Manage Biol Invasions 6:127–135
- Parker JD, Torchin ME, Hufbauer RA, Lemoine NP, Alba C, Blumenthal DM, Bossdorf O, Byers JE, Dunn AM, Heckman RW, Hejda M, Jarošík V, Kanarek AR, Martin LB, Perkins SE, Pyšek P, Schierenbeck K, Schlöder C, van Klinken R, Vaughn KJ, Williams W, Wolfe LM (2013) Do invasive species perform better in their new ranges? Ecology 94:985–994. doi:10.1890/12-1810.1
- Pauls SU, Nowak C, Bálint M, Pfenninger M (2013) The impact of global climate change on genetic diversity within populations and species. Mol Ecol 22:925–946
- Petersen AM, Pavlidis I, Semendeferi I (2014) A quantitative perspective on ethics in large team science. Sci Engin Ethics 20:923–945. doi:10.1007/s11948-014-9562-8
- Pohl C (2005) Transdisciplinary collaboration in environmental research. Futures 37:1159–1178
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological invasions, Ecological studies 193. Springer-Verlag, Berlin, pp 97–125
- Pyšek P, Richardson DM, Jarošík V (2006) Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. Preslia 78:437–468
- Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244. doi:10.1016/j.tree. 2008.02.002
- Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek jun J, Sádlo J (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Divers Distrib 15(5):891–903
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau A-M, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proc Natl Acad Sci USA 107:12157–12162. doi:10. 1073/pnas.1002314107
- Pyšek P, Manceur AM, Alba C, McGregor KF, Pergl J, Štajerová K, Chytrý M, Danihelka J, Kartesz J, Klimešová J, Lučanová M, Moravcová L, Nishino M, Sádlo J, Suda J, Tichý L, Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96:762–774. doi:10. 1890/14-1005.1
- Rapo C, Muller-Scharer H, Vrieling K, Schaffner U (2010) Is there rapid evolutionary response in introduced populations of tansy ragwort, *Jacobaea vulgaris*, when exposed to biological control? Evol Ecol 24:1081–1099
- Ravenscroft CH, Whitlock R, Fridley JD (2015) Rapid genetic divergence in response to 15 years of simulated climate change. Glob Change Biol 21:4165–4176

Springer

- Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species—2013 update of the global database. Diversity Distrib 19:1093–1094
- Ricciardi A, Steiner WWM, Mack RN, Simberloff D (2000) Toward a global information system for invasive species. Bioscience 50:239–244. doi:10.1641/0006-3568(2000)050[0239:TAGISF]2.3.CO:2
- Richardson DM (2011) Invasion science: the roads travelled and the roads ahead. In: Richardson DM (ed) Fifty years of invasion ecology. The legacy of Charles Elton. Wiley-Blackwell, Oxford, pp 397–407. doi: 10.1002/ 9781444329988.ch29
- Richardson DM, Bond WJ (1991) Determinants of plant distribution: evidence from pine invasions. Am Nat 137:639–668
- Richardson BJ, Lefroy T (2016) Restoration dialogues: improving the governance of ecological restoration. Restor Ecol 24:668–673. doi:10.1111/rec.12391
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progr Phys Geogr 30:409–431
- Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographic patterns. New Phytol 196:383–396
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions: the role of mutualisms. Biol Rev 75:65–93
- Richardson DM, Rouget M, Rejmánek M (2004) Using natural experiments in the study of alien tree invasions: opportunities and limitations. In: Gordon MS, Bartol SM (eds) Experimental approaches to conservation biology. University of California Press, Berkeley, pp 180–201
- Richardson DM, van Wilgen BW, Nunez MA (2008) Alien conifer invasions in South America: short fuse burning? Biol Invasions 10:573–577
- Richardson DM, Daehler CC, Leishman MR, Pauchard A, Pyšek P (2010) Plant invasions: theoretical and practical challenges. Biol Invasions 12:3907–3911
- Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU (2011) Human-mediated introductions of Australian acacias: a global experiment in biogeography. Diversity Distrib 17:771–787
- Rodríguez-Echeverría S (2010) Rhizobial hitchhikers from Down Under: invasional meltdown in a plant-bacteria mutualism? J Biogeogr 37:1611–1622
- Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. J Appl Ecol 41:561–570
- Roques A, Fan J-T, Courtial B, Zhang Y-Z, Yart A, Auger-Rozenberg M-A, Denux O, Kenis M, Baker R, Sun J-H (2015) Planting sentinel European trees in Eastern Asia as a novel method to identify potential insect pest invaders. PLoS ONE 10:e0120864
- Schrey AW, Alvarez M, Foust CM, Kilvitis HJ, Lee JD, Liebl LB, Martin CL, Richards M, Robertson AW (2013) Ecological epigenetics: beyond MS-AFLP. Integr Comp Biol 53(2):340–350. doi:10.1093/icb/ict012

