Assessing the invasiveness of alien aroids using modelling techniques and ecological assessments

by

Desika Moodley

Submitted in fulfilment of the academic requirements for the degree of
Doctor of Philosophy in the School of Agricultural, Earth and
Environmental Sciences, University of KwaZulu-Natal,
Westville campus

UNIVERSITY OF
KWAZULU-NATAL

December 2016

As the candidate's supervisor I have approved this thesis for submission.

Signed: _____   Name: _____   Date: _____

Abstract

Biological invasions represent one of the main drivers of the present decline in biodiversity worldwide and are difficult and costly to control. Consequently, identifying which factors allow a small proportion of species to successfully invade is a key area of research in invasion biology and is essential for effective management. In this thesis, I studied invasion patterns of the Araceae family, explored some of their ecological drivers, and unravelled mechanistic relationships that caused species to become successful. There are several emerging generalizations in invasion biology, but often the factors determining invasiveness are group-specific. Therefore the primary aim of this thesis was to establish whether general patterns of invasion biology also applied to Araceae. At a global scale, I found that, similar to other plant families, species with large native ranges and those that have been widely introduced were more likely to become invasive. What is unique to the family is the great diversity of growth forms, some of which are more likely to become invasive than others. I identified nine lineages in the family that have a greater tendency to invasiveness and recommended a precautionary approach be taken for these clades. At a regional scale, I used *Epipremnum aureum* as my case study species, because of the detection of the species in the country, as well as knowledge on its invasive cogener. In the KwaZulu-Natal province of South Africa, I found 78 naturalized *E. aureum* populations and 321 cultivated populations, of which the naturalized populations covered nearly 3 hectares in total. Disturbance played a major role in facilitating invasions and species distribution models indicated that *E. aureum* has a high probability of expanding its current range. Due to the invasion threat of this species, I recommended that all plants outside cultivation be removed. Lastly, I assessed a unique case where a widely planted species, *Monstera deliciosa*, has not yet become a global invader. I explored whether introduction history drives invasiveness in the Monsteroideae subfamily. I found that long residence times and high propagule pressure facilitated invasiveness in this subfamily. This was followed by as a local scale approach to identify factors influencing invasion success. The naturalization of *Monstera deliciosa* was largely driven by anthropogenic effects in Limpopo, South Africa, despite the plants' occurence in suitable habitat. Therefore, I concluded that *M. deliciosa* poses a low

invasion risk to South Africa. Overall, this thesis demonstrated the importance of using a taxonomic group to identify the contribution of multiple factors in the success of invasive species, but that species-specific assessments will still be required for effective management.

Preface

The work described in this thesis was carried out in the School of Sciences, University of KwaZulu-Natal, Westville campus from June 2013 to December 2016, under the supervision of Professor Şerban Procheş and co-supervision of Professor John R. Wilson.

I hereby declare that the entirety of the work contained in this thesis is my own, original work, that I am the sole author thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any degree or diploma to any tertiary institution.

_____   _____

Desika Moodley   Date

Declaration 1 - Plagiarism

I, …………………………………………… declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
   a. Their words have been re-written but the general information attributed to them has been referenced
   b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.

5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed: ………………………………………………………

Declaration 2 - Publications

Publication 1: Moodley, D., Procheş, Ş., Wilson, J.R.U., 2016. A global assessment of a large monocot family highlights the need for group-specific analyses of invasiveness. AoB PLANTS 8, 1–14. (Editor's choice)

Contribution of each author:

DM, ŞP & JRUW: Planning and discussion of the study.

DM: Database compilation, statistical analyses, led the writing.

ŞP & JRUW: Provided comments on the manuscript.

Publication 2: Moodley, D., Procheş, Ş., Wilson, J.R.U. (2017). Assessing and managing the threat posed by *Epipremnum aureum* in South Africa. South African Journal of Botany 109, 178–188

Contribution of each author:

DM, ŞP & JRUW: Planning and discussion of the study.

DM: Data collection, statistical analyses, led the writing.

ŞP & JRUW: Provided comments on the manuscript.

Signed: ……………………………………………………

Poem – Entropy

Sunlight raced towards Earth's embrace,

and in that twilit moment,

love seemed to fill the air.

peace prevailed as sunlight unveiled

the magnificence of mother nature.

life received a borrowed grandeur

sunlight was the enlightening lender.

have you ever seen such a beauty?

as the moment passed, entropy!

the gradual decline into disorder,

with humans circumventing the natural borders

causing unnatural movements of fauna and flora

to regions near and far, opening up pandora.

the sunlight bore witness to such calamities!

silent cries of dying trees filled the air,

leaving mother nature in much despair!

the hands of time sing a song with a constant rhyme

each hand takes away a moment, and never gives it back again,

soon only echoes and silent cries of dying trees will be heard.

the bees will dance no more, the birds will never sing,

the flowers will cease to bloom, the forests will be doomed

wild and scenic rivers will become a remnant,

only then will man be repentant

and as sunlight becomes disasters spotlight,

life will never again receive a borrowed light!

now is the time to step up to the plate,

to conserve Earth's natural habitats, before it's too late!

Acknowledgements

Time flies (especially when you are doing a PhD), but memories last forever. Now, at the end of this journey, it is probably the best time to thank all the people, who made the completion of my PhD possible by providing significant guidance, advice, and encouragement which culminated in a wonderful experience.

First and foremost, I am filled with gratitude to the indivisible invisible frequency (God) that always resonated words of confidence and faith; I offer my profound thankfulness unto He, the Guru perceptor, whom has always guided me; and my sincere thanks and appreciation to my beloved grandmother, mom and brother for their continuous support, patience, and confidence in me.

A heartfelt thank you to my supervisors, Prof. Şerban Procheş and Prof. John Wilson, for their excellent academic guidance, ideas, and comments. Their support and assistance throughout this project has been invaluable.

A special thanks to all my friends for standing by my side when times got rough and and for making me laugh when I didn't even want to smile. All of you have given me the strength to persevere and warmed my heart. I am truly greateful.

Finally, I acknowledge financial support from the South African National Department of Environment Affairs through its funding of the South African National Biodiversity Institute Invasive Species Programme.

For further details see the acknowledgement sections in chapters two and three.

Table of contents

Chapter 1: Introduction

For millions of years the distribution of the global flora and fauna was restricted by natural barriers such as mountains, deserts, rivers, and oceans. Anthropogenic activities have circumvented these barriers and provided a conduit for some species to disperse much farther than they could naturally and subsequently increased the rate and spread of alien species (Hulme, 2009; Meyerson and Mooney, 2007b; Wilson *et al.*, 2009b). As such, biological invasions can broadly be defined by the expansion of a species' geographic range into novel regions. The study of invasion biology has allowed us to progress in our understanding of invasions and our ability to manage them.

Following species introductions, many of the alien species remain innocuous and some eventually die out. For plants, only a small proportion are able to produce self-sustaining populations, and an even smaller proportion are able to spread great distances from their point of introduction (Blackburn *et al.*, 2011a; Williamson, 1996). This small percentage of species has caused significant environmental, economic and social impacts (Levine and D'Antonio, 2003; Mack *et al.*, 2000; Pimentel, 2011). Accordingly, this phenomena has directed some of the key research questions in invasion biology, such as: 1) why do some species become invasive once introduced, while others either fail or remain innocuous; 2) why are some habitats more vulnerable to invasions than other habitats; and 3) how can the knowledge developed in response to these two questions be used to predict invasion patterns, as well as develop effective policies and prioritize the management of biological invasions.

Many hypotheses have been proposed to explain and predict biological invasions. For example, Baker (1965; 1974) discussed the ability of plants to reproduce both sexually and asexually, as well as adapt to environmental stress (i.e. phenotypic plasticity), while Goodwin *et al.* (1999) showed that invasion success was related to plant life form. In addition, higher specific leaf area (Gallagher *et al.*, 2015; Grotkopp and Rejmánek, 2007) and the capability to climb (Paul and Yavitt, 2011) also predispose plant species to invasiveness.

In the same way, not all habitats are equally vulnerable to invasion, and indeed habitats vary in their plant invasion level. Often, invaded habitats are commonly associated with anthropogenic disturbances, however, many invasive alien plants also thrive in natural habitats (Chytrý *et al.*, 2008; Pyšek *et al.*, 2010a; Pyšek *et al.*, 2010b). Disturbance increases invasibility because it eliminates resident species, disrupts species interactions, and increases the amount of available resources such as space, light, water and nutrients, consequently reducing the effects of competition and creating opportunities which an alien species may be able to exploit (Davis *et al.*, 2000; Shea and Chesson, 2002). In addition, favourable climatic factors and the availability of resources such as light, water, and fertile soil also predispose a habitat to invasion (Parepa *et al.*, 2013; Richardson and Pyšek, 2006a; Thuiller *et al.*, 2007).

Some species are, however, not immediately successful at invading. They remain at low numbers for many years (i.e. lag phase) before the population suddenly explodes, turning a quiescent alien species into an invader (Kowarik, 1995; Zenni and Nuñez, 2013). Lag phases can be associated with several factors, such as delayed introduction of a required mutualist (Richardson *et al.*, 2000b), the absence of disturbance events such as fire for fire-dependent species (Geerts *et al.*, 2013), genetic constraints (Ellstrand and Schierenbeck, 2000), climate change (Salo, 2004), and the build up to achieve significant propagule pressure. It is also possible that lag phases are an artefact of sampling effort over time (Cousens and Mortimer, 1995). Consequently, lag phases can vary greatly across species and are difficult to predict.

Numerous studies have shown that aspects of the species' introduction history are also important drivers of plant invasions and therefore should complement studies that are looking at invasiveness. In particular, a greater influx of propagules (i.e. propagule pressure) and a longer time since a species was first introduced into a region (i.e. residence time) often correlates well with successful invasions (Colautti *et al.*, 2006; Lockwood *et al.*, 2005b; Pyšek *et al.*, 2009b; Simberloff, 2009; Wilson *et al.*, 2007). Given these complex drivers of biological invasions, it is evident that understanding these context-dependent effects across species, habitats and spatial scales will provide important insights to develop successful management strategies and ultimately transform invasion biology into a predictive science.

Finally, in order to advance our understanding of invasion patterns and processes we need to consider two other important components for invasion biology research comprising taxonomy and the stages of invasion. Although a combination of traits (some of which have been cited above) has been shown to have high predictive power in identifying drivers of invasiveness, it has not yet been possible to generalize these factors across all but fairly narrow taxonomic groups. This highlights the context-dependent nature of invasions and suggests the need to study invasions using the appropriate taxonomic level. Model groups studied to date have provided important insights, and even though they share similar drivers of invasiveness (e.g. native range size), they also differ in their mechanism associated with invasion success. For instance, the level of susceptibility to the root rot fungus (*Phytophthora*) significantly influenced naturalization success in Proteaceae (Moodley *et al.*, 2013); specific growth forms facilitate vegetative dispersal in Cactaceae which correlates with invasiveness (Novoa *et al.*, 2015); long-distance seed dispersal drives invasiveness in *Pinus* (Richardson, 2006); and the ability of Australian acacias to form effective mutualisms with nitrogen-fixing bacteria and their long-lived seed banks are important for their invasion success (Gibson *et al.,* 2011; Le Maitre *et al.,* 2011)*.*

In addition, since the relative importance of factors influencing invasiveness vary at different stages along the introduction-naturalization-invasion continuum (Figure 1; Gravuer *et al.*, 2008; Lloret *et al.*, 2005a; Pyšek *et al.*, 2009b; Richardson and Pyšek, 2006a; Williamson, 2006), it is important to take into account how different traits play a role at different invasion stages, as failure to do so can obscure the results. Moreover, this integrative line of research (i.e. species traits, habitat characteristics, cognizance of lag phases, introduction history, and invasion stages) using taxonomic groups will provide a greater understanding of the context dependencies of biological invasions.
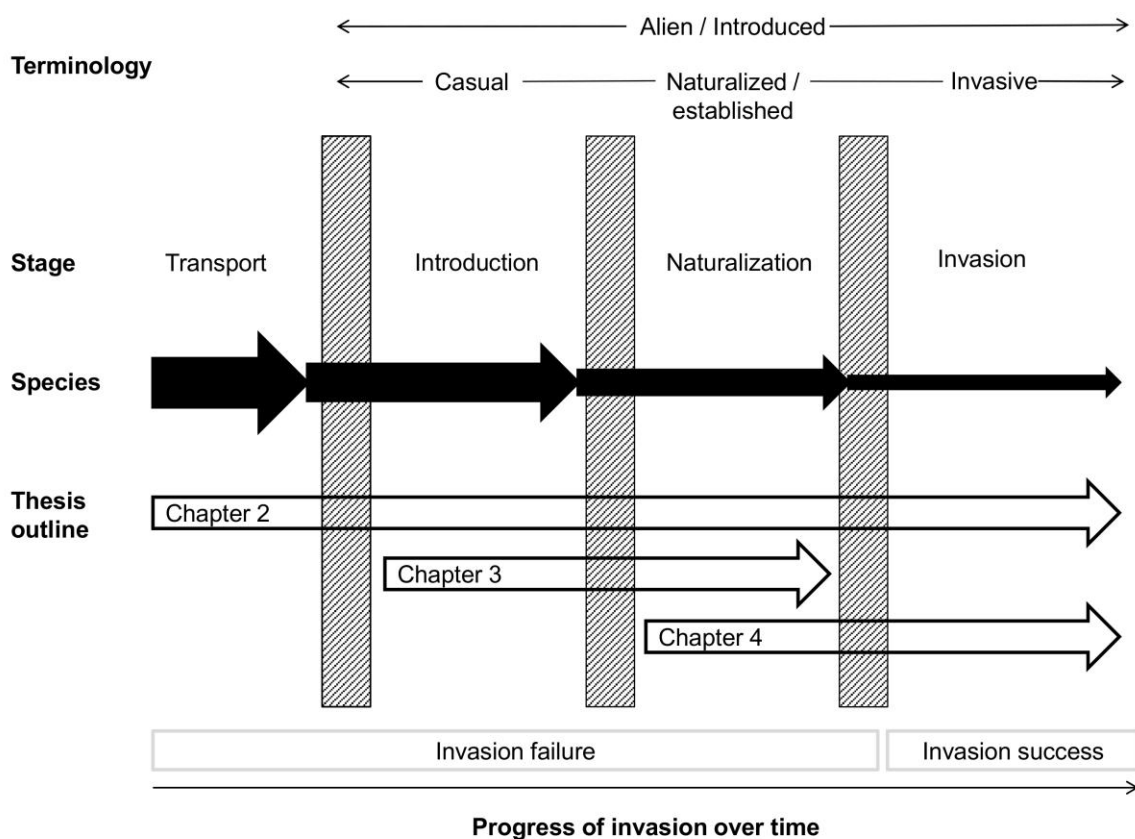
Fig. 1.1. A simplified illustration of the invasion process as a series of distinct stages (i.e. introduction-naturalization-invasion) which a species must transition through in order to successfully invade (adapted from Blackburn *et al.*, 2011a). Species statuses are defined according to the stage they occupy. Alien species refers to those that are intentionally introduced by humans only; casual are those alien species that do not form self-replacing populations thereby depending on repeated introductions; naturalized or established are those alien species that can form self-sustaining populations for at least 10 years for plants without direct human intervention, or despite human intervention; and invasive species are a subset of naturalized species that reproduce in large numbers, spread great distances from the initial point of introduction (i.e. > 100 m; < 50 years for taxa spreading by seeds and 6 m/3 years for taxa spreading vegetatively), and cause impacts to the economy, environment or health (Richardson *et al.*, 2011b). Geographic barriers and survival rates are important for overcoming the introduction stage, whereas overcoming various barriers to reproduction is important for naturalization, and dispersal ability is an important barrier for invasion (Richardson *et al.*, 2000a). These progressive stages are recognized as the introduction-naturalization-invasion (INI)

continnum. Intuitively, a species fails to become invasive if it fails to progress through the barriers at any stage of the invasion process. The stages investigated throughout the thesis are also outlined. The hatched bars represent the various barriers and the black arrows show that the proportion of species that progress from one stage to the next is less than the previous one.

Pinus L. (Richardson, 2006), Australian acacias Mill. (sensu lato, Castro-Díez *et al.*, 2011; Hui *et al.*, 2011; Richardson *et al.*, 2011a), and Proteaceae (Moodley *et al.*, 2013) are model groups of woody plants that have been well studied in invasion biology and generated useful insights on traits that are important for invasiveness. However, much less work has been done on herbaceous plants. For this thesis I chose to explore the Araceae Juss., or the aroid family, as I will argue that this family which contains many well-known species of horticultural importance provides an excellent study group for identifying determinants of species invasiveness and habitat invasibility in herbaceous plants.

THE ARACEAE

The Araceae is recognized as a diverse family of monocotyledonous herbs, the third largest monocotyledon family after orchids and grasses, and the seventh largest of all flowering plants (Mayo *et al.*, 1997; Nauheimer *et al.*, 2012). The uniqueness of this ancient family is evident by its diversity in life forms, morphology and anatomy (Bogner, 1987; Cabrera *et al.*, 2008; Croat, 1990; Cusimano *et al.*, 2011; Grayum, 1990). Species range from gigantic to tiny, from arborescent to floating plants, and they occupy terrestrial, epiphytic and aquatic habitats (although most species in the family are epiphytes and climbers) (Boyce and Croat, 2011 onwards).

The Araceae occur naturally on every continent except for Antarctica, however their distribution is predominantly tropical with two main centers of diversity, tropical Asia and tropical America (Grayum, 1990; Nauheimer *et al.*, 2012). Although the paleotropics comprise more genera, the neotropics comprise most of the total species resulting in regions such as America being extremely species rich (Mayo *et al.*, 1997). Ecologically, the Araceae is an important herbaceous family because of the species' dominance of the understory and inter-canopy herb layer (Croat, 1990; Nadkami *et al.*, 2001), which subsequently also serve as indicators of forest

5

condition. Conversely, the ability to dominate on the ground and in the sub- or inter-canopy may also pre-adapt these species to become invasive. Furthermore, aroids have been used for many decades as a food source and for medicinal purposes, and they are amongst the most horticulturally important families (Acebey *et al.*, 2010; Bienz, 1980; Boyce and Croat, 2011 onwards; Croat, 1994; Kubitzki, 1998). Consequently, comparable to the above-mentioned model groups, many species have had a long history of introduction to regions outside their native ranges.

Because of the increasing interest in this family in horticulture, introduction pathways are increasing. Certain introduction pathways enhance the likelihood of invasive success by ensuring high propagule pressure (Wilson *et al.*, 2009b). Since many Araceae species are popular in horticulture (e.g. ornamentals in gardens and inside homes, decoration in public spaces, and grown in aquariums) which is as an important pathway for invasive alien plants in general (Dehnen-Schmutz *et al.*, 2007b; Reichard and White, 2001; Richardson and Rejmánek, 2011), this group may exhibit different invasion patterns compared to *Pinus* and Australian acacias. *Pinus* and Australian acacia species were mainly planted for forestry purposes worldwide. Although species introduced through horticulture and forestry are categorized under the same introduction pathway (i.e. the importation of a commodity), they differ in several aspects such as their cultivation, trade, propagule pressure, residence time, and probability of escape. Hence, these different human effects may result in different invasion patterns. Additionally, compared to *Pinus* and Australian acacias, only a few Araceae species are currently known to be invasive globally and some others are naturalized. Given these dynamics, important insights can be gleaned from seeking patterns and correlations from a group with large numbers of introduced species over large geographical areas. Consequently, the long history of widespread transfers and planting of Araceae in many parts of the world has created a natural global-scale experiment with many opportunities to explore different aspects of plant invasion biology. This makes the Araceae an excellent taxonomic group for uncovering invasion patterns and processes in herbaceous plants, and this thesis will therefore also supplement studies on model groups.

HYPOTHESES PROPOSED TO EXPLAIN THE INVASION SUCCESS IN ARACEAE

The global problem of biological invasions is multifaceted and therefore, as outlined above, there are several ecological attributes and hypotheses proposed to explain the success of invasive species (Catford *et al.*, 2009). Furthermore, a single theory cannot account for invasion success among all environments since this varies spatially and temporally. Therefore, in order to develop appropriate management plans for invasive species, it is necessary to develop a synoptic view of the dynamic processes involved in the invasion process. In the past, studies mostly focused on species invasiveness and habitat invasibility (Alpert *et al.*, 2000; Rejmánek *et al.*, 2005b; Richardson and Pyšek, 2006a). More recently, an increasing number of studies recognized the importance of quantifying the likelihood of invasion by also focusing on pathways (Essl *et al.*, 2015a; Kumschick *et al.*, 2015a; McGeoch *et al.*, 2016; Puth and Post, 2005). This complementary approach of targeting all three aspects (species, sites and pathways) is necessary to facilitate reactive and proactive management, and develop effective invasion policies.

Species

Given the introduction history of Araceae, as well as a very invasive genus in the family (Lemnaceae), I expect that the tens rule, traits of an ideal weed, propagule pressure, and the residence time hypotheses will play a role in driving species invasiveness at broad and small spatial scales. The tens rule was proposed as the quantitative estimate of the proportion of introduced species becoming invasive (Williamson and Fitter, 1996). As such, I expect to find that 10% of Araceae will be introduced, of which 1 in 10 introduced species will become naturalized and that 1 in 10 of those naturalized species becomes invasive. Several studies have attempted to profile successful invaders by identifying which traits and attributes facilitate their invasion (Baker, 1965; Elton, 1958; Goodwin *et al.*, 1999; Grotkopp *et al.*, 2002; Pyšek *et al.*, 2003; Rejmánek *et al.*, 2005a; van Kleunen *et al.*, 2016). I will attempt to identify traits driving invasiveness within Araceae based on evidence of other successful invaders, as well as data availability.

Propagule pressure, both in space (by widespread distribution and abundant plantings) and/or temporally (by a long history of cultivation) increases the chance of

successful invasions (Lonsdale, 1999; Rouget and Richardson, 2003). Propagules include seeds, seedlings, adult plants and reproductive vegetative fragments. Due to the challenges of measuring propagule pressure, this frequently cited determinant is studied in many different forms in the invasion biology literature. These associated proxy variables encompass propagule abundance, propagule richness and propagule frequency to better understand the processes involved (Ricciardi *et al.*, 2010). In the chapters that ensue I will use the number of introduced regions (i.e. propagule frequency) and the number of stems (i.e. propagule abundance) as proxies for propagule pressure. As a result, I predict that introduced Araceae with widespread dissemination and/or species planted in large numbers will have a higher probability of invasion. One of the most robust generalizations in invasion biology is that the probability of invasion increases with the time since introduction (i.e. residence time or time lag; Hulme, 2003; Kowarik, 1995; Pyšek and Jarošík, 2005). In addition, the importance of residence time is also associated with propagule pressure, because species that were introduced a long time ago are likely to have been introduced many times since their first introduction. In the case of Araceae, I expect that species present in their new ranges for a longer period of time will be naturalized and/or invasive since they had the opportunity to fulfil more life cycles and spread further. On the other hand, given the context dependency of invasions, I also expect to find that propagule pressure and residence time are dependent on optimal site conditions at a local scale.

Sites

The capacity of species to tolerate the abiotic conditions of the site it was introduced in is another predictor coinciding with successful establishment. Hypotheses attributing invasion success to environmental factors are often based on fluctuation in resource availability and anthropogenic or natural disturbances (Funk and Vitousek, 2007; Levine and D'Antonio, 1999; Seabloom *et al.*, 2003). Resource availability can fluctuate following an increase in resource supply (e.g. water, light and nutrients) which will facilitate invasion success in the new site as long as the alien species can outcompete the resident species (Blumenthal, 2006; Davis *et al.*, 2000). In addition, natural and anthropogenic disturbances increase resource levels which give alien species a better chance of success at survival and establishment (Mack *et al.*, 2000). Therefore, I predict that successful Araceae will comprise of

species that are in the right place (i.e. suitable environmental conditions) at the right time (i.e. have access to available resources and also occupy disturbed areas which increase resource levels and decrease competition).

Pathways

Recent studies have highlighted the significance between pathways of introduction and invasion success (Essl *et al.*, 2015a; Faulkner *et al.*, 2016; Perrings *et al.*, 2005; Pyšek *et al.*, 2011). Prioritizing pathways uses information on vectors and routes of introduced species, thereby ensuring pre-border management and regulation of high-risk invasion pathways, as well as post-border management and legislation (Carlton and Ruiz, 2005; Hulme *et al.*, 2008). Hulme *et al.* (2008) outlined six principal pathways which was later refined into categories by Essl *et al.* (2015a). These six principal pathway categories comprise intentional release, escape from containment, transport as contaminant, transport as a stowaway, spread through corridors, and spread through unaided natural dispersal. Because Araceae are mainly introduced for horticultural purposes, I postulate that intentional releases and escape from containment are the main pathways since these include ornamental species.

THESIS STRUCTURE

This thesis comprises five chapters, three of which have been written in manuscript-style and are intended for publication in peer-reviewed journals. The chapters are structured as follows:

Chapter 1 provides a general introduction to biological invasions and includes a background, some of the research conducted, gaps in our knowledge, and objectives of this thesis.

Studies have shown that the determinants of naturalization and invasion success vary across taxonomic groups, invasion stages, and spatial scales. In chapter 2, I explore this variation for the Araceae family, a group remarkable through its life form diversity and horticultural importance globally. To do this, I created a species inventory of the family, described the invasion status of all species, identified factors influencing introduction, naturalization and invasion success and tested whether this

varied for different life forms, and then predicted which species will become invasive in future.

Chapter 3 explores the invasion risk posed by *Epipremnum aureum* in South Africa, a species that was recently recognized as a potential invader in the country, but a well-known invader in tropical regions. Here, I demarcate the species' current distribution in South Africa, describe factors driving naturalization, identify potential areas suitable for spread that are currently unoccupied by the species, and finally provide management options.

In chapter 4, I examine a paradoxical case in invasion biology; a popular horticultural species (*Monstera deliciosa*) that has been grown in most of the warm countries of the world for many decades, however it is not yet a major invader. Hence, this species does not conform to the established invasion theories. To unravel the mechanisms and factors behind the dynamics of this poorly studied species, I first assess whether attributes related to introduction history influences the invasion status of the Monsteroideae subfamily globally, subsequently I quantify the invasion risk of Monsteroideae in South Africa, and finally, at a local scale (i.e. using the only known invasive population in the Limpopo province) I describe the potential conditions under which *M. deliciosa* can become naturalized.

Chapter 5 provides a synthesis of the results of the three research studies and highlights the knowledge added to invasion biology by assessing the practicality of using a taxonomic group to explain invasion successes and failures. I emphasize the effectiveness of this approach in revealing the mechanisms of both successful and failed invasions, and encourage future comparisons within taxonomic groups.

THESIS OBJECTIVES

While research to date has described a multitude of factors influencing biological invasions (Hui and Richardson, 2017; Kolar and Lodge, 2001; Pyšek and Richardson, 2007; Richardson and Pyšek, 2012; van Kleunen *et al.*, 2015; Wilson *et al.*, 2017), the conclusions that can be drawn are limited by the lack of taxonomic group studies that identify drivers affecting invasion successes and failures. Using Araceae as a test case, this thesis examines the role of drivers of invasiveness (i.e.

the inherent ability of a species to invade) and invasibility (i.e. the susceptibility of the habitat to being invaded) in relation to the different invasion stages, spatial scales and introduction pathways. This approach will also account for the taxonomic bias in Araceae regarding general invasion principles in an herbaceous plant group since the invasion biology aspect is currently understudied. The overall goal of my research is to conduct a global assessment of the invasion processes driving Araceae invasions and to examine these processes at multiple spatial scales (Fig. 1.2).
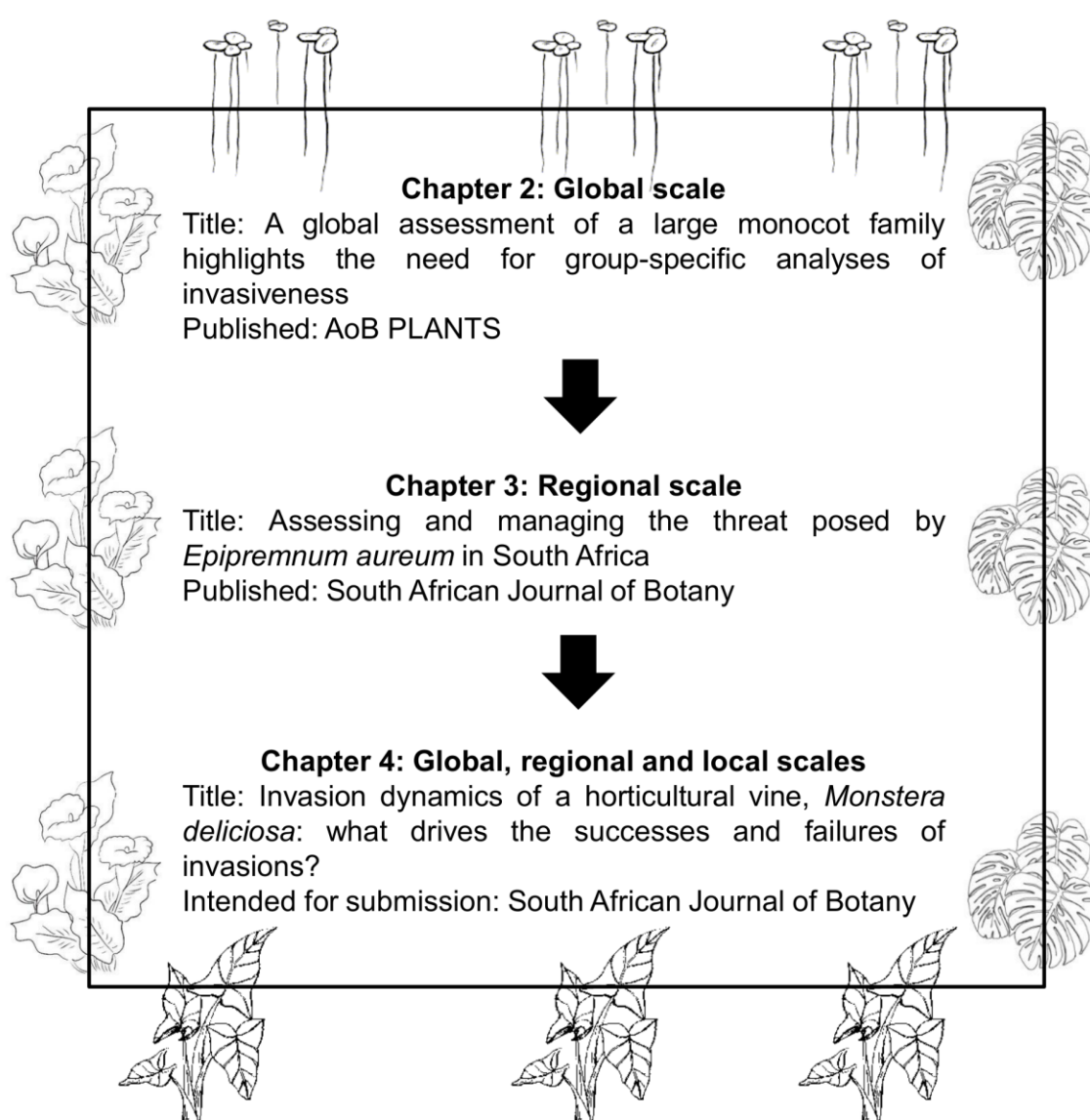
Chapter 2: Global scale
Title: A global assessment of a large monocot family highlights the need for group-specific analyses of invasiveness
Published: AoB PLANTS

Chapter 3: Regional scale
Title: Assessing and managing the threat posed by *Epipremnum aureum* in South Africa
Published: South African Journal of Botany

Chapter 4: Global, regional and local scales
Title: Invasion dynamics of a horticultural vine, *Monstera deliciosa*: what drives the successes and failures of invasions?
Intended for submission: South African Journal of Botany

Fig. 1.2. The titles of each chapter, the associated spatial scales studied and the journal where it was published or submitted. The box encapsulating the chapters

symbolizes the unique taxonomic group used, which ranges from tiny floating aquatic plants to forest climbers and tuberous plants.

My specific research questions were:

1. What are the suites of factors underlying invasion success in Araceae?

2. Does *Epipremnum aureum* pose an invasion threat in South Africa?

3. Why is the world's most common house plant (*Monstera deliciosa*) not yet a major invader?

REFERENCES

Acebey A, Krömer T, Maass BL and Kessler M (2010) Ecoregional distribution of potentially useful species of Araceae and Bromeliaceae as non-timber forest products in Bolivia. Biodiversity and Conservation 19: 2553-2564

Alpert P, Bone E and Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52-66

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG and Stebbins GL (eds) The genetics of colonizing species, Academic Press, New York, USA

Baker HG (1974) The evolution of weeds. Annual Review of Ecology and Systematics 5: 1-24

Bienz DR (1980) The why and how of home horticulture. W. H. Freeman and Co., San Francisco

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

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9: 887-895

Bogner J (1987) Morphological variation in Aroids. Aroideana 10: 4-16

Boyce PC and Croat TB (2011 onwards) The Überlist of Araceae, Totals for published and estimated number of species in aroid genera.