- Simberloff D, Nuñez M, Ledgard NJ, Pauchard A, Richardson DM, Sarasola M, van Wilgen BW, Zalba SM, Zenni RD, Bustamante R, Peña E, Ziller SR (2010) Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. Austral Ecol 35:489–504. doi:10.1111/j.1442-9993.2009.02058.x
- Strayer DL (2012) Eight questions about invasions and ecosystem functioning. Ecol Lett 15:1199–1210. doi:10. 1111/j.1461-0248.2012.01817.x
- Suda J, Meyerson LA, Leitch I, Pyšek P (2015) The hidden side of plant invasions: the role of genome size. New Phytol 205:994–1007. doi:10.1111/nph.13107
- Tho BT, Sorrell BK, Lambertini C, Eller F, Brix H (2016) *Phragmites australis*: how do genotypes of different phylogeographic origin differ from their invasive genotypes in growth, nitrogen allocation and gas exchange? Biol Invasions 18:2563–2576. doi:10.1007/s10530-016-1158-6
- Thompson GD, Bellstedt DU, Richardson DM, Wilson JRU, Le Roux JJ (2015) A tree well travelled: global genetic structure of the invasive tree Acacia saligna. J Biogeogr 42:305–314. doi:10.1111/jbi.12436
- van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245
- van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelser PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu W, Thomas J, Velayos M, Wieringa JJ, Pyšek P (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. doi:10.1038/nature14910
- van Wilgen BW, Davies SJ, Richardson DM (2014) Invasion science for society: a decade of contributions from the Centre for Invasion Biology. S Afr J Sci. doi:10.1590/sajs. 2014/a0074
- Walther GR, Gritti ES, Berger S, Hickler T, Tang ZY, Sykes MT (2007) Palms tracking climate change. Global Ecol Biogeogr 16:801–809
- Wickson F, Carew AL, Russell AW (2006) Transdisciplinary research: characteristics, quandaries and quality. Futures 38:1046–1059. doi:10.1016/j.futures.2006.02.011
- Wilson JRU, Caplat P, Dickie IA, Hui C, Maxwell BD, Nuñez MA, Pauchard A, Rejmánek M, Richardson DM, Robertson MP, Spear D, Webber BL, van Wilgen BW, Zenni RD (2014) A standardized set of metrics to assess and monitor tree invasions. Biol Invasions 16:535–551. doi:10.1007/ s10530-013-0605-x
- Woodford DJ, Richardson DM, MacIsaac HJ, Mandrak NE, van Wilgen BW, Wilson JRU, Weyl OLF (2016) Confronting the wicked problem of managing biological invasions. Neobiota 31:63–86
- Zenetos A. (ed.), 2015. Illustrated Guide of Marine Alien species in the Mediterranean for Students and Citizen Scientists. COST1209 Action: Alien Challenge, 22 pp

Deringer

GENERAL CONCLUSIONS AND RECOMMENDATIONS

This Thesis has proposed and applied novel methodologies for the inventorying and the study of biological invasions in inland water in a poorly investigated continent such as South America.

Among the main achievements, an original data-base was established, holding reviewed information on native and non-native aquatic plant species in South America (SA). Although the data collected for SA from 2015 stored more than 1,000 species with their basic information, at the moment very detailed information is available only for 250 aquatic species. The most detailed information hold in the inventory was used for further analyses including macroecological studies. It was also possible use the DB to apply and test the USAqWRA as a screening protocol for South American alien aquatic plant species, providing a rapid assessment scheme that may help reduce the costs of control in the future.

With the predicted global change and the large numbers of aquatic plants species in trade (e.g., ornamentals, phytodepuration and other uses), new species will have the potential to establish if introduced, and possibly become invasive. Therefore, it is necessary to consider that native species presently invasive in South America might spread to continents like Europe or Central and North America and become invasive. However, aquatic plant species might have a larger tolerance than revealed by ecological niche models.

Based on the results obtained in this Thesis, it is possible to provide some very general recommendations in the field of biological invasions are:

(1) Country-based or Continent-based inventory of non-native plants are a very important tool for basic and applied research in plant invasions;

(2) A comparison of available information in the scientific literature reveals that more scientific long-term studies are necessary to understand fully the interaction between ecological niche dynamics and invasive alien species and more species-specific information are needed for improved management.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

(3) Attempts to incorporate scenarios of climate change should be considered in future integrated water resource management efforts, but scenarios should be condensed to realistic ranges starting with projections based on detectable (if any) trends in the historical climatic and hydrological records.

Findings from this Thesis confirm and illustrate the potential usefulness of a variety of modelling approaches in projecting potential invasive species distributions under current climate. Challenges still remain in integrating climate change projections and mechanisms of invasions, particularly in aquatic ecosystems and in translating model results into information useful to managers and decision-makers.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

BIBLIOGRAPHY

Abell R, Thieme M, Ricketts TH, Olwero N, Ng R, Petry P, Hoekstra J (2011). Concordance of freshwater and terrestrial biodiversity. Conservation Letters, 4: 127–136.

Assessment, Millennium Ecosystem (MEA) (2005). Ecosystems and human well-being: wetlands and water. World resources institute, Washington, DC 5.

Crawley MJ, Harvey PH, Purvis ANDA (1996). Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 351(1345): 1251–1259.

Dudgeon D, Arthington AH, Gessner MO (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, 81:163–182.

Elton CS (1958). The ecology of invasions by plants and animals. Methuen, London 18.

FAO/LEG (1996). Regional compendium on aquaculture and inland fisheries legislation (Asian Region). FAO Development Law Service. Rome, FAO.

Fuentes N, Ugarte E, Kühn I, Klotz S (2010). Alien plants in southern South America. A framework for evaluation and management of mutual risk of invasion between Chile and Argentina. Biological Invasions, 12: 3227–3236. doi: 10.1007/s10530-010-9716-9

Fuentes N, Ugarte E, Kühn I, Klotz S (2008). Alien plants in Chile: inferring invasion periods from herbarium records. Biological Invasions, 10:649–657. doi: 10.1007/s10530-007-9159-0

Gallardo B, Aldridge DC (2013). The "dirty dozen": socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. Journal Applied Ecology, 50: 757–766.

Gardener M, Bustamante R, Herrera I, Durigan G, Pivello V, Moro M, Stoll A, Langdon B, Baruch Z, Rico A, Arredondo-Nunez A, Flores S (2011). Plant invasion in Latin America: fast track to a more focused agenda. Plant Ecology and Diversity, 0: 1–8.

Goodwin BJ, McAllister AJ, Fahrig L (1999). Predicting invasiveness of plant species based on biological information. Conservation biology, 13(2): 422–426.

Hussner A (2012). Alien aquatic plant species in European countries: Alien aquatic plant species in European countries. Weed Res, 52: 297–306.

IUCN (1999). IUCN guidelines for the prevention of biodiversity loss due to biological invasion. Species, 31–32, 28–42.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

Murphy K (2002). Plant communities and plant diversity in softwater lakes of northern Europe. Aquatic Botany, 73: 287–324.

Pyšek P, Richardson D, Rejmánek M, Webster G, Williamson M, Kirschner J (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon, 53: 131–143.

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000). Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distribution, 6: 93–107.

Revenga C, Campbell I, Abell R, De Villiers P, Bryer M (2005). Prospects for monitoring freshwater ecosystems towards the 2010 targets. Philosophical Transactions of the Royal Society of London. Series B, 360: 397–413.

Strayer DL (2010). Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology, 55:152–174.