Cabrera LI, Salazar GA, Chase MW, Mayo SJ, Bogner J and Davila P (2008) Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. American Journal of Botany 95: 1153-1165

Carlton JT and Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ and Waage JK (eds) Invasive alien species: a new synthesis, pp 36-58, Island Press, Washington

Castro-Díez P, Godoy O, Saldaña A and Richardson DM (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Diversity and Distributions 17: 934-945

Catford JA, Jansson R and Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22-40

Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L and Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89: 1541-1553

Colautti RI, Grigorovich IA and MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Cousens R and Mortimer M (1995) Dynamics of weed populations. Cambridge University Press, 348 pp

Croat TB (1990) Ecology and life forms of Araceae. Aroideana 11: 4-55

Croat TB (1994) The use of New World Araceae as drug plants. Japanese Journal of Botany 69: 185-203

Cusimano N, Bogner J, Mayo SJ, Boyce PC, Wong SY, Hesse M, Hetterscheid WLA, Keating RC and French JC (2011) Relationships within the araceae:

comparison of morphological patterns with molecular phylogenies. American Journal of Botany 98: 654-668

Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528-534

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224-231

Ellstrand NC and Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences of the United States of America 97: 7043-7050

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso A-C, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JRU, Zenetos A and Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769-782

Faulkner KT, Robertson MP, Rouget M and Wilson JRU (2016) Understanding and managing the introduction pathways of alien taxa: South Africa as a case study. Biological Invasions 18: 73-87

Funk JL and Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446: 1079-1081

Gallagher RV, Randall RP and Leishman MR (2015) Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. Conservation Biology 29: 360-369

Geerts S, Moodley D, Gaertner M, Le Roux JJ, McGeoch MA, Muofhe C, Richardson DM and Wilson JRU (2013) The absence of fire can cause a lag phase-the invasion dynamics of *Banksia ericifolia* (Proteaceae). Austral Ecology 38: 931-941

Gibson MR, Richardson DM, Marchante E, Marchante H, Rodger JG, Stone GN, Byrne M, Fuentes-Ramírez A, George N, Harris C, Johnson SD, Le Roux JJ, Miller JT, Murphy DJ, Pauw A, Prescott MN, Wandrag EM and Wilson JRU (2011) Reproductive biology of Australian acacias: important mediator of invasiveness? Diversity and Distributions 17: 911-933

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

Gravuer K, Sullivan JJ, Williams PA and Duncan RP (2008) Strong human association with plant invasion success for Trifolium introductions to New Zealand. PNAS 105: 6344-6349

Grayum MH (1990) Evolution and phylogeny of the Araceae. Annals of the Missouri Botanical Garden 77: 628-697

Grotkopp E and Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. American Journal of Botany 94: 526-532

Grotkopp E, Rejmanek M and Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. The American Naturalist 159: 396-419

Hui C and Richardson DM (2017) Invasion dynamics, Oxford, 384 pp

Hui C, Richardson DM, Robertson MP, Wilson JRU and Yates CJ (2011) Macroecology meets invasion ecology: linking the native distributions of Australian acacias to invasiveness. Diversity and Distributions 17: 872-883

Hulme PE (2003) Biological invasions: winning the science battles but losing the conservation war? Oryx 37: 178-193

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10-18

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W and Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45: 403-414

Kolar CS and Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204

Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek P, Prach K, Rejmánek M and Wade M (eds) Plant invasions, general aspects and special problems, pp 15-38, SPB Academic Publishers, Amsterdam, Netherlands

Kubitzki K (1998) The Families and genera of vascular plants. Springer, 511 pp

Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer G, Vilà M and Nentwig W (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. Journal of Applied Ecology 52: 552-561

Le Maitre DC, Gaertner M, Marchante E, Ens E-J, Holmes PM, Pauchard A, O'Farrell PJ, Rogers AM, Blanchard R, Blignaut J and Richardson DM (2011) Impacts of invasive Australian acacias: implications for management and restoration. Diversity and Distributions 17: 1015-1029

Levine JM and D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conservation Biology 17: 322-326

Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26

Lloret F, Médail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon P and Hulme PE (2005) Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology 93: 512-520

Lockwood JL, Cassey P and Blackburn TM (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223-228

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536

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

Mayo SJ, Bogner J and Boyce PC (1997) The genera of Araceae. Royal Botanic Gardens, Kew, 370 pp

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C and Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299-314

Meyerson LA and Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5: 199-208

Moodley D, Geerts S, Richardson DM and Wilson JRU (2013) Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. PLoS ONE 8: e75078

Nadkami NM, Mewin MC and Niedert J (2001) Forest canopies, plant diversity. Encyclopedia of Biodiversity 3: 27-40

Nauheimer L, Metzler D and Renner SS (2012) Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. New Phytologist 95: 938-950

Novoa A, Le Roux JJ, Robertson MP, Wilson JRU and Richardson DM (2015) Introduced and invasive cactus species: a global review. AoB PLANTS 7: plu078

Parepa M, Fischer M and Bossdorf O (2013) Environmental variability promotes plant invasion. Nature Communications 4: 1604

Paul GS and Yavitt JB (2011) Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. Botanical Review 77: 11-30

Perrings C, Dehnen-Schmutz K, Touza J and Williamson M (2005) How to manage invasive species under globalization. Trends in Ecology & Evolution 20: 212-215

Pimentel D (2011) Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton

Puth LM and Post DM (2005) Studying invasion: have we missed the boat? Ecology Letters 8: 715-721

Pyšek P, Bacher S, Chytrý M, Jarošík V, Wild J, Celesti-Grapow L, Gassó N, Kenis M, Lambdon PW, Nentwig W, Pergl J, Roques A, Sádlo J, Solarz W, Vilà M and Hulme PE (2010a) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. Global Ecology and Biogeography 19: 317-331

Pyšek P, Chytrý M and Jarošik V (2010b) Habitats and land use as determinants of plant invasions in the temperate zone of Europe. Oxford University Press, 66-79 pp

Pyšek P and Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit (ed) Invasive plants: ecological and agricultural aspects, pp 77-96, Birkhäuser Basel, Switzerland

Pyšek P, Jarošík V and Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. PLoS ONE 6: e24890

Pyšek P, Krivánek M and Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90: 2734-2744

Pyšek P and Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological Invasions, pp 97-125, Springer, Berlin.

Pyšek P, Sadlo J, Mandak B and Jarošík V (2003) Czech alien flora and the historical pattern of its formation: what came first to Central Europe? Oecologia 135: 122-130

Reichard SH and White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103-113

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ and Grotkopp E (2005a) Ecology of invasive plants: state of the art. In: Mooney HA, Mack RM, McNeely JA, Neville L, Schei P and Waage J (eds) Invasive alien species: a new synthesis, pp 104-161, Island Press, Washington, DC

Rejmánek M, Richardson DM and Pyšek P (2005b) Plant invasions and invasibility of plant communities. In: van der Maarel E (ed) Vegetation Ecology, pp 332-355, Blackwell Publishing, Oxford

Ricciardi, A., Jones, L. A., Kestrup, Å. M. and Ward, J. M. (2010) Expanding the propagule pressure concept to understand the impact of biological invasions, in fifty years of invasion ecology: the legacy of Charles Elton (ed D. M. Richardson), pp 225-235, Wiley-Blackwell, Oxford, UK

Richardson D and Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30: 409-431

Richardson D, Pyšek P, Rejmánek M, Barbour M, Panetta F and West C (2000a) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93-107

Richardson D and Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. Diversity and Distributions 17: 788-809

Richardson DM (2006) Pinus: a model group for unlocking the secrets of alien plant invasions? Preslia 78: 375-388

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ and Rejmánek M (2000b) Plant invasions - the role of mutualisms. Biological Reviews 75: 65-93

Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ and Wilson JRU (2011a) Human-mediated introductions of Australian acacias – a global experiment in biogeography. Diversity and Distributions 17: 771-787

Richardson DM and Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383-396

Richardson DM, Pyšek P and Carlton JT (2011b) A compendium of essential concepts and terminology in invasion ecology. Wiley-Blackwell, Oxford, 409-420 pp

Rouget M and Richardson DM (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. The American Naturalist 162: 713-724

Salo LF (2004) Population dynamics of red brome (*Bromus madritensis* subsp *rubens*): times for concern, opportunities for management. Journal of Arid Environments 57: 291-296

Seabloom EW, Borer ET, Boucher VL, Burton RS, Cottingham KL, Goldwasser L, Gram WK, Kendall BE and Micheli F (2003) Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications 13: 575-592

Shea K and Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170-176

Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40: 81-102

Thuiller W, Richardson DM and Midgley GF (2007) Will climate change promote alien plant invasions? Berlin Heidelberg: Springer-Verlag, 197-211 pp

van Kleunen M, Dawson W and Maurel N (2015) Characteristics of successful alien plants. Molecular Ecology 24: 1954-1968

van Kleunen M, Dawson W and Maurel N (2016) Characteristics of successful alien plants. In: Barrett SCH, Colautti RI, Dlugosch KM and Rieseberg LH (eds) Invasion genetics: the Baker and Stebbins legacy, John Wiley & Sons, Chichester, UK

Williamson M (1996) Biological invasions. Chapman and Hall, London

Williamson M (2006) Explaining and predicting the success of invading species at different stages of invasion. Biological Invasions 8: 1561-1568

Williamson M and Fitter A (1996) The varying success of invaders. Ecology 77: 1661-1666

Wilson JR, Panetta FD and Lindgren C (2017) Detecting and responding to alien plant incursions. Cambridge University Press, 286 pp

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ and Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution 24: 136-144

Wilson JRU, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L and Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13: 11-22

Zenni RD and Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122: 801-815

Chapter 2: A global assessment of a large monocot family highlights the need for group-specific analyses of invasiveness

ABSTRACT

Significant progress has been made in understanding biological invasions recently and one of the key findings is that the determinants of naturalization and invasion success vary from group to group. Here we explore this variation for one of the largest plant families in the world, the Araceae. This group provides an excellent opportunity for identifying determinants of invasiveness in herbaceous plants, since it is one of the families most popular with horticulturalists, with species occupying various habitats and comprising many different life forms. We first developed a checklist of 3,494 species of Araceae using online databases and literature sources. We aimed to determine whether invasiveness across the introduction-naturalization-invasion continuum is associated to particular traits within the family, and whether analyses focused on specific life-forms can reveal any mechanistic correlates. Boosted regression tree models were based on species invasion statuses as the response variables and traits associated with human use, biological characteristics, and distribution as the explanatory variables. The models indicate that biological traits such as plant life form and pollinator type are consistently strong correlates of invasiveness. Additionally, large scale drivers such as the number of native floristic regions and numbers of introduced regions are also influential at particular stages in the invasion continuum. We used these traits to build a phenogram showing groups defined by the similarity of characters. We identified nine groups that have a greater tendency to invasiveness (including *Alocasia*, the Lemnoideae and *Epipremnum*). From this we propose a list of species that are not currently invasive for which we would recommend a precautionary approach be taken. The successful management of plant invasions will depend on understanding such context-dependent effects across taxonomic groups, and across the different stages of the invasion process.

KEYWORDS: Araceae, biological invasions, boosted regression trees, invasiveness, predictions, stages of invasion, traits.

INTRODUCTION

Trade and transport of goods by humans have connected regions across the globe (Hulme, 2009; Pyšek *et al.*, 2010c). These pathways break down geographic barriers which results in thousands of species being introduced outside their native ranges (Pyšek *et al.*, 2011; Wilson *et al.*, 2009a). Of the introduced species, some are able to reproduce and form self-replacing populations to become naturalized but only a small subset progress to become invasive (Blackburn *et al.*, 2011b; Lockwood *et al.*, 2005a; Richardson *et al.*, 2000c; Williamson and Fitter, 1996). Identifying why some species become invasive in the introduced range while others do not, is one of the most important but challenging questions in invasion ecology. By improving our understanding of the drivers linked to biological invasions we can also develop better management practices and predict potential invasions.

The conceptualized invasion process comprises a series of barriers which a species must overcome to become naturalized and invasive in the introduced range (Blackburn *et al.*, 2011b; Richardson *et al.*, 2000c). A general understanding over the last several decades is that invasive species possess particular traits which allow them to overcome the invasion barriers in the introduced range. In the literature, species traits such as rapid growth rates and high reproductive output (Grotkopp and Rejmánek, 2007; Pyšek and Richardson, 2007; van Kleunen *et al.*, 2010), as well as, their introduction history, such as high propagule pressure and a long residence time (Pyšek *et al.*, 2009b; Simberloff, 2009) have been shown to be important determinants of invasiveness, but their relative importance varies across studies. The likelihood of invasiveness has also been predicted by attributes of the native range, such as large range sizes, and environmental similarity with the introduced range (Guisan and Thuiller, 2005; Hui *et al.*, 2011). In addition, different traits become important at different stages of the invasion process (Richardson and Pyšek, 2012). For example, a large proportion of the alien plants have been introduced by humans over many years via the horticultural pathway, and this facilitates invasions through high propagule pressure and long residence times (Dehnen-Schmutz and Touza, 2008; Lambdon *et al.*, 2008; Pyšek *et al.*, 2009b).

Although there are several hypotheses explaining traits driving invasiveness, identifying a general suite of traits has proved difficult (Jeschke *et al.*, 2012;

Richardson and Pyšek, 2006b). To date, empirical evidence shows that different sets of traits become important in different situations and the determinants of invasiveness are context-dependent (e.g. Funk, 2013; Moodley *et al.*, 2013; Prinzing *et al.*, 2002; Pyšek *et al.*, 2009a; Rejmánek, 1996; Thompson *et al.*, 1995; van Kleunen *et al.*, 2010). Furthermore, while some species perform better with the predicted invasive traits, it is not a feature shared by all invasive species (Alpert *et al.*, 2000; Lloret *et al.*, 2005b; Richardson and Pyšek, 2006b; Tecco *et al.*, 2010). One line of reasoning is that invasive species are associated with invasion syndromes. For example, invasion success may be specific to particular taxonomic groups, habitats or species life history traits (Kueffer *et al.*, 2013; Perkins and Nowak, 2013; Pyšek *et al.*, 2012). Therefore, instead of trying to identify general trends between invasive and non-invasive species across a wide range of taxa, it would be ideal to conduct in-depth case studies within taxonomic groups.

Araceae, also known as the arum or aroid family, is one of the oldest and the third largest monocotyledonous family in the world, after orchids and grasses (Mayo *et al.*, 1997; Nauheimer *et al.*, 2012). A unique feature of all species in this family is that their inflorescences consist of a spadix and a spathe (Chartier *et al.*, 2014). Aroids mostly occur in the tropics where they are concentrated in Southeast Asia, tropical America and the Malay Archipelago, and they comprise diverse life forms which occupy a wide range of habitats such as aquatic, terrestrial and ephiphytic (Cabrera *et al.*, 2008; Grayum, 1990; Mayo *et al.*, 1997). In addition, aroids have been used for decades as a food source, for medicinal purposes and in horticulture (Croat, 1994; Kubitzki, 1998; Mayo *et al.*, 1997). Given their large diversity and distribution, as well as their long history of introduction, Araceae serves as an excellent taxonomic group for identifying determinants of invasiveness in herbaceous plants.

In this study, we focused on introduction dynamics, characteristics of species' native ranges and biological traits to identify correlates of invasiveness within the Araceae family. Given that there are a variety of life-forms in Araceae, we hypothesized that when all species were analysed together, the only factors that would be significantly correlated to invasiveness would be factors seen to have a consistent influence across previously studied groups (e.g. native range size). However, repeating the analyses separately for different life forms would reveal specific mechanistic

correlates of invasiveness. Our objectives were therefore to: (1) create a species inventory using databases and literature sources, (2) describe the invasion status of all species, (3) identify which factors (native range characteristics, introduction dynamics and biological traits), influence introduction, naturalization and invasion success and whether this varied for different life forms, and (4) predict which species will become invasive in future.

METHODS

Global aroid database

Currently, there are no global databases listing all species belonging to Araceae. However, recent publications by Boyce and Croat (2011 onwards) provide the number of published and estimated species for each genus. This key resource gave us an initial idea of the aroid taxonomy. In order to create a comprehensive species inventory which includes data on accepted genera, species and synonyms, we surveyed a wide range of online databases (eMonocot, International aroid society, The Plant List, USDA Germplasm Resources Information Network, and World Checklist of Selected Plant Families). Given the large number of estimated and undescribed species in this family, it is likely there are aroid species that we did not include in our list.

Species status

The status of introduced, naturalized and invasive species is described in a wide variety of sources (e.g. on the internet, in published and unpublished literature). Since the criteria for defining naturalized and invasive species differ across studies, it is important to use reliable sources (Falk-Petersen *et al.*, 2006). We used multiple sources which contain a broad range of taxa, habitats and ecosystem types. This included 1) online databases (Atlas of living Australia, Calflora, Center for invasive species and ecosystem health, DAISIE, eMonocot, FloraBase, GBIF, GCW, GISD, HEAR, Invasive species of Japan, Randall (2007), and The PLANTS database), 2) published literature (New Zealand naturalized plant checklist), and 3) expert opinion (Haigh, A., Köster, N., Li, R., Seznec, G., Boyce, P., pers.comm.).

Determinants of invasiveness

Explanatory variables related to biological traits, biogeographical factors and human usage were selected to predict invasiveness (Table 2.1). We used these traits and factors because they were shown to be important drivers of invasiveness in other taxonomic groups such as Australian acacias (Castro-Díez *et al.*, 2011; Gibson *et al.*, 2011), Cactaceae (Novoa *et al.*, 2015), pines (Zenni and Simberloff, 2013), and Proteaceae (Moodley *et al.*, 2013). Binary response variables were categorized into three groups: non-introduced vs introduced (but not naturalized) species; introduced (but not naturalized) vs naturalized (but not invasive) species; and naturalized (but not invasive) vs invasive species. These groupings describe the stages that species need to successfully transition through to become invasive (Blackburn *et al.*, 2011b).

Table 2.1. Summary of traits used as explanatory variables in the analyses for identifying potential drivers of invasiveness in Araceae. The number of species is indicative of available data in terms of the listed traits (out of a total of 3,494 species). The range and median values for integer variables are shown in parentheses.

Trait	Levels	Number of species	Type of variable
Introduction dynamics	Use (food source; medicine; fibre production; horticulture; agroforestry; phytoremediation)	546	Categorical
	Total number of uses	546	Integer (1-5;1)
	Number of introduced regions (proxy for propagule pressure)	514	Integer (1-50;1)
Native range	34 floristic native regions classified according to Ronald Good (1974)	3490	Categorical, binary
	Total number of native regions (proxy for range size)	3490	Integer (1-31;1)
	Habitat (desert & xeric shrubland; mediterranean forests, woodland and scrub; temperate mixed forest; tropical dry forest; tropical moist forest)	3494	Categorical
Biological traits	Pollinator type (bees; beetles; flies; combination)	3250	Categorical

Flower sexuality (bisexual; unisexual)	3470	Categorical, binary
Regeneration mechanism (seed; vegetative; both)	444	Categorical
Life form chamaephyte; epiphyte; geophyte; helophyte; hemicryptophyte; hemiepiphyte; hyrdophyte; lithophyte; phanerophyte)	3426	Categorical

Statistical analyses

All analyses were performed in the R software version 2.15.1 (R Development Core Team, 2012). We used boosted regression trees (BRTs) to assess the relationship of the explanatory variables with the three transition stages, first using all species belonging to Araceae, followed by models developed for particular life forms. The BRT models were fitted using the 'gbm.step' function from the gbm package version 1.6-3.2 (Ridgeway, 2012).

Boosted regression trees are an advanced machine learning technique that applies an iterative method which sequentially builds multiple simple models, using the residuals from each subset of data during model fitting, to produce one ensemble model (Elith *et al.*, 2008; Friedman, 2001). This technique improves the models' predictive performance (Elith *et al.*, 2006). Among some of the advantages of this technique are that it can be fitted to a variety of response types (e.g. Gaussian, Poisson and binomial), it handles complex interactions between variables more efficiently than traditional methods (i.e. generalized linear models), it identifies important predictor variables, and it addresses issues like missing data and outliers (Elith *et al.*, 2008; Friedman, 2002).

Elith *et al.* (2008) provide details on selecting optimal settings for model fitting. These settings include the learning rate (shrinkage parameter that determines the contribution of each tree to the growing model) and tree complexity (specifies the number of nodes on each tree which controls whether interactions are fitted) which must be adjusted to produce a model comprising at least 1000 trees. BRT results include a measure of the comparative strength of association between the response variable and predictor variables (i.e. percentage deviance explained), and a cross-

validation coefficient (CV) which indicates the degree to which the model fits withheld data.

For this study, we first built preliminary models for each stage of the invasion continuum using all the predictor variables listed in Table 2.1 so that we could identify those with the greatest predictive contributions and reduce the overall number of variables in our analyses. The models were built with the default 10-fold cross-validation. The relative influence of predictor variables are determined by how often a variable was selected for splitting, weighted by the improvement of the models results (Elith *et al.*, 2008). From these results, we only kept predictors that contributed at least 5% to the models. From those, we performed a correlation test using Kendall's rank correlation to remove correlated variables ($r^2 > 0.65$); however all variables conformed to the correlation criterion. The models that were developed for particular life forms were only run for the introduction stage because of small datasets.

Boosted regression tree model calibration is prone to overfitting, and there are several ways to reduce this behaviour. A key approach of the model building process is to use validation processes which require a proportion of the dataset to be withheld. Here, cross-validation was performed using 75% of the data for training the model and the remaining 25% for testing. We used the caret package, version 6.0-24 (Kuhn, 2014), which creates random training and test sets while stratifying by the y variable. To evaluate model performance we used the average percentage deviance explained and the average cross-validation area under the receiver operating characteristic (AUC). Hosmer and Lemeshow (2000) state that an AUC value between 0.7–0.8 can be regarded as an acceptable model performance, 0.8–0.9 is excellent and higher than 0.9 is considered outstanding. A value of 0.5 or lower indicates predictions are worse than random. Due to the relatively low number of invasive Araceae, we could not fit training and testing datasets for the invasion model. Therefore, we only used 10-fold CV for model development and the cross-validation AUC-value for evaluation (Elith *et al.*, 2008). CV provides a means for testing the model on withheld portions of data, while still using the full data set at some stage to fit the model. The optimal parameter settings that were used in the final models are presented in Table 2.2.

Lastly, using predictors that met the BRT criteria (i.e. predictors that contributed at least 5% to the model) we either built generalized linear models with binomial errors, or used independent t-tests. This step provided insight into the individual explanation potential of each variable.

Table 2.2. Optimal parameter settings used in calibrating the boosted regression trees that produced the best performing introduction-naturalization-invasion models. To reduce overfitting, we used cross-validation which was performed by splitting 75% of the data for training the model and 25% for testing. We tested various learning rates (0.1–0.0005), bag 10 fractions (0.1–0.8) and levels of tree complexity (1–5). By trial-and-error we determined the most effective algorithm parameters for our dataset which is depicted below.

	Introduction Model	Naturalization Model	Invasion Model
Sample size (*n*):			
Full dataset	3,494	514	46
Training Data	2,621	386	–
Test Data	873	128	–
Parameters:			
Learning rate	0.001	0.001	0.001
Tree complexity	3	3	3
Bag Fraction	0.5	0.5	0.75

Predicting potentially invasive species

Using published literature, the first step was to examine the family tree and only select monophyletic groups. This selection controlled for phylogenetic effects as best as possible. Given that very few genera have published species level phylogenies, and most genera contain only non-introduced species, we decided to only include genera with known invasive species records. However, most of the invasive genera also lacked complete species level phylogenies. Selecting groups with invasive genera was important as it allowed inferring potentially invasive species in a more insightful manner (i.e. the selected groups comprised traits that are already known to confer invasiveness). In addition, it is assumed that species that have the potential to become invasive will be ones that 1) have relatives that are invasive, and 2) have

similar traits as invasive species. These two assumptions were used to formulate criteria to shortlist genera that have a known history of invasiveness.

Second, using the results from the BRT analyses, we scored species on traits that have already been shown to facilitate naturalization and invasion success in Araceae (Appendix 1). Following species scoring, we removed uninformative character states from the matrix. Finally, we constructed the phenograms using Jaccard's index and the unweighted pair group method with arithmetic mean (UPGMA) implemented in the Freetree software version 0.9.1.50 (Pavlicek *et al.*, 1999) which ranked species based on their overall similarity of characters. The phenograms clustered species based on the statistical similarity of their traits and also reflect evolutionary relatedness since only monophyletic groups were selected (see above). This allowed us to match species clusters with their associated invasion status. We used this approach as a tool to predict species that are not yet invasive but potentially pose an invasion risk.

RESULTS

Global aroid list

The Araceae database comprises 115 genera with 3,494 species worldwide (see Appendix 2), predominantly tropical in their distribution. Relatively few species 468 (13%) have been introduced (not yet naturalized or invasive) outside their native ranges, of which 27 (5% of the introduced species pool) species are classified as naturalized (not yet invasive) and 19 (4% of the introduced species pool) as invasive (Fig. 2.1A). Chamaephytes (Fig. 2.1B) and geophytes (Fig. 2.1C) contain the largest numbers of species, as well as, large proportions of introduced (not naturalized or invasive) species (11.98% and 17.34%, respectively), but they have low numbers of invasive species. Helophytes have the greatest proportion of introduced (not naturalized or invasive) species (23.86%) and also a relatively high proportion of naturalized (not invasive) and invasive species (Fig. 2.1D). Hemicryptophytes had 17.50% introduced (not naturalized or invasive) species, no naturalized (not invasive) species and 1% of the species are invasive (Fig. 2.1E). Hydrophytes seem to be the most successful with 13.15% introduced (not naturalized or invasive) species, 10.52% naturalized (not invasive) species and 13.15% invasive species (Fig. 2.1F). In contrast, phanerophytes have a large proportion of introduced (not

naturalized or invasive) species and naturalized (not invasive) species (16.67%) but no invasive species (Fig. 2.1g).

	a) All species	b) Chamae-phyte	c) Geophyte	d) Helophyte	e) Hemicryp-tophyte	f) Hydro-phyte	g) Phanero-phyte
Species Pool	3494	893	980	88	257	38	12
Introduced (not yet naturalized or invasive)	468	107	170	21	45	5	2
Naturalized (not yet invasive)	27	6	11	1	0	4	2
Invasive	19	1	4	2	3	5	0

Fig. 2.1. Numbers of Araceae species at different stages along the introduction-naturalization-invasion continuum. The selected plant life forms that are depicted here tend to be introduced more often.

Model performance

The predictive performance of the models varied from acceptable (for the introduction and invasion model) to outstanding (for the naturalization model). The final BRT introduction model explained 13% of the mean total deviance (1 - mean residual deviance/mean total deviance). The test data AUC score was 0.72 and the full dataset cross-validation coefficient AUC score was 0.70 ± 0.011 (mean ± standard error). The naturalization model accounted for 59% of the total deviance and the test data AUC score was 0.98 while the cross-validation coefficient AUC score was 0.93 ± 0.021. The invasion model accounted for 36% of the total deviance and the cross-validation coefficient AUC score was 0.74 ± 0.072.

Factors associated with species' native range, introduction dynamics and biological traits in explaining INI success

The number of native floristic regions, which we used as a proxy for range size, was an important predictor for introduction (Table 2.3; Appendix 3). Species that occur over more floristic regions in their native range tend to be introduced more often (Fig. 2.2A; $F_{3,3490} = 46.7$, $p < 0.001$).

Table 2.3. Variables shown in the boosted regression tree analyses to have the greatest influence on the prediction of introduction, naturalization and invasion. The percentage contribution of a variable is based on the number of times the variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. For each model, the contribution of the variables is scaled to add up to 100%, with higher numbers indicating stronger influence on the response.

Model	Variable	Percentage contribution
Introduction	Number of native regions	30.00
	Life form	26.00
	Pollinator type	17.70
	Species native to Polynesia	9.90
	Flower sexuality	8.20
	Habitat	8.20
Naturalization	Number of introduced regions	65.90
	Life form	16.00
	Habitat	9.80
	Number of uses	8.30
Invasion	Life form	48.90
	Number of introduced regions	35.30
	Pollinator type	15.90

The number of introduced regions, which we used as a proxy for propagule pressure, was an important predictor of naturalization and invasion (Table 2.3). This suggests that species that are introduced to more regions in their new range tend to overcome the naturalization and invasion barriers (Fig. 2.2B; $F_{2,511} = 266$, $p < 0.001$).

Flower sexuality was significant for species overcoming the introduction barrier (Table 2.3). Relative to non-introduced species there are significantly more unisexual flowers among introduced species, but there are no significant differences across the naturalization and invasion stages (Fig. 2.2C; $F_{3,3466} = 11.29$, $p < 0.001$). Tropical climbers largely comprise species with unisexual flowers which explains why species with this flower type is likely to be introduced.

Data on the purpose of introduction were limited, as only 12% (n = 409) of the species had information on human usage. Nevertheless, we found number of uses to be an important predictor of naturalization (Table 2.3). Introduced species that had failed to naturalize tended to have fewer uses than naturalized and invasive species (Fig. 2.2D; $F_{2,406} = 53.55$, $p < 0.001$).

In comparison to other plant life forms, chamaephytes (z = -19.165; p < 0.001), geophytes (z = 3.587; p < 0.001), helophytes (z = 3.626; p < 0.001), hemicryptophytes (z = 2.386; p = 0.0170), hydrophytes (z = 3.940; p < 0.001), and phanerophytes (z = 1.980; p = 0.0477) have been introduced more frequently outside their native ranges. After introduction, hydrophytes (z = 4.870; p < 0.001) are the most successful in overcoming the naturalization barriers (Fig. 2.2E). These successful species are mainly used as ornamentals (including plants used in gardens, landscaping, cut flowers, aquariums and ponds) or as a food source. This demonstrates that horticulture provides a major pathway for plant invasions in Araceae. Even though life form was the most important factor across all stages (Table 2.3), we did not find a significant difference between the different life forms for the invasion stage. This can be attributed to the large number of naturalized species across the range of life forms that were able to become invasive.

The method of pollination was an important correlate for species introduction and invasion (Table 2.3). Species pollinated by bees (z = -7.930; p < 0.001) and flies (z = 3.149; p = 0.00164) were introduced more often. Although not significant, the combination of pollinators (z = 0.007; p > 0.05) and fly-pollinated (z = 0.007; p > 0.05) species are more invasive (Fig. 2.2F). Pollination by flies is typical of plants in the Araceae family. Fly-pollinated species being able to overcome the introduction barrier is probably an artefact of human use, since fly-pollinated species comprise

popular ornamental plants that are used for their unique inflorescences (e.g. *Amorphophallus*, *Anthurium*, *Arisaema* and *Zantedeschia*), decorative foliage (e.g. *Philodendron* and *Schismatoglottis*), or as aquarium plants (e.g. *Cryptocoryne*). Nevertheless, these pollinators highlight a specialized pollination syndrome in Araceae.

The type of habitat a species occupies in its native range was an important correlate of introduction and naturalization (Table 2.3). Although most of the species originating in desert and xeric shrublands are introduced ($z = -2.587$; $p = 0.00969$), they have not yet been recorded to naturalize or invade (Fig. 2.2G). Species native to humid regions, mediterranean forests ($z = -3.569$; $p = 0.00289$) and temperate mixed forests ($z = -3.922$; $p < 0.001$) in particular, tend to overcome the introduction and naturalization barriers.

From the thirty-four native floristic regions that Araceae occupy, species native to the Polynesian province were introduced more often (Table 2.3). While larger native floristic regions such as Malaysia and Euro-Siberia were more important in terms of the total number of invasive species originating there, Polynesia had the largest proportion of introduced species (64%), with 24% classified as naturalized and 12% as invasive.