Strayer DL, Dudgeon D (2010). Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society, 29:344–358.

Ugarte E, Fuentes N, Klotz S (2010) European plants in southern South America unwanted visitors? In: Settele J, Penev L, Georgiev T, Grabaum R, Grobelnik V, Hammen V, Klotz S, Kotarac M, Kuhn I (eds) Atlas of biodiversity risk. Pensoft Sofia, Bulgaria, pp 148–149.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters, 14: 702–708.

Willby NJ (2007). Managing invasive aquatic plants: problems and prospects. Aquatic Conservation: Marine and Freshwater Ecosystems, 17: 659–665.

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.

APPENDIX I

A. The inventory for native and non-native aquatic plants of South America.

Qualitative categorization for the sub-set of 250 native and non-native aquatic plant species in the 16 regions of South America, based on the expert opinion and literature: IND = native, ALNNA = alien not assessed, ALNCULT = alien cultivated, ALNNAT = alien naturalized and ALNINV = alien invasive, ALN IN = alien in, ALN TO = alien to, ABS = absent.

Species	Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	Falkland Islands	French Guiana	Galapagos	Guyana	Paraguay	Peru	SG and SSI	Suriname	Uruguay	Venezuela
Agrostis capillaris L.	ALNNA	RNA	ALNNA	ALNNA	ALNNA	RNA	ALNNAT	RNA	RNA	RNA	RNA	RNA	ALNNAT	RNA	RNA	ALNNA
Agrostis stolonifera L.	ALNNAT	ALNNA	RNA	ALNINV	ALNNA	ALNNA	ALNNAT	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	RREF	ALNNAT
Alternanthera brasiliana (L.) Kuntze	RNA	IND	IND	IND	RNA	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RREF	IND
Alternanthera halimifolia (Lam.) Standl. ex Pittier	RNA	RNA	IND	IND	IND	IND	RNA	IND	RNA	IND	RREF	IND	RNA	IND	RREF	IND
Alternanthera philoxeroides (Mart.) Griseb.	IND	IND	ALNNA	ALNNAT	RNA	RNA	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Andronogon hicornis I.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RREF	IND
Aneilema umbrosum (Vahl) Kunth	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Arundo donar I			AI NINV	AI NINV	AI NINV	AI NCULT	RNA		AI NCULT	RNA	RRFF		RNA		ALNINV	
Astraga lobata (L.) Klotzsch	IND	RNA	IND	RNA	IND	RNA	RNA	IND	RNA	IND	RREF	IND	RNA	RNA	IND	IND
Azolla caroliniana Willd	PPEF	PPEE	RREE	RNA	IND	IND	RNA	IND	PNA	IND	IND		RNA	IND	IND	IND
A clic Clic lei les Les	IND	IND	NID				DNIA	IND	DNA	IND	IND	ALINIA	DNA	IND	IND	IND
Azona juiculoides Lam.	IND	IND	IND	ALNNA-INL	ALMINV-INL	IND	RNA	IND	KINA	IND	IND	IND	RNA	IND	IND	IND
Azolla microphylla Kaulf.	IND	IND	IND	RNA AL NNA T		IND	RNA	IND	IND	IND	KNA	IND	RNA	RNA	IND	IND
Bidens idevis (L.) Britton, Sterns & Poggenb.	IND	IND	IND	ALNINAI	ALININ V-IINL	KNA	KNA	KNA	KINA	RNA	IND	IND	RNA	RNA	IND	ABS
Bidens pilosa L.	IND	IND	IND	ALNNAI-INI	IND	ALNNAI -IN	L KNA	IND	ALNNAI	IND	RREF	IND	RNA	IND	IND	IND
Blechnum cordatum (Desv.) Hieron.	IND	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RREF	IND	RNA	RNA	RREF	IND
Bolboschoenus maritimus (L.) Palla	IND	RNA	IND	ALNNAI-INI	. KNA	RNA	RNA	RNA	RNA	RNA	RREF	IND	RNA	IND	RREF	ABS
Brachiaria arrecta (T.Durand & Schinz) Stent	ALNNA	RNA	ALNINV	RNA	ALNNA	RNA	RNA	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	RNA	ALNINV
Brachiaria brizantha (A.Rich.) Stapf	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	RNA	ALNNA	ALNNA	ALNNA	ALNNA	RNA	RNA	RNA	ALNNA
Brachiaria mutica (Forssk.) Stapt	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	ALNNA	ALNNA	ALNNA	RNA	ALNNA	RNA	ALNNA
Cabomba caroliniana A.Gray	IND	IND	ALNNA	RNA	RREF	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	IND	IND
Cabomba furcata Schult. & Schult.f.	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RREF	IND	RNA	IND	RNA	IND
Cabomba warmingii Casp.	RNA	RNA	ALNCULT	RNA	IND	IND	RNA	IND	RNA	IND	RREF	IND	RNA	IND	RNA	IND
Callitriche deflexa A.Braun ex Hegelm.	IND	IND	IND	IND	IND	IND	RNA	RNA	ALNNA	RNA	IND	RREF	RNA	RNA	IND	IND
Callitriche heterophylla Pursh	IND	RNA	IND	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RREF	IND
Callitriche terrestris Rat.	IND	RNA	IND	IND	RREF	IND	RNA	RNA	RNA	RNA	RREF	IND	RNA	RNA	RREF	ABS
Canna indica L.	IND	IND	IND	IND	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	ALNCULT-IND
Caperonia castaneifolia (L.) A.StHil.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Cardamine bonariensis Juss. ex Pers.	IND	IND	IND	ALNNA	IND	IND	RNA	RNA	ALNNA	RNA	IND	IND	RNA	RNA	IND	IND
Carex aematorrhyncha Desv.	IND	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ABS
Centella erecta (L.f.) Fernald	IND	RNA	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND	IND
Ceratophyllum demersum L.	IND	IND	ALNNA-IND	ALNNA	IND	IND	RNA	RNA	RNA	RNA	RREF	IND	RNA	RNA	IND	IND
Ceratophyllum muricatum subsp. australe (Griseb.) Les	IND	IND	IND	RNA	IND	IND	RNA	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND
Chamaecrista nictitans (L.) Moench	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	RREF	RNA	IND	RNA	IND
Chloris barbata Sw.	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	ALNNA-IND	ALNNA	ALNNA	ALNNA	ALNNA	RNA	ALNNA-IND	ALNNA	ALNNA-IND
Coix lacryma-jobi L.	ALNNA	ALNCULT	ALNNA	RNA	RNA	ALNCULT	RNA	ALNNAT	ALNNA	ALNNAT	RREF	ALNCULT	RNA	ALNNAT	RNA	ALNNAT
Commelina diffusa Burm.f.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RREF	IND
Commelina obliqua Vahl	IND	IND	IND	RNA	RREF	IND	RNA	IND	RNA	IND	IND	RNA	RNA	IND	RNA	IND
Conium maculatum L.	ALNNAT	ALNNAT	ALNNAT	ALNNAT	ALNNA	ALNNAT	ALNNAT	RNA	RNA	RNA	RNA	ALNNAT	RNA	RREF	ALNNAT	ABS
Cotula australis (Sieber ex Spreng.) Hook.f.	RNA	ALNNAT	ALNNA	ALNNAT	RNA	ALNNA	RNA	RNA	RNA	RNA	RNA	ALNNAT	RNA	RNA	ALNNA	ABS
Cotula coronopifolia L.	RNA	ALNNAT	ALNNAT	ALNINV	ALNNAT	ALNNA	RNA	RNA	RNA	RNA	ALNCULT	ALNNA	RNA	RNA	RNA	ABS
Crassula venezuelensis (Steyerm.) M.Bywater & Wickens	IND	IND	RNA	RNA	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND
Crotalaria retusa L.	RNA	RNA	ALNNAT	RNA	ALNNA	ALNNA	RNA	ALNNA	ALNINV	ALNNA	ALNNA	ALNNA	RNA	ALNNA	RNA	ALNNA
Cuphea racemosa (L.f.) Spreng.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	RNA	ALNNA	RNA	IND	IND	RNA	RNA	IND	IND
Cyperus alternifolius L.	RNA	RNA	ALNNAT	ALNNAT	ALNNAT	RREF	RNA	RNA	ALNNA	RNA	RREF	RREF	RNA	RNA	RREF	ALNNA
Cyperus articulatus L.	IND	IND	IND	ALNNAT	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Cyperus difformis L.	RNA	ALNNA	ALNNA	ALNINV	RREF	ALNINV	RNA	RNA	RNA	ALNNA	ALNNA	ALNINV	RNA	RNA	RNA	ALNNA
Cyperus digitatus Roxb.	IND	IND	IND	RNA	IND	IND	RNA	RNA	ALNNA	IND	IND	IND	RNA	IND	IND	IND
Cyperus eragrostis Lam.	IND	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RREF	IND	RNA	IND	IND	ABS
Cyperus esculentus L.	IND	IND	IND	ALNNA	IND	IND	RNA	RNA	IND	RREF	IND	IND	RNA	RNA	IND	IND
Cyperus giganteus Vahl	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND

Cyperus haspan L.	IND	IND	IND	ALNNAT	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RREF	IND
Cyperus iria L.	ALNNAT	ALNNA	ALNNA	RNA	RREF	ALNNA	RNA	ALNCULT	RNA	ALNNA	RREF	ALNNA	RNA	RNA	ALNNA	ALNNA
Cyperus laevigatus L.	IND	IND	RNA	ALNNAT-INI	RREF	IND	RNA	RNA	IND	RNA	RNA	IND	RNA	RNA	RNA	IND
Cyperus ligularis L.	RREF	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Cyperus luzulae (L.) Retz.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	ALNNA
Cyperus odoratus L.	IND	IND	IND	ALNNAT	IND	IND	RNA	IND	ALNNA	IND	IND	RREF	RNA	IND	IND	IND
Cyperus reflexus Vahl	IND	IND	IND	IND	RNA	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND	IND
Cyperus rotundus L.	IND	IND	ALNNA	ALNNAT	ALNNA	ALNNA	RNA	ALNNA	ALNNA	ALNNA	IND	ALNNA	RNA	ALNNA	IND	ALNNA-IND
Cyperus sauarrosus L.	IND	IND	IND	ALNNAT-INI	IND	IND	RNA	RNA	IND	RREF	IND	IND	RNA	RNA	IND	IND
Cyperus surinamensis Rotth	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	ALNINV-IND
Cyperus hermanhroditus (Jaca) Standl	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	RNA	RNA	IND
Desmodium adscendens (Sw) DC	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RREF	IND	RNA	IND	IND	IND
Desmodium harbatum (L.) Benth	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Desmodium incanum DC	IND	IND	IND	RNA	IND	IND	RNA	IND		IND	IND	IND	RNA	IND	ALNINV	IND
Digitaria ciliaris (Betz.) Koeler	ALNNA						RNA						RNA		ALNNA	
Dioclea virgata (Pich) Amshoff	IND	IND	IND	RNA	IND	IND	RNA	IND	AI NCULT	IND	IND	IND	RNA	IND	RNA	IND
Distichlis spigsta (L.) Greene	IND	IND	PNA	IND	IND	IND	DNA	PNA	IND	PNA	DNA	IND	DNA	PNA	IND	DDEE
Dysnhania ambrosioidas (L.) Mosyakin & Clamants	IND	IND	DNA PNA		IND	AI NCULT	DNA	ALNNAT IND	ALNNAT	AL NINAT INF	IND	IND	DNA	AL NIMAT INF	ALNCULT	ALNNAT IND
Echinochlog colong (L.) Link	ALNNA			ALININA-IIND	AL NNA	ALNCOLI	DNA	ALININAI -IIND	ALININAT	ALININAI -IINI	AL NNA		DNA	ALINIA I -IINL	ALNCOLI	ALINIAI -IND
Echinochiou colonu (E.) Eliik	ALNINA	DNA	ALNINA	ALNNA	ALMNA	DNA	DNIA	DNA	ALININA	DNA	ALININA	ALININA	DNA	DNA	ALNINA	ALININA
Echinochioa crusgatti (L.) F. Beauv.	ALMINV		ALININA	ALININA	ALININA		DNA		DNA		ALININA	ALININA	DNA		ALININA	ALININA
Echinochioa crus-pavonis (Kunth) Schut.	ALNNA	ALININA	ALNNA	ALININA	ALININA	ALNNA	RNA	ALININA	RINA	ALININA	ALNINA	ALINIA	RNA	ALNNA	ALININA	ALNNA
Echinochioa polystachya (Kunth) Hitche.	IND	IND	IND	RINA	IND	IND	RNA	IND	RINA	IND	IND	IND	RNA	IND	IND	
Echinodorus grandiflorus (Cham. & Schildl.) Micheli	IND	IND	IND	RNA	IND	RREF	RNA	ABS	RNA	ABS	IND	IND	RNA	ABS	IND	ALNNA-IND
Echinodorus horizontalis Rataj	RNA	KNA	IND	RNA	IND	IND	RNA	ABS	RNA	IND	KNA	ALNCULI	RNA	ABS	RNA	IND
Echinodorus paniculatus Micheli	IND	IND	IND	RNA	IND	IND	RNA	ABS	RNA	IND	IND	IND	RNA	IND	KNA	IND
Eclipta prostrata (L.) L.	IND	IND	IND	ALNNAI	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	ALNINV
Egeria densa Planch.	ALNNAI -INL	ALNNA	ALNNAI -IND	ALNINV	ALNINV	RNA	RNA	RNA	RNA	RNA	ALNINV	RNA	RNA	RNA	ALNNA I -INI	ALNNAI
Egeria najas Planch.	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ALNINV	RNA	RNA	RNA	IND	ABS
Eichhornia azurea (Sw.) Kunth	IND	IND	ALNINV-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Eichhornia crassipes (Mart.) Solms	IND	IND	IND	ALNINV	ALNINV	ALNINV	RNA	ALNINV	RNA	ALNINV	IND	IND	RNA	ALNINV	ALNINV	ALNINV-IND
Eichhornia paniculata (Spreng.) Solms	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	ALNNAT	RNA	ALNNAT	IND	RNA	RNA	ABS	RNA	IND
Eleocharis acicularis Roem et Schult.	RNA	IND	IND	ALNINV	IND	IND	RNA	RNA	RNA	RNA	IND	RREF	RNA	RNA	IND	IND
Eleocharis acutangula (Roxb.) Schult.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	ABS	IND	IND	IND	IND	RNA	IND	RREF	IND
Eleocharis bonariensis Nees	IND	IND	IND	IND	RNA	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND	ABS
Eleocharis elegans (Kunth) Roem. & Schult.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Eleocharis exigua (Kunth.) Roem. & Schult.	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Eleocharis geniculata (L.) Roem. & Schult.	IND	IND	IND	RNA	RREF	IND	RNA	IND	ALNNA	IND	IND	IND	RNA	IND	IND	IND
Eleocharis interstincta (Vahl) Roem. & Schult.	ABS	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	RREF	RNA	IND	RNA	IND
Eleocharis minima Kunth	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RREF	IND
Eleocharis montana (Kunth) Roem. & Schult.	IND	IND	IND	IND	IND	IND	RNA	ABS	IND	ABS	IND	IND	RNA	IND	IND	IND
Eleocharis mutata (L.) Roem. & Schult.	RNA	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Eleocharis sellowiana Kunth	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	RNA	RNA	ABS	IND	IND
Elodea canadensis Michx.	IND	RNA	RNA	ALN	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	IND	NAT
Elodea granatensis Humb. & Bonpl.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	ALNNA-IND
Eragrostis ciliaris (L.) R.Br.	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	ALNNAT	RNA	ALNNAT	ALNNA	ALNNA	RNA	ALNNAT	RNA	ALNNAT
Eragrostis hypnoides (Lam.) Britton, Stern & Poggenb.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Eragrostis pectinacea (Michx.) Nees	ALNNAT-INE	IND	IND	RNA	IND	IND	RNA	IND	RNA	ABS	RNA	IND	RNA	IND	ALNNA	ALNINV-IND
Euphorbia heterophylla L.	IND	RNA	IND	RNA	RNA	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	IND	IND
Fimbristylis autumnalis (L.) Roem. & Schult.	IND	RREF	ALNNA-IND	RNA	RREF	IND	RNA	IND	RNA	IND	IND	RNA	RNA	IND	IND	IND
Fimbristylis complanata (Retz.) Link	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Fuirena umbellata Rottb.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	RNA	RNA	IND	RNA	IND

Glyceria fluitans (L.) R.Br.	RNA	RNA	RNA	ALNNAT	ALNNA	ALNNA	RNA	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	ALNNAT	ABS
Habenaria trifida Kunth.	IND	IND	IND	IND	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Hedychium coronarium J.Koenig	ALNINV	ALNNAT	ALNINV	RNA	RREF	ALNNA	RNA	ALNNA	ALNNA	ALNNA	ALNNA	ALNNA	RNA	ALNNA	RNA	ALNNAT
Helanthium bolivianum (Rusby) Lehtonen & Myllys	IND	IND	IND	RNA	IND	IND	RNA	RNA	RNA	IND	IND	IND	RNA	RNA	RNA	IND
Helanthium tenellum (Mart. ex Schult.f.) J.G.Sm.	IND	IND	IND	RNA	IND	IND	RNA	ABS	RNA	IND	IND	IND	RNA	IND	RNA	IND
Hippuris vulgaris L.	IND	RNA	RNA	ALN	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ABS
Holcus lanatus L.	ALNNA	ALNNA	ALNNA	ALNNA	ALNNA	ALNNA	ALNNAT	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	ALNNA	ALNNA
Hydrilla verticillata (L.f.) Royle	ALNINV	RNA	ALNINV	RNA	ALNINV	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ALNINV
Hydrocleys nymphoides (Humb. & Bonpl. ex Willd.)	DID	DUD	DUD		D ID	DID	DNIA	DID	DNIA	nin	DID	DDEE	DATA	DID	DUD.	
Buchenau	IND	IND	IND	ALNNAI	IND	IND	RNA	IND	KNA	IND	IND	RREF	KNA	IND	IND	ALNCULI-IND
Hydrocotyle ranunculoides L.f.	IND	ALNNA-INI	IND	ALNINV-IND	ALNNA-IND	ALNNA	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Hydrocotyle umbellata L.	RNA	IND	IND	ALNNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Hydrolea spinosa L.	RREF	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	RREF	RNA	IND	IND	IND
Hymenachne amplexicaulis (Rudge) Nees	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Hymenachne donacifolia (Raddi) Chase	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Hymenachne pernambucensis (Spreng.) Zuloaga	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Hypoxis decumbens L.	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Isachne polygonoides (Lam.) Döll	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Isolepis cernua (Vahl) Roem. & Schult.	IND	IND	IND	IND	RREF	IND	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	RREF
Juncus balticus Willd.	IND	IND	RNA	ALNNA-IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND
Juncus bufonius L.	IND	IND	IND	ALNNA-IND	IND	IND	ALNNAT	RNA	RNA	RNA	IND	IND	RNA	RREF	IND	IND
Juncus capillaceus Lam.	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	IND
Juncus cyperoides Laharpe	IND	IND	RNA	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	ABS
Juncus effusus L.	IND	IND	IND	ALNNA	IND	IND	ALNNAT	RNA	RNA	RNA	RNA	IND	RNA	RNA	RREF	IND
Juncus imbricatus Laharpe	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	ABS
Juncus microcephalus Kunth	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Juncus pallescens Lam.	IND	IND	IND	IND	IND	IND	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	ABS
Juncus tenuis Willd.	ALNNA	RREF	ALNNA	ALNNA	ALNNA	ALNNA	RNA	RNA	RNA	RNA	ALNNA	RREF	RNA	RNA	ALNNA	ALNNA
Justicia laevilinguis (Nees) Lindau	RREF	IND	IND	RNA	IND	RNA	RNA	IND	RNA	RREF	IND	IND	RNA	IND	IND	IND
Kyllinga brevifolia Rottb.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Kyllinga vaginata Lam.	IND	IND	IND	RNA	RREF	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Lasthenia kunthii (Less.) Hook. & Arn.	IND	IND	IND	IND	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Leersia hexandra Sw.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	ALNNA	IND	IND	IND	RNA	IND	IND	IND
Lemna aequinoctialis Welw.	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	ALNCULT	RNA	IND	RNA	IND
Lemna gibba L.	IND	IND	IND	IND	ALNNAT	IND	RNA	ABS	RNA	ABS	IND	IND	RNA	ABS	IND	IND
Lemna minor L.	IND	RNA	IND	IND	ALNNA	RREF	RNA	ABS	IND	ABS	RNA	RREF	RNA	ABS	RNA	ALNNAT
Lemna minuta Kunth	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Lemna valdiviana Phil.	IND	IND	IND	IND	IND	IND	RNA	RNA	IND	ABS	IND	IND	RNA	IND	IND	IND
Leptochlog virgata (L.) P.Beauv.	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Lilaeonsis macloviana (Gand.) A.W. Hill	IND	IND	RNA	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	ABS
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	IND	IND	IND	ALNINV-IND	ALNINV-IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Limnocharis flava (L.) Buchenau	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	RNA	IND	IND	RNA	RNA	RNA	IND
Limosella australis R.Br.	IND	ALNNAT	RNA	IND	RREF	RREF	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	ABS
Ludwigia grandiflora (Michx.) Greuter & Burdet	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	ABS
Ludwigia hexapetala (Hook. & Arn.) Zardini, H.Y. Gu & P.]	ALNINV	IND	ALNNAT-INE	RNA	IND	IND	RNA	RNA	RNA	RNA	ALNNAT	IND	RNA	RNA	RREF	IND
Ludwigia leptocarpa (Nutt.) H.Hara	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Ludwigia octovalvis (Jacq.) P.H.Raven	IND	IND	IND	ALNNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RREF	IND
Ludwigia peploides (Kunth) P.H.Raven	IND	IND	IND	ALNNA-IND	IND	IND	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	IND
Ludwigia peruviana (L.) H.Hara	IND	IND	IND	IND	IND	IND	RNA	ABS	RNA	RNA	RNA	IND	RNA	RNA	IND	IND
Luziola bahiensis (Steud.) Hitchc.	IND	IND	IND	RNA	IND	RNA	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Luziola subintegra Swallen	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Mauritia flexuosa L.f.	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	RREF	RNA	IND	RNA	IND