Lastly, after incorporating particular life forms into the analyses, we did not find specific correlates of invasiveness that differed from the original model, therefore we rejected the second hypothesis. We found the number of introduced regions and reproductive characteristics to be important for chamaephytes; the number of native floristic regions, pollinator type, species native to West African rainforests and human use were important for epiphytes; and the number of introduced regions and reproductive characteristics were important for geophytes. In addition, we did not find a strong clustering in life forms across the family (see Appendix 4).
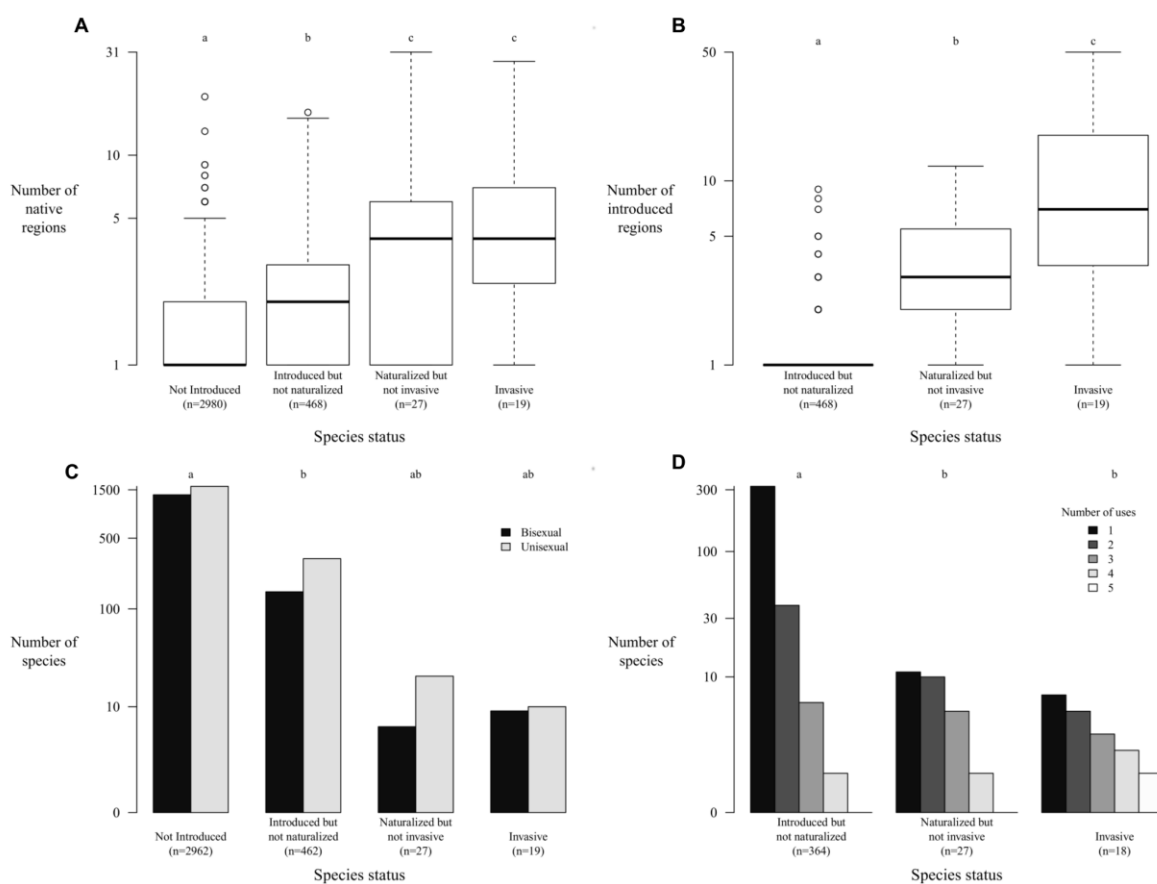
Fig. 2.2. The relationship between the introduction status of Araceae species and the parameters found to have a significant effect using boosted regression trees. **A)** Invasive taxa have larger native range sizes. Native range size is measured here in terms of the number of floristic regions based on Good's (1974) classification. Araceae naturally occur in 34 of the 37 floristic regions. **B)** Invasive species tend to have been introduced to more regions than naturalized species, and almost 90% of species which have been introduced to only one region have not yet naturalized. **C)** Species with unisexual flowers tend to have overcome more of the barriers to invasion than species with bisexual flowers. **D)** Species with a broad range of uses have naturalized and become invasive more often. Five different categories of human usage were considered: food source, medicine, fibre production, horticulture, agroforestry, and phytoremediation. **E)** Different life forms varied in their importance at different stages of the invasion. Introduced hydrophytes have naturalized far more than any other life form. **F)** Species that were fly-pollinated or had a combination of pollinator types became invasive compared to bee or beetle pollinated species. **G)** Species native to mediterranean and temperate mixed forests tend to naturalize more often. There were few data on the human uses of species that had not been

introduced outside their native range and so this category was excluded. In panels A and B, the box is the interquartile range, and the bold centre line is the median. Different letters denote different values using Tukey's multiple comparisons of means test. In panels E-G, tests were done using the original data, though the panels actually show plots of the fitted functions produced by boosted regression trees which indicate the effect on species presence/absence across the INI stages (y-axes) by each predictor variable (x-axes). For the relative contribution of each variable to the total deviance explained see Table 2.3. Grey panels indicate factors with low importance in the INI continuum, and therefore exclusion from the model.
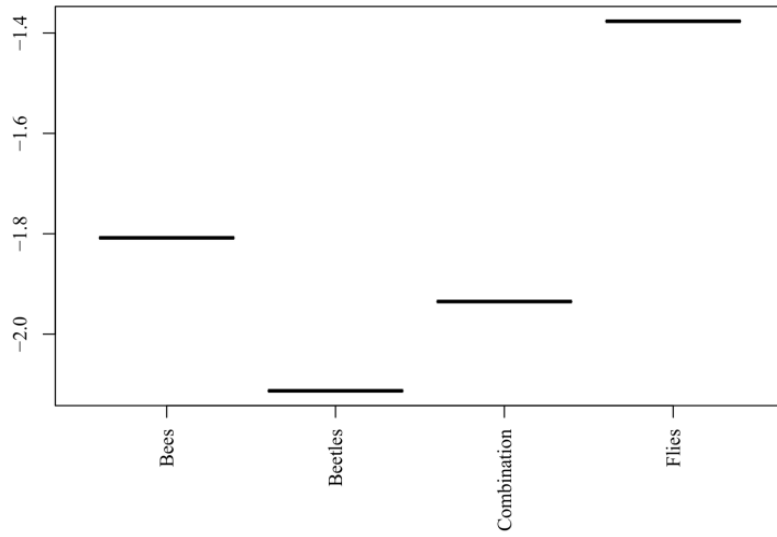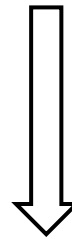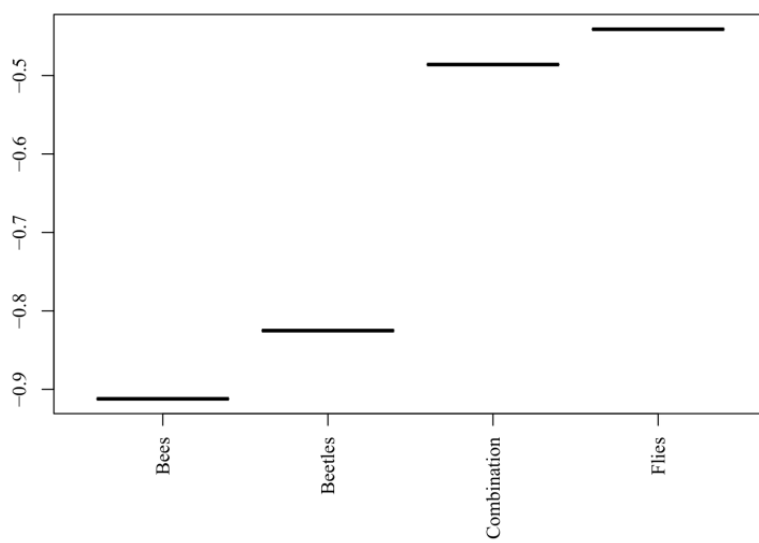
Not Introduced

vs.

introduced

Introduced not

naturalized

vs.

naturalized

and invasive

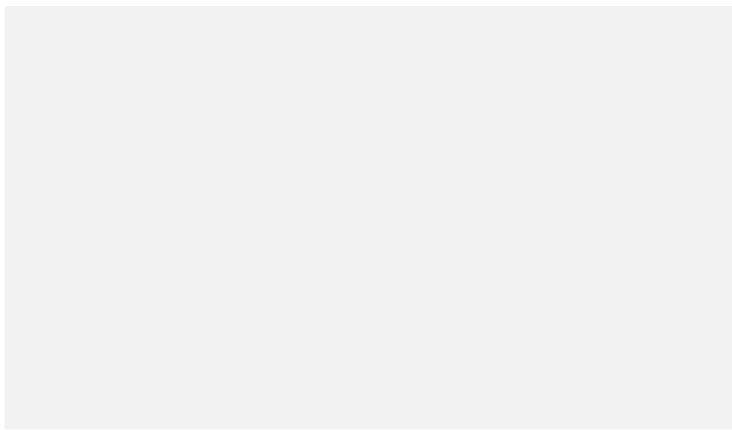**Naturalized not**

invasive

vs.

invasive

Fig. 2.2E. Continued

Not Introduced

vs.

introduced

Introduced not

naturalized

vs.

naturalized
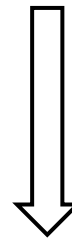
and invasive

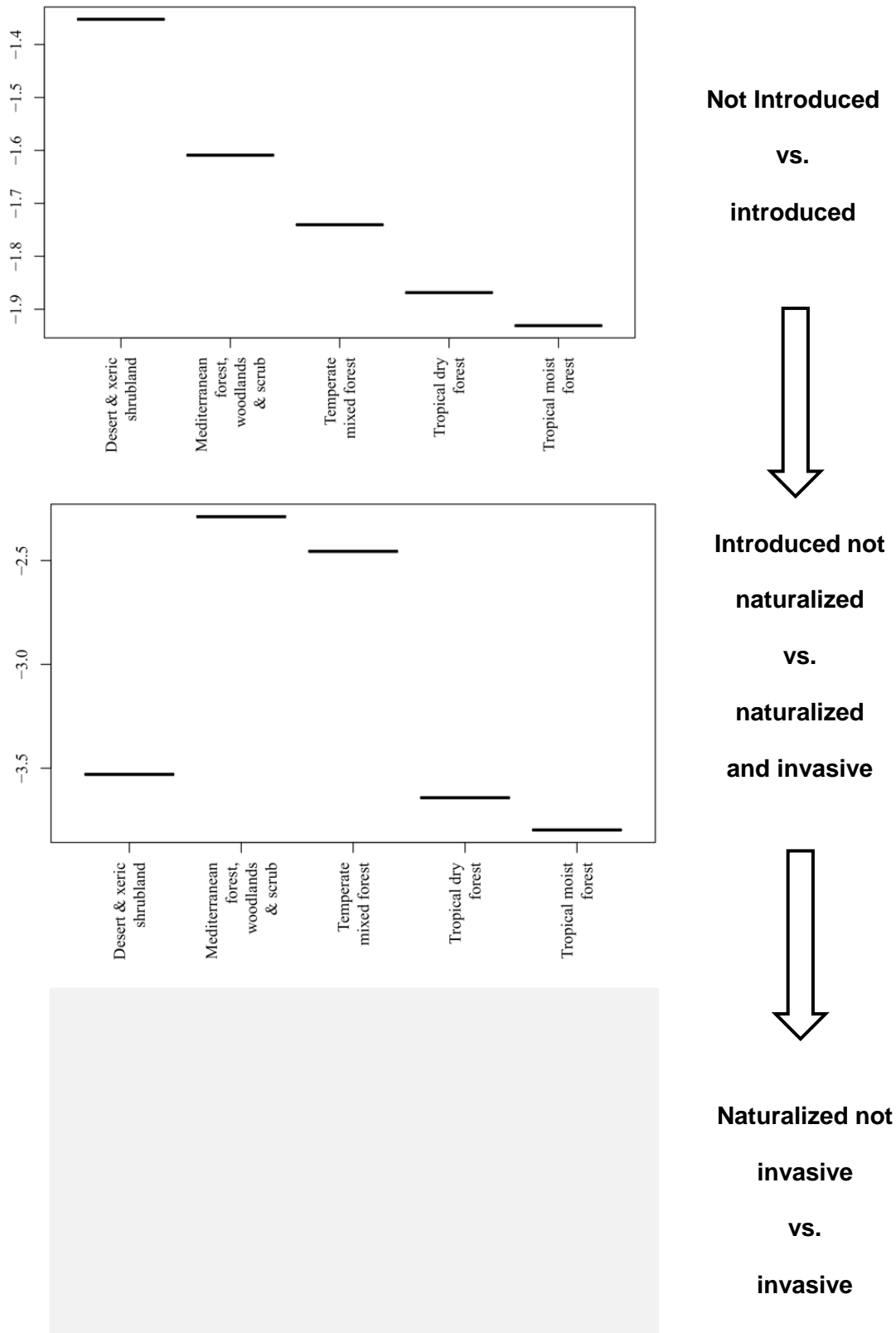Naturalized not

invasive

vs.

invasive

Fig. 2.2F. Continued

Fig. 2.2G. Continued

Predicting potentially invasive species

From the BRT models, we identified eight characteristics which facilitate species to overcome the INI barriers (see Appendix 1). Of the fifteen invasive genera in Araceae, we constructed phenograms inclusive of fourteen genera. The arguments used to identify potentially invasive species from the phenogram were based on 1) overall similarity in the character states of species, 2) whether species group with naturalized or invasive species, and 3) whether species cluster with naturalized or invasive sister groups. From the nine monophyletic groups, species with a high risk of becoming invasive are listed in Table 2.4 and their respective phenograms are illustrated in Appendix 5.

Table 2.4. A list of potentially invasive Araceae species constructed from model-based statistical inferences (i.e. UPGMA phenograms). These species are placed into groupings that are based on evolutionary relatedness (i.e. monophyletic groups) and similar ecological traits. Phenograms are illustrated in Appendix 5.

Monophyletic group	No. of species evaluated	No. of potentially high risk species	Potentially invasive species list [see Appendix 5]	Comments
Alocasia	77	5	*Alocasia longiloba*, *Alocasia odora*, *Alocasia acuminata*, *Alocasia brisbanensis*, *Alocasia hypnosa*	High likelihood for the listed non-introduced and introduced species to become invasive.
Amydrium, Anadendrum, Epipremnum, Monstera, Rhaphidophora, Scindapsus	82	38	*Monstera adansonii* var. *adansonii*, *Monstera deliciosa*, *Anadendrum microstachyum*, *Anadendrum latifolium*	Most species in this group are not yet introduced, however since this group already contains two invasive species, all species that are not listed requires further evaluation.

Ariopsis, Colocasia, Remusatia, Steudnera	20	11	*Remusatia hookeriana*, *Remusatia pumila*, *Colocasia affinis*	One cluster contains the invasive *Colocasia esculenta*, therefore, species in this group requires more attention.
Arophyton, Carlephyton, Colletogyne, Peltandra, Typhonodorum	2	1	*Peltandra sagittifolia*	*Peltandra virginica* is invasive and sister species *Peltandra sagittifolia* has been introduced outside its native range.
Arum, Biarum, Dracunculus, Eminium, Helicodiceros, Sauromatum, Theriophonum, Typhonium	55	23	*Arum maculatum*, *Dracunculus vulgaris*, *Typhonium blumei*, *Typhonium roxburghii*, *Sauromatum venosum*, *Sauromatum horsfieldii*, *Typhonium trilobatum*	Many species require further evaluation. Risk assessments must be conducted prior to species introductions.
Caladium, Chlorospatha, Filarum, Hapaline, Jasarum, Scaphispatha, Syngonium, Ulearum, Xanthosoma, Zomicarpa and Zomicarpella	169	~107	See clusters marked with asterisks in Appendix 5	Large group with five naturalized, but not invasive species and three invasive species scattered in the phenogram. All groups containing high risk species need to be evaluated further.

Cryptocoryne, Lagenandra	86	65	All species that clusters with invasive species	Phenogram shows very little structure (i.e. many species nested within groups) because fewer informative traits were used. Nevertheless, a single cluster contains the naturalized and invasive species. Therefore all species within this group pose an invasion risk.
Gymnostachys, Lysichiton, Orontium, Symplocarpus	8	6	*Lysichiton camtschatcensis*, *Symplocarpus egorovii*, *Symplocarpus foetidus*, *Symplocarpus nabekuraensis*, *Symplocarpus nipponicus*, *Symplocarpus renifolius*	High likelihood for non-introduced and introduced species to become invasive.
Lemna, Spirodela, Wolffia and *Wolffiella*	31	8	*Lemna aequinoctialis, Lemna minor, Lemna perpusilla, Spirodela oligorrhiza, Wolffia arrhiza, Wolffia brasiliensis, Wolffiella lingulata, Wolffiella welwitschii*	Many invasive species in this group. The listed non-invasive species have a high invasion risk because they cluster with the invasive species.

DISCUSSION

Identifying characteristics of successful invaders has been a major goal in invasion biology (Pyšek and Richardson, 2007; Rejmánek, 1996; Rejmánek and Richardson, 1996; Rejmánek *et al.*, 2005b; Richardson *et al.*, 2011a; Richardson and Pyšek,

2012). Although there are quite a few studies that have looked at traits in this family, these are mainly restricted to the most invasive group, the Duckweeds, and do not necessarily examine drivers of invasiveness. Some examples of studies conducted to date include; life traits and nutrient uptake of *Lemna minuta* and *Landoltia punctata* (Gérard and Triest, 2014); duckweeds as a valuable meal for domestic animals and fish due to their high protein content (Leng *et al.*, 1995); nutrient responses of *Lemna minuta* and *Lemna minor* to different nutrient availabilities (Paolaccia *et al.*, 2016); dispersal of the invasive *Lemna minuta* mediated by mallard ducks (Coughlan *et al.*, 2015); traits driving invasiveness of the first invasive *Colocasia esculenta* population in the Iberian Peninsula (García-de-Lomas *et al.*, 2012); and the phytochemical, pharmacological, medicinal, bioremediation potential, allelopathy, utilization and management of *Pistia stratiotes* (Khan *et al.*, 2014). Evidently, literature on the traits and mechanisms facilitating invasions in the Araceae family is resource poor, making this one of the most comprehensive studies to improve our understanding of invasion patterns in this family.

Our study supports the understanding that although some invasive traits are shared between invasive species, this is not consistent among all taxa and they are context-specific (Alpert *et al.*, 2000; Moodley *et al.*, 2013; Novoa *et al.*, 2015; Potgieter *et al.*, 2014; Richardson and Pyšek, 2006b; Theoharides and Dukes, 2007). Our main observations were that species that have large native floristic ranges are more likely to be introduced, and introduced species that are introduced to more regions are more likely to naturalize and invade; life form is consistently a major predictor; pollinator type might also be an important correlate and this is arguably specific to Araceae. Additionally, we found that particular traits or a combination of traits become important at different stages of the invasion continuum.

The importance of native range size (measured here in terms of the number of native floristic regions) is consistent with other studies (Hui *et al.*, 2011; Moodley *et al.*, 2013; Procheş *et al.*, 2012; Pyšek *et al.*, 2009a; Rejmánek, 1996), which also showed that species with larger native ranges are more likely to be introduced and become naturalized. A large native distribution is often correlated with invasiveness because there is a higher probability that wide ranging species will be picked up and intentionally or accidentally introduced (Blackburn and Jeschke, 2009). It is also

reflective of species being tolerant to a wide range of environmental conditions which pre-adapts them to survive and become established in the new region (Goodwin *et al.*, 1999; Pyšek *et al.*, 2009a).

High introduction efforts across novel ranges translate to a high propagule pressure. This finding is also in agreement with other studies (Colautti *et al.*, 2006; Moodley *et al.*, 2013; Pauchard and Shea, 2006; Zenni and Simberloff, 2013), where higher propagule pressure facilitates naturalization and invasion. This concept is based on the principle that species which are introduced across a wide area of the new region have a better chance of landing in localities that are suitable for establishment (Lockwood *et al.*, 2005a).

A large proportion of plant invasions result from horticultural introductions (Dehnen-Schmutz *et al.*, 2007b; Keller *et al.*, 2011; Reichard and White, 2001). Araceae are often used in horticulture, with hundreds of species and cultivars. Araceae that are used by humans for more purposes have a higher probability of being introduced and becoming naturalized. In addition, the invasion stage included species with the most number of uses. Other studies also found that species used by humans have a greater chance of becoming established in the introduced region because of a higher probability of being transported, and higher propagule pressure (Pyšek *et al.*, 2003; Thuiller *et al.*, 2006; van Kleunen *et al.*, 2007).

Plant life form is a common predictor of invasiveness for Araceae species since this trait is shared across the INI stages. This includes species (a) that are classified as hydrophytes; and (b) used for ornamental purposes. Araceae species that conform to these categories often reproduce vegetatively and this regeneration strategy is frequently linked to invasiveness (Kolar and Lodge, 2001). Although vegetative reproduction is not associated with long-distance spread, it can play an important role in the establishment of invasive species under suitable conditions in their new range (Daehler, 1998; Lloret *et al.*, 2005b). Given that hydrophytes are more likely to overcome the introduction and naturalization barriers, species belonging to this life form pose a greater invasion risk. Furthermore, once species overcome the introduction and naturalization barriers, species of any life form have the potential to become invasive.

Ornamental species topped the list of invasive Araceae. It is well known that species deliberately introduced for ornamental purposes are associated with successful invasion because high market availability allows for high propagule pressure (Dehnen-Schmutz, 2011; Dehnen-Schmutz *et al.*, 2007a). Species comprising invasive life forms with a potential for ornamental use should be carefully evaluated prior to introduction and management plans specific for these plants should be put in place. In addition, any species that is likely to be introduced with high propagule pressure poses a high risk and therefore efforts to reduce propagule pressure may successfully prevent a proportion of invasions. Propagules include seeds, seedlings, adult plants and reproductive vegetative fragments, and a high propagule pressure refers to propagules introduced or planted in large numbers, disseminated across a wide area, and/or with several introduction events. Efforts to reduce such pressures include regulating high-risk species that have not yet been introduced (i.e. pre-border management), as well as, regulating high invasion risk species that have already been introduced accompanied by management efforts that aim to eradicate, contain and control (i.e. post-border management). Additionally, control of propagules through effective management of the transport pathways and vectors (i.e. the importation of a commodity is the mechanism through which Araceae is introduced) will serve as a superior tool for the management and control of human-mediated biological introductions.

The main centres of origin and diversity of aroids are tropical regions such as tropical Asia and tropical America (Croat, 1998). However we found that species native to the Polynesian province were more successful in overcoming the introduction barriers. Forests in these Paleotropical regions are classified as one of the most wide-ranging and species-rich terrestrial habitats in the world (Whitmore, 1984) across taxa, and the Araceae are no exception. A higher introduction effort of wide-ranging species could be attributable to a higher abundance and tolerance to diverse conditions in any new area and so a relatively higher ease of cultivation (Dehnen-Schmutz *et al.*, 2007b; Forcella and Wood, 1984; Goodwin *et al.*, 1999; Prinzing *et al.*, 2002). In addition, since Polynesia is made up of islands, introduction effort from these islands is a key driver for Araceae dispersal. It is also possible that some of

these "native" Polynesian species were introduced by humans (and so pre-selected for an ability to be introduced), though this remains to be determined.

Some model groups demonstrate strong mechanistic correlation to invasion, such as *Phytophthora* susceptibility in Proteaceae (Moodley *et al.*, 2013) and the many growth forms in Cactaceae which contain detachable vegetative propagules (Novoa *et al.*, 2015). In Araceae we found that most correlates are universal. However, specialized pollinator types (e.g. flies and beetles) were important for introduction and invasion and this factor might be specific to Araceae. Most Araceae species are dependent on specialized pollinators (n = 900 beetles, n = 653 flies), and this may be limiting species that cannot spread vegetatively from becoming invasive. Species that require specialized pollination can encounter barriers to invasion when there is a lack of suitable pollinators or pollinator functional groups in their new range (Geerts and Pauw, 2012). The prevention and management of potentially high-risk species is required to help reduce the threats posed by invasive alien species. On one hand, there should be management plans put in place for species that are already introduced or species with a few naturalized populations, but which pose an invasion risk (e.g. prohibit further dissemination of potentially invasive species, remove high-risk species or issue permits for the possession of high-risk species, and consider attempting eradication or containment).

On the other hand, prevention is the best line of defence and can be applied to species that are not yet introduced but have similar traits to naturalized and invasive species. For instance, groups that so far lack invasive species may contain potentially invasive species which haven't been given an opportunity to invade. Therefore, phenograms should also be used for non-invasive groups that comprise species with the same suite of characteristics as the invasive groups. Screening high-risk species using a simple method based on evolutionary history and trait similarity is a conceptual step forward that provides a general framework in trying to predict invasiveness, however, this has ample room for improvement. In practice this will contribute towards the battle against invasive species, since risk assessment has its greatest impact when integrated into early invasive species management planning (Hulme, 2012; Wilson *et al.*, 2013)*.*

CONCLUSION

Araceae conforms to some, but not all, of the emerging generalizations in invasion biology. As in other studies with other taxa, Araceae species that have been widely introduced (i.e. high propagule pressure) and which have large native range sizes are more likely to be invasive. However, unlike many other groups, there was little evidence of a link between invasiveness and regeneration mechanism (i.e. by seed, vegetative or both). Instead, there was a significant effect of plant life form and pollinator syndrome. Moreover, the importance of factors varied across the INI continuum.

Since the mechanisms associated with invasiveness differ between taxa and across the INI continuum, group and stage-specific analyses are required. As more complete phylogenies and better knowledge of traits become available, these analyses are likely to become increasingly sophisticated and able to produce valuable insights into risk assessments.

ACKNOWLEDGEMENTS

REFERENCES

Alpert P, Bone E and Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52-66

Blackburn TM and Jeschke JM (2009) Invasion success and threat status: Two sides of a different coin? Ecography 32: 83-88

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

Boyce PC and Croat TB (2011 onwards) The Überlist of Araceae, Totals for published and estimated number of species in aroid genera.

Cabrera LI, Salazar GA, Chase MW, Mayo SJ, Bogner J and Davila P (2008) Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. American Journal of Botany 95: 1153-1165

Castro-Díez P, Godoy O, Saldaña A and Richardson DM (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Diversity and Distributions 17: 934-945

Chartier M, Gibernau M and Renner SS (2014) The evolution of pollinator-plant interaction types in the Araceae. Evolution 68: 1533-1543

Colautti RI, Grigorovich IA and MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Coughlan NE, Kelly TC and Jansen MAK (2015) Mallard duck (*Anas platyrhynchos*)-mediated dispersal of Lemnaceae: a contributing factor in the spread of invasive *Lemna minuta*?. Plant Biology 17: 108-114

Croat TB (1994) The use of New World Araceae as drug plants. Japanese Journal of Botany 69: 185-203

Croat TB (1998) Tropical aroids: taxonomy, diversity and ecology. In: Mathew P and Sivadasan M (eds) Diversity and Taxonomy of Tropical Flowering Plants, pp 235-286, Mentor Books, Calicut

Daehler CC (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biological Conservation 84: 167-180

Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. Journal of Applied Ecology 48: 1374-1380

Dehnen-Schmutz K and Touza J (2008) Plant invasions and ornamental horticulture: pathway, propagule pressure and the legal framework. In: Teixeira da Silva JA (ed) Floriculture, Ornamental and Plant Biotechnology Advances and Topical Issues, pp 15-21, Global Science Book, United Kingdom

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007a) A century of the ornamental plant trade and its impact on invasion success. Diversity and Distributions 13: 527-534

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007b) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224-231

Elith J, Leathwick JR and Hastie T (2008) A working guide to boosted regression trees. Journal of Animal Ecology 77: 802-813

Elith JH, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS and Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129-151

Falk-Petersen J, Bøhn T and Sandlund OT (2006) On the numerous concepts in invasion biology. Biological Invasions 8: 1409-1424

Forcella F and Wood JT (1984) Colonization potentials of alien weeds are related to their "native" distributions: Implications for plant quarantine. Journal of the Australian Institute of Agricultural Science 50: 35-40

Friedman JH (2001) Greedy function approximation: a gradient boosting machine. Annals of Statistics 29: 1189-1232

Friedman JH (2002) Stochastic gradient boosting. Computational statistics & data analysis 38: 367-378

Funk JL (2013) The physiology of invasive plants in low-resource environments. Conservation Physiology 1: 1-17

García-de-Lomas J, Dana ED and Ceballos G (2012) First report of an invading population of *Colocasia esculenta* (L.) Schott in the Iberian Peninsula. BioInvasions Records 1: 139-143

Geerts S and Pauw A (2012) The cost of being specialized: Pollinator limitation in the endangered geophyte Brunsvigia litoralis (Amaryllidaceae) in the Cape Floristic Region of South Africa. South African Journal of Botany 78: 159-164

Gérard J and Triest L (2014) The effect of phosphorus reduction and competition on invasive lemnids: life traits and nutrient uptake. ISRN Botany 2014: 1-9

Gibson MR, Richardson DM, Marchante E, Marchante H, Rodger JG, Stone GN, Byrne M, Fuentes-Ramírez A, George N, Harris C, Johnson SD, Le Roux JJ, Miller JT, Murphy DJ, Pauw A, Prescott MN, Wandrag EM and Wilson JRU (2011) Reproductive biology of Australian acacias: important mediator of invasiveness? Diversity and Distributions 17: 911-933

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

Grayum MH (1990) Evolution and phylogeny of the Araceae. Annals of the Missouri Botanical Garden 77: 628-697

Grotkopp E and Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. American Journal of Botany 94: 526-532

Guisan A and Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993-1009

Hosmer DW and Lemeshow S (2000) Applied logistic regression. Wiley, New York

Hui C, Richardson DM, Robertson MP, Wilson JRU and Yates CJ (2011) Macroecology meets invasion ecology: linking the native distributions of Australian acacias to invasiveness. Diversity and Distributions 17: 872-883

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10-18

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

Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P and Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14: 1-20

Khan M, Gul B, Wahid F, Hashim S and Marwat KB (2014) *Pistia stratiotes* l (Araceae): phytochemistry, use in medicines, phytoremediation, biogas and management options. Pakistan Journal of Botany 46: 851-860

Keller RP, Geist J, Jeschke JM and Kühn I (2011) Invasive species in Europe: ecology, status, and policy. Environmental Sciences Europe 23: 23

Kolar CS and Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204

Kubitzki K (1998) The Families and genera of vascular plants. Springer, Berlin, 511 pp

Kueffer C, Pyšek P and Richardson DM (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist 200: 615-633

Kuhn M (2014) Classification and regression Training. R package version 6.0-24

Lambdon PW, Lloret F and Hulme PE (2008) How do introduction characteristics influence the invasion success of Mediterranean alien plants? Perspectives in Plant Ecology Evolution and Systematics 10: 143-159

Leng, R.A., Stambolic, J.H., and Bell, R. 1995. Duckweed - a potential high-protein feed resource for domestic animals and fish. Volume 7. Livestock Research for Rural Development.

Lloret F, Médail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon P and Hulme PE (2005) Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology 93: 512-520

Lockwood JL, Cassey P and Blackburn TM (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20: 223-228

Mayo SJ, Bogner J and Boyce PC (1997) The genera of Araceae. Royal Botanic Gardens, Kew, Belgium, 370 pp

Moodley D, Geerts S, Richardson DM and Wilson JRU (2013) Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. PLoS ONE 8: e75078

Nauheimer L, Metzler D and Renner SS (2012) Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. New Phytologist 95: 938-950

New Zealand naturalized plant checklist www.nzpcn.org.nz/publications/Naturalised-list-06-new.pdf, accessed August 2011.

Novoa A, Le Roux JJ, Robertson MP, Wilson JRU and Richardson DM (2015) Introduced and invasive cactus species: a global review. AoB PLANTS 7: plu078

Paolaccia S, Harrison S, and Jansen MAK (2016) A comparative study of the nutrient responses of the invasive duckweed *Lemna minuta*, and the native, co-generic species *Lemna minor*. Aquatic Botany 134: 47-53

Pauchard A and Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399-413

Pavlicek A, Hrdá S and Flegr J (1999) FreeTree - freeware program for construction of phylogenetic trees on the basis of distance data and bootstrap jacknife analysis of the tree robustness. Application in the RAPD analysis of genus Frenkelia. Folia Biologica 45: 97-99

Perkins LB and Nowak RS (2013) Invasion syndromes: hypotheses on relationships among invasive species attributes and characteristics of invaded sites. Journal of Arid Land 5: 275-283

Potgieter LJ, Richardson DM and Wilson JRU (2014) Casuarina: biogeography and ecology of an important tree genus in a changing world. Biological Invasions 16: 609-633

Prinzing A, Durka W, Klotz S and Brandl R (2002) Which species become aliens? Evolutionary Ecology Research 4: 385-405

Procheş Ş, Wilson JRU, Richardson DM and Rejmánek M (2012) Native and naturalized range size in Pinus: relative importance of biogeography, introduction effort and species traits. Global Ecology and Biogeography 21: 513-523

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essli F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M and Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the USA 107: 12157-12162

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U and Vilà M (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

Pyšek P, Jarošík V and Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. PLoS ONE 6: e24890

Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek jun J and Sádlo J (2009a) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Diversity and Distributions 15: 891-903

Pyšek P, Krivánek M and Jarošík V (2009b) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90: 2734-2744

Pyšek P and Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological Invasions, pp 97-125, Springer, Berlin.

Pyšek P, Sadlo J, Mandak B and Jarošík V (2003) Czech alien flora and the historical pattern of its formation: what came first to Central Europe? Oecologia 135: 122-130

R Development Core Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reichard SH and White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103-113

Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. Biological Conservation 78: 171-181

Rejmánek M and Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655-1661

Rejmánek M, Richardson DM and Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (ed) Vegetation Ecology, pp 332-355, Blackwell Publishing, Oxford

Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ and Wilson JRU (2011) Human-mediated introductions of Australian acacias – a global experiment in biogeography. Diversity and Distributions 17: 771-787

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

Richardson DM and Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383-396

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

Ridgeway G (2012) Generalized Boosted Regression Models. R package version 1.6-3.2

Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40: 81-102

Tecco PA, Diaz S, Cabido M and Urcelay C (2010) Functional traits of alien plants across contrasting climatic and landuse regimes: do aliens join the locals or try harder than them? Journal of Ecology 98: 17-27

Theoharides KA and Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256-273

Thompson K, Hodgson JG and Rich TCG (1995) Native and alien invasive plants: more of the same? Ecography 18: 390-402

Thuiller W, Richardson DM, Rouget M, Procheş Ş and Wilson JRU (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87: 1755-1769

van Kleunen M, Johnson SD and Fischer M (2007) Predicting naturalization of Southern African Iridaceae in other regions. Journal of Applied Ecology 44: 594-603

van Kleunen M, Weber E and Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235-245

Whitmore TC (1984) Tropical rain forests of the far east. Clarendon Press, Oxford

Williamson M and Fitter A (1996) The varying success of invaders. Ecology 77: 1661-1666

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ and Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology and Evolution 24: 136-144

Wilson JRU, Ivey P, Manyama P and Nänni I (2013) A new national unit for invasive species detection, assessment and eradication planning. South African Journal of Science 109: 1-13

Zenni RD and Simberloff D (2013) Number of source populations as a potential driver of pine invasions in Brazil. Biological Invasions 15: 1623-1639

Chapter 3: Assessing and managing the threat posed by *Epipremnum aureum* in South Africa

ABSTRACT

The predictive success of risk assessments is still largely a function of invasiveness elsewhere. Therefore, species that are invasive elsewhere should be prioritised for management, and where possible eradicated. We set out to investigate the threat posed by the alien climber *Epipremnum aureum* (Araceae) and assess techniques for controlling the spread of the species in South Africa. *Epipremnum aureum* is highly invasive in Hawaii and Sri Lanka, and has recently been considered as a potential invader in South Africa. However, no study has examined the invasion dynamics of the species. We mapped the species' current distribution in South Africa, modelled its potential distribution globally, and explored control methods. We only recorded the species in the KwaZulu-Natal province of South Africa, which comprised 78 naturalized populations and 321 cultivated populations. Delimitation surveys of the naturalized populations revealed ~187,000 plants over ~3 hectares. Several of these populations comprised plants as tall as the trees they were growing on, and were often found flourishing in dump sites, along roadsides or as a result of escaping cultivation. Species distribution models showed that *E. aureum* has a high probability of expanding its current range primarily along the coastal regions of South Africa and into neighbouring countries on Africa's eastern seaboard. Due to the invasion threat of the species, we recommend that all plants outside cultivation be removed. To achieve this, we found that applying herbicides to freshly cut stems significantly reduced plant growth. Given the species' limited dispersal ability and effective chemical control methods, we propose that *E. aureum* should be listed as category 3 under South Africa's National Environmental Management: Biodiversity Act (10/2004) Alien and Invasive Species regulations, i.e. naturalized populations need to be managed, it cannot be propagated or sold in future, but current garden plantings may remain.

Keywords: Biological invasions, climatic suitability, management, post-border risk assessment, South Africa

INTRODUCTION

Biological invasions are a global threat to agriculture, natural ecosystems, human and animal health, biodiversity and the economy (Davis, 2009; Drake *et al.*, 1989; Mazza *et al.*, 2014; McNeely, 2001a; Pimentel, 2011; Vitousek *et al.*, 1997). The mechanisms that underlie plant invasions are multifaceted, and for this reason no single predictor exists. Factors that facilitate the success of invasive alien plants include a combination of species invasiveness (i.e. intrinsic properties of a species), habitat invasibility (i.e. properties of a community that make it vulnerable or resistant), and the history of introduction (i.e. propagule pressure and residence time) (Lockwood *et al.*, 2005a; Nentwig, 2007; Richardson and Pyšek, 2006b; Wilson *et al.*, 2007). Understanding the conditions that facilitate biological invasions is a critical step in the prevention and management of invasions.

Understanding pathways of introductions is also important if species invasions are to be effectively regulated (Essl *et al.*, 2015b). Humans have both intentionally (e.g. import for horticulture) and unintentionally (e.g. as contaminants or stowaways) introduced species into new environments (Dehnen-Schmutz *et al.*, 2007b; Lambdon *et al.*, 2008; Mack and Lonsdale, 2001; Pyšek *et al.*, 2011; Reichard and White, 2001). With increased globalization, the number of introduced species has increased exponentially, and the number of pathways by which species may spread has also increased (Hulme, 2009; Hulme *et al.*, 2008; Pyšek *et al.*, 2011). The impact of biological invasions will inevitably continue increasing if management efforts against those species and pathways that pose the greatest threat are not prioritised (Rouget *et al.*, 2016).

Consequently, the development of country-level risk assessments, spanning the pre-border, border and post-border stages, has become a high priority for managing invasive species. Weed risk assessments (WRA) represent a tool that is used to support the exclusion of potentially invasive alien species (IAS) from being introduced (i.e. pre-border screening), as well as assessing the potential impact of already introduced species that occupy different stages along the introduction-naturalization-invasion continuum (i.e. post-border prioritization and management) (Conser *et al.*, 2015; Groves *et al.*, 2001; Hulme, 2012; Pheloung *et al.*, 1999a; Reichard and Hamilton, 1997; Weber and Gut, 2004). WRA tools are developed

through classification of consistent patterns in traits of species that have previously become invasive. The Australian WRA (Pheloung *et al.*, 1999a) is widely recognised as one of the best systems to identify plant species, particularly terrestrial plant species, that are likely to become invasive and cause negative impacts. Several peer-reviewed papers have supported the accuracy of the Australian WRA system and recommend its wider application (Gordon *et al.*, 2008a; Hulme, 2012).