Mayaca fluviatilis Aubl.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Mayaca madida (Vell.) Stellfeld	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Myriophyllum aquaticum (Vell.) Verdc.	ALNNAT-INI	ALNNAT	ALNNAT-IN	CALNINV-IND	IND	ALNNAT	RNA	IND	RNA	IND	ALNNAT-IN	FALNNAT-INI	RNA	RNA	IND	IND
Myriophyllum quitense Kunth	IND	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	IND
Najas guadalupensis (Spreng.) Magnus	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	RNA	RNA	IND	RNA	RNA	IND	IND
Najas marina L.	IND	IND	IND	RNA	RNA	IND	RNA	IND	IND	RNA	IND	RNA	RNA	RNA	RREF	IND
Nasturtium officinale R.Br.	ALNNAT	ALNNAT	ALNNA	ALNINV	ALNNAT	ALNCULT	ALNNAT	ALNNA	ALNNA	RNA	ALNNA	RREF	RNA	RNA	ALNNA	ALNNAT
Nelumbo nucifera Gaertn.	RNA	RNA	CUL	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	CUL
Nymphaea alba L.	RNA	ALNCULT	ALNNA	ALNINV	RREF	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ALNCULT	ALNCULT
Nymphaea amazonum Mart. & Zucc.	IND	IND	IND	ABS	IND	IND	RNA	IND	ABS	IND	IND	IND	RNA	IND	RNA	ALNNA-IND
Nymphaea ampla (Salisb.) DC.	ABS	IND	IND	ABS	IND	IND	ABS	IND	IND	IND	IND	IND	IND	IND	IND	IND
Nymphaea lotus L.	RNA	RNA	ALNNAT	RNA	ALNNAT	RNA	RNA	ALNCULT	RNA	ALNNAT	RNA	RNA	RNA	ALNCULT	ALNCULT	ALNNAT
Nymphaea mexicana Zucc.	RNA	RNA	RNA	RNA	CUL	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	CUL
Nymphaea micrantha Guill. & Perr.	RNA	RNA	ALNCUL	RNA	ALNCUL	ALNCUL	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ALNCUL
Nymphaea rubra Roxb. ex Andrews	RNA	RNA	ALNCULT	RNA	ALNCULT	ALNCULT	RNA	ALNNAT	RNA	ALNNAT	RNA	RNA	RNA	ALNNAT	RNA	ALNCULT
Nymphoides fallax Ornduff	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ALN
Nymphoides indica (L.) Kuntze	IND	RREF	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Oryza grandiglumis (Döll) Prodoehl	RNA	IND	IND	RNA	IND	RNA	RNA	IND	RNA	RNA	RNA	IND	RNA	RNA	RNA	IND
Oryza latifolia Desv.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Oryza rufipogon Griff.	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	ALNNA	RNA	ALNNA	ALNNA	RNA	RNA	ALNNA	RNA	ALNNA
Oryza sativa L.	RNA	ALNNA	ALNCULT	ALNNA	ALNNA	ALNNA	RNA	ALNNAT	ALNCULT	RNA	RREF	ALNNA	RNA	RNA	ALNCULT	ALNCULT
Oxycaryum cubense (Poepp. & Kunth) Palla	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	IND	ALNINV-IND
Panicum elephantipes Nees ex Trin.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	IND	IND
Panicum grande Hitchc. & Chase	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Panicum hylaeicum Mez	IND	IND	IND	RNA	IND	RNA	RNA	IND	RNA	IND	IND	RREF	RNA	IND	IND	IND
Panicum maximum Jacq.	ALNNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	RNA	ALNNA	ALNNA	ALNNA	ALNNA	ALNNA	RNA	ALNNA	RNA	ALNNA
Panicum repens L.	ALNNA	ALNCULT	ALNINV	RNA	RREF	RNA	RNA	RNA	RNA	RNA	RREF	RNA	RNA	RNA	RREF	ABS
Paspalidium geminatum (Forssk.) Stapf	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Paspalum conjugatum P.J.Bergius	IND	IND	IND	RNA	IND	IND	RNA	IND	ALNNA	IND	IND	IND	RNA	IND	RNA	IND
Paspalum dilatatum Poir.	IND	IND	IND	IND	ALNNA	RNA	RNA	ALNNAT	RNA	ALNNAT	IND	RNA	RNA	ALNNA	IND	ALNNA
Paspalum distichum L.	IND	IND	IND	ALNNA-IND	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Paspalum fasciculatum Willd. ex Flüggé	IND	IND	IND	RNA	IND	IND	RNA	ALNNAT	ALNNA	ABS	IND	IND	RNA	ALNNAT	IND	ALNNAT-IND
Paspalum pallens Swallen	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Paspalum paniculatum L.	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	ALNINV-IND
Paspalum repens P.J.Bergius	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Paspalum vaginatum Sw.	IND	IND	IND	IND	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	ALNINV
Paspalum wrightii Hitchc. & Chase	IND	IND	IND	RNA	IND	RNA	RNA	ABS	RNA	IND	IND	RNA	RNA	ABS	RNA	ALNINV
Passiflora foetida L.	IND	IND	IND	IND	IND	IND	IND	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Persicaria hydropiperoides (Michx.) Small	IND	IND	IND	ALNINV	RNA	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Persicaria punctata (Elliott) Small	ALNNAT	IND	IND	RNA	ALNINV	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Phalaris arundinacea L.	ALNNA	RNA	ALNNA	ALNNA	ALNNA	RNA	ALNNAT	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	ALNNA	ABS
Phragmites australis (Cav.) Trin. ex Steud.	IND	IND	ALNNA	ALNNAT-INI	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	IND	IND
Pistia stratiotes L.	IND	IND	ALNNA-INL) ALNNAT	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Polypogon viridis (Gouan.) Breistr.	ALNNA	ALNNA	RNA	ALNNA	ALNNA	ALNNA	RNA	RNA	RNA	RNA	RNA	ALNNA	RNA	RNA	ALNNA	ALNNA
Pontederia cordata L.	IND	IND	IND	RNA	IND	IND	RNA	ABS	RNA	ABS	IND	RNA	RNA	ABS	IND	IND
Pontederia rotundifolia L.f.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Potamogeton illinoensis Morong	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	ABS
Potamogeton lucens L.	KNA	KNA	RNA	ALN	KNA	KNA	KNA	RNA	KNA	KNA	KNA	KNA	KNA	KNA	KNA	ABS
Potamogeton natans L.	RNA	RNA	RNA	ALN	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ABS

Potentilla anserina L.	ALNINV	RNA	RNA	ALN	RNA	RNA	ALNNAT	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	ABS
Pycreus polystachyos (Rottb.) P.Beauy.	IND	IND	IND	IND	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Pvcreus unioloides (R.Br.) Urb.	IND	IND	IND	RNA	IND	IND	RNA	RNA	RNA	RREF	IND	IND	RNA	IND	IND	IND
Ranunculus aquatilis L.	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA
Rhabdadenia madida (Vell.) Miers	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Rhvnchospora holoschoenoides (Rich.) Herter	IND	IND	IND	RNA	IND	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	IND	IND
Rhynchospora nervosa (Vahl) Boeckeler	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	RNA	IND
Rhynchospora tenuis Link	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	RREF	RNA	IND	IND	IND
Rumex acetosella L.	ALNNA	ALNNA	ALNNA	ALNINV	ALNNA	ALNNA	ALNNAT	RNA	RNA	RNA	RNA	ALNNA	ALNNAT	RNA	ALNNA	ALNNA
Ruppia maritima L.	IND	IND	IND	IND	RREF	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Sagittaria guayanensis Kunth	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Sagittaria montevidensis Cham. & Schltdl.	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	ALNNA
Sagittaria rhombifolia Cham.	IND	IND	IND	IND	IND	RNA	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Sagittaria sagittifolia L.	RNA	RNA	ALNCULT	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA
Salvinia auriculata Aubl.	IND	IND	ALNINV-IND	ALNNA	IND	IND	RNA	IND	IND	IND	IND	RREF	RNA	IND	IND	IND
Sauvagesia erecta L.	IND	IND	IND	IND	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	RNA	IND
Schoenoplectus californicus (C.A.Mey.) Soják	IND	IND	IND	IND	ALNINV-IND	IND	IND	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	ABS
Scleria gaertneri Raddi	IND	IND	ALNNA-IND	RNA	IND	IND	RNA	IND	IND	IND	RREF	IND	RNA	IND	RNA	IND
Setaria parviflora (Poir.) M.Kerguelen	IND	IND	IND	IND	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	ALNINV
Spermacoce verticillata L.	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	IND
Sphagneticola trilobata (L.) Pruski	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Spirodela punctata (G.Mey.) C.H.Thomps.	IND	IND	IND	IND	IND	IND	RNA	ABS	RNA	RNA	IND	IND	RNA	IND	IND	IND
Stachytarpheta indica (L.) Vahl	RNA	IND	IND	RNA	IND	RNA	RNA	IND	RNA	IND	IND	RNA	RNA	IND	RNA	IND
Steinchisma laxum (Sw.) Zuloaga	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Stratiotes aloides L.	RNA	RNA	CUL	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA
Stuckenia filiformis (Pers.) Börner	IND	IND	RNA	IND	RNA	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	ABS
Stuckenia pectinata (L.) Börner	IND	IND	IND	IND	IND	IND	RNA	RNA	IND	RNA	RNA	IND	RNA	RNA	RNA	IND
Stuckenia striata (Ruiz & Pav.) Holub	IND	IND	ABS	IND	RNA	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Syngonanthus caulescens (Poir.) Ruhland	IND	IND	IND	RNA	IND	RNA	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Thalia geniculata L.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	IND	RREF	RNA	IND	IND	IND
Trapa natans L.	RNA	RNA	ALN	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA
Triglochin scilloides (Poir.) Mering & Kadereit	IND	RREF	IND	IND	IND	IND	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	ABS
Typha angustifolia L.	RREF	RREF	ALNNA	ALNNA	ALNINV	RREF	RNA	ABS	RNA	ABS	RNA	RREF	RNA	ABS	RREF	ABS
Typha domingensis Pers.	ALNINV	IND	ALNINV-IND	ALNNAT	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Typha latifolia L.	IND	IND	IND	RNA	ALNINV	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	RNA	ABS
Urena lobata L.	ALNNAT	IND	IND	IND	IND	IND	RNA	IND	ALNINV	IND	ALNINV-IND	ALNINV-IND) RNA	IND	RNA	IND
Utricularia foliosa L.	IND	IND	IND	RNA	IND	IND	RNA	IND	IND	IND	IND	IND	RNA	IND	IND	IND
Utricularia gibba L.	IND	IND	IND	IND	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	IND	IND
Vallisneria americana Michx.	ALNINV	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA	RNA
Veronica anagallis-aquatica L.	IND	ALNNAT	ALNNAT	ALNINV	RNA	RNA	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	IND	ABS
Victoria amazonica (Poepp.) J.C. Sowerby	RNA	IND	IND	RNA	ALNCULT	RNA	RNA	ALNCULT	RNA	IND	RREF	IND	RNA	RNA	RNA	ALNCULT
Victoria cruziana A.D. Orb.	IND	IND	IND	RNA	ALNCULT	RNA	RNA	RNA	RNA	RNA	IND	RNA	RNA	RNA	RNA	ALNCULT
Vigna luteola (Jacq.) Benth.	ALNNAT	IND	ALNNAT	RNA	ALNNAT	IND	RNA	ALNNAT	ALNNAT	IND	ALNNAT	ALNNAT	RNA	IND	IND	ALNNAT
Wolffia brasiliensis Wedd.	IND	IND	ALNNA-IND	IND	IND	IND	RNA	ABS	RNA	RNA	IND	IND	RNA	IND	IND	IND
Wolffiella lingulata (Hegelm.) Hegelm.	IND	IND	IND	RNA	IND	IND	RNA	IND	RNA	RNA	IND	RNA	RNA	IND	IND	IND
Wolffiella oblonga (Phil.) Hegelm.	IND	IND	IND	IND	IND	IND	RNA	RNA	RNA	RNA	IND	IND	RNA	RNA	IND	IND
Wolffiella wetwitschii (Hegelm.) Monod	RNA	IND	IND	RNA	IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND	RNA	IND
Xyris laxifolia Mart.	RNA	IND	IND	ABS	IND	IND	RNA	IND	RNA	IND	IND	IND	RNA	IND	ABS	IND
Zannichellia palustris L.	IND	IND	IND	ALNNAT-INI	. IND	IND	RNA	IND	RNA	IND	RNA	IND	RNA	RNA	IND	IND