Once a species has been introduced and becomes established at a site (i.e. post-border), preventing its spread through containment or eradication becomes a priority. However, to fully understand the risks of IAS and to develop effective invasion policies and management, post-border weed risk assessments also need to take into account the context of the invasion. For example, introduction pathways (Hulme, 2009), species traits and their associated impacts (Blackburn *et al.*, 2014; Pyšek and Richardson, 2010), and the sites' susceptibility to invasion (Catford *et al.*, 2011), depict the plethora of conditions that can facilitate the success of IAS. As a result, the context for prioritization can vary widely across taxa, habitats and countries. Furthermore, delimiting the current geographic extent of the species and estimating their abundance are crucial steps towards understanding the likelihood of successfully implementing control and eradication plans (Panetta and Lawes, 2005; Wilson *et al.*, 2014). Consequently, standardized approaches for prioritizing pathways, sites and species impacts have recently been proposed (Dawson *et al.*, 2015; Essl *et al.*, 2015b; Kumschick *et al.*, 2015a; McGeoch *et al.*, 2016).

Araceae, one of the largest plant families, has been introduced globally through the horticultural pathway and currently contains 19 invasive species (Moodley *et al.*, 2016b). Of these, *Epipremnum aureum* has recently been detected in KwaZulu-Natal (KZN), South Africa (Sithole and Nzama, 2012). The global invasive status of *E. aureum* incited an evaluation of the species invasion risk and management in South Africa by the South African National Biodiversity Institute's Invasive Species Programme, which is responsible for detecting new invasions, conducting post-border risk assessments, and coordinating the eradication of high risk species that have a limited distribution (Wilson *et al.*, 2013).

Epipremnum aureum (Linden & André) G.S. Bunting, commonly referred to as devil's ivy, silver vine and golden pothos, is an evergreen epiphyte and a widely planted invasive species in subtropical and tropical climates around the world (Moodley *et al.*, 2016b; PIER). This species, a creeper and climber, is widely cultivated for ornamental use (i.e. as garden and indoor plants) because of its popular variegated foliage, reputation as a low maintenance plant and its efficiency in removing indoor pollutants such as formaldehyde and benzene (Dela Cruz *et al.*, 2014; Xu *et al.*, 2011). *E. aureum* reproduces easily from cuttings and detached pieces of stem, and is mainly dispersed vegetatively. The species rarely flowers in the wild, and in South Africa the species has not been seen in flower (pers.obs.).

The botanical classification of *E. aureum* has been controversial throughout its history. The species is sometimes considered a variety of *Epipremnum pinnatum* (L.) A. Engler, however Boyce (2004) identified *E. aureum* as a completely different species. There are quite a few distinctions between *E. pinnatum* and *E. aureum*; in *E. pinnatum* mature leaves are strongly pinnatifid, resembling the foliage of *Monstera deliciosa* Liebm. more than that of *E. aureum*; *E. pinnatum* has lanceolate to elliptic adult leaves while *E. aureum* has ovate to ovate-lanceolate leaves; and *E. pinnatum* flowers abundantly in the wild and in cultivation whereas *E. aureum* seldom flowers in the wild and flowering in cultivation is extremely rare (Boyce, 2004). *E. pinnatum* has not been recorded in South African herbaria, and based on morphology, the species was also not found during our field surveys.

While *E. pinnatum* is known to have a broad native range (i.e. temperate and tropical Asia, Australia, and the Pacific Islands; GISD), until 2004, there was uncertainty surrounding the origin of *E. aureum*. Finally, aroid botanist Peter Boyce established that the species was originally collected as *Epipremnum mooreense* Nadeaud (a synonym of *E. aureum*) from natural forest on the island of Moorea in French Polynesia (Boyce, 2004). Following the release of imported plants, *E. aureum* is now common in many countries including several Pacific Islands, the Caribbean, China, Hawaii, Central and South America, Southeast Asia, India, Pakistan and Singapore (eMonocot; HEAR; PIER).

One criterion commonly used to infer the status of a species as an invasion risk, is evidence that the species has a history of being invasive elsewhere, especially under similar climatic conditions (Faulkner *et al.*, 2014; Kolar and Lodge, 2001; Reichard and Hamilton, 1997; Thuiller *et al.*, 2005). *Epipremnum aureum* has a pan-tropical distribution and is regarded as a species of considerable concern because it has invaded several tropical and sub-tropical forests in Asia and the new world (Center for invasive species and ecosystem health; FLEPPC; PIER). Additionally, in Sri Lanka the species densely covers the forest floor and the trunks of trees, causing severe ecological disruption (Nyanatusita and Dissanayake, 2013). In South Africa, *E. aureum* was first detected in the Southbroom and Durban areas in the KZN province were it was observed to be invading forest margins (Sithole and Nzama, 2012). The identity of the species has been confirmed as *E. aureum* and specimens are lodged at the KZN herbarium (Appendix 6).

The purpose of this study is to determine the risk posed by *E. aureum* in South Africa. Specifically, we aim to: 1) delineate the current distribution of the species in South Africa; 2) describe factors that have contributed to its successful invasion; 3) identify the threat *E. aureum* poses in South Africa and globally using bioclimatic models, the Australian WRA, and notes on its behaviour in South Africa; 4) investigate best management practices to control the species; and 5) provide a recommendation as to whether regulation should be considered. This study is the first focussing on the invasion dynamics of *E. aureum*.

MATERIALS AND METHODS

Identifying study sites

Detection is important to ensure that new invasive species are promptly identified, reported, and contained or eradicated. A systematic search for the invasive species is the first component when managing a newly detected incursion (Wilson *et al.*, 2017). Initial localities of *E. aureum* were identified using the Southern African Plant Invaders Atlas (SAPIA) database in which there were 6 records (Henderson, 2007). To identify additional localities in the country, we contacted eight herbaria which cover five South African provinces (i.e. Bews, Bolus, Charles E. Moss, Compton, H.G.W.J. Schweickerdt, KwaZulu-Natal, Larry Leach and Selmar Schonland herbaria). As far as the species on record are concerned, *E. aureum* was only

recorded in KZN. For that reason, to determine if there are other populations in the province we distributed information flyers in KZN (Appendix 7). The flyers were targeted at spotter networks (i.e. groups of volunteers located in different towns or provinces in South Africa who identify and report invasive species) in the south coast area, however, many of the spotters often travelled throughout KZN. Spotters comprised members from the Pondoland custodians of rare and endangered wildflowers (CREW) group, members affiliated with the south coast conservancies, and residents.

Delimiting the extent of *E. aureum* populations in South Africa

Delimiting the spatial extent of the detected populations is necessary to determine the area to which the species has already spread (i.e. size of populations). Such delimitation surveys are also important for selecting appropriate control actions (e.g. eradication, containment, or no action) and assessing management feasibility (Hauser *et al.*, 2016; Moore *et al.*, 2011; Panetta and Lawes, 2005; Tobin *et al.*, 2013). Once a locality was confirmed through our detection efforts, we scanned the entire town using road surveys at a driving speed limited to 20km/hr. In addition, during our ad hoc drives through the nearby towns we detected populations that were previously not recorded. When we spotted *E. aureum*, we marked the locality with a handheld GPS (Garmin GPSMAP 64s). We also recorded whether the species was planted in a garden or in the wild (i.e. unmanaged area), and for populations growing in the wild, we collected information about the plants and the site (e.g. area, abundance, and disturbance).

Field assessments of wild populations

The extent of occurrence of invasive species is often used as proxy of success, and over time can be used as a measure of spread (Wilson *et al.*, 2014). In addition, understanding the occupied area inhabited by IAS will assist in guiding management strategies. We determined the extent of occurrence for each population by connecting the outlying GPS waypoints for each population and then calculating the enclosed area (m^2), using the mapping software ExpertGPS 5.71.

Species abundance is another important indicator used to characterize the risk of IAS because it is associated with the impact of biological invasions (Kumschick *et*

al., 2015b). In addition, the number of stems is important for the expansion of *E. aureum* populations because the main mode of reproduction occurs vegetatively and seldom via seed. Consequently, since most populations comprised extremely dense plants and it was difficult to count all individuals, we measured abundance in terms of the number of stems in a population (i.e. each stem was considered as a single plant). To count the number of stems we laid three 1×1 m^2 transects, oriented perpendicular to the plant and its climbing structure, on different plant cover types (i.e. a representation from dense to sparse cover) and counted every stem within the transect. Plant abundance was then estimated using the average numbers of stems counted in a 1×1 m^2 perpendicular transect and multiplied by the populations extent of occurrence (m^2).

A number of studies have shown that plant height is a consistent trait facilitating invasion success (Pyšek and Richardson, 2007). One explanation is that height is a major determinant of a plants' ability to compete for limiting resources, such as light (Moles *et al.*, 2009; Westoby *et al.*, 2002). For vines, the maximum height will, however, be limited by the height of the supporting structures on which they grow. Therefore, we estimated the height of the tallest *E. aureum* plant and the height of its associated support structure in order to demonstrate the competitive ability of the species. Height was estimated by one person holding a 2 m stick against the supporting structure and the other person standing 10 m away used their index finger and thumb to count the number of sticks from the ground to the top of the structure and to the top of the tallest *E. aureum* plants. If a vine can overtop a tree or shrub, then they can potentially have much greater impacts. Where the support structures were trees, the trees were grouped into size classes and the height of the tallest *E. aureum* plants relative to the height of the tree species they were growing on (one sample per population) were plotted on a boxplot and analysed using a generalized linear model with a Poisson distribution.

Lastly, we looked at land-use types where the study species occurred and their associated disturbance levels. Disturbance is commonly linked to increasing habitat invasibility (Alpert *et al.*, 2000; Pyšek *et al.*, 2010b; Rejmánek *et al.*, 2005b). Disturbance creates a window of opportunity during which IAS might benefit if they can reproduce and thrive better than the native species under such conditions (Davis

et al., 2000). For example, there is a strong correlation between plant invasions and disturbed habitats such as roadsides (Gelbard and Belnap, 2003; Meunier and Lavoie, 2012; Parendes and Jones, 2000). The land-use types at each site were initially categorized in the same way as the data collected for the SAPIA database but this was modified during field work. The following categories were used: canal, garden escapee (i.e. most of the population is still thriving in a garden but the species is in the early stages of spreading into the adjacent land), natural vegetation, roadside, transformed vegetation (i.e. sites dominated with alien plants), vacant land (i.e. land set aside for development which also includes vacant or abandoned properties), or wasteland (i.e. dump sites). We plotted the frequency of the number of populations and their land-use types, and analyzed the data using Pearson's Chi-squared Test for Count Data. All statistical analyses were performed using R Studio software (R Development Core Team, 2012).

Predicting potentially suitable climatic areas for *E. aureum*

The predictive success of invasive weed risk assessments is still largely a function of invasiveness elsewhere, as well as, climatic suitability, therefore an understanding of these criteria provides significant value for management (Rouget *et al.*, 2004; Thuiller *et al.*, 2005).

There are no geo-referenced records of *E. aureum* in its native range. Moreover, although a number of sources report on the species invasiveness in several countries, very few global geo-referenced records exist (18 in total). Therefore, our presence-only data included the global records and the South African records obtained from field surveys conducted in this study (*N* = 171 with duplicate records removed).

To develop the niche model, current environmental data (1950–2000) were downloaded from the WorldClim database at a resolution of 30 arc-seconds (www.worldclim.org, accessed June 2012). The entire dataset of the 19 raster predictor variables was reduced through pairwise evaluation (Kendall rank correlation coefficient < 0.65) to reduce multi-collinearity among the predictors (Elith *et al.*, 2010). We chose mean temperature of the coldest quarter as a primary predictor variable because *E. aureum* is limited by cold tolerance (http://aggie-

horticulture.tamu.edu/syllabi/308/Lists/Fourth%20Edition/Epipremnumaureum.pdf,
accessed June 2012; Floridata plant encyclopedia,
http://floridata.com/Plants/Araceae/Epipremnum%20aureum/1210, accessed June
2012). Subsequent variable selection was based on predictors with the lowest pair-
wise correlations. The resulting variables included four predictors; one rainfall (i.e.
annual precipitation) and three temperature (i.e. minimum temperature of the coldest
month, mean temperature of the wettest quarter and mean temperature of the
coldest quarter) variables.

We used maximum entropy modelling to quantify habitats at potential risk of invasion
and map the potential global geographic distribution of *E. aureum* (MaxEnt version
3.3.3 k; Phillips *et al.*, 2006). The selection of MaxEnt was based on the following
reasons: (1) MaxEnt provides an appropriate strategy for working with presence-only
data such as our *E. aureum* data set, (2) MaxEnt consistently outperformed other
species distribution model implementations across taxa and geographic regions
(Elith *et al.*, 2006), and (3) models are not strongly influenced by small sample sizes
or irregularly sampled data and hence prediction is relatively robust (Pearson *et al.*,
2007, Elith *et al.*, 2011).

We generally opted for default MaxEnt settings: 10,000 random background points
(i.e. pseudo-absences), from which the algorithm will select random points that are
assumed as pseudo-absences, create response curves to evaluate *E. aureum*
response to individual variables, logistic output to produce a continuous map, and
jackknife procedure to measure variable importance. Appropriate selection of
background points is essential for presence-only species distribution modelling
because these points are generated from a random sample of non-occurrences in
the region of interest. We ensured that the background points were geographically
(i.e. selected from the spatial extent of presence records) and environmentally (i.e.
selected from intersecting climate classes using the Köppen-Geiger climate
classification) stratified. Furthermore, occurrence data is often spatially biased which
generally results in environmental bias. However, spatial aggregation is reduced
when using background data with the same bias as occurrence data but this does
not correct for the lack of data due to low sampling effort. This selection method,
together with 10,000 pseudo-absence points, is recommended when using a

machine learning technique in order to improve the models predictive accuracy (Barbet-Massin *et al.* 2012; Phillips and Dudik, 2008; VanDerWal *et al.* 2009).

In addition, we changed the following settings for model parameterization: (1) selected hinge features for smoother response curves, (2) regularization parameter = 1 to control over-fitting and clamping, (3) selected a random seed, (4) set random test percentage at 25 to evaluate model performance and reduce bias (75% of the data trained the model), (5) set replicates at 10 to ensure variability, (6) replicated run-type was set as subsample, and (7) set maximum iterations to 5,000 allowing the model adequate time for convergence.

The percent contribution of each variable and jackknife procedures were used to investigate the relative importance of the bioclimatic predictors while the 'area under the curve' (AUC) of the receiver operating characteristic was used to evaluate model performance. The AUC is a threshold-independent measure of model performance that ranges from 0 to 1. From the 10 replicates that were run we used the average AUC values for training and test datasets. Values > 0.9 indicate high accuracy, 0.7–0.9 indicates moderate accuracy, 0.5–0.7 indicates poor performance and values below 0.5 indicate that predictions are worse than random (Townsend Peterson *et al.*, 2011). Finally, using ArcMap version 10.2.2, the ASCII file containing the average model results were converted to binary maps in raster format. The colour distribution from light to dark represents increasing habitat suitability for *E. aureum*.

Weed risk assessment

We used the Australian Weed Risk Assessment protocol (A-WRA) to categorize the risk of invasiveness of *E. aureum* in South Africa based on its biology and ecology, climatic requirements, history, and biogeography (Pheloung *et al.*, 1999a). In the absence of any direct measure of impact, we used the A-WRA as a tool to predict potential weed impacts.

The A-WRA is a question-based scoring system, subdivided into sections on biology and ecology, climatic requirements, history, and biogeography. The assessment involves answering up to 49 questions and each question is awarded between -3 and 5 points. The final WRA score is the sum of points for all answered questions.

The answers generate a numerical score relating to the plants' invasive potential and the score is then used to determine one of three outcomes: the species is accepted for introduction (score < 1); rejected (score > 6); or rejected pending further evaluation of invasive potential (score 1–6). A minimum of 10 answers are needed for a species to be evaluated. The A-WRA system can therefore be used to identify useful non-problematic plants, as well as to predict potentially invasive plants of the agricultural and/or environmental sectors. In our study, questions related to geography and climate, were modified to reflect the conditions of South Africa (i.e. question 2.01).

Identifying best methods for control

We selected one research site in Umtentwini, KZN (-30.7224 °S, 30.464 °E), because this site contained many *E. aureum* plants growing on many trees over a large area (4,262 m^2). This accounted for independent treatments and replication. Additionally, this selection intentionally factored in soil properties and climatic conditions. The uniformity of these variables across the trial site is essential because changes in these factors can influence the effects of the herbicide. The objectives of this trial were to evaluate the performance of three methods for *E. aureum* control: 1) cut treatment: cutting plants at 1.5 m above ground level with no herbicide application (i.e. the stem was severed completely); 2) glyphosate treatment: cutting plants at 1.5 m and tying plastic packets filled with 100 ml of herbicide mixture (2% Clearout 360 diluted with actipron, water and a marker dye) to the fresh cut stem on the aerial part of the plant, as well as, spraying the mixture on the fresh cut stem on the rooted plant; and 3) triclopyr and picloram treatment: cutting plants at 1.5 m and applying the herbicide gel (Kaput 100 Gel) with a brush to the fresh cut aerial and rooted parts of the plant. The control group, located at the same study site, received no treatment.

Measurements were done on the width of the stems using callipers 100 mm above the cut-stem and 100 mm below cut-stem. For the control we measured the width of the stem once at 1.5 m, i.e. height at which the plants were cut for the treatments. Stem width was used as a measure for effective control because previous trials that attempted to control this species revealed that the deterioration of the stems is more symptomatic of plant death compared to wilting leaves (Skene, pers. comm.). In

addition, measurements were taken above and below the cut-stem because the plants above the cut may still survive as they will be reliant on stored root reserves, while plants below the cut will primarily rely on nutrients obtained from the soil (Skene, pers. comm.). The reason for cutting the plants at 1.5 m was to ensure that the dead rooted part of the plant could be pulled out of the ground.

Glyphosate is the active ingredient in the 2% Clearout 360 herbicide, and triclopyr and picloram are the active ingredients in the Kaput 100 Gel. These two systemic herbicides were selected because literature searches suggest that these herbicides are commonly used to treat other Araceae species (e.g. *Colocasia esculenta, Philodendron* spp., *Pistia stratiotes* and *Syngonium podophyllum*). The experimental and control groups were set up on 27 August 2015 using 20 climbing *E. aureum* plants per treatment. The treatments and control group were not pseudo-replicated (n = 80). Thereafter, evaluations of the groups were done once a week for 6 weeks (3, 10, 17, 24 September; 1, 8 October). Statistical analyses were performed using the Kruskal-Wallis rank sum test.

RESULTS

Current distribution

Epipremnum aureum is present in several coastal towns in the KZN province, South Africa (Table 3.1; Appendix 8). From our information flyers, spotter networks and enquiries with staff from other herbaria across South Africa, we did not discover additional localities in other parts of the country. However, it must be noted that during this study our field survey effort was focussed in KZN because we only found records of naturalized *E. aureum* populations in this province (i.e. there may be populations in other provinces). Through road surveys, we found a total of 399 populations in the KZN province, of which 321 occur in gardens and 78 populations were growing in unmanaged sites which increases the species' potential to spread. Furthermore, these populations were distributed across 35 towns in KZN and populations in 9 of these towns were reported by spotters. This implies that although passive surveillance (e.g. through spotters) is valuable and less costly, active surveillance provides more accurate and timely information which is fundamental for post-border risk assessments.

Table 3.1. The distribution of *Epipremnum aureum* across KwaZulu-Natal, South Africa, as determined by spotters and road-side surveys. For wild populations, we collected information about the plants and the site. However, for populations that were cultivated in gardens, we only recorded their locality. Some towns are grouped together because they are located in close proximity.

Town	No. of garden populations	No. of unmanaged populations
Anerley	7	–
Bazley Beach	1	–
Durban North	12	–
Eshowe	9	–
Glenwood	8	–
Hibberdene	1	–
Margate + Uvongo	15	9
Marina Beach	–	1
Melville	15	–
Mtwalume	3	–
Munster	7	–
Oslo Beach	8	–
Park Rynie	7	1
Pendale + Pennington + Kelso	37	5
Port Edward	–	8
Port Shepstone	–	5
Ramsgate	1	23
Scottburgh	15	1
Seapark	24	–
Sezela	2	–
Shelly Beach	7	3
Southbroom	4	4
St. Michael's on Sea	7	–
Sunwich Port	8	3
Trafalgar	3	–
Umgeni Park	7	–
Umkomaas	5	–
Umtentwini	16	9
Virginia	1	1
Westville	86	3
Winkelspruit + Warner Beach	5	2

Status of wild populations

The majority of the surveyed wild populations were observed as naturalized given that the plants were self-sustaining (i.e. reproducing), healthy and in large numbers.

This is a problem of great concern because these populations are wild (i.e. they are currently not managed) and therefore require active management. We found a total of 76 invasion foci requiring management across KZN with their extent of occurrence ranging from 1 m^2 to 3,383 m^2 within a population to a total occupancy area of 25,660.20 m^2 across all populations. Invasion foci were defined by populations that are clearly distinct containing the parent and/or initial site of introduction. For example, a garden population and the adjacent land in which the plants escaped reflected one invasion foci.

Abundance (i.e. the number of stems) varied widely across the populations, with sites comprising 3–34,011 plants. The total abundance across all sites was estimated at 186,667 individual stems (this can be interpreted as the estimated number of plants). Given the extent and abundance of the species, we classify *E. aureum* as category E under the Blackburn scheme (Blackburn *et al.*, 2011b). This category classifies *E. aureum* as a fully invasive species since there are several invasion foci comprising self-sustaining individuals that are distributed across a wide area.
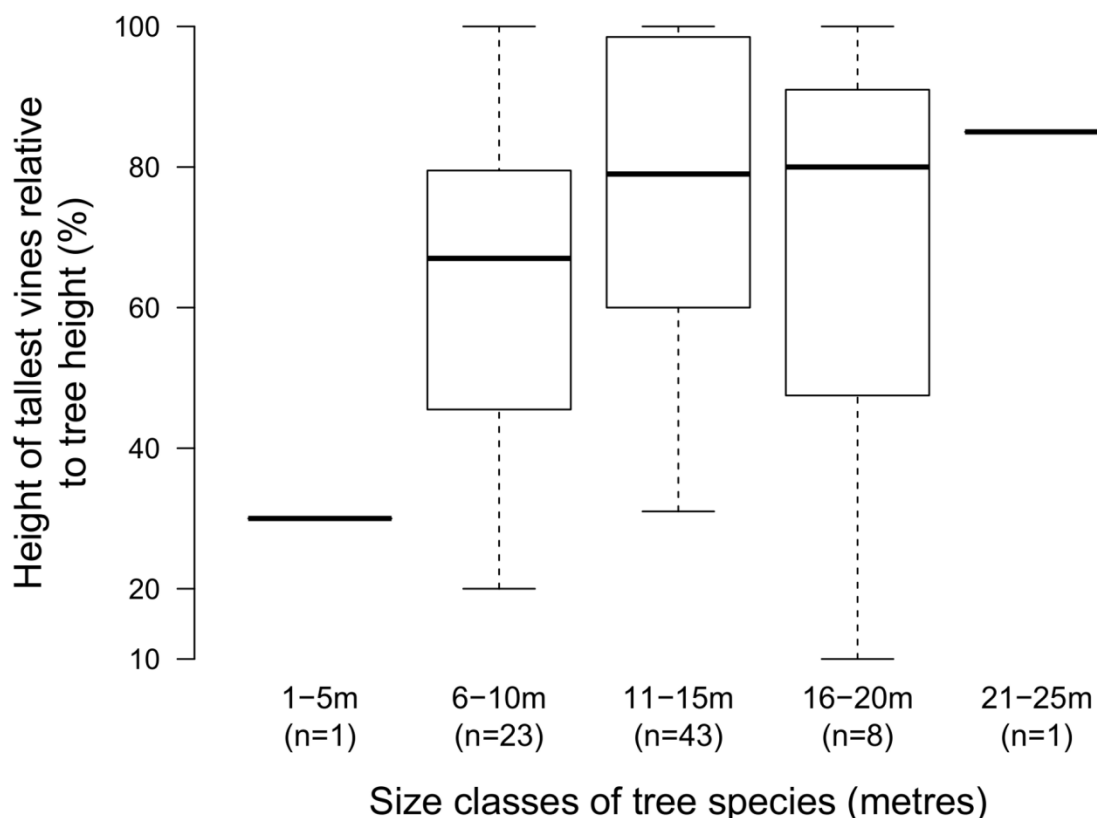
Fig. 3.1. Boxplot showing the relationship between the heights of the tallest vines relative to the heights of the supporting trees across 76 of the 77 populations surveyed. One population was supported by a boundary wall and therefore not included. Tree height was categorized according to size classes with population sample sizes shown in parentheses: 1–5 m (n = 1), 6–10 m (n = 23), 11–15 m (n = 43), 16–20 m (n = 8), 21–25 m (n = 1). The box is the interquartile range, and the bold centre line is the median.

The height of *E. aureum* also varied across populations (Fig. 3.1). Most of the populations comprised plants that were growing on trees ranging from 6 to 10 m (30%), 11–15 m (57%), and 16–20 m (11%). Of concern is that many populations consist of vines that have already reached the canopy. Furthermore, we observed that *E. aureum* does not have any preference for the support structures they climb. The species climbs up anything in its path, native or alien plant species, telephone poles, light poles and walls (Fig. 3.2A–C). When no structures were available to climb, *E. aureum* rapidly grows on the ground with a dense cover of its variegated foliage.

Fig. 3.2. Examples depicting the behaviour of *E. aureum* populations outside cultivation. **A)** Plants escaping from a garden and spreading in the neighbouring transformed vegetation, **B)** plants climbing up electricity poles, **C)** plants covering a telephone box, **D)** dense stands of *E. aureum* as a result of dumping garden refuse, and **E)** an additional example of illegal dump sites as a major source of *E. aureum* populations.

In South Africa, naturalized populations of *E. aureum* were primarily found in land-use types associated with some level of disturbance (Fig. 3.3). A chi-square goodness of fit test revealed a significant difference across the seven disturbance types and the number of *E. aureum* populations (x^2 = 98.63, df = 6, *P* < 0.001). This also demonstrates that the species can succeed across a range of land-use types. Furthermore, when comparing all land use types, significantly more populations were present in wastelands and this is a result of the disposal of garden cuttings (Fig. 3.2D–E). Thus, wastelands are a major source of *E. aureum* populations and characterize habitats in which the species flourishes. Garden escapees and roadsides also contributed significantly to the naturalization of *E. aureum*

populations. Of concern is the one population growing in natural vegetation and this population already covers a large area. Since we only found one population in natural vegetation this may represent an anomaly, however if left unmanaged, this could portray the future (i.e. many naturalized populations overgrowing natural vegetation).
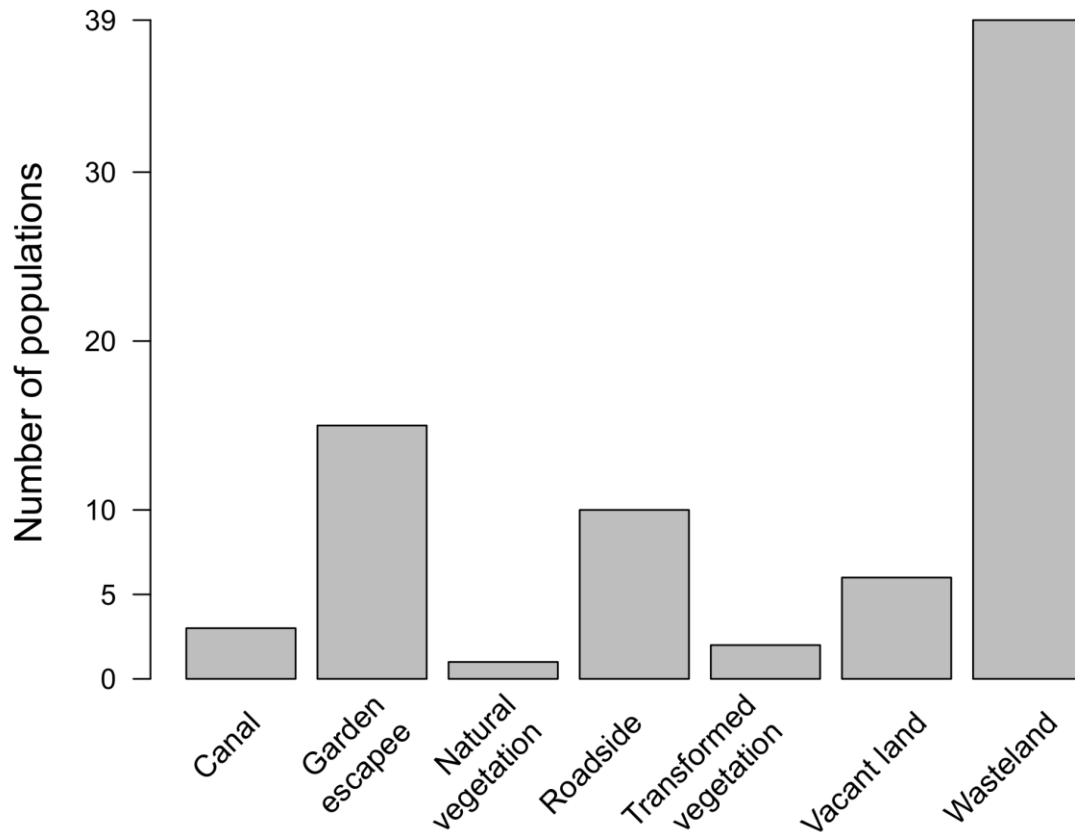

Fig. 3.3. Bar plot depicting land-use types in which *E. aureum* populations have naturalized.

Potentially suitable climatic areas for *E. aureum*

The average testing AUC value across the 10 iterations of the MaxEnt model was 0.967 ± 0.0156 (± standard deviation) which indicates good model performance for predicting suitable climatic conditions for *E. aureum*. The major contributors to invasion risk in descending order included minimum temperature of the coldest month (39.0730%) annual precipitation (33.546%), mean temperature of the coldest quarter (23.606%), and mean temperature of the wettest quarter (3.775%).

Based on model projections, many coastal tropical and sub-tropical regions provide suitable habitats for the species (Fig. 3.4A), including large parts of Mexico, Brazil, Angola, South Africa through to Mozambique and up to Kenya extending inland, India, Vietnam, and Australia (Queensland). The most climatically suitable islands for *E. aureum* include the Bahamas, Hawaii, Madagascar, Réunion Island, New Caledonia and several islands in Southeast Asia.

In South Africa, potential climatic suitability for *E. aureum* was largely restricted to the Indian Ocean coast (Fig. 3.4B). Projected habitat suitability occurs from Cape St. Francis in the Eastern Cape to KZN and its two neighbouring countries (Swaziland and Mozambique). Suitability also extends inland into the Mpumalanga and Limpopo provinces. On the southern Cape and west coast, Knysna and the Cape Peninsula were projected to be climatically suitable. Although we did not expect this region to be suitable, we must include it as a high risk region because both areas are home to National Parks. In addition, the entire predicted range includes many coastal towns within South Africa that are not yet known to be colonized. As such, there is a potential for further spread within South Africa, as well as, across the borders into Swaziland and Mozambique. This further highlights high priority locations for early detection and invasion control.
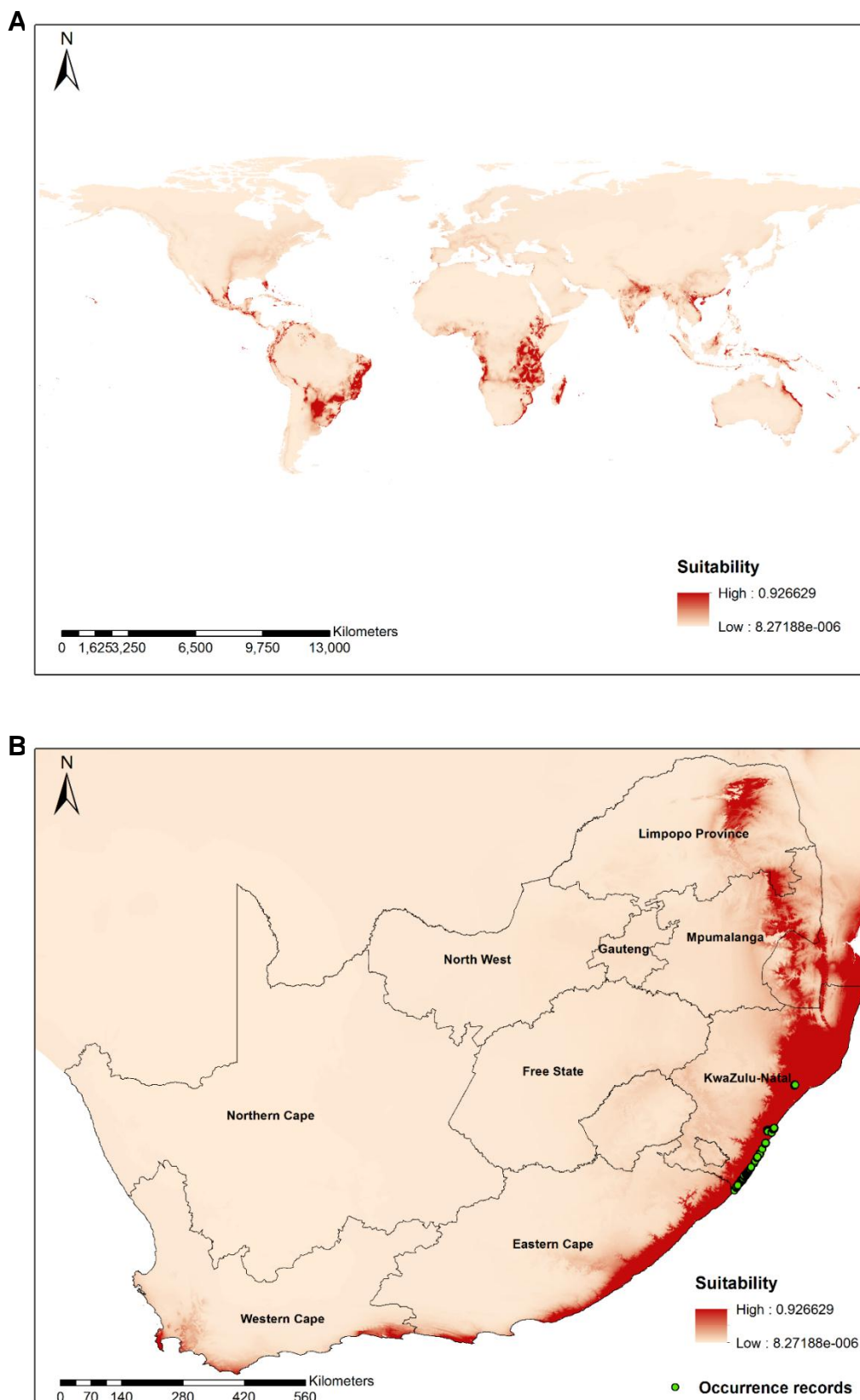
Fig. 3.4. Average suitability map showing the potential distribution of *E. aureum*, **A)** globally and **B)** zoomed into South Africa, based on existing occurrence data and climate variables modelled using MaxEnt. The maps represent an average of 10

replicates created using the subsampling method. The scale is a logistic probability with values between 0 (low probability; light shading) and 1 (high probability; darker shading).