B. Records of aquatic plant species in the 16 regions of South America



Figure 1. The map shows the records of aquatic plant species in each of the 16 regions of South America. The records given an idea of the reliability of the floristic inventory of 1,463 plants distributed in the regions. The 16 South American regions considered in the study were defined as follows: (1) Argentina, (2) Bolivia, (3) Brazil, (4) Chile, (5) Colombia, (6) Ecuador, (7) Falklands Islands, (8) French Guiana, (9) Galapagos, (10) Guyana, (11) Paraguay, (12) Peru, (13) South Georgia and South Sandwich Islands, (14) Suriname, (15) Uruguay and (16) Venezuela.

C. Relevant illustrative pictures (for information)



Figure 1. Invasion of Eichhornia crassipes (Sardinia, IT)

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.



Figure 2. An example of the literature used in the data collection for this manuscript, Biodiversity Heritage Library, BHL (https://www.biodiversitylibrary.org/item/97287#page/1/mode/1up)

Vanessa Lucia Lozano Masellis – Invasive alien aquatic plants in South American Inland waters: inventory, prioritisation and distribution models – Tesi di Dottorato in Scienze Agrarie – Curriculum "Monitoraggio e controllo degli ecosistemi agrari e forestali in ambiente mediterraneo" – Ciclo XXX – Università degli Studi di Sassari.