Weed risk assessment

We were able to complete the A-WRA for *E. aureum*, answering 39 of the 49 questions (Table 3.2). Main gaps of knowledge correspond to reproductive characteristics (5 unanswered questions). This scheme predicted *E. aureum* to have a high probability of invasion in South Africa with a resulting score of 9. Consequently, pre-border screening should deny species entry into South Africa. Moreover, the environmental sector has a higher risk of impacts by *E. aureum* than the agricultural sector. The domestication of the species, climatic suitability, invasion history, weedy growth habit, high species densities, and vegetative propagation, pre-adapts *E. aureum* to becoming invasive. In addition, these characteristics suggest that *E. aureum* is likely to have profound negative impacts similar to other invasive vines (Blaustein, 2001; Pavlovic and Leicht-Young, 2011; *et al.*Yurkonis and Meiners, 2004; Zhang *et al.*, 2004).

Table 3.2. Australian weed risk assessment for *Epipremnum aureum*.

Question	Answer	Score	Possible scores
1.01 Is the species highly domesticated?	y[a]	-3	0 or -3
1.02 Has the species become naturalized where grown?	y[b]	1	-1 or 1
1.03 Does the species have weedy races?	n[c]	-1	-1 or 1
2.01 Species suited to South African climates	1[d]	1	0, 1 or 2
2.02 Quality of climate match data (0-low; 1-intermediate; 2-high)	2[d]	2	0, 1 or 2
2.03 Broad climate suitability (environmental versatility)	n[d]	0	0, 1 or 2
2.04 Native or naturalized in regions with tropical or subtropical climates	n[e]	0	0 or 1
2.05 Does the species have a history of repeated introductions outside its natural range?	y[f]	1	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.01 Naturalized beyond native range	y[d]	1	Refer to "lookup" table (Appendix 2) from

Pheloung *et al.*, 1999

3.02 Garden/amenity/disturbance weed	y[g]	1	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.03 Weed of agriculture/horticulture/forestry	y[h]	2	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.04 Environmental weed	y[c]	2	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.05 Congeneric weed	y[g]	1	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
4.01 Produces spines, thorns or burrs	n[d]	0	0 or 1
4.02 Allelopathic	n[c]	0	0 or 1
4.03 Parasitic	n[c]	0	0 or 1
4.04 Unpalatable to grazing animals	[f]		-1 or 1
4.05 Toxic to animals	y[a]	1	0 or 1
4.06 Host for recognised pests and pathogens	y[i]	1	0 or 1
4.07 Causes allergies or is otherwise toxic to humans	y[j]	1	0 or 1
4.08 Creates a fire hazard in natural ecosystems	n[c]	0	0 or 1
4.09 Is a shade tolerant plant at some stage of its life cycle	y[k]	1	0 or 1
4.10 Grows on infertile soils	y[k]	1	0 or 1
4.11 Climbing or smothering growth habit	y[l]	1	0 or 1
4.12 Forms dense thickets	y[m]	1	0 or 1
5.01 Aquatic	n[h]	0	0 or 5
5.02 Grass	n[h]	0	0 or 1
5.03 Nitrogen fixing woody plant	n[h]	0	0 or 1
5.04 Geophyte	n[h]	0	0 or 1
6.01 Evidence of substantial reproductive failure in native habitat	n[c]	0	0 or 1
6.02 Produces viable seed	[f]		-1 or 1
6.03 Hybridises naturally	[f]		-1 or 1
6.04 Self-fertilisation	[f]		-1 or 1

6.05 Requires specialist pollinators	[f]		0 or -1
6.06 Reproduction by vegetative propagation	y[n]	1	-1 or 1
6.07 Minimum generative time (years)	[f]		-1, 0, or 1
7.01 Propagules likely to be dispersed unintentionally	y[d]	1	-1 or 1
7.02 Propagules dispersed intentionally by people	y[d]	1	-1 or 1
7.03 Propagules likely to disperse as a produce contaminant	n[c]	-1	-1 or 1
7.04 Propagules adapted to wind dispersal	n[n]	-1	-1 or 1
7.05 Propagules buoyant	n[c]	-1	-1 or 1
7.06 Propagules bird dispersed	[f]		-1 or 1
7.07 Propagules dispersed by other animals (externally)	[f]		-1 or 1
7.08 Propagules dispersed by other animals (internally)	[f]		-1 or 1
8.01 Prolific seed production	n[f]	-1	-1 or 1
8.02 Evidence that a persistent propagule bank is formed (>1 yr)	n[f]	-1	-1 or 1
8.03 Well controlled by herbicides	y[d]	-1	-1 or 1
8.04 Tolerates or benefits from mutilation, cultivation or fire	y[a]	1	-1 or 1
8.05 Effective natural enemies present in South Africa	[f]		-1 or 1

[a]Meshram, A. and Srivastava, N. 2014. Molecular and physiological role of Epipremnum aureum. International Journal of Green Pharmacy. 8: 73-76; [b]PIER. Pacific Island Ecosystems at Risk, http://www.hear.org/pier/species/epipremnum_pinnatum_cv_aureum.htm, accessed February 2016; [c]No evidence; [d]This paper; [e]http://mobile.floridata.com/Plants/Araceae/Epipremnum%20aureum/1210; [f]Unknown; [g]Global compendium of weeds, http://www.hear.org/gcw/species, accessed February 2016; [h]Boyce, P., 2004. A review of Epipremnum (araceae) in cultivation. Aroideana 27, 199-205; [i]Wick, R.L. and Dicklow, M.B. 2002. Epipremnum, a new host for *Phytophthora capsici*. Plant Disease 86 (9): 1050; [j]Spoerke, D.G. and Smolinske, S.C. 1990. Toxicity of houseplants.CRC Press, Florida; [k]https://edis.ifas.ufl.edu/fp194, accessed March 2016; [l]https://plantdatabase.kpu.ca/plant/plantDetail/54, accessed March 2016; [m]Nyanatusita, B., Dissanayake, R., 2013. Udawattakele: a sanctuary destroyed from within. Journal of the

Wildlife and Nature Protection Society of Sri Lanka 26; [n]http://aggie-horticulture.tamu.edu/syllabi/308/Lists/Fourth%20Edition/Epipremnumaureum.pdf, accessed March 2016.

Best management practices

The impacts of the control group (i.e. no treatment) on stem widths did not differ significantly to plants above the cut stem treatment (Fig. 3.5A). In both cases 35% of the plants had no change in their stem width while some of the plants continued to flourish (indicated by the 20% increase in stem width of the control group and 7% in cut treatment). However, although not significant, there was also some decrease in stem width (control group: 19% and the cut treatment: 11%). Interestingly, seeing as plants cut off from their roots were still able to grow and persist without any indication of new roots being produced, we can deduce that *E. aureum* does not only absorb nutrients from the soil but also from the air and/or stored reserves. The herbicide treatments were significantly superior since stem widths deteriorated by 47% after Clearout 360 (i.e. glyphosate) and 41% after the Kaput treatment (i.e. triclopyr and picloram). Furthermore, the herbicide treatments resulted in mortality of three plants during the trial (i.e. whole plants dropped to the ground with no chance of recovery).

The impacts of the treatments below the fresh cut stem showed a similar trend to the aerial part of the plant (Fig. 3.5B). However, Clearout 360 performed significantly better (56% decrease in stem width) on the roots of *E. aureum* than Kaput (31% decrease in stem width). Furthermore, triclopyr and picloram did not appear to be translocated into the roots because three weeks into the trial we observed growth of new shoots in plants treated with Kaput, but this was not observed in the glyphosate treatment.
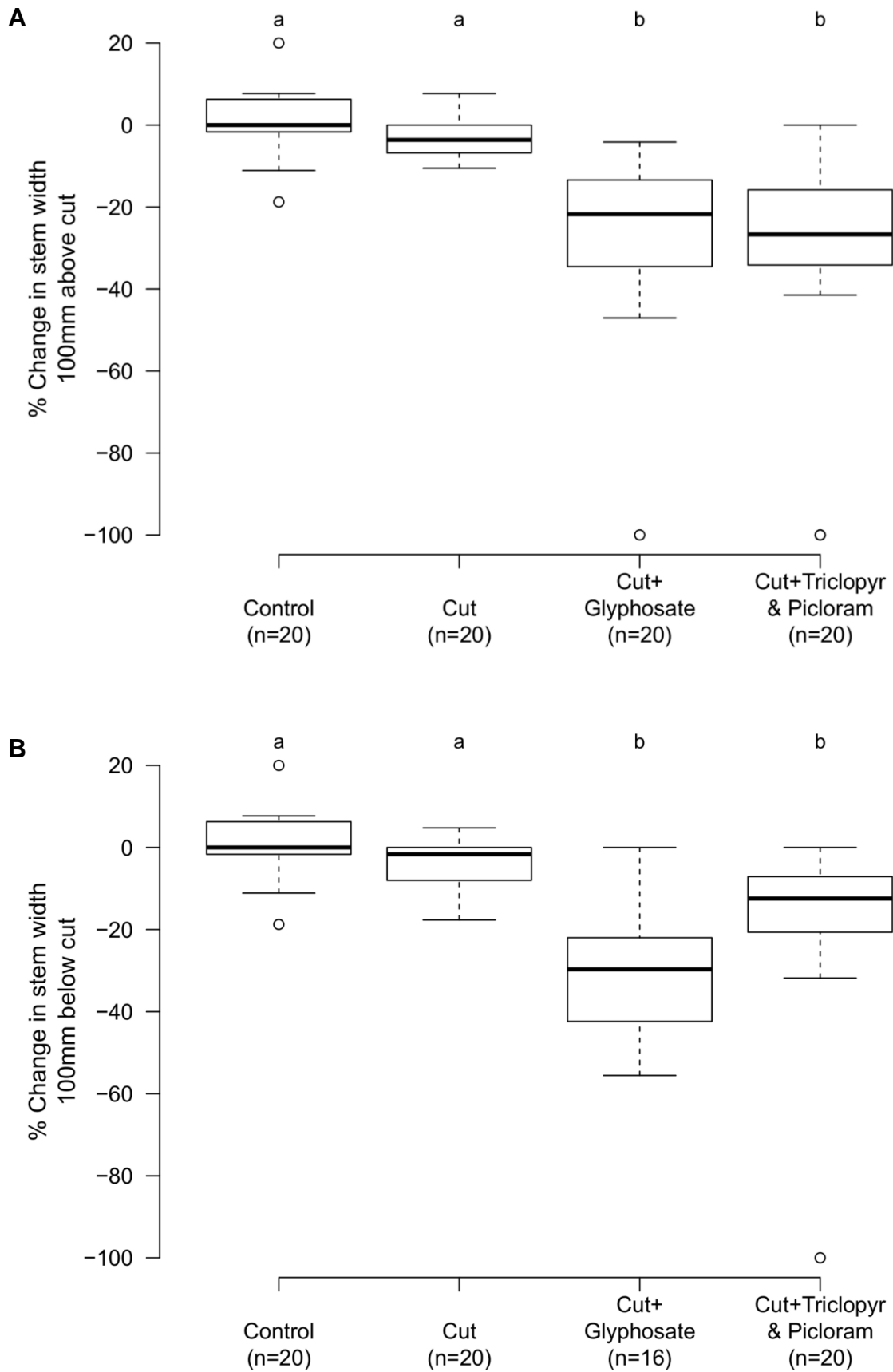
Fig. 3.5. Change in stem width **A)** 100 mm above the fresh cut and **B)** 100 mm below the fresh cut *E. aureum* plants. Stem width was measured across four

treatment groups during a six week trial. Boxplots display the median with a solid line, 25th and 75th percentiles in the lower and upper boxes, respectively, and the data range is indicated by the whiskers. Open circles indicate outliers (values > 1.5 times interquartile distance below 25th percentile). We used the non-parametric Kruskal-Wallis test to compare means ranks between treatment groups. Letters denote significance of the mean ranks ($P < 0.05$).

DISCUSSION

The most cost-effective strategy against IAS following post-border introductions is early detection and eradication when populations are small and localized. Following quantification of the spatial extent, abundance, competitive ability, potential for further spread into suitable habitats, and the high invasion risk of *E. aureum* it can be concluded that this evergreen climber poses a significant but currently manageable threat to biodiversity in the KZN province of South Africa. Our results suggest that it is possible to control naturalized populations of *E. aureum* because, although the species is spread across the coastal areas of the KZN province, the total condensed extent of occurrence (~3 hectares) and vine abundance (i.e. number of plant stems, ~187,000) are still low. For these reasons it is necessary to take action and manage the species in order to curb potential impacts on the ecosystem. We believe that containment is a viable strategy for managing *E. aureum* in South Africa.

During our field surveys (i.e. over a 2 year period) no flowers were seen, therefore reproduction and spread via seeds might be negligible. As a result, the more stems in a population, the higher the propagule pressure for establishment and spread. Propagule pressure is regarded as a major driver of invasive success of alien species (Colautti *et al.*, 2006; Lockwood *et al.*, 2005a; Simberloff, 2009), and our results on plant abundance also supports this hypothesis. This is based on the idea that increasing the number of individuals should increase the success of establishment. *Epipremnum aureum* grows rapidly and sustains its populations via vegetative reproduction and stem fragments. Therefore maintaining its populations with high plant numbers was expected.

Despite the thick stems (e.g. largest stem measured was 48 mm in diameter) and large leaves, this vine can still grow high into the canopies (e.g. tallest vine was 18

m). The maximum height that a species can reach is an indicator of its light capture strategy and competitive ability. Moreover, tall plants are associated with invasion success (Bucharova and Van Kleunen, 2009; Pyšek and Richardson, 2007). Climbing capacity enables climbers to ascend up to a height to compete for light and space and this facilitates their success as an invader (Paul and Yavitt, 2011). *Epipremnum aureum* thrives under high light conditions and therefore creeps, trails and clings around anything in its path. In doing so, the species shades out its competitors and monopolizes the light environment for photosynthesis (cf. Hejda *et al.*, 2009).

Epipremnum aureum is commonly grown as an ornamental plant in gardens, worldwide and in South Africa (for example, we found 321 cultivated populations in KZN, South Africa). Humans also contribute significantly to the spread of *E. aureum*, by dumping their garden waste in unmanaged spaces, illegal dumping sites, parks and natural areas, as well as allowing their garden plants to skip the fence. Seeing as invasive species often establish more frequently in disturbed rather than pristine habitats (Didham *et al.*, 2005), it is clear that anthropogenic disturbances exacerbate the threat of *E. aureum*. In the field we also observed a striking correlation between dump sites and numerous dense *E. aureum* populations. Being a vegetatively-propagated plant, *E. aureum* is able to rapidly spread and become established in dense monocultures on the ground, up the trees and telephone poles, and across walls and fences. Repeated patterns of human-mediated disturbances give alien plants a chance to establish and spread. Populations growing along roadsides were also common. Roads are particularly good corridors as they alter conditions, stress indigenous species, and allow easier access of humans as vectors of plant dispersal. They also have higher light conditions and bare soil, which favour alien plant establishment (Gelbard and Belnap, 2003; Mortensen *et al.*, 2009; Pauchard and Alaback, 2004). Therefore, management measures to reduce human disturbance need to be implemented. For example, increase awareness and knowledge of invasive plants within the community and encourage the disposal of garden waste through the local municipalities.

From a management point of view, it is imperative to identify areas that are not yet invaded but where early warning, detection, and control programmes can be

implemented. *Epipremnum aureum* has a wide potential distribution across the coastal regions of South Africa including numerous unoccupied regions by the species. In view of the fact that *E. aureum* has only been reported in KZN thus far, there is a high possibility of control and eradication. If not contained, there is a high invasion risk in the Eastern Cape, southern Cape and parts of the Mpumalanga and Limpopo regions which provides suitable habitats. Among many management activities, monitoring and mapping the occurrence of invasive species is important for control action. The model presented in this study can be used for informing management plans and guiding monitoring efforts in preventing further spread of *E. aureum* in South Africa.

Since *E. aureum* is already a problem in the KZN province, and given its high potential habitat suitability in regions that it is currently not known to occupy, it has a high potential to expand its range. Therefore control efforts of populations present in KZN must be prioritised. Mechanical control, by itself, of *E. aureum* is not feasible given the vines' abundance in a single population, thick stems and great heights reached on trees. In addition, although cutting weakened the plant, the vegetative nature and rapid growth of *E. aureum* allows the species to persist and quickly reoccupy the space. Hence, the problem is alleviated only temporarily. Fortunately, chemical control on cut stems proved successful in destroying plants.

Between the two chemicals tested, field observations and experiments indicate that glyphosate is more successful in affecting *E. aureum*. This treatment works from the canopy down to the ground seeing as both leaf chlorosis and the loss of stem turgor were observed in that order. The triclopyr and picloram treatment primarily affected the stems causing them to lose turgor and change colour. Therefore, chemical control is preferable to mechanical control and indicates promising potential for the control of *E. aureum*. Cost–benefit analyses of biological control programs usually show an overpowering economic justification for the use of biological control agents (De Clercq *et al.*, 2011; Olckers, 2004). However, for *E. aureum* biological control is probably not ideal since a) there is no tested agent available, b) effective chemical control methods are available, and c) most populations detected to date are accessible with low levels of spread.

CONCLUSION

Epipremnum aureum is a highly invasive species in Hawaii and many parts of Asia. In South Africa, given the large number of naturalized populations and the lack of records from the other provinces, the KZN province appears to be an invasion hotspot. The species has a high potential to become invasive under favourable conditions and therefore has a high risk of becoming invasive along the east and south coasts of South Africa. Although many of the populations comprise a large number of plants, herbicidal control appears to be effective and feasible.

To minimise the threat posed, we recommend that new plantings be prohibited and all populations outside cultivation (i.e. 78 naturalized populations) be controlled and ideally extirpated. However, given the fact that the species appears to be relatively limited in its dispersal ability, has no seed banks, and no chance of maintaining populations vegetatively if treated with herbicides, it might pose a manageable threat if allowed to remain on a property provided that the species is contained within the property. However, we recommend that the species should not be further propagated or sold (i.e. category 3 under South Africa's National Environmental Management: Biodiversity Act (10/2004) A&IS regulations).

ACKNOWLEDGEMENTS

REFERENCES

Alpert P, Bone E and Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52-66

Barbet-Massin M, Jiguet F, Albert, CH and Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many?. Methods in Ecology and Evolution, 3: 327-338.

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P and Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology 12: e1001850

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

Blaustein RJ (2001) Kudzu's invasion into Southern United states life and culture. In: McNeeley JA (ed) The great reshuffling: human dimensions of invasive alien species, pp 55-62, IUCN, Gland, Switzerland and Cambridge, UK

Boyce P (2004) A review of *Epipremnum* (Araceae) in cultivation. Aroideana 27: 199-205

Bucharova A and Van Kleunen M (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. Journal of Ecology 97: 230-238

Catford JA, Vesk PA, White MD and Wintle BA (2011) Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. Diversity and Distributions 17: 1099-1110

Center for invasive species and ecosystem health http://invasive.org/, accessed November 2013.

Colautti RI, Grigorovich IA and MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Conser C, Seebacher L, Fujino DW, Reichard S and DiTomaso JM (2015) The development of a Plant Risk Evaluation (PRE) tool for assessing the invasive potential of ornamental plants. PLoS ONE 10: e0121053

Davis MA (2009) Invasion biology. Oxford University Press, Oxford, UK

Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528-534

Dawson J, Oppel S, Cuthbert RJ, Holmes N, Bird JP, Butchart SHM, Spatz DR and Tershy B (2015) Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. Conservation Biology 29: 143-153

De Clercq P, Mason PG and Babendreier D (2011) Benefits and risks of exotic biological control agents. BioControl 56: 681-698

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224-231

Dela Cruz M, Christensen JH, Thomsen JD and Müller R (2014) Can ornamental potted plants remove volatile organic compounds from indoor air? - a review. Environmental Science and Pollution Research 21: 13909-13928

Didham RK, Tylianakis JM, Hutchinson MA, Ewers RM and Gemmell NJ (2005) Are invasive species the drivers of ecological change? Trends in Ecology & Evolution 20: 470-474

Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M and Williamson M (1989) Biological invasions: a global perspective. Wiley and Sons, New York

Elith J, Kearney M and Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330-342

eMonocot http://emonocot.org/, accessed August 2013.

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso A-C, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JRU, Zenetos A and Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. Bioscience 65: 769-782

Faulkner KT, Robertson MP, Rouget M and Wilson JRU (2014) A simple, rapid methodology for developing invasive species watch lists. Biological Conservation 179: 25-32

FLEPPC Florida Exotic Pest Plant Council, http://www.fleppc.org/list/2009/09list.htm, accessed February 2016.

Gelbard JL and Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17: 420-432

GISD Global invasive species database, http://www.issg.org/, accessed November 2013.

Gordon DR, Onderdonk DA, Fox AM and Stocker RK (2008) Consistent accuracy of the Australian Weed Risk Assessment system across varied geographies. Diversity and Distributions 14: 234-242

Groves RH, Panetta FD and Virtue JG (2001) Weed risk assessment. CSIRO Publishing, Collingwood

Hauser CE, Giljohann KM, Rigby M, Herbert K, Curran I, Pascoe C, Williams NSG, Cousens RD and Moore JL (2016) Practicable methods for delimiting a plant invasion. Diversity and Distributions 22: 136-147

HEAR Hawaiian ecosystems at risk project, http://www.hear.org/plants/, accessed November 2013.

Hejda M, Pyšek P and Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97: 393-403

Henderson L (2007) Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia. 37: 215-248

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10-18

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

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W and Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45: 403-414

Kolar CS and Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204

Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer G, Vilà M and Nentwig W (2015a) Comparing impacts of alien plants and animals in Europe using a standard scoring system. Journal of Applied Ecology 52: 552-561

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kuhn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A and Winter M (2015b) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. BioScience 65: 55-63

Lambdon PW, Lloret F and Hulme PE (2008) How do introduction characteristics influence the invasion success of Mediterranean alien plants? Perspectives in Plant Ecology Evolution and Systematics 10: 143-159

Lockwood JL, Cassey P and Blackburn TM (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20: 223-228

Mack RN and Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. BioScience 51: 95-102

Mazza G, Tricarico E, Genovesi P and Gherardi F (2014) Biological invaders are threats to human health: an overview. Ethology Ecology & Evolution 26: 112-129

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C and Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299-314

McNeely J (2001) Invasive species: a costly catastrophe for native biodiversity. Land Use and Water Resources Research 1: 1-10

Meunier G and Lavoie C (2012) Roads as corridors for invasive plant species: new evidence from smooth bedstraw (*Galium mollugo*). Invasive Plant Science and Management 5: 92-100

Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, Pitman A, Hemmings FA and Leishman MR (2009) Global patterns in plant height. Journal of Ecology 97: 923-932

Moodley D, Procheş Ş and Wilson JRU (2016) A global assessment of a large monocot family highlights the need for group-specific analyses of invasiveness. AoB PLANTS 8: 1-14

Moore JL, Runge MC, Webber BL and Wilson JRU (2011) Contain or eradicate? Optimizing the management goal for Australian acacia invasions in the face of uncertainty. Diversity and Distributions 17: 1047-1059

Mortensen DA, Rauschert ESJ, Nord AN and Jones BP (2009) Forest roads facilitate the spread of invasive plants. Invasive Plant Science and Management 2: 191-199

Nentwig W (2007) Biological invasions. Springer-Verlag, Berlin Heidelberg, 446 pp

Nyanatusita B and Dissanayake R (2013) Udawattakele: a sanctuary destroyed from within. Journal of the Wildlife and Nature Protection Society of Sri Lanka 26: 38-47

Olckers T (2004) Targeting emerging weeds for biological control in South Africa: the benefits of halting the spread of alien plants at an early stage of their invasion. South African Journal of Science 100: 64-68

Panetta FD and Lawes R (2005) Evaluation of weed eradication programs: the delimitation of extent. Diversity and Distributions 11: 435-442

Parendes LA and Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conservation Biology 14: 64-75

Pauchard A and Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. Conservation Biology 18: 238-248

Paul GS and Yavitt JB (2011) Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. Botanical Review 77: 11-30

Pavlovic NB and Leicht-Young SA (2011) Are temperate mature forests buffered from invasive lianas? Journal of the Torrey Botanical Society 138: 85-92

Pheloung PC, Williams PA and Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57: 239-251

Phillips SJ and Dudik M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31: 161-175.

PIER Pacific Island Ecosystems at Risk, http://www.hear.org/pier/species/epipremnum_pinnatum_cv_aureum.htm, accessed February 2016.

Pimentel D (2011) Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton

Pyšek P, Chytrý M and Jarošik V (2010) Habitats and land use as determinants of plant invasions in the temperate zone of Europe. Oxford University Press, Oxford, 66-79 pp

Pyšek P, Jarošík V and Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. PLoS ONE 6: e24890

Pyšek P and Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological Invasions, pp 97-125, Springer, Berlin.

Pyšek P and Richardson DM (2010) Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35: 25-55

R Development Core Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reichard SH and Hamilton MA (1997) Predicting Invasions of Woody Plants Introduced into North America. Conservation Biology 11: 193-203

Reichard SH and White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103-113

Rejmánek M, Richardson DM and Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (ed) Vegetation Ecology, pp 332-355, Blackwell Publishing,, Oxford

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

Rouget M, Richardson DM, Nel JL, Le Maitre DC, Egoh B and Mgidi T (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. Diversity and Distributions 10: 475-484

Rouget M, Robertson MP, Wilson JRU, Hui C, Essl F, Rentería JL and Richardson DM (2016) Invasion debt - quantifying future biological invasions. Diversity and Distributions 22: 445-456

Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40: 81-102

Sithole J and Nzama S (2012) Silver vine: watch out for a new potential weed on the southcoast of KwaZulu-Natal. SAPIA NEWS: Invasive Aroids, pp 1-5, ARC-Plant Protection Research Institute, Pretoria

Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO and Rouget M (2005) Niche-based modelling as a tool for prediciting the risk of alien plant invasions at a global scale. Global change biology 11: 2234-2250

Tobin PC, Blackburn LM, Gray RH, Lettau CT, Liebhold AM and Raffa KF (2013) Using delimiting surveys to characterize the spatiotemporal dynamics facilitates the management of an invasive non-native insect. Population Ecology 55: 545-555

VanDerWal J, Shoo LP, Graham C and Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know?. Ecological Modelling 220: 589-594

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1-16

Weber E and Gut D (2004) Assessing the risk of potentially invasive plant species in central Europe. Journal for Nature Conservation 12: 171-179

Westoby M, Falster DS, Moles AT, Vesk PA and Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33: 125-159

Wilson JR, Panetta FD and Lindgren C (2017) Detecting and responding to alien plant incursions. Cambridge University Press, 286 pp

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 and Zenni RD (2014) A standardized set of metrics to assess and monitor tree invasions. Biological Invasions 16: 535-551

Wilson JRU, Ivey P, Manyama P and Nänni I (2013) A new national unit for invasive species detection, assessment and eradication planning. South African Journal of Science 109: 1-13

Wilson JRU, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L and Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13: 11-22

Xu Z, Wang L and Hou H (2011) Formaldehyde removal by potted plant-soil systems. Journal of Hazardous Materials 192: 314-318

Yurkonis KA and Meiners SJ (2004) Invasion impacts local species turnover in a successional system. Ecology Letters 7: 764-769

Zhang LY, Ye WH, Cao HL and Feng HL (2004) *Mikania micrantha* H. B. K. in China – an overview. Weed Research 44: 42-49

Chapter 4: Invasion dynamics of a horticultural vine, *Monstera deliciosa*: what drives the successes and failures of invasions?

ABSTRACT

To understand the success of invading species, knowledge on factors driving invasiveness is needed. Here, we look at *Monstera deliciosa* (Araceae) and its relatives in a South African and global context. First, we explore the subfamily Monsteroideae to assess whether attributes related to introduction history influences the invasion status of species. Next, we classify the invasion risk of *M. deliciosa* in South Africa using a weed risk assessment and species distribution models. Lastly, using a local scale study, we identify potential conditions under which *M. deliciosa* can become naturalized. Overall, Monsteroideae species that have been introduced for a longer period of time, and those that have been introduced to several new regions have a significantly higher likelihood of becoming naturalized and invasive. *Monstera deliciosa* was ranked as having a high impact risk in South Africa and also modelled to have a wide potential global distribution. On a local scale, naturalization success was driven by warm temperatures and sufficient water. However, despite the risk, we conclude that *M. deliciosa* will not become a rampant invader based on the fact that the species already had a sufficiently long minimum residence time and high propagule pressure in South Africa and in several currently occupied regions globally, yet there are no records of invasiveness or impacts. Even if the species becomes invasive under ideal conditions, it can be controlled manually. As such, *M. deliciosa* can be recommended to the horticultural trade, landscaping sector and gardeners.

Keywords

Biological invasion, green list, horticulture, low risk, Monsteroideae, time lag

INTRODUCTION

The growing magnitude of worldwide interconnectedness through globalization has intensified the flow of trade, transport, and travel. Consequently, this increased mobility of people and their goods removes natural barriers between and across ecosystems. This facilitates the introduction of new species to ecosystems, as well as, intensifies the spread of invasive alien species (IAS) through intentional or accidental introductions (Hulme, 2009; McNeely, 2001b; Meyerson and Mooney, 2007a; Perrings *et al.*, 2010). In addition, IAS are now widely cited as the second greatest global threat to biodiversity. Therefore, understanding the factors that facilitate or limit invasions is an important step towards predicting and managing invasive species, and ultimately conserving biodiversity.

For a species to become invasive, it must be: introduced deliberately or unintentionally through human activities to an area where it is not native; resistant enough to survive in the new area; establish self-sustaining populations; disperse; and spread (Blackburn *et al.*, 2011a; Richardson *et al.*, 2000a). However, not all species become invasive when introduced to novel systems. Only a proportion of species introduced to novel systems become naturalized, and of those, a small subset spread and become invasive (Richardson and Pyšek, 2006a; Williamson and Fitter, 1996). Although only a small percentage of species become invasive, their negative impacts (i.e. ecological, economic, and/or social impacts) can be extensive, and over time causes substantial damage which requires high control costs (Mack *et al.*, 2000; Pimentel, 2011; Pimentel *et al.*, 2005; Vilá *et al.*, 2010). For that reason urgent action is required.

Furthermore, although many introduced species fail to become invasive (e.g. Bufford and Daehler, 2014; Copp *et al.*, 2007; Miller *et al.*, 2007; Reichard and Hamilton, 1997; Rejmánek and Richardson, 1996; Young, 2015), there are many studies looking at species that were able to persist and comparatively fewer studies that have addressed the issue of failed invasions. Instances of failed invasions can highlight factors that limit the expansion of an invasive species (Lonsdale, 1999; Zenni and Nuñez, 2013). This type of knowledge will further our understanding of biological invasions and also identify species with a low invasion risk that can be recommended for introduction.

Identifying and prioritizing pathways of introduction is major component of managing biological invasions (McGeoch *et al.*, 2016). Species introduced for horticulture, ornamental use in particular, are dominating invasion pathways worldwide (Dehnen-Schmutz and Touza, 2008; Ööpik *et al.*, 2013; Reichard and White, 2001; Richardson and Rejmánek, 2011). The invasion success of plants introduced via this pathway is a result of importers selecting plants with specific characteristics that inadvertently also match characteristics associated with invasiveness (Bucharova and Van Kleunen, 2009; Dehnen-Schmutz *et al.*, 2007b). Furthermore, ornamentals that are marketed at a good price also influence invasion success. For example, Dehnen-Schmutz *et al.* (2007b) showed that species marketed at low prices and species that were regularly available in the 19th and 20th centuries were strong predictors of the current range of alien plants in Britain. Lastly, the high number of introduction events and the nurturing of plants by gardeners also enable species to overcome the various barriers to invasion (Kowarik, 2003).

Preventing biological invasions is the most cost-effective and efficient approach, however, if the IAS has already been introduced, then early detection and management become important to prevent establishment. As a general rule, it is understood that under certain conditions any widely planted species will have a greater likelihood of becoming naturalized and invasive, even more so, when species have been introduced long ago. Introduction history has been identified as an important driver of invasiveness because it usually influences a high propagule pressure (Cassey *et al.,* 2004; Colautti *et al.*, 2006; Lockwood *et al.*, 2005b; Simberloff, 2009; Von Holle and Simberloff, 2005) and sufficiently long residence time (Dehnen-Schmutz *et al.*, 2007a; Phillips *et al.*, 2010; Pyšek and Jarošík, 2005; Wilson *et al.*, 2007) which are significant drivers of invasion. In addition, introduction history as a correlate of invasiveness (i.e. residence time in particular) also facilitates invasiveness in alien vines (Harris *et al.*, 2007).

Another challenge in invasion biology, which led to the premise of this study, is to understand the patterns and conditional nature of invasions. Across the spectrum of species introduced to novel systems there are; species that clearly become a problem; species that will not become a problem; and a unique category of species that fall somewhere in between – widely planted but not yet a major invader. This

unique pattern may be explained by a poorly studied species, *Monstera deliciosa* Liebm., which is widely planted yet it has seemingly minimal records of being invasive.

Although *M. deliciosa* is our focal case study species, we first selected the subfamily Monsteroideae to assess whether attributes related to introduction history influences the invasion status of species within this clade. Residence time is one of the most important correlates of vine invasiveness (Harris *et al.*, 2007). The reasoning behind this is that species that are present for a longer time have a higher probability of spreading more propagules and forming new populations (Wilson *et al.*, 2007). Propagule pressure has also been identified as one of the most consistent predictors of invasiveness (Colautti *et al.*, 2006; Simberloff, 2009). Species that are introduced across a wider area in a new environment have a better chance of landing in localities that are suitable for establishment (Lockwood *et al.*, 2005b). Therefore, to identify whether species that are introduced into more regions have a greater chance of becoming invasive, we used the number of introduced regions as a proxy for propagule pressure. Additionally, a species' continent of origin is another important predictor associated with introduction history (Zenni, 2014). This attribute takes into account the chance of dispersal by humans from particular source areas.

We then explore these trait findings to unravel possible explanations of the global status of *M. deliciosa*. Next, at a regional scale, we aim to classify the invasion risk of *M. deliciosa* in South Africa using a weed risk assessment and species distribution models. Finally, on a local scale, we describe potential conditions under which *M. deliciosa* can become invasive.

MATERIALS AND METHODS

Study species

Monstera deliciosa, commonly known as the Swiss cheese plant, is an evergreen climber native to tropical moist forests in Mexico, Costa Rica, Guatemala, Honduras, Nicaragua, and Panama (eMonocot, http://emonocot.org/, accessed August 2013). This climber has been recorded to reach 20 m or more in height, often depending on the height of the support structure, and can also form a dense mat on the ground when unsupported. *Monstera deliciosa'*s attractive large leaves and tolerance of

shade and humidity make it one of the most widely cultivated ornamental plants (Madison, 1977). *Monstera deliciosa* is now grown in most of the warm countries of the world (temperate and tropical regions) as a potted indoor plant or as a garden plant. However, it has only been recorded as naturalized in a few regions, and is surprisingly not a major invader (Table 4.1).

Table 4.1. List of introduced regions where *M. deliciosa* is grown and its associated invasion status. This list relies on published literature and online databases. Searches used for identifying the relevant literature and databases were undertaken online using the following combination of terms in Google: *M. deliciosa* was used in conjunction with "grown", "cultivated", "alien", "exotic", "introduced", "naturalized", "invasive", "impact".

Region	Year of record	Status	Reference
Ascension	2005	Introduced	Varnham, K. 2005. Non-native species in UK Overseas Territories: a review. JNCC Report 372. Peterborough, United Kingdom
Australia	1991	Introduced	Global Compendium of Weeds (GCW). http://www.hear.org/gcw/species/monstera_deliciosa/, accessed September 2016
Azores	–	Naturalized	Delivering Alien Invasive Species In Europe (DAISIE). http://www.europe-aliens.org/speciesFactsheet.do?speciesId=717#, accessed September 2016
Bermuda	2005	Introduced	Varnham, K. 2005. Non-native species in UK Overseas Territories: a review. JNCC Report 372. Peterborough, United Kingdom

California	2002	Introduced	Jepsen, E.P.B., and Murdock, A.G. 2002. Inventory of native and non-native vegetation on John Muir national historic site, Eugene O'Neill national historic site, and Port Chicago national monument, http://www.sfnps.org/download_product/2 606/0, accessed September 2016
England	1752	Introduced	http://floridata.com/Plants/Araceae/Monste ra+deliciosa/794, accessed November 2016; http://edis.ifas.ufl.edu/hs311, accessed November 2016
Florida	1976	Introduced	Morton, J.F. 1976. Pestiferous spread of many ornamental and fruit species in south Florida. Proceedings of the Florida State Horticultural Society, 89: 348-353
Galapagos	2004	Naturalized	Global Compendium of Weeds (GCW). http://www.hear.org/gcw/species/monstera _deliciosa/, accessed September 2016
Hawaii	2010	Introduced	Benitez, D.M., R. Loh, T. Tunison, N.G. Zimmer, J. Makaike, R. Mattos and M. Casali. 2012. The distribution of invasive plant species of concern in the Kīlauea and Mauna Loa strip areas of Hawai'i Volcanoes National Park, 2000-2010. Technical Report No. 179. The Hawai`i-Pacific Islands Cooperative Ecosystem Studies Unit & Pacific Cooperative Studies Unit, University of Hawai`i, Honolulu, Hawai`i. 120 pp.
India	1878	Introduced	http://edis.ifas.ufl.edu/hs311, accessed November 2016

London	–	Introduced	http://www.clifton.co.uk/cg-monstera_deliciosa.htm, accessed November 2016
Madeira	2002	Naturalized	Delivering Alien Invasive Species In Europe (DAISIE). http://www.europe-aliens.org/speciesFactsheet.do?speciesId=717#, accessed September 2016
Mediterranean	2012	Introduced	Heywood, V.H. 2012. The role of New World biodiversity in the transformation of mediterranean landscapes and culture. Bocconea 24: 69-93
Motuora Island, Hauraki Gulf	2006	Introduced	Heiss-Dunlop, S., and Fillery, J. 2006. Vascular flora of Motuora Island, Hauraki Gulf. Auckland Botanical Society Journal, 61(2): 113-120
Pitcairn Islands	2009	Introduced	Varnham, K. 2009. Non-native species in UK Overseas Territories: an updated review. JNCC Report 372. Peterborough, United Kingdom
Puerto Rico	2000	Introduced	Global Compendium of Weeds (GCW). http://www.hear.org/gcw/species/monstera_deliciosa/, accessed September 2016
Saint Helena	2005	Introduced	Varnham, K. 2005. Non-native species in UK Overseas Territories: a review. JNCC Report 372. Peterborough, United Kingdom
Singapore	1877	Introduced	http://edis.ifas.ufl.edu/hs311, accessed November 2016
South Africa	1989	Naturalized	Henderson, L. 1989. Invasive alien woody plants of Natal and the north-eastern Orange Free State. Bothalia 19(2): 237-261

| Spain | – | Introduced | Delivering Alien Invasive Species In Europe (DAISIE). http://www.europe-aliens.org/speciesFactsheet.do?speciesId=717#, accessed September 2016 |
| New Zealand | – | Naturalized | Howell, C. 2008. Consolidated list of environmental weeds in New Zealand. DOC Research & Development Series 292. Department of Conservation, Wellington. 42 pp.; Global Compendium of Weeds (GCW). http://www.hear.org/gcw/species/monstera_deliciosa/, accessed September 2016 |

Global introduction history of Monsteroideae

To assess whether introduction history drives invasiveness in this subfamily we only looked at species that are introduced but not yet naturalized versus naturalized and invasive species. This included a total of 42 species belonging to 9 genera (Moodley *et al.*, 2016a). Since we usually do not know exactly when a species was introduced, we used minimum residence time (MRT) based on the year in which the first herbarium specimen was collected. We estimated MRT using the formula 2016-x, with x being the earliest introduced record of the species and 2016 being the current year. Herbarium records were obtained from the Global Biodiversity Information Facility (http://www.gbif.org/, accessed September 2016) and Tropicos (http://www.tropicos.org, accessed September 2016). We identified the species' continent of origin by first obtaining their countries of origin using eMonocot and then assigning them to Africa, Asia, Australia/Oceania, Europe, North America, and South America. The number of introduced regions were extracted from a recently complied Araceae database (Moodley *et al.*, 2016a).

Statistical Analysis

To explore whether minimum residence time, country of origin, and the number of introduced regions (i.e. explanatory variables) influences the invasion status (i.e.

response variable) of introduced Monsteroideae, a one-way analysis of variance (ANOVA) or the non-parametric alternative (Kruskal-Wallis rank sum test) were used. The ANOVA was used if the data satisfied the following assumptions: observations are independent; have a normal distribution; and scores in different groups have homogeneous variances (i.e. minimum residence time and country of origin). We used the Kruskal-Wallis rank sum test when the assumptions were violated (i.e. number of introduced regions). All statistical analyses were performed in R (version 3.3.1, R Development Core Team, 2016).

Weed risk assessment of *M. deliciosa* in South Africa

One of the most popular screening tools to date is the Australian Weed Risk Assessment (A-WRA), which consists of 49 questions that categorizes the risk of species becoming invasive (Pheloung *et al.*, 1999b). The questions focus on biogeography, biology/ecology, and undesirable plant attributes, and the answers are scored from least likely (−3) to most likely (5). Several studies demonstrated the consistency and accuracy of the A-WRA in predicting invaders (Daehler *et al.*, 2004; Gassó *et al.*, 2010; Gordon *et al.*, 2008b; Gordon *et al.*, 2008c; Křivánek and Pyšek, 2006). Hence, we selected this screening protocol. In our study, questions related to geography and climate, were modified to reflect the conditions of South Africa. Suitability of species to Australian climate was changed to suitability to South African climate (question 2.01) and native or naturalized in regions with extended dry periods was changed to native or naturalized in regions with tropical or subtropical climates (question 2.04). Species are identified as potentially high risk and rejected for import if the score is > 6, potentially low risk and accepted for import if the score is < 1, and species with intermediate scores (1–6) are recommended for further evaluation.

Potential global distribution of *M. deliciosa* based on climate

We used the widely accepted maximum entropy model (MaxEnt version 3.3.3k) to predict the probability of *M. deliciosa* occurrence and map its potential geographic distribution (Phillips *et al.*, 2006). MaxEnt estimates the probability distribution of a species based on the maximum entropy principle by comparing environmental conditions and associated presence records to background points (Elith *et al.*, 2011;

Phillips and Dudík, 2008). This software was implemented in R (version 3.3.1, R Development Core Team, 2016).

Occurrence records, background data and environmental layers

We downloaded georeferenced occurrence records from both the native and introduced ranges because this distribution encompassed the most realistic estimation of *M. deliciosa's* climate niche. We also downloaded georeferenced records for two closely related introduced *Monstera* species (i.e. *Monstera obliqua* Miq. and *Monstera punctulata* (Schott) Schott ex Engl.) to use as background data (i.e. pseudo-absence). These two species were native to the same regions as *M. deliciosa*. This method is referred to as target group sampling and is recommended over randomly generated background points because it accounts for sampling bias (Phillips *et al.*, 2009). All records were downloaded from GBIF (http://www.gbif.org/) using the package rgbif (Chamberlain *et al.*, 2016). We used the "getData" function from the raster package (Hijmans, 2016) to download bioclimatic data from the WorldClim database at a spatial resolution of 10 arc-minutes. This database provides climatic data averaged over the years 1950–2000.

The 19 climatic variables were reduced through pair-wise correlation to avoid multicollinearity among these variables (Kendall rank correlation coefficient < 0.65), as suggested by Elith *et al.* (2010). We chose annual mean temperature as our primary predictor variable because *M. deliciosa* grows best between 20–30°C and is killed by frost (Lim, 2011). Subsequent variable selection was based on predictors with the lowest pair-wise correlations. The resulting variables included four predictors; two temperature (annual mean temperature, temperature annual range (i.e. maximum temperature of the warmest month - minimum temperature of the coldest month)) and two rainfall (annual precipitation, precipitation seasonality) variables. Lastly, the biogeo package (Robertson, 2016) was used for data cleaning and this involved removing fossil records, duplicates within 10' grid cells, points in the sea, points that do not have environmental data, as well as pseudo-absences with the same coordinates as presence points. In addition, *M. deliciosa* records present in areas that experience frost, such as in Europe and the United States of America, were also removed to ensure data reliability. This resulted in 210 occurrences and 390 pseudo-absences.

Model building and evaluation

We used the dismo package (Hijmans *et al.*, 2016) to build the model using the occurrence records mentioned above and 10,000 pseudo-absence records. Pseudo-absence data are used in lieu of observed absence data to define environmental conditions in which the species has not been recorded. This means that biased sampling can influence the accuracy of the model (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009). Therefore, MaxEnt assumes that species occurrence data are unbiased (Phillips *et al.*, 2006). As such, we limited the spatial extent from which MaxEnt could select pseudo-absence points to locations within 2 degree (i.e. ~240 kilometres) of occurrence records (Merow *et al.*, 2013). Bias in occurrence records was further addressed by producing a bias grid derived from a Gaussian kernel density map of the occurrence locations (Elith *et al.*, 2010).

MaxEnt was run using only linear, quadratic and hinge features. This reduces the chances of model overfitting and results in smoother response curves, as well as, models that are focussed on the strongest trends in the data (Elith *et al.*, 2010; Merow *et al.*, 2013). Models were trained using a randomly selected 70% of the data (both occurrences and pseudo-absences) and model accuracy was then tested on the remaining 30%. This process was repeated 100 times in order to account for variability in model performance arising from the selection of training and testing data. From this, we received training and testing area under the receiver operating characteristic curve (ROC) values, also known as AUC. The AUC value is a widely used measure of model performance and is interpreted as the probability that a randomly selected pair of occupied and unoccupied sites are correctly predicted (Elith *et al.*, 2006). Values range from 0 to 1, and values > 0.9 indicate high accuracy, values of 0.7–0.9 indicate good accuracy, and values < 0.7 indicate low accuracy (Swets, 1988). Lastly, since the regularization coefficient in Maxent (β) can impact on model predictions, we set the model to explore different values for β and select a model based on the best AUC value (Merow *et al.*, 2013).

Model projection

We used the raw output from MaxEnt to predict the potential distribution of *M. deliciosa* based on climatic suitability. Using the raw output is preferable to the logistic transformation output since it is based on the probability of climatic suitability

(Merow *et al.*, 2013). The final MaxEnt output provides a calculation of the percent contribution each variable has on the model building process and also reveals a surface with a continuous climatic suitability gradient with values ranging from 0 (least suitable) to 1 (most suitable).

A qualitative assessment of an invasive population in the Limpopo Province, South Africa

Only two entries of *M. deliciosa* populations in South Africa are recorded in the Southern African Plant Invader Atlas (Henderson, 2007). This database lists one population in the KwaZulu-Natal Province, with no additional information provided, and the other in the Limpopo province. Hence, we could only follow up one the Limpopo record. This record was lodged in 2012 and describes the population as a garden escapee that is invading the moist high-rainfall southern slopes of the Soutpansberg Mountain. The garden, surrounding the main house and originally created by the first landowner, is situated within the lajuma research centre high up in the Soutpansberg mountain range. Lajuma has been declared a natural heritage site and comprises a variety of veld types, including montane forests and grasslands, and a remarkable diversity of plants and animals.

Field work in 2016 for this study involved mapping the extent of this garden population and evaluating reasons for its spread. The extent was determined by calculating the area of a convex hull drawn around the most outlying points in ArcGIS 10.4. Spread was measured by identifying the initial plantings by the landowners and then mapping the plants expansion. Given the ruggered terrain, surveys were conducted by foot along the roads, trails and fence lines in the reserve in order to track every plant in the garden, as well as those which may have escaped into the surrounding reserve. Because this was a qualitative assessment of the first detected naturalized population, we were more interested in the land use type, whether the area was managed, modes of spread, and the total area of spread.

RESULTS

Global introduction history of Monsteroideae

The Monsteroideae subfamily comprises 362 species belonging to 9 genera. Out of these, 39 species (11%) have been introduced but are not yet naturalized and 3

species (0.82%) have become naturalized or invasive (Fig. 4.1A, Appendix 9). Species that have been introduced over a longer period of time were more likely to naturalize and invade in their new region (F (1, 31) = 6.41, P = 0.017) (Fig. 4.1B). The most common native continent for introduced Monsteroideae was the American continent (n = 21), followed by Asia (n = 8) and Oceania (n = 7) (Fig. 4.1C). However, continent of origin was not significantly related to invasion status (F (4, 37) = 0.81, P = 0.52). Species that were introduced into more regions had a higher incidence of naturalizing and invading than those that were introduced into fewer regions (X^2 = 10.98, df = 1, P = 0.00091) (Fig. 4.1D).
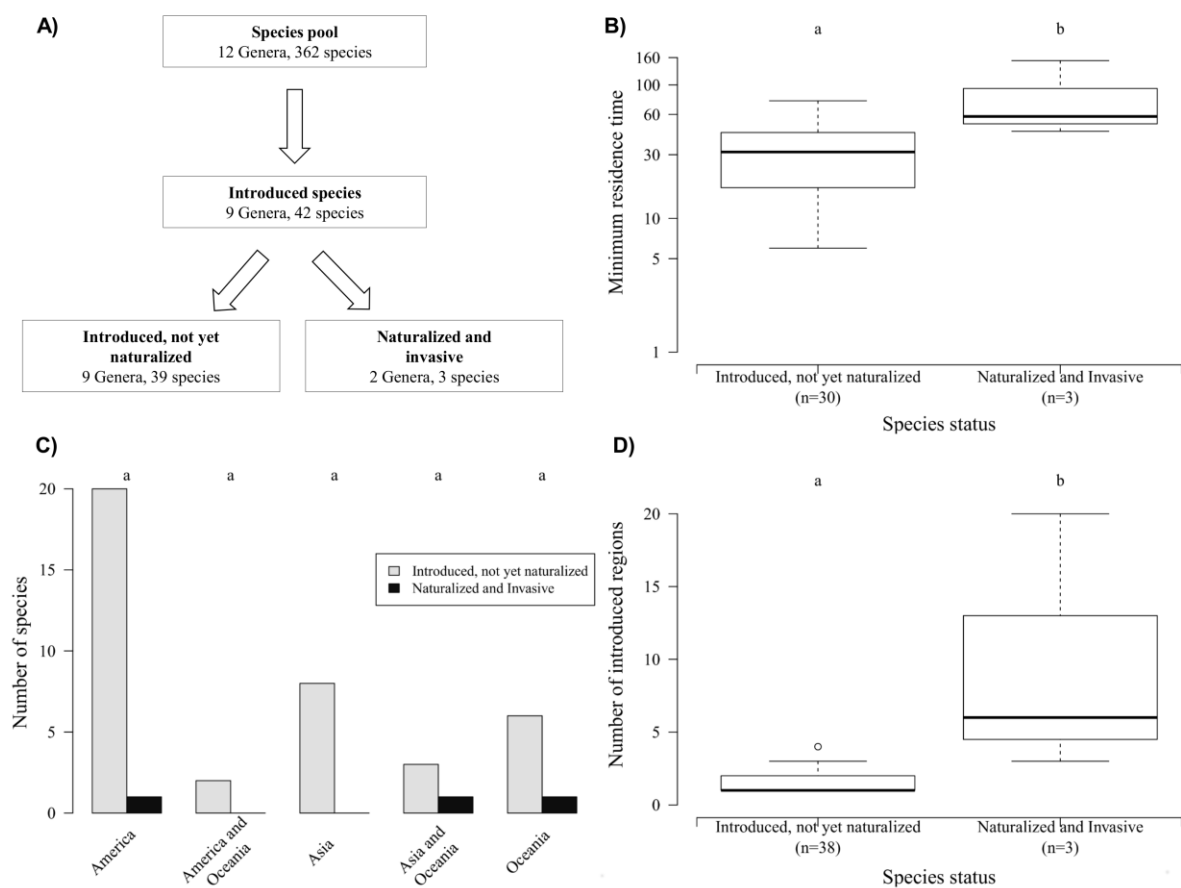
Fig. 4.1. Factors associated with invasion success in Monsteroideae. **A)** a narrative on the introduction history of the species pool; **B)** the minimum residence time; **C)** country of origin; and **D)** number of introduced regions. Different lower-case letters denote significant differences (P < 0.05) amongst invasion categories.

Weed risk assessment of *M. deliciosa* in South Africa

Out of the 49 questions in the weed risk assessment, 39 were answered based on published literature and online databases (Appendix 10). *Monstera deliciosa* scored a total of 7 points, with the biology/ecology of the species contributing the most to the total score. This score portrays a high probability of invasion and would have resulted in the species being rejected in a pre-border evaluation. In addition, we also attempted to perform an impact-based risk assessment following the generic impact scoring system (Nentwig *et al.*, 2016). However, this scoring system relies on published evidence of environmental and socio-economic impact and after searching the literature we could not find any reports of impact.

Potential global distribution of *M. deliciosa* based on climate

The MaxEnt model exhibited a high degree of predictive accuracy (AUC = 0.90 ± 0.0041 95% CI). *M. deliciosa* occurrence is predicted across much of the tropical countries and a few temperate countries. In particular, Mexico (the species' native range), the west coast of the United States, Hawaii, Chile, parts of Argentina and Brazil, England, Ireland, Spain, France, Italy, southern Africa, Madagascar, Iran, Nepal, Bhutan, west coast of India, parts of Southeast Asia, large parts of China, south Korea, Japan, Taiwan, Australia, and New Zealand (Fig. 4.2). Analysis of variable contribution indicates that among the four climatic parameters, annual mean temperature was the most influential predictor of *M. deliciosa* occurrence (84.8%), followed by temperature annual range (9.4%), precipitation seasonality (3.8%), and annual precipitation (2%). In addition, the relationship between the most influential predictor (annual mean temperature) and probability of occurrence is bell shaped (Appendix 11). This indicates reduced suitability as the annual mean temperatures shift from the optimums of 10–20 °C. This is particularly observable in the lowest and highest temperature ranges. Additionally, suitable climate ranges for the remaining variables comprised regions experiencing 12–28 °C as their temperature annual range; an increasing trend was observed for precipitation seasonality with a spike in regions receiving more than 110 mm of rain seasonally; and the likelihood of suitability increased in regions experiencing 1,000–4,000 mm of rain annually but suitability decreased in regions experiencing more than 4,000 mm of rain which could be indicative of winter rainfall regions.
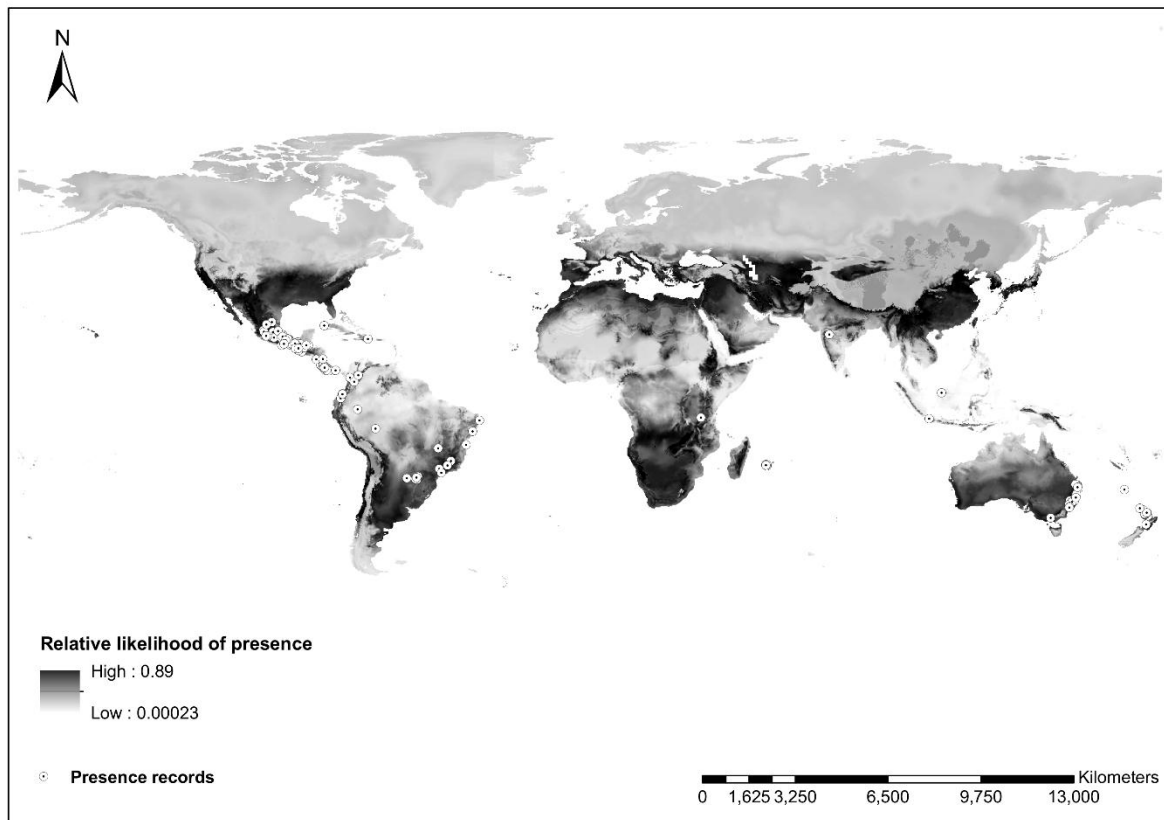
Fig. 4.2. Predicted global distribution of *M. deliciosa* based on occurrences in both its native and introduced ranges. Occurrences are indicated by white dots and projected presences are shown on a gradient from dark shading (high suitability) to white shading (low suitability).

A qualitative assessment of an invasive population in the Limpopo Province, South Africa

A densely scattered population was found growing and spreading at the site, covering approximately 1.4 ha (Fig. 4.3). The garden was established in 1948 at this site and *M. deliciosa* is believed to be grown here since the creation of the garden (68 years ago, I. Gaigher, pers. comm.). This species is now the dominant plant in the garden (Fig. 4.4). The plants have moved outside the garden through dispersal by vegetative means which is occurring at a very slow rate since they are currently not too far from the garden area. The garden has a lot of trees and is therefore suitable to support the growth and spread of *M. deliciosa* within the garden, and the dense clusters of trees in the Bushveld surrounding the garden also provide sufficient host structures. This site also receives a lot of shade since most of the plants were under 40–80% shade.

97
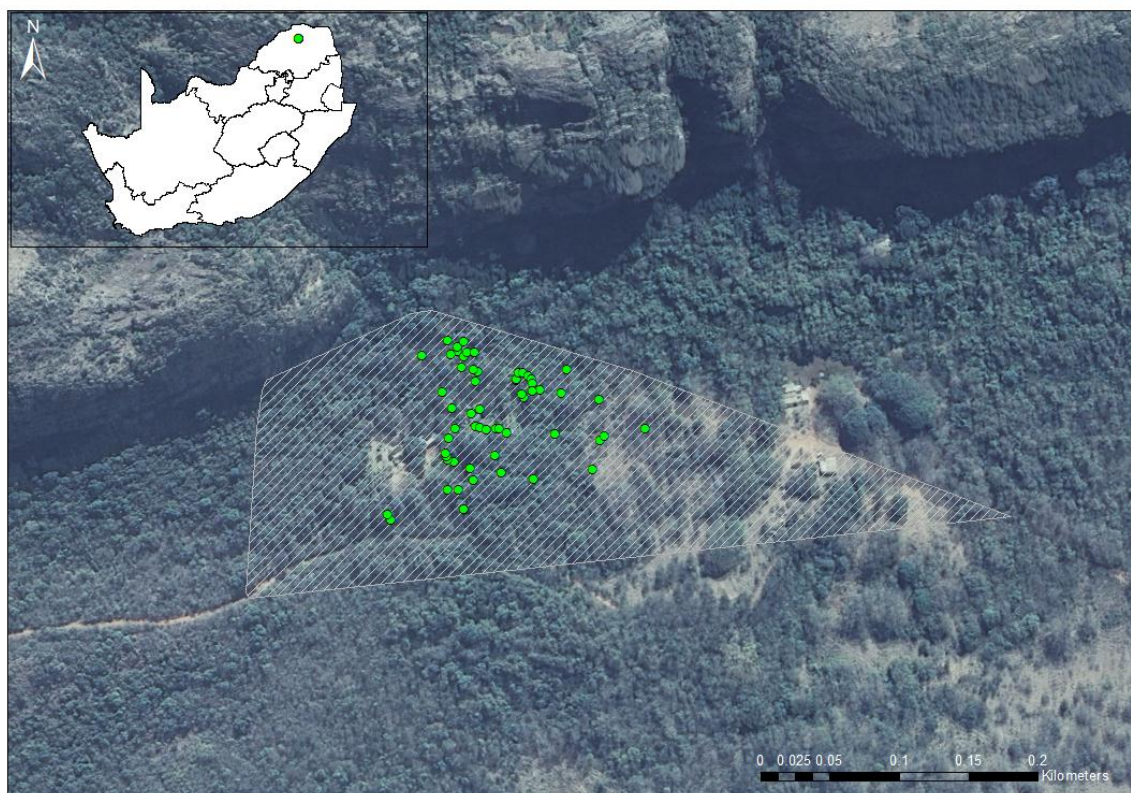
Fig. 4.3. The naturalized *M. deliciosa* population on the Soutpansberg Mountains in the Limpopo province, South Africa. The striped area represents the total area surveyed (~59331.50 m^2) and the green dots depicts where we found the plants.

On the northern slopes of the garden (i.e. dry soils) we observed that *M. deliciosa's* distribution clearly follows an irrigation system occurring along the garden just outside the garden fence. On the southern slopes (i.e. wetter soils), the plants are much more abundant and dense and they are slowly moving downhill vegetatively, but the plants are only concentrated along the waterway. Over the years the landowner has tried to restrict the plants to the garden and commented that manual removal of the plants is effective. *M. deliciosa* can be cleared by chopping off the base stem and removing the rooted base, as well as, removing any aerial roots hanging down. The rest of the plant will then slowly die in the trees and/or on the ground.

Fig. 4.4. *Monstera deliciosa* in Limpopo, South Africa. **A)** Climbing 10 m high, **B)** aerial roots growing downward out of the thick stems and taking root where they touch the ground, **C)** creeping densely on the ground, and **D)** showing off its massive leathery leaves with deep splits and oblong holes.

DISCUSSION

Many different mechanisms promoting invasions have been proposed, however recent studies have shown that invasions are context dependent (González-Moreno *et al.*, 2014; Kueffer *et al.*, 2013; Perkins and Nowak, 2013; Pyšek *et al.*, 2012). These context dependent effects include interactions between climate, species traits, introduction history, conditions of the local habitat, and human activity. We support the argument that many cases are different, but strongly advocate that future research which aims to identify factors facilitating plant invasions should focus on species in particular functional groups (Moodley *et al.*, 2013; Moodley *et al.*, 2016a; Novoa *et al.*, 2015).

In general, species within the Monsteroideae subfamily are likely to naturalize and become successful invaders if they have been introduced for a longer period of time. The likelihood of alien species becoming naturalized increases with residence time because the longer a species is present in a specific region, more propagules can be produced and dispersed (Pyšek and Jarošík, 2005; Pyšek *et al.*, 2011). Additionally, Monsteroideae species that are introduced to several new regions are more likely to overcome the naturalization and invasion barriers. This can be attributed to species having a better chance of landing in localities that are suitable for establishment if they are introduced across a wider area (Lockwood *et al.*, 2005b). Similar patterns have been reported for other alien flora (Dawson *et al.*, 2009; Moodley *et al.*, 2013; Trueman *et al.*, 2010). Even though *M. deliciosa* possesses these introduction history traits, it is not considered a major invader.

Monstera deliciosa has a high impact risk in South Africa. This is largely driven by the species' intrinsic traits and undesirable attributes in particular (e.g. toxicity, climbing growth habit, tolerates infertile soils and shade). This suggests that intrinsic traits which have been shown to drive invasiveness are not sufficient, and *M. deliciosa* requires additional interactions to overcome the invasion barriers.

Globally, the species is generally present in climatic regions that are moderately to highly suitable (Fig. 4.2). In addition, *M. deliciosa* has a wide potential geographical range. Therefore, it is possible that the species may become an invader with impacts if introduced to regions that have highly suitable climatic conditions but are currently unoccupied by the species (i.e. such as Korea or Southwest China).

On a local scale we found that water availability was the most important limiting factor since the plants were confined around an irrigation system or a stream (i.e. human intervention). Additionally, though the population occurs in a moderately suitable region (50–70% relative likelihood of presence), human intervention was necessary to sustain the population. Furthermore, while the population is naturalized and spreading within the modified landscape, it is not yet widespread. Taking into consideration the naturalized status as well as the restricted spread, the population can be classified as D1 under the Blackburn scheme (Blackburn *et al.*, 2011a). This

status denotes that the population is self-sustaining with individuals surviving a significant distance from the original point of introduction.

Following an introduction event, many species are not immediately successful at establishing and it often takes a considerable amount of time for an invasive species to transition to an exponential growth phase in the new geographical area. Herbaceous invasive plants can show a delay in invasion in the order of decades (Pyśek and Prach, 1993). Initially, growth rate is seemingly slow, but after a trigger there may be rapid population expansion. This is either due to the slow initial phase of exponential growth from small populations or a true lag phase (Aikio *et al.*, 2010). Understanding this dynamic is critical for management success (Essl *et al.*, 2011; Wilson *et al.*, 2017).

The determinants for the naturalization success of *M. deliciosa* at the Limpopo site comprise a suite of characters. This includes the undesirable attributes, climatically suitable regions, and a continuous source of water, which was facilitated by human-mediated opportunities in the Limpopo population. In the absence of these characteristics, populations remain in a lag phase. Similar aspects inducing a lag phase were identified for other taxa (Larkins, 2012).

Another example of a species that overcame a lag phase, even though it possessed all the traits of an invader, is *Banksia ericifolia*. This species required a trigger, such as disturbance, to influence the species establishment, growth and spread. A large population (n = 100 plants) in the Western Cape province, South Africa, had a sufficiently long residence time (35 years) but remained under the invasion radar until multiple fire events caused the population to spread rapidly and form dense monotypic stands (Geerts *et al.*, 2013). Consequently, this highlights that the lag phase is the best time to eradicate an invasive species population.

Using several examples, the role of failed invasions is also clearly demonstrated by a single species that can be highly invasive at one site and either fail or have minor impact at another (Zenni and Nuñez, 2013). However, much is still unknown on this crucial topic and such instances are often difficult to detect. Nevertheless, more detailed studies on invasion failures (e.g. why invasions are unsuccessful and what

changes in the natural landscape contribute to these failures) are required to advance our understanding of invasions.

Even though we identified several reasons why *M. deliciosa* should be invasive such as; widespread planting (globally and locally); non-reliance on pollinators and dispersal vectors in the introduced region due to vegetative reproduction; and a high likelihood of invasion risk, there is still a question of why *M. deliciosa* is in a lag phase and what will trigger an exponential phase. Species may establish in an area because they are better competitors than the resident species, but in order to become dominant, their competitive advantage must be persistent. We postulate that this is where *M. deliciosa* is failing. The species can become established and densified within a restricted area over a period of time, but its growth rate may be limiting its ability to spread fast enough. It is probable that given sufficient time and if left unmanaged the species may become an invader, however this should be explored in future studies.

CONCLUSION

Our analyses highlights that there are a number of characters, both of *M. deliciosa* (e.g. the species contains characteristics that pose a high invasion risk) and of the introduced habitats (e.g. warm temperatures and sufficient water) that increases the probability of the species naturalizing. However, even though these attributes favoured successful naturalization, the species is not a predominant invader. Moreover, when populations have naturalized it appears that manual control is effective and cost-efficient. Therefore, we recommend that *M. deliciosa* should not be regulated under South Africa's National Environmental Management: Biodiversity Act (10/2004) Alien and Invasive Species regulations. Given the sufficiently long minimum residence time, high propagule pressure, and no records of invasiveness or impacts elsewhere in the globe, we would also suggest that in many situations the species should be considered as "safe" and added to green lists of species that, despite lots of opportunities to invade, have never caused significant negative impacts (Dehnen-Schmutz, 2011).

REFERENCES

Aikio S, Duncan RP and Hulme PE (2010) Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos 119: 370-378

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

Bucharova A and Van Kleunen M (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. Journal of Ecology 97: 230-238

Bufford JL and Daehler CC (2014) Sterility and lack of pollinator services explain reproductive failure in non-invasive ornamental plants. Diversity and Distributions 20: 975-985

Cassey P, Blackburn TM, Sol S, Duncan RP and Lockwood JL (2004) Global patterns of introduction effort and establishment success in birds. Proceedings of the Royal Society of London Series B-Biological Sciences 271: S405-S408

Chamberlain S, Ram K, Barve V and Mcglinn D (2016) rgbif: Interface to the Global 'Biodiversity' Information Facility 'API'. R package version 0.9.4. https://CRAN.R-project.org/package=rgbif.

Colautti RI, Grigorovich IA and MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Copp GH, Wesley KJ, Verreycken H and Russell IC (2007) When an 'invasive' fish species fails to invade! Example of the topmouth gudgeon Pseudorasbora parva. Aquatic Invasions 2: 107-112

Daehler CC, Denslow J, Ansari S and Kuo H-C (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. Conservation Biology 18: 360-368

Dawson W, Burslem DFRP and Hulme PE (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. Journal of Ecology 97: 657-665

Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. Journal of Applied Ecology 48: 1374-1380

Dehnen-Schmutz K and Touza J (2008) Plant invasions and ornamental horticulture: pathway, propagule pressure and the legal framework. Floriculture, Ornamental and Plant Biotechnology Advances and Topical Issues, pp 15-21, Global Science Book, United Kingdom

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007a) A century of the ornamental plant trade and its impact on invasion success. Diversity and Distributions 13: 527-534

Dehnen-Schmutz K, Touza J, Perrings C and Williamson M (2007b) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224-231

Elith J, Kearney M and Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330-342

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE and Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17: 43-57

Elith JH, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT,

Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS and Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129-151

Essl F, Dullinger. S., Rabitsch W, Hulme PE, Hülber K, Jarošík V, Kleinbauer I, Krausmann F, Kühn I, Nentwig W, Vilà M, Genovesi P, Gherardi F, Desprez-Loustau M-L, Roques A and Pyšek P (2011) lllllSocioeconomic legacy yields an invasion debt. Proc Natl Acad Sci USA 108: 203-207

Gassó N, Basnou C and Vilá M (2010) Predicting plant invaders in the mediterranean through a weed risk assessment system. Biological Invasions 12: 463-476

Geerts S, Moodley D, Gaertner M, Le Roux JJ, McGeoch MA, Muofhe C, Richardson DM and Wilson JRU (2013) The absence of fire can cause a lag phase-the invasion dynamics of *Banksia ericifolia* (Proteaceae). Austral Ecology 38: 931-941

González-Moreno P, Diez JM, Ibáñez I, Font X and Vilà M (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions 20: 720-731

Gordon DR, Onderdonk DA, Fox AM and Stocker RK (2008a) Consistent accuracy of the Australian weed risk assessment system across varied geographies. Diversity and Distributions 14: 234-242

Gordon DR, Onderdonk DA, Fox AM, Stocker RK and Gantz C (2008b) Predicting invasive plants in Florida using the Australian weed risk assessment. Invasive Plant Science Management 1: 178-195

Harris CJ, Murray BR, Hose GC and Hamilton MA (2007) Introduction history and invasion success in exotic vines introduced to Australia. Diversity and Distributions 13: 467-475

Henderson L (2007) Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia. 37: 215-248

Hijmans RJ (2016) raster: Geographic Data Analysis and Modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster.

Hijmans RJ, Phillips S, Leathwick J and Elith J (2016) dismo: Species distribution modeling. R package version 1.1-1. https://CRAN.R-project.org/package=dismo.

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10-18

Kowarik I (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. Biological Invasions 5: 293-312

Křivánek M and Pyšek P (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). Diversity and Distributions 12: 319-327

Kueffer C, Pyšek P and Richardson DM (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist 200: 615-633

Larkins DJ (2012) Lengths and correlates of lag phases in upper-Midwest plant invasions. Biological Invasions 14: 827-838

Lim TK (2011) Monstera deliciosa in Edible Medicinal and Non-Medicinal Plants: Volume 1, Fruits. pp 252-256, Springer, Netherlands

Lockwood JL, Cassey P and Blackburn TM (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223-228

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536

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

Madison M (1977) A revision of Monstera (Araceae). Contributions from the Gray Herbarium of Harvard University: 3-100

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C and Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299-314

McNeely JA (2001) An introduction to human dimensions of invasive alien species. In: McNeely JA (ed) The great reshuffling: human dimensions of invasive alien species, pp 5-20, IUCN Switzerland

Merow C, Smith MJ and Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36: 1058-1069

Meyerson LA and Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5: 199-208

Miller AW, Ruiz GM, Minton MS and Ambrose RF (2007) Differentiating successful and failed molluscan invaders in estuarine ecosystems. Marine Ecology Progress Series 332: 41-51

Moodley D, Geerts S, Richardson DM and Wilson JRU (2013) Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. PLoS ONE 8: e75078

Moodley D, Procheş Ş and Wilson JRU (2016) A global assessment of a large monocot family highlights the need for group-specific analyses of invasiveness. AoB PLANTS 8: plw009

Nentwig W, Bacher S, Pyšek P, Vilà M and Kumschick S (2016) The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species. Environmental Monitoring and Assessment 188: 315

Novoa A, Le Roux JJ, Robertson MP, Wilson JRU and Richardson DM (2015) Introduced and invasive cactus species: a global review. AoB PLANTS 7: plu078

Ööpik M, Bunce RGH and Tischler M (2013) Horticultural markets promote alien species invasions: an Estonian case study of herbaceous perennials. NeoBiota 17: 19-37

Perkins LB and Nowak RS (2013) Invasion syndromes: hypotheses on relationships among invasive species attributes and characteristics of invaded sites. Journal of Arid Land 5: 275-283

Perrings C, Burgiel S, Lonsdale WM, Mooney H and Williamson M (2010) International cooperation in the solution to trade-related invasive species risks. Annals of the New York Academy of Sciences 1195: 198-212

Pheloung PC, Williams PA and Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57: 239-251

Phillips ML, Murray BR, Pyšek P, Pergl J, Jarošík V, Chytrý M and Kühn I (2010) Plants species of the Central European flora as aliens in Australia. Preslia 82: 465-482

Phillips SJ, Anderson RP and Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259

Phillips SJ and Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161-175

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J and Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19: 181-197

Pimentel D (2011) Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton

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

Pyšek P and Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit (ed) Invasive plants: ecological and agricultural aspects, pp 77-96, Birkhäuser Basel, Switzerland

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U and Vilà M (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

Pyšek P, Jarošík V and Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. PLoS ONE 6: e24890

Pyśek P and Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. Journal of Biogeography 20: 413-420

Reichard SH and Hamilton MA (1997) Predicting Invasions of Woody Plants Introduced into North America. Conservation Biology 11: 193-203

Reichard SH and White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103-113

Rejmánek M and Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655-1661

Richardson D and Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30: 409-431

Richardson D, Pyšek P, Rejmánek M, Barbour M, Panetta F and West C (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93-107

Richardson D and Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. Diversity and Distributions 17: 788-809

Robertson M (2016) biogeo: Point Data Quality Assessment and Coordinate Conversion. R package version 1.0. https://CRAN.R-project.org/package=biogeo.

Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40: 81-102

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240: 1285-1293

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

VanDerWal J, Shoo LP, Graham C and Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? . Ecological Modelling 220: 589-594

Vilá M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE and Daisie Partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8: 135-144

Von Holle B and Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86: 3212-3218

Williamson M and Fitter A (1996) The varying success of invaders. Ecology 77: 1661-1666

Wilson JR, Panetta FD and Lindgren C (2017) Detecting and responding to alien plant incursions. Cambridge University Press, 286 pp

Wilson JRU, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L and Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13: 11-22

Young SL (2015) When an invasive plant fails to invade. Frontiers in Ecology and the Environment 13: 450-451

Zenni RD (2014) Analysis of introduction history of invasive plants in Brazil reveals patterns of association between biogeographical origin and reason for introduction. Austral Ecology, 39: 401-407

Zenni RD and Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122: 801-815

Chapter 5: Synthesis

THEORY

This thesis uncovered patterns, processes and invasion risks of a very popular horticultural plant group, the Araceae, which is not well represented in the invasion biology literature. Comparable to other model groups (e.g. Australian acacias, Cactaceae, Eucalyptus, *Pinus* and Proteaceae), the global distribution of the Araceae has been radically changed by humans in the last few centuries. However, in contrast to these groups, very little is known about the invasion status of such a widely introduced family, as well as the determinants underlying species' introduction, naturalization and invasion. The findings presented in this thesis address these knowledge gaps and assist in developing management approaches. Each study evaluated determinants of invasions at different stages along the introduction-naturalization-invasion (INI) continuum. The following predictions were tested:

(i)   A taxonomic group approach which explores invasiveness across the INI continuum to reveal specific mechanistic correlates within the family, as well as correlates that similarly influence other model groups. To identify these correlates I created the first comprehensive species inventory of Araceae using databases and literature sources; described the invasion status of all species; identified whether factors associated with the native range characteristics, introduction dynamics and biological traits influenced INI success and whether this varied for different life forms; and predicted which species have the potential to become invasive in future (Chapter 2).

(ii)   Invasion history elsewhere and/or impact elsewhere are reliable predictors of potential invasiveness and invasibility (Blackburn *et al.*, 2014; Williamson, 1996; Wilson *et al.*, 2011). For that reason, the global invasive status of *Epipremnum aureum* incited an evaluation of the species' invasion risk and management in South Africa, and was also the first invasion study of this species. To determine the potential risk posed by *E. aureum*, I delineated the current distribution of the species in South Africa; described factors that have contributed to its successful invasion;

identified the threat *E. aureum* poses globally and in South Africa; tested best management practices to control the species; and provided a recommendation on regulating the species (Chapter 3).

(iii) Invasion failure can occur at any stage of the INI continuum (Blackburn *et al.*, 2011a; Zenni and Nuñez, 2013). Consequently, understanding why some alien plant species fail to become invasive provides insights on the relative importance of drivers of invasiveness and invasibility, and also help inform suitable management strategies. To unravel why *Monstera deliciosa* has failed to invade in much of its novel ranges, I assessed whether the popular hypotheses related to introduction history influences the invasion status of species within the Monsteroideae clade; and at a regional scale, I classified the invasion risk of *M. deliciosa* in South Africa; and on a local scale, I described potential conditions under which *M. deliciosa* can become naturalized (Chapter 4).

SUMMARY OF MAJOR FINDINGS

The Araceae conform to some, but not all, of the emerging generalizations in the invasion biology literature (Chapter 2; Table 5.1). My findings closely parallel those in many other studies; Araceae species that have been widely introduced (i.e. high propagule pressure) and which have large native range sizes were more likely to be invasive. However, unlike many other groups, there was little evidence of a link between invasiveness and regeneration mechanism (i.e. by seed, vegetative or both). Instead, there was a significant effect of plant life form and pollinator syndrome. Moreover, the importance of these factors varied across the INI continuum. I found that species classified as hydrophytes were more likely to overcome the introduction and naturalization barriers, and these species were mainly used as ornamentals. In addition, species requiring specialized pollinator types (e.g. flies and beetles) were able to overcome the invasion barriers, and this factor might be specific to Araceae. The type of habitat a species occupied in its native range was also an important correlate of introduction and naturalization success. Species native to humid regions, such as mediterranean forests and temperate mixed forests, were more likely to be introduced and become naturalized. Furthermore, I identified nine monophyletic groups that comprise species that are not currently invasive but have a high risk of becoming invasive in future, and I recommend a precautionary

approach be taken for these species. This includes species belonging to the following clades: *Alocasia*, *Amydrium*, *Ariopsis*, *Arum*, *Caladium*, *Cryptocoryne*, *Gymnostachys*, Lemnoideae, and *Peltandra*.

The global invasion patterns of *Epipremnum aureum* are mirrored in South Africa (Chapter 3; Table 5.1). In particular, the KwaZulu-Natal province of South Africa appears to be an invasion hotspot for *E. aureum*, with 78 naturalized populations and 321 cultivated populations. The naturalized populations consist of ~187,000 plants over ~3 hectares. Many of these extremely successful populations comprised plants as tall as the trees they were growing on, and were often found flourishing in dump sites, along roadsides or as a result of escaping cultivation. In addition, *E. aureum* has a high probability of expanding its current range along the coastal regions of South Africa, as well as, into neighbouring countries on Africa's eastern seaboard. Due to the invasion threat of the species, I recommend that all plants outside cultivation be removed, but current garden plantings could remain (though are not replaced). To control populations outside of cultivation, I found that applying herbicides to freshly cut stems effectively reduced plant growth. In view of that, I proposed that *E. aureum* should be listed as category 3 under South Africa's National Environmental Management: Biodiversity Act (10/2004) Alien and Invasive Species regulations, i.e. naturalized populations need to be managed, existing cultivated indivudals may remain, but the plant may not be propagated or sold in future.

It is well acknowledged that not all species become invasive when introduced to novel systems and the illustrious *Monstera deliciosa* distinctly falls into this category (Chapter 4; Table 5.1). Following an introduction event it often takes a considerable amount of time for an invasive species to transition to an exponential growth phase in the new geographical area. Globally, *M. deliciosa* has been subjected to a long period of time in the introduced regions, high propagule pressure, and suitable climatic conditions, while possessing undesirable species attributes, yet the species has not been documented as invasive, neither has there been any impacts. A qualitative local scale investigation of the only recorded naturalized population in South Africa, highlights that, invasions are in essence human driven. At the site in Limpopo the climate is suitable, the propagules are plentiful but the species only

spreads where a continual water supply is available, and this pattern follows the irrigation systems. Furthermore, the species can be removed manually which is a very efficient and cost effective means of control. Taking all aspects into account, the sufficiently long minimum residence time, high propagule pressure, and no records of invasiveness or impacts elsewhere, I recommended that *M. deliciosa* should not be regulated under South Africa's National Environmental Management: Biodiversity Act (10/2004) Alien and Invasive Species regulations, but should rather be considered as "safe" and added to green lists of species that, despite lots of opportunities to invade, have never caused significant negative impacts.

Table 5.1. Hypotheses evaluated in playing a role in Araceae invasions for each chapter and their associated traits tested. It is important to note that these findings vary across the INI continuum, as well as spatially and temporally. Empty cells indicate hypotheses not included in a chapter.

	Chapter 2	**Chapter 3**	**Chapter 4**
Species			
1. Tens rule	15% of the species pool have been introduced, of which 10% have naturalized, and 70% of the naturalized species are invasive	–	–
2. Traits of an ideal weed	The number of native floristic regions (i.e.proxy for native range size), life form (e.g. hydrophytes), pollinator type, native floristic	Growth habit (climbing and creeping), height, and vegetative reproduction	Continent of origin

	regions (e.g. Polynesia), flower sexuality, habitat type (e.g. Mediterranean forests and temperate mixed forests), and the number of uses		
3. Propagule pressure	The number of introduced regions (i.e. proxy for propagule pressure)	The number of stems in a population (i.e. proxy for propagule pressure)	The number of introduced regions (i.e. proxy for propagule pressure)
4. Residence time	–	–	Minimum residence time (i.e. the year in which the first herbarium specimen was collected)

Sites

1. Resource availability	–	Habitat suitability (i.e. temperature and precipitation)	Habitat suitability (i.e. temperature and precipitation) and water supply
2. Disturbances	–	Land-use types (i.e. canal, garden escapee, natural vegetation, open area, roadside, transformed	–

vegetation,

vacant land or

wasteland)

Pathways

1. Intentional release	Phytoremediation	–	–
2. Escape from containment	Agroforestry, food source, fibre production, horticulture, and medicine	Cultivation	Cultivation

IMPLICATIONS FOR THE THEORY OF INVASION BIOLOGY

In general, the analytical, experimental and observational aspects of this thesis supported the invasion biology literature which shows that invasions are complex processes synergistically driven by factors associated with introduction history, intrinsic species traits, characteristics of the recipient environment, and anthropogenic influences. What is more, the role of these factors differed at different stages of the INI continuum, and this facet is lacking in the literature.

There are a few universal attributes associated with plant invasions, the most common being propagule pressure, native range size and residence time (Hui and Richardson, 2017; Pyšek *et al.*, 2009a; Pyšek *et al.*, 2015; Richardson and Pyšek, 2012). These findings are also supported by Araceae. However, progress towards understanding the invasion process has largely been made by examining these invasion correlates, in isolation, rather than linking their degree of success to particular stages of the continuum. As a result, robust conclusions about which species will make the shift from introduced to naturalized and invasive, as well as the mechanisms driving these transitions, remain somewhat elusive. These comparisons provide critical insights into the transitions along the INI continuum and this thesis helps to bridge this gap. This approach helped to identify processes relevant for understanding invasions and their underlying mechanisms.

In addition to the invasion stages, the patterns of plant invasions and the mechanisms which generate these patterns, vary across spatial scales (Hamilton *et al.*, 2005; Pauchard and Shea, 2006; Pyšek and Hulme, 2005). Considering spatial scales in invasion studies offered insights into appropriate management strategies. For instance, if I only looked at *Monstera deliciosa* on a local scale in South Africa, I would have initially deemed the species as invasive. However, taking into account the global invasion dynamics of the species, fittingly changed the status to being a low invasion risk, and compelled me to identify the fine scale drivers of invasions.

Lastly, analyzing a single taxonomic or functional group provides a relatively accurate understanding of the mechanisms facilitating invasions. For example, specialized pollination syndromes were identified as a driver of invasiveness in Araceae, and this is unique to the family. Vegetative reproduction has been shown to be a common predictor of invasiveness in other groups (Kolar and Lodge, 2001; Lloret *et al.*, 2005a), but it was not significant in Araceae (chapter 2). In addition, a comprehensive look at two case study species with different invasion patterns revealed important information on species invasion, such as why some species become invasive (chapter 3 – primarily driven by human-mediated disturbances) while others fail (chapter 4 – lag phase). As a result, future studies need to continue looking at different groups in order to develop robust generalizations in invasion biology.

IMPLICATIONS FOR METHODOLOGY

This project successfully revealed the suitability of various approaches when studying processes that promote invasions. I demonstrated that collating a comprehensive species list, compiling trait databases, mapping species distributions, conducting population surveys and performing field experiments are useful for understanding invasion dynamics. In addition, risk assessments and species distribution models are also valuable tools for, among other things, informing management.

IMPLICATIONS FOR INVASIVE ALIEN SPECIES MANAGEMENT

Whilst research in invasion biology has progressed rapidly over the last few decades, a recurring criticism is linking existing knowledge into policies and management strategies (Hulme, 2006; Lodge, 1993). The results of this thesis have practical implications for invasion biologists, conservation managers and legislation. In chapter 2, I predicted which species have the potential to become invasive in the future and therefore recommended a precautionary approach be taken for these species. In chapter 3, I recommended that *E. aureum* be regulated, and in chapter 4, I recommended that *M. deliciosa* is reasonably innocuous and can continue being introduced and planted.

FUTURE RESEARCH

A stage-based approach to improve our understanding of the factors important throughout the invasion process should consider the themes proposed below (in combination):

- Identification of species traits combined with characteristics of the recipient habitats. In the global study, I established that hydrophytes pose a greater invasion risk than most other life forms. One of the limitations of this study was the exclusion of dispersal vectors due to the lack of available information. The inclusion of this trait will identify which trait is more important in driving hydrophyte invasiveness, regeneration mechanism or dispersal vectors;

- Research focused on particular taxonomic or functional groups;

- Studies should also consider traits of non-introduced species. This was a major limitation in this thesis. This information will be crucial for refining methods of predicting which species are likely to become invasive which will facilitate prevention methods, as well as better management of invasions;

- Ignoring failed invasions may hinder our understanding of the invasion process and these types of studies are still rare. For that reason, we should focus more effort on compiling and analyzing data on failed invasions. In the local case study of a failed invasion one of the major limitations was the lack of additional *M. deliciosa* localities for comaprisons. Other localities would have significantly strengthened the study.

CONCLUSION

The study of invasion biology contributes to a better understanding of processes that facilitate or limit invasions. This thesis illustrated that the mechanisms associated with invasiveness differ between taxa and across the INI continuum, therefore group and stage-specific analyses are essential. Despite the advances made through this work, much remains to be done to improve our knowledge and control of invasive alien species. To achieve the goal of predicting successful invasions, the recommendations mentioned above (i.e. spatial scale, invasion stage, species traits and characteristics of the recipient habitat) must be jointly accounted for in order to increase our predictive power. I strongly recommend that future studies use a similar framework for other plant groups.

These types of studies will provide a better understanding of why some introduced species become invasive while others fail, and will ultimately assist in managing biological invasions. In addition, similar studies of other plant groups are necessary to confirm the general applicability of these results. As more complete phylogenies and better knowledge of traits become available, these analyses are likely to become increasingly sophisticated and able to produce valuable insights into risk assessments. The work presented in this thesis contributes to understanding the causes and mechanisms of plant invasions and addresses questions of species invasiveness and community invasibility. Consequently, this research improves our ability to predict and manage the invasion risk of existing, emerging and potential invasive Araceae species, which is the ultimate research mission in invasion biology.

REFERENCES

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P and Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology 12: e1001850

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

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ and Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecology Letters 8: 1066-1074

Hui C and Richardson DM (2017) Invasion dynamics, Oxford, 384 pp

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835-847

Kolar CS and Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204

Lloret F, Médail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon P and Hulme PE (2005) Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology 93: 512-520

Lodge DM (1993) Biological invasions: lessons for ecology. Trends in Ecology & Evolution 8: 133-137

Pauchard A and Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399-413

Pyšek P and Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. Écoscience 12: 302-315

Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek jun J and Sádlo J (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Diversity and Distributions 15: 891-903

Pyšek P, Manceur AM, Alba C, McGregor KF, Pergl J, Stajerová K, Chytrý M, Danihelka J, Kartesz J, Klimesova J, Lucanova M, Moravcová L, Nishino M, Sadlo J, Suda J, Tichy L and Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96: 762-774

Richardson DM and Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383-396

Williamson M (1996) Biological invasions. Chapman and Hall, London

Wilson JRU, Gairifo C, Gibson MR, Arianoutsou M, Bakar BB, Baret S, Celesti-Grapow L, DiTomaso JM, Dufour-Dror J-M, Kueffer C, Kull CA, Hoffmann JH, Impson FAC, Loope LL, Marchante E, Marchante H, Moore JL, Murphy DJ, Tassin J, Witt A, Zenni RD and Richardson DM (2011) Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. Diversity and Distributions 17: 1030-1046

Zenni RD and Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122: 801-815

Appendices

Appendix 1. Eight characteristics used to construct phenograms for invasive genera.

Characteristics	Reason for selection	Binary code
Number of native regions	Species occurring over a larger range have a greater chance of becoming introduced and naturalized (proxy for range size).	Native regions ≥ 3 = 1; Native regions < 3 = 0
Plant life form	Chamaephytes, geophytes, helophytes, hemicryptophytes or hydrophytes were found to be the most important life forms for Araceae to overcome the introduction and naturalization barriers.	Chamaephytes, geophytes, helophytes, hemicryptophytes or hydrophytes = 1; Other life forms = 0
Pollinator type	Fly pollinated species have a higher likelihood of being introduced by humans.	Fly pollinated = 1; Other pollinators = 0
Native floristic regions	Species native to the Polynesian province had a higher likelihood of being introduced.	Polynesian = 1; Non-Polynesian = 0
Flower sexuality	Unisexual flowers were favoured over bisexual flowers.	Unisexual = 1; Bisexual = 0
Habitat	Araceae genera are concentrated in the tropics. Species from tropical moist forests have a greater chance of being introduced.	Tropical moist forests = 1; Other habitats = 0
Number of introduced regions	Species introduced into more regions have a greater chance of becoming naturalized and invasive (proxy for propagule pressure).	Introduced regions ≥ 3 = 1; Introduced regions < 3 = 0
Number of uses	Species with more uses overcame the naturalization barriers.	Number of uses ≥ 3 = 1; Number of uses < 3 = 0

Appendix 2. A comprehensive species checklist developed for Araceae in 2013–2014.

Scientific name

Aglaodorum griffithii
Aglaonema brevispathum
Aglaonema chermsiriwattanae
Aglaonema cochinchinense
Aglaonema commutatum var.commutatum
Aglaonema commutatum var. elegans
Aglaonema commutatum var. maculatum
Aglaonema commutatum var. warburgii
Aglaonema cordifolium
Aglaonema costatum
Aglaonema crispum
Aglaonema densinervium
Aglaonema flemingianum
Aglaonema hookerianum
Aglaonema marantifolium
Aglaonema modestum
Aglaonema nebulosum
Aglaonema nitidum
Aglaonema ovatum
Aglaonema philippinense var. philippinense
Aglaonema philippinense var. stenophyllum
Aglaonema pictum
Aglaonema pumilum
Aglaonema rotundum
Aglaonema simplex
Aglaonema tricolor
Aglaonema vittatum
Alloschemone inopinata
Alloschemone occidentalis
Alocasia acuminata
Alocasia aequiloba
Alocasia alba
Alocasia arifolia
Alocasia atropurpurea
Alocasia augustiana
Alocasia baginda
Alocasia balgooyi
Alocasia beccarii
Alocasia boa
Alocasia boyceana
Alocasia brancifolia
Alocasia brisbanensis

Scientific name

Alocasia cadieri
Alocasia celebica
Alocasia chaii
Alocasia clypeolata
Alocasia cucullata
Alocasia culionensis
Alocasia cuprea
Alocasia decipiens
Alocasia decumbens
Alocasia devansayana
Alocasia fallax
Alocasia flabellifera
Alocasia flemingiana
Alocasia fornicata
Alocasia gageana
Alocasia grata
Alocasia hainanica
Alocasia heterophylla
Alocasia hollrungii
Alocasia hypnosa
Alocasia hypoleuca
Alocasia infernalis
Alocasia inornata
Alocasia jiewhoei
Alocasia kerinciensis
Alocasia lancifolia
Alocasia lauterbachiana
Alocasia lecomtei
Alocasia longiloba
Alocasia macrorrhizos
Alocasia maquilingensis
Alocasia megawatiae
Alocasia melo
Alocasia micholitziana
Alocasia miniuscula
Alocasia monticola
Alocasia navicularis
Alocasia nebula
Alocasia nicolsonii
Alocasia nycteris
Alocasia odora
Alocasia pangeran
Alocasia peltata
Alocasia perakensis
Alocasia portei
Alocasia princeps
Alocasia principiculus
Alocasia puber
Alocasia puteri
Alocasia pyrospatha
Alocasia ramosii
Alocasia reginae
Alocasia reginula
Alocasia reversa
Alocasia ridleyi
Alocasia robusta
Alocasia sanderi

Scientific name

Alocasia sarawakensis
Alocasia scabriuscula
Alocasia scalprum
Alocasia simonsiana
Alocasia sinuata
Alocasia suhirmaniana
Alocasia venusta
Alocasia wentii
Alocasia wongii
Alocasia zebrina
Ambrosina bassii
Amorphophallus aberrans
Amorphophallus abyssinicus subsp. abyssinicus
Amorphophallus abyssinicus subsp. akeassii
Amorphophallus abyssinicus subsp. unyikae
Amorphophallus albispathus
Amorphophallus albus
Amorphophallus amygdaloides
Amorphophallus andranogidroensis
Amorphophallus angolensis subsp. angolensis
Amorphophallus angolensis subsp. maculatus
Amorphophallus angulatus
Amorphophallus angustispathus
Amorphophallus ankarana
Amorphophallus annulifer
Amorphophallus antsingyensis
Amorphophallus aphyllus
Amorphophallus asper
Amorphophallus asterostigmatus
Amorphophallus atrorubens
Amorphophallus atroviridis
Amorphophallus bangkokensis
Amorphophallus barthlottii
Amorphophallus baumannii
Amorphophallus beccarii
Amorphophallus bequaertii
Amorphophallus bonaccordensis
Amorphophallus borneensis
Amorphophallus boyceanus
Amorphophallus brachyphyllus
Amorphophallus brevispathus
Amorphophallus bufo
Amorphophallus bulbifer
Amorphophallus calabaricus subsp. calabaricus
Amorphophallus calabaricus subsp. mayoi
Amorphophallus canaliculatus
Amorphophallus carneus
Amorphophallus chlorospathus
Amorphophallus cicatricifer

Scientific name

Amorphophallus cirrifer
Amorphophallus coaetaneus
Amorphophallus commutatus
Amorphophallus consimilis
Amorphophallus corrugatus
Amorphophallus costatus
Amorphophallus coudercii
Amorphophallus croatii
Amorphophallus curvistylis
Amorphophallus dactylifer
Amorphophallus declinatus
Amorphophallus decus-silvae
Amorphophallus discophorus
Amorphophallus dracontioides
Amorphophallus dunnii
Amorphophallus dzui
Amorphophallus eburneus
Amorphophallus echinatus
Amorphophallus eichleri
Amorphophallus elatus
Amorphophallus elegans
Amorphophallus elliottii
Amorphophallus erythrororrhachis
Amorphophallus excentricus
Amorphophallus flotoi
Amorphophallus forbesii
Amorphophallus fuscus
Amorphophallus galbra
Amorphophallus gallaensis
Amorphophallus gallowayi
Amorphophallus gigas
Amorphophallus glaucophyllus
Amorphophallus gliruroides
Amorphophallus glossophyllus
Amorphophallus goetzei
Amorphophallus gomboczianus
Amorphophallus gracilior
Amorphophallus gracilis
Amorphophallus haematospadix
Amorphophallus harmandii
Amorphophallus hayi
Amorphophallus henryi
Amorphophallus hetterscheidii
Amorphophallus hewittii
Amorphophallus hildebrandtii
Amorphophallus hirsutus
Amorphophallus hirtus
Amorphophallus hohenackeri
Amorphophallus hottae
Amorphophallus impressus
Amorphophallus incurvatus
Amorphophallus infundibuliformis
Amorphophallus interruptus
Amorphophallus johnsonii
Amorphophallus josefbogneri

Scientific name	Scientific name	Scientific name	Scientific name
Amorphophallus julaihii	*Amorphophallus pendulus*	*Amorphophallus yuloensis*	*Anthurium albovirescens*
Amorphophallus juliae	*Amorphophallus perakensis*	*Amorphophallus yunnanensis*	*Anthurium alcatrazense*
Amorphophallus kachinensis	*Amorphophallus pilosus*	*Amorphophallus zenkeri subsp. zenkeri*	*Anthurium alegriasense*
Amorphophallus kiusianus	*Amorphophallus plicatus*	*Amorphophallus zenkeri subsp. mannii*	*Anthurium algentryi*
Amorphophallus konjac	*Amorphophallus polyanthus*	*Amydrium hainanense*	*Anthurium alluriquinense*
Amorphophallus konkanensis	*Amorphophallus prainii*	*Amydrium humile*	*Anthurium alstonii*
Amorphophallus koratensis	*Amorphophallus preussii*	*Amydrium medium*	*Anthurium alticola*
Amorphophallus krausei	*Amorphophallus prolificus*	*Amydrium sinense*	*Anthurium amargalense*
Amorphophallus lacourii	*Amorphophallus purpurascens*	*Amydrium zippelianum*	*Anthurium ameliae*
Amorphophallus lambii	*Amorphophallus pusillus*	*Anadendrum affine var. affine*	*Anthurium amnicola*
Amorphophallus lanuginosus	*Amorphophallus putii*	*Anadendrum affine var. semivestitum*	*Anthurium amoenum var. amoenum*
Amorphophallus laoticus	*Amorphophallus pygmaeus*	*Anadendrum angustifolium*	*Anthurium amoenum var. humile*
Amorphophallus lewallei	*Amorphophallus ranchanensis*	*Anadendrum badium*	*Anthurium anceps*
Amorphophallus linearis	*Amorphophallus reflexus*	*Anadendrum cordatum*	*Anthurium anchicayense*
Amorphophallus linguiformis	*Amorphophallus rhizomatosus*	*Anadendrum ellipticum*	*Anthurium ancuashii*
Amorphophallus longicomus	*Amorphophallus richardsiae*	*Anadendrum griseum*	*Anthurium andicola*
Amorphophallus longiconnectivus	*Amorphophallus rostratus*	*Anadendrum latifolium*	*Anthurium andinum*
Amorphophallus longispathaceus	*Amorphophallus rugosus*	*Anadendrum marcesovaginatum*	*Anthurium andraeanum*
Amorphophallus longistylus	*Amorphophallus sagittarius*	*Anadendrum marginatum*	*Anthurium andreslovinense*
Amorphophallus longituberosus	*Amorphophallus salmoneus*	*Anadendrum microstachyum*	*Anthurium angelopolinense*
Amorphophallus lunatus	*Amorphophallus saraburensis*	*Anadendrum montanum*	*Anthurium angosturense*
Amorphophallus luzoniensis	*Amorphophallus saururus*	*Anadendrum superans*	*Anthurium angustatum*
Amorphophallus lyratus	*Amorphophallus scaber*	*Anaphyllopsis americana*	*Anthurium angustilaminatum subsp. angustilaminatum*
Amorphophallus macrorhizus	*Amorphophallus schmidtiae*	*Anaphyllopsis cururuana*	*Anthurium angustilaminatum subsp. cibuserpentis*
Amorphophallus mangelsdorffii	*Amorphophallus scutatus*	*Anaphyllopsis pinnata*	
Amorphophallus manta	*Amorphophallus serrulatus*	*Anaphyllum beddomei*	*Anthurium angustilobum*
Amorphophallus margaritifer	*Amorphophallus sinuatus*	*Anaphyllum wightii*	*Anthurium angustisectum*
Amorphophallus margretae	*Amorphophallus sizemoreae*	*Anchomanes abbreviatus*	*Anthurium angustispadix*
Amorphophallus maximus subsp. maximus	*Amorphophallus smithsonianus*	*Anchomanes boehmii*	*Anthurium anorianum*
Amorphophallus maximus subsp. fischeri	*Amorphophallus sparsiflorus*	*Anchomanes dalzielii*	*Anthurium antioquiense*
Amorphophallus maxwellii	*Amorphophallus spectabilis*	*Anchomanes difformis*	*Anthurium antonioanum*
Amorphophallus mekongensis	*Amorphophallus staudtii*	*Anchomanes giganteus*	*Anthurium antrophyoides*
Amorphophallus merrillii	*Amorphophallus stuhlmannii subsp. stuhlmannii*	*Anchomanes nigritianus*	*Anthurium apanui*
Amorphophallus mildbraedii	*Amorphophallus stuhlmannii subsp. congoensis*	*Anthurium abelaezii*	*Anthurium apaporanum*
Amorphophallus minor	*Amorphophallus subcymbiformis*	*Anthurium acanthospadix*	*Anthurium apiaense*
Amorphophallus mossambicensis	*Amorphophallus sumawongii*	*Anthurium acaule*	*Anthurium arenasense*
Amorphophallus muelleri	*Amorphophallus suwidjianus*	*Anthurium acebeyae*	*Anthurium argyrostachyum*
Amorphophallus mullendersii	*Amorphophallus sylvaticus*	*Anthurium achupallense*	*Anthurium aripoense*
Amorphophallus myosuroides	*Amorphophallus symonianus*	*Anthurium acutangulum*	*Anthurium arisaemoides*
Amorphophallus mysorensis	*Amorphophallus synandrifer*	*Anthurium acutibacca*	*Anthurium aristatum*
Amorphophallus napalensis	*Amorphophallus taurostigma*	*Anthurium acutifolium var. acutifolium*	*Anthurium armeniense*
Amorphophallus napiger	*Amorphophallus tenuispadix*	*Anthurium acutifolium var. herrerae*	*Anthurium aroense*
Amorphophallus natolii	*Amorphophallus tenuistylis*	*Anthurium acutissimum*	*Anthurium arusiense*
Amorphophallus niahensis	*Amorphophallus teuszii*	*Anthurium acutum*	*Anthurium asplundii*
Amorphophallus nicolsonianus	*Amorphophallus thaiensis*	*Anthurium aduncum*	*Anthurium atamainii*
Amorphophallus obovoideus	*Amorphophallus tinekeae*	*Anthurium affine*	*Anthurium atramentarium*
Amorphophallus obscurus	*Amorphophallus titanum*	*Anthurium agnatum*	*Anthurium atropurpureum var. atropurpureum*
Amorphophallus ochroleucus	*Amorphophallus tonkinensis*	*Anthurium alatipedunculatum*	*Anthurium atropurpureum var. arenicola*
Amorphophallus ongsakulii	*Amorphophallus tuberculatus*	*Anthurium alatum*	*Anthurium atropurpureum var. thomasii*
Amorphophallus operculatus	*Amorphophallus variabilis*	*Anthurium albertiae*	*Anthurium atroviride*
Amorphophallus opertus	*Amorphophallus venustus*	*Anthurium albidum*	*Anthurium augustinum*
Amorphophallus paeoniifolius	*Amorphophallus verticillatus*	*Anthurium albispatha*	*Anthurium aureum*
Amorphophallus palawanensis	*Amorphophallus vogelianus*	*Anthurium albobueyense*	*Anthurium auritum*
Amorphophallus paucisectus	*Amorphophallus xiei*		

Scientific name	Scientific name	Scientific name	Scientific name
Anthurium austin-smithii	*Anthurium bushii*	*Anthurium citrifolium*	*Anthurium crystallinum*
Anthurium aylwardianum	*Anthurium cabrerense*	*Anthurium clarinervium*	*Anthurium cuasicanum*
Anthurium baguense	*Anthurium cabuyalense*	*Anthurium clarkei*	*Anthurium cubense*
Anthurium bakeri	*Anthurium cachabianum*	*Anthurium clathratum*	*Anthurium cucullispathum*
Anthurium balaoanum	*Anthurium cainarachense*	*Anthurium clavatum*	*Anthurium cultrifolium*
Anthurium balslevii	*Anthurium caldodsonii*	*Anthurium clavigerum*	*Anthurium cupreonitens*
Anthurium barbacoasense	*Anthurium calimense*	*Anthurium cleistanthum*	*Anthurium cupreum*
Anthurium barclayanum	*Anthurium callejasii*	*Anthurium clidemioides subsp. clidemioides*	*Anthurium cupulispathum*
Anthurium barreranum	*Anthurium caloveboranum*	*Anthurium clidemioides subsp. pacificum*	*Anthurium curicuriariense*
Anthurium barrieri	*Anthurium campii*	*Anthurium coclense*	*Anthurium curtispadix*
Anthurium barryi	*Anthurium camposii*	*Anthurium cocornaense*	*Anthurium curvilaminum*
Anthurium basirotundum	*Anthurium canaliculatum*	*Anthurium coerulescens*	*Anthurium curvispadix*
Anthurium bayae	*Anthurium candolleanum*	*Anthurium cogolloanum*	*Anthurium cuspidatum*
Anthurium beckii	*Anthurium caperatum*	*Anthurium coleomischum*	*Anthurium cuspidiferum*
Anthurium bellum	*Anthurium caraboboense*	*Anthurium coleorrhiza*	*Anthurium cutucuense*
Anthurium beltianum	*Anthurium caramantae*	*Anthurium collettianum*	*Anthurium cuyabenoense*
Anthurium benktsparrei	*Anthurium carchiense*	*Anthurium collinsii*	*Anthurium cylindratum*
Anthurium bernardii	*Anthurium cardenasii*	*Anthurium colonchense*	*Anthurium cymbiforme*
Anthurium berriozabalense	*Anthurium carinatum*	*Anthurium colonense*	*Anthurium cymbispatha*
Anthurium berryi	*Anthurium caripense*	*Anthurium colonicum*	*Anthurium daguense*
Anthurium besseae	*Anthurium carneospadix*	*Anthurium coloradense*	*Anthurium darcyi*
Anthurium betanianum	*Anthurium carnosum*	*Anthurium comtum*	*Anthurium davidsei*
Anthurium bicordoense	*Anthurium carpishense*	*Anthurium concinnatum*	*Anthurium davidsoniae*
Anthurium bimarginatum	*Anthurium cartiense*	*Anthurium concolor*	*Anthurium debilipeltatum*
Anthurium binotii	*Anthurium cartilagineum*	*Anthurium conjunctum*	*Anthurium debilis*
Anthurium birdseyanum	*Anthurium cataniapoense*	*Anthurium consimile*	*Anthurium decurrens*
Anthurium bittneri	*Anthurium caucanum*	*Anthurium consobrinum*	*Anthurium deflexum*
Anthurium bocainense	*Anthurium caucavallense*	*Anthurium conspicuum*	*Anthurium delannayi*
Anthurium boekei	*Anthurium caulorrhizum*	*Anthurium constrictum*	*Anthurium dendrobates*
Anthurium bogneri	*Anthurium ceratiinum*	*Anthurium conterminum*	*Anthurium denudatum*
Anthurium bogotense	*Anthurium ceronii*	*Anthurium corallinum*	*Anthurium diazii*
Anthurium bonplandii subsp. bonplandii	*Anthurium cerrateae*	*Anthurium cordatotriangulum*	*Anthurium digitatum*
Anthurium bonplandii subsp. guayanum	*Anthurium cerrobaulense*	*Anthurium cordatum*	*Anthurium diversicaudex*
Anthurium boosianum	*Anthurium cerrocampanense*	*Anthurium cordiforme*	*Anthurium dolichocnemum*
Anthurium boudetii	*Anthurium cerropelonense*	*Anthurium cordobense*	*Anthurium dolichophyllum*
Anthurium brachypodum	*Anthurium cerropirrense*	*Anthurium cordulatum*	*Anthurium dolichostachyum*
Anthurium bradeanum	*Anthurium chacoense*	*Anthurium coriaceum*	*Anthurium dombeyanum*
Anthurium bragae	*Anthurium chamberlainii*	*Anthurium coripatense*	*Anthurium dominicense*
Anthurium bredemeyeri	*Anthurium chamulense subsp. chamulense*	*Anthurium correae*	*Anthurium dorbayae*
Anthurium brenesii	*Anthurium chamulense subsp. oaxacanum*	*Anthurium corrugatum*	*Anthurium draconopterum*
Anthurium brent-berlinii	*Anthurium chiapasense subsp. chiapasense*	*Anthurium cotejense*	*Anthurium dressleri*
Anthurium brevipedunculatum	*Anthurium chiapasense subsp. tlaxiacense*	*Anthurium cotobrusii*	*Anthurium dukei*
Anthurium brevipes	*Anthurium chimborazense*	*Anthurium cowanii*	*Anthurium durandii*
Anthurium breviscapum	*Anthurium chinchipense*	*Anthurium crassifolium*	*Anthurium dussii*
Anthurium brevispadix	*Anthurium chinimense*	*Anthurium crassilaminum*	*Anthurium dwyeri*
Anthurium brittonianum	*Anthurium chiriquense*	*Anthurium crassinervium var. crassinervium*	*Anthurium dylanii*
Anthurium bromelicola subsp. bromelicola	*Anthurium chocoense*	*Anthurium crassinervium var. caatingae*	*Anthurium ecuadorense*
Anthurium bromelicola subsp. bahiense	*Anthurium chorense*	*Anthurium crassiradix var. crassiradix*	*Anthurium effusilobum subsp. effusilobum*
Anthurium brownii	*Anthurium chorranum*	*Anthurium crassiradix var. purpureospadix*	*Anthurium effusilobum subsp.pallidispadix*
Anthurium bucayanum	*Anthurium chrysolithos*	*Anthurium crassitepalum*	*Anthurium effusispathum*
Anthurium buchtienii	*Anthurium churutense*	*Anthurium crassivenium*	*Anthurium eggersii*
Anthurium buganum	*Anthurium cinereopetiolatum*	*Anthurium cremersii*	*Anthurium eichleri*
Anthurium bullianum	*Anthurium cipoense*	*Anthurium crenatum*	*Anthurium emarginatum*
Anthurium bullosum	*Anthurium circinatum*	*Anthurium croatii*	*Anthurium eminens subsp. eminens*
Anthurium burgeri	*Anthurium cirinoi*		*Anthurium eminens subsp. longispadix*

Scientific name

Anthurium ensifolium
Anthurium ericae
Anthurium ernestii var. ernestii
Anthurium ernestii var. oellgaardii
Anthurium erskinei
Anthurium erythrostachyum
Anthurium esmeraldense
Anthurium espinae
Anthurium eximium
Anthurium expansum
Anthurium exstipulatum
Anthurium fasciale
Anthurium fatoense
Anthurium faustomirandae
Anthurium fendleri
Anthurium fernandezii
Anthurium filiforme
Anthurium flavescens
Anthurium flavidum
Anthurium flavolineatum
Anthurium flavoviride
Anthurium flexile subsp. flexile
Anthurium flexile subsp. muelleri
Anthurium folsomianum
Anthurium fontellanum
Anthurium fontoides
Anthurium foreroanum
Anthurium forgetii
Anthurium formosum
Anthurium fornicifolium
Anthurium fosteri
Anthurium fragae
Anthurium fragrans
Anthurium fragrantissimum
Anthurium fraseri
Anthurium friedrichsthalii
Anthurium funiferum
Anthurium furcatum
Anthurium fuscopunctatum
Anthurium fusiforme
Anthurium gaffurii
Anthurium galactospadix
Anthurium galeanoae
Anthurium galeottii
Anthurium galileanum
Anthurium gaskinii
Anthurium gaudichaudianum
Anthurium gehrigeri
Anthurium geitnerianum
Anthurium genferryae
Anthurium geniculatum
Anthurium gentryi
Anthurium giganteum
Anthurium ginesii
Anthurium giraldoi

Scientific name

Anthurium gladiifolium
Anthurium glanduligerum
Anthurium glaucophyllum
Anthurium glaucospadix
Anthurium globosum
Anthurium gomesianum
Anthurium gonzalezii
Anthurium gracile
Anthurium gracililaminum
Anthurium gracilipedunculatum
Anthurium gracilispadix
Anthurium grande
Anthurium grandicataphyllum
Anthurium grandifolium
Anthurium grex-avium
Anthurium gualeanum
Anthurium guanacense
Anthurium guanchezii
Anthurium guatemalense
Anthurium guayaquilense
Anthurium gustavii
Anthurium gymnopus
Anthurium hacumense
Anthurium hagsaterianum
Anthurium halmoorei
Anthurium hamiltonii
Anthurium hammelii
Anthurium harrisii
Anthurium hastifolium
Anthurium hatschbachii
Anthurium hebetatilaminum
Anthurium hebetatum
Anthurium herthae
Anthurium hieronymi
Anthurium hinoideum
Anthurium hodgei
Anthurium hoehnei
Anthurium hoffmannii
Anthurium holm-nielsenii
Anthurium holquinianum
Anthurium hookeri
Anthurium hornitense
Anthurium huacamayoense
Anthurium huallagense
Anthurium huampamiense
Anthurium huanucense
Anthurium huashikatii
Anthurium huautlense
Anthurium huberi
Anthurium huixtlense
Anthurium humboldtianum subsp. humboldtianum
Anthurium humboldtianum subsp. viridispadix
Anthurium humoense
Anthurium hutchisonii
Anthurium hygrophilum
Anthurium ianthinopodum

Scientific name

Anthurium icanense
Anthurium idmense
Anthurium illepidum
Anthurium iltisii
Anthurium imperiale
Anthurium impolitum
Anthurium incomptum
Anthurium inconspicuum
Anthurium incurvatum
Anthurium incurvum
Anthurium infectorium
Anthurium intermedium
Anthurium interruptum
Anthurium inzanum
Anthurium ionanthum
Anthurium iramireziae
Anthurium isidroense
Anthurium jaramilloi
Anthurium jefense
Anthurium jenmanii
Anthurium jesusii
Anthurium jilekii
Anthurium jimenae
Anthurium joaquinense
Anthurium johnmackii
Anthurium johnsoniae
Anthurium josei
Anthurium julianii
Anthurium julospadix
Anthurium jureianum
Anthurium kajekai
Anthurium kallunkiae
Anthurium kamemotoanum
Anthurium karstenianum
Anthurium kastelskii
Anthurium kayapii
Anthurium knappiae
Anthurium krukovii
Anthurium kugkumasii
Anthurium kunayalense
Anthurium kunthii var. kunthii
Anthurium kunthii var. cylindricum
Anthurium kusuense
Anthurium lacerdae
Anthurium laciniosum
Anthurium lactifructum
Anthurium lancea
Anthurium lancetillense
Anthurium lancifolium var. lancifolium
Anthurium lancifolium var. albifructum
Anthurium langendoenii
Anthurium langsdorffii
Anthurium lanjouwii
Anthurium latemarginatum
Anthurium latissimum

Scientific name

Anthurium laucheanum
Anthurium lautum
Anthurium lechlerianum
Anthurium lehmannii
Anthurium lennartii
Anthurium lentii
Anthurium leonianum
Anthurium leonii
Anthurium leptocaule
Anthurium leuconeurum
Anthurium leveaui
Anthurium lezamae
Anthurium lhotzkyanum
Anthurium libanoense
Anthurium licium
Anthurium lievenii
Anthurium ligulare
Anthurium lilacinum
Anthurium limonense
Anthurium lindenianum
Anthurium lindmanianum
Anthurium lineolatum
Anthurium linganii
Anthurium lingua
Anthurium linguifolium
Anthurium llanense
Anthurium llewellynii
Anthurium lloense
Anthurium loefgrenii
Anthurium lojtnantii
Anthurium longicaudatum
Anthurium longicuspidatum
Anthurium longifolium
Anthurium longigeniculatum
Anthurium longipeltatum
Anthurium longipes
Anthurium longispadiceum
Anthurium longissimilobum
Anthurium longissimum subsp. longissimum
Anthurium longissimum subsp. nirguense
Anthurium longistamineum
Anthurium longistipitatum
Anthurium longiusculum
Anthurium loretense
Anthurium louisii
Anthurium lucens
Anthurium lucidum
Anthurium lucioi
Anthurium lucorum
Anthurium luschnathianum
Anthurium lutescens
Anthurium luteynii
Anthurium luxurians
Anthurium lygrum
Anthurium lynniae
Anthurium maasii

Scientific name	Scientific name	Scientific name	Scientific name
Anthurium macarenense	*Anthurium moonenii*	*Anthurium oxyanthum*	*Anthurium pichindense*
Anthurium macbridei	*Anthurium morae*	*Anthurium oxybelium*	*Anthurium pilonense*
Anthurium macdanielii	*Anthurium morii*	*Anthurium oxycarpum*	*Anthurium pinkleyi*
Anthurium machetioides	*Anthurium moronense*	*Anthurium oxyphyllum*	*Anthurium pirottae*
Anthurium macleanii	*Anthurium mostaceroi*	*Anthurium oxystachyum*	*Anthurium pirrense*
Anthurium macphersonii	*Anthurium mourae*	*Anthurium pachylaminum*	*Anthurium pittieri var. pittieri*
Anthurium macrocephalum	*Anthurium multinervium*	*Anthurium pachyspathum*	*Anthurium pittieri var. fogdeniorum*
Anthurium macrolonchium	*Anthurium multisulcatum*	*Anthurium pageanum*	*Anthurium pittieri var. morii*
Anthurium macrophyllum	*Anthurium munchiquense*	*Anthurium palacioanum*	*Anthurium piurensis*
Anthurium macropodum	*Anthurium myosuroides*	*Anthurium palenquense*	*Anthurium plantagineum*
Anthurium macrospadix	*Anthurium myosurus*	*Anthurium pallatangense*	*Anthurium platyglossum*
Anthurium macrourum	*Anthurium nakamurae*	*Anthurium pallens*	*Anthurium platyrhizum*
Anthurium maculosum	*Anthurium nangaritense*	*Anthurium pallidicaudex*	*Anthurium plowmanii*
Anthurium madisonianum	*Anthurium nanum*	*Anthurium pallidiflorum*	*Anthurium plurisulcatum*
Anthurium magdae	*Anthurium napaeum*	*Anthurium palmarense*	*Anthurium pluviaticum*
Anthurium magnificum	*Anthurium narinoense*	*Anthurium palmatum*	*Anthurium podophyllum*
Anthurium magnifolium	*Anthurium navasii*	*Anthurium paludosum*	*Anthurium pohlianum*
Anthurium maguirei	*Anthurium naviculare*	*Anthurium panamense*	*Anthurium polydactylum*
Anthurium malagaense	*Anthurium nelsonii*	*Anthurium panduriforme*	*Anthurium polynervium*
Anthurium malianum	*Anthurium nemorale*	*Anthurium papillilaminum*	*Anthurium polyneuron*
Anthurium manabianum	*Anthurium nemoricola*	*Anthurium paradisicum*	*Anthurium polyphlebium*
Anthurium mancuniense	*Anthurium nervatum*	*Anthurium paraguasense*	*Anthurium polyschistum*
Anthurium manuanum	*Anthurium nicolasianum*	*Anthurium paraguayense var. paraguayense*	*Anthurium polystictum*
Anthurium marense	*Anthurium nigrescens*	*Anthurium paraguayense var. coroicoanum*	*Anthurium porcesitoense*
Anthurium margaricarpum	*Anthurium nigropunctatum*	*Anthurium parambae*	*Anthurium potarense*
Anthurium marginellum	*Anthurium niqueanum*	*Anthurium parasiticum*	*Anthurium pradoense*
Anthurium mariae	*Anthurium nitens*	*Anthurium pariense*	*Anthurium praealtum*
Anthurium maricense	*Anthurium nitidulum*	*Anthurium parile*	*Anthurium pranceanum*
Anthurium marinoanum	*Anthurium nitidum*	*Anthurium parvispathum*	*Anthurium prolatum*
Anthurium marleenianum	*Anthurium nizandense*	*Anthurium parvum*	*Anthurium prominens*
Anthurium marmoratum	*Anthurium novitaense*	*Anthurium pastasanum*	*Anthurium promininerve*
Anthurium martianum	*Anthurium nubicola*	*Anthurium patens*	*Anthurium protensum subsp. protensum*
Anthurium masfense	*Anthurium nutibarense*	*Anthurium pauciflorum*	*Anthurium protensum subsp. arcuatum*
Anthurium maximiliani	*Anthurium nymphaeifolium*	*Anthurium paucinerve*	*Anthurium pseudospectabile*
Anthurium maximum	*Anthurium obliquatum*	*Anthurium payaminoense*	*Anthurium psilostachyum*
Anthurium megapetiolatum	*Anthurium oblongocordatum*	*Anthurium pedatoradiatum subsp. pedatoradiatum*	*Anthurium ptarianum*
Anthurium melastomatis	*Anthurium obpyriforme*	*Anthurium pedatoradiatum subsp. helleborifolium*	*Anthurium puberulinervium*
Anthurium membranaceum	*Anthurium obscurinervium*	*Anthurium pedatum*	*Anthurium puberulum*
Anthurium mendietae	*Anthurium obtusatum*	*Anthurium pedunculare*	*Anthurium pucayacuense*
Anthurium merlei	*Anthurium obtusifolium*	*Anthurium pellucidopunctatum*	*Anthurium pulcachense*
Anthurium metallicum	*Anthurium obtusilobum*	*Anthurium peltatum*	*Anthurium pulchellum*
Anthurium miaziense	*Anthurium obtusum subsp. obtusum*	*Anthurium peltigerum*	*Anthurium pulidoae*
Anthurium michelii	*Anthurium obtusum subsp. puntarenense*	*Anthurium penae*	*Anthurium pulverulentum var. pulverulentum*
Anthurium microphyllum	*Anthurium occidentale*	*Anthurium pendens*	*Anthurium pulverulentum var. adsimile*
Anthurium microspadix	*Anthurium ochranthum*	*Anthurium pendulifolium*	*Anthurium punctatum*
Anthurium minarum	*Anthurium ochreatum*	*Anthurium penningtonii*	*Anthurium punkuyocense*
Anthurium mindense	*Anthurium ocotepecense*	*Anthurium pentaphyllum var. pentaphyllum*	*Anthurium purdieanum*
Anthurium miniatum	*Anthurium oerstedianum*	*Anthurium pentaphyllum var. bombacifolium*	*Anthurium purpureospathum*
Anthurium modicum	*Anthurium oreodoxa*	*Anthurium perijanum*	*Anthurium purpureum*
Anthurium molaui	*Anthurium oreophilum*	*Anthurium perviride*	*Anthurium queirozianum*
Anthurium molle	*Anthurium organense*	*Anthurium pescadilloense*	*Anthurium quinindense*
Anthurium montanum	*Anthurium orientale*	*Anthurium petrophilum*	*Anthurium quinquenervium*
Anthurium monteverdense	*Anthurium orteganum*	*Anthurium phyllobaris*	*Anthurium quinquesulcatum*
Anthurium monticola var. monticola	*Anthurium ottobuchtienii*	*Anthurium pichinchae*	
Anthurium monticola var. attenuatum	*Anthurium ottonis*		
Anthurium monzonense	*Anthurium ovatifolium*		

123

Scientific name	Scientific name	Scientific name	Scientific name
Anthurium quipuscoae	*Anthurium sanguineum*	*Anthurium subcarinatum*	*Anthurium triciafrankiae*
Anthurium radiatum	*Anthurium santaritensis*	*Anthurium subcaudatum*	*Anthurium trifidum*
Anthurium radicans	*Anthurium santiagoense*	*Anthurium subcoerulescens*	*Anthurium trilobum*
Anthurium raimundii	*Anthurium sapense*	*Anthurium subcordatum subsp. subcordatum*	*Anthurium trinervium*
Anthurium ramoncaracasii	*Anthurium sarmentosum*	*Anthurium subcordatum subsp. chlorocardium*	*Anthurium triphyllum*
Anthurium ramonense	*Anthurium sarukhanianum*	*Anthurium subhastatum*	*Anthurium trisectum*
Anthurium ramosense	*Anthurium scaberulum*	*Anthurium subovatum*	*Anthurium truncatulum*
Anthurium ramosii	*Anthurium scandens subsp. scandens*	*Anthurium subrotundum*	*Anthurium truncatum*
Anthurium ranchoanum	*Anthurium scandens subsp. pusillum*	*Anthurium subsagittatum*	*Anthurium truncicola*
Anthurium ravenii	*Anthurium scherzerianum*	*Anthurium subscriptum*	*Anthurium tsamajainii*
Anthurium recavum	*Anthurium schlechtendalii subsp. schlechtendalii*	*Anthurium subsignatum*	*Anthurium tunquii*
Anthurium redolens	*Anthurium schlechtendalii subsp. jimenezii*	*Anthurium subtriangulare*	*Anthurium tutense*
Anthurium reflexinervium	*Anthurium schottianum*	*Anthurium subtrilobum*	*Anthurium tysonii*
Anthurium regale	*Anthurium schunkei*	*Anthurium subtruncatum*	*Anthurium uasadiensis*
Anthurium remotigeniculatum	*Anthurium sebastianense*	*Anthurium subulatum*	*Anthurium uleanum var. uleanum*
Anthurium remotum	*Anthurium seibertii*	*Anthurium sucrii*	*Anthurium uleanum var. nanayense*
Anthurium renteriae	*Anthurium seleri*	*Anthurium sulcatum*	*Anthurium umbraculum*
Anthurium resectum	*Anthurium sellowianum*	*Anthurium superbum subsp. superbum*	*Anthurium umbricola*
Anthurium reticulatum	*Anthurium septuplinervium*	*Anthurium superbum subsp. brentberlinii*	*Anthurium umbrosum*
Anthurium retiferum	*Anthurium shinumas*	*Anthurium supianum*	*Anthurium unense*
Anthurium rhizophorum	*Anthurium siccisilvarum*	*Anthurium supraglandulum*	*Anthurium upalaense*
Anthurium rhodorhizum	*Anthurium sidneyi*	*Anthurium suramaense*	*Anthurium urbanii*
Anthurium ribeiroi	*Anthurium sierpense*	*Anthurium sylvestre*	*Anthurium urvilleanum*
Anthurium rigidifolium	*Anthurium signatum*	*Anthurium sytsmae*	*Anthurium utleyorum*
Anthurium rimbachii	*Anthurium silanchense*	*Anthurium tacarcunense*	*Anthurium validifolium*
Anthurium riodocense	*Anthurium silverstonei*	*Anthurium tachiranum*	*Anthurium validinervium*
Anthurium riofrioi	*Anthurium silvicola*	*Anthurium talmonii*	*Anthurium vallense*
Anthurium riograndicola	*Anthurium silvigaudens*	*Anthurium tamaense*	*Anthurium vanderknaapii*
Anthurium riojaense	*Anthurium simonii*	*Anthurium tarapotense*	*Anthurium variegatum*
Anthurium rionegrense	*Anthurium simpsonii*	*Anthurium tatei*	*Anthurium variilobum*
Anthurium riparium	*Anthurium sinuatum*	*Anthurium teimosoanum*	*Anthurium vaupesianum*
Anthurium rivulare	*Anthurium siqueirae*	*Anthurium tenaense*	*Anthurium veitchii*
Anthurium rodrigueziae	*Anthurium smaragdinum*	*Anthurium tenerum*	*Anthurium velutinum*
Anthurium roezlii	*Anthurium smithii*	*Anthurium tenuicaule*	*Anthurium venadoense*
Anthurium rojasiae	*Anthurium sodiroanum*	*Anthurium tenuifolium*	*Anthurium venosum*
Anthurium roraimense	*Anthurium soejartoi subsp. soejartoi*	*Anthurium tenuispica*	*Anthurium ventanasense*
Anthurium roseospadix	*Anthurium soejartoi subsp. ascendens*	*Anthurium teribense*	*Anthurium verapazense*
Anthurium rotundatum	*Anthurium solitarium*	*Anthurium ternifolium*	*Anthurium verrucosum*
Anthurium rotundilobum	*Anthurium solomonii*	*Anthurium terryae*	*Anthurium versicolor var. versicolor*
Anthurium rotundistigmatum	*Anthurium soukupii*	*Anthurium testaceum*	*Anthurium versicolor var. azuayense*
Anthurium rubrifructum	*Anthurium sparreorum*	*Anthurium thompsoniae*	*Anthurium vestitum*
Anthurium rubrivellus	*Anthurium spathiphyllum*	*Anthurium thrinax*	*Anthurium victorii*
Anthurium rugulosum	*Anthurium spathulifolium*	*Anthurium tikunorum*	*Anthurium vientense*
Anthurium rupestre	*Anthurium spectabile*	*Anthurium tilaranense*	*Anthurium vinillense*
Anthurium rupicola	*Anthurium splendidum*	*Anthurium timplowmanii*	*Anthurium viridescens*
Anthurium rzedowskii	*Anthurium standleyi*	*Anthurium titanium*	*Anthurium viridispathum*
Anthurium saccardoi	*Anthurium stephanii*	*Anthurium tolimense*	*Anthurium vittariifolium*
Anthurium sagawae	*Anthurium stipitatum*	*Anthurium tomasiae*	*Anthurium vomeriforme*
Anthurium sagittale	*Anthurium straminopetiolum*	*Anthurium tonduzii*	*Anthurium wagenerianum*
Anthurium sagittaria	*Anthurium striatipes*	*Anthurium tonianum*	*Anthurium wallisii*
Anthurium sagittatum	*Anthurium striatum*	*Anthurium torraense*	*Anthurium walujewii*
Anthurium sagittellum	*Anthurium striolatum*	*Anthurium treleasei*	*Anthurium warintsense*
Anthurium salgarense	*Anthurium stuebelii*	*Anthurium tremulum*	*Anthurium warocqueanum*
Anthurium salvadorense	*Anthurium subaequans*	*Anthurium trianae*	*Anthurium watermaliense*
Anthurium salvinii		*Anthurium tricarinatum*	*Anthurium wattii*
Anthurium samamaense			
Anthurium sanctifidense			

124

Scientific name	Scientific name	Scientific name	Scientific name
Anthurium weberbaueri	*Aridarum montanum*	*Arisaema flavum subsp. flavum*	*Arisaema monophyllum var. monophyllum*
Anthurium wedelianum subsp. wedelianum	*Aridarum nicolsonii*	*Arisaema flavum subsp. tibeticum*	*Arisaema monophyllum var. atrolinguum*
Anthurium wedelianum subsp. viridispadix	*Aridarum purseglovei*	*Arisaema formosanum*	*Arisaema mooneyanum*
Anthurium wendlingeri	*Aridarum rostratum*	*Arisaema franchetianum*	*Arisaema muratae*
Anthurium werffii	*Ariopsis peltata*	*Arisaema fraternum*	*Arisaema muricaudatum*
Anthurium werneri	*Ariopsis protanthera*	*Arisaema galeatum*	*Arisaema murrayi var. murrayi*
Anthurium whitmorei	*Arisaema abei*	*Arisaema garrettii*	*Arisaema murrayi var. sahyadricum*
Anthurium willdenowii	*Arisaema aequinoctiale*	*Arisaema ghaticum*	*Arisaema murrayi var. sonubeniae*
Anthurium willifordii	*Arisaema agasthyanum*	*Arisaema grapsospadix*	*Arisaema nagiense*
Anthurium wintersii	*Arisaema album*	*Arisaema griffithii*	*Arisaema nambae*
Anthurium wurdackii	*Arisaema amurense*	*Arisaema hainanense*	*Arisaema negishii*
Anthurium xanthoneurum	*Arisaema anomalum*	*Arisaema handelii*	*Arisaema nepenthoides*
Anthurium xanthophylloides	*Arisaema aprile*	*Arisaema heterocephalum subsp. heterocephalum*	*Arisaema nikoense var. nikoense*
Anthurium yamayakatense	*Arisaema aridum*	*Arisaema heterocephalum subsp. okinawaense*	*Arisaema nikoense var. australe*
Anthurium yarumalense	*Arisaema asperatum*	*Arisaema heterophyllum*	*Arisaema nikoense var. kaimontanum*
Anthurium yatacuense	*Arisaema auriculatum*	*Arisaema hunanense*	*Arisaema nilamburense*
Anthurium yetlense	*Arisaema austroyunnanense*	*Arisaema ilanense*	*Arisaema odoratum*
Anthurium yungasense	*Arisaema averyanovii*	*Arisaema inclusum*	*Arisaema ogatae*
Anthurium yurimaguense	*Arisaema balansae*	*Arisaema intermedium*	*Arisaema omkoiense*
Anthurium yutajense	*Arisaema bannaense*	*Arisaema ishizuchiense subsp. ishizuchiense*	*Arisaema ornatum var. ornatum*
Anthurium zappiae	*Arisaema barbatum*	*Arisaema ishizuchiense subsp. brevicollum*	*Arisaema ovale var. ovale*
Anthurium zeneidae	*Arisaema barnesii*	*Arisaema iyoanum*	*Arisaema ovale var. inaense*
Anthurium zuloagae	*Arisaema bockii*	*Arisaema jacquemontii*	*Arisaema ovale var. sadoense*
Anubias afzelii	*Arisaema bonatianum*	*Arisaema jethompsonii*	*Arisaema pachystachyum*
Anubias barteri var. barteri	*Arisaema bottae*	*Arisaema jingdongense*	*Arisaema pallidum*
Anubias barteri var. angustifolia	*Arisaema brucei*	*Arisaema kawashimae*	*Arisaema parisifolia*
Anubias barteri var. caladiifolia	*Arisaema calcareum*	*Arisaema kerrii*	*Arisaema parvum*
Anubias barteri var. glabra	*Arisaema candidissimum*	*Arisaema kishidae*	*Arisaema pattaniense*
Anubias barteri var. nana	*Arisaema caudatum*	*Arisaema kiushianum*	*Arisaema penicillatum*
Anubias gigantea	*Arisaema chuanxiense*	*Arisaema kuratae*	*Arisaema petelotii*
Anubias gilletii	*Arisaema chumponense*	*Arisaema lackneri*	*Arisaema petiolulatum*
Anubias gracilis	*Arisaema ciliatum*	*Arisaema laminatum*	*Arisaema pianmaense*
Anubias hastifolia	*Arisaema clavatum*	*Arisaema leschenaultii*	*Arisaema pingbianense*
Anubias heterophylla	*Arisaema concinnum*	*Arisaema lichiangense*	*Arisaema polyphyllum*
Anubias pynaertii	*Arisaema condaoense*	*Arisaema lidaense*	*Arisaema prazeri*
Apoballis acuminatissima	*Arisaema consanguineum subsp. consanguineum*	*Arisaema lihengianum*	*Arisaema propinquum*
Apoballis belophylla	*Arisaema consanguineum subsp. kelung-insulare*	*Arisaema limbatum*	*Arisaema psittacus*
Apoballis brevipes	*Arisaema constrictum*	*Arisaema linearifolium*	*Arisaema quinatum*
Apoballis grandiflora	*Arisaema cordatum*	*Arisaema lingyunense*	*Arisaema quinquelobatum*
Apoballis hastifolia	*Arisaema costatum*	*Arisaema lobatum*	*Arisaema ramulosum*
Apoballis javanica	*Arisaema cucullatum*	*Arisaema longipedunculatum*	*Arisaema ringens*
Apoballis longicaulis	*Arisaema dahaiense*	*Arisaema macrospathum*	*Arisaema rostratum*
Apoballis mutata	*Arisaema decipiens*	*Arisaema maekawae*	*Arisaema roxburghii*
Apoballis okadae	*Arisaema dracontium*	*Arisaema mairei*	*Arisaema rubrirhizomatum*
Apoballis ovata	*Arisaema echinatum*	*Arisaema maximowiczii subsp. maximowiczii*	*Arisaema ruwenzoricum*
Apoballis rupestris	*Arisaema echinoides*	*Arisaema maximowiczii subsp. tashiroi*	*Arisaema sachalinense*
Apoballis sagittifolia	*Arisaema ehimense*	*Arisaema maxwellii*	*Arisaema saddlepeakense*
Aridarum borneense	*Arisaema elephas*	*Arisaema meleagris*	*Arisaema sarracenioides*
Aridarum burttii	*Arisaema enneaphyllum*	*Arisaema menglaense*	*Arisaema saxatile*
Aridarum caulescens	*Arisaema erubescens*	*Arisaema microspadix*	*Arisaema sazensoo*
Aridarum crassum	*Arisaema exappendiculatum*	*Arisaema mildbraedii*	*Arisaema schimperianum*
Aridarum incavatum	*Arisaema fargesii*	*Arisaema minamitanii*	
Aridarum minimum	*Arisaema filiforme*	*Arisaema minus*	
	Arisaema fimbriatum subsp. fimbriatum		
	Arisaema fimbriatum subsp. bakerianum		

Scientific name	Scientific name	Scientific name	Scientific name
Arisaema scortechinii	*Arisaema wrayi*	*Arum megobrebi*	*Bucephalandra motleyana*
Arisaema seppikoense	*Arisaema xuanweiense*	*Arum nigrum*	*Caladium andreanum*
Arisaema serratum var. serratum	*Arisaema yamatense subsp. yamatense*	*Arum orientale subsp. orientale*	*Caladium bicolor*
Arisaema serratum var. izuense	*Arisaema yamatense subsp. sugimotoi*	*Arum orientale subsp. longispathum*	*Caladium clavatum*
Arisaema serratum var. mayebarae	*Arisaema yanxianum*	*Arum palaestinum*	*Caladium coerulescens*
Arisaema serratum var. suwoense	*Arisaema yunnanense*	*Arum pictum*	*Caladium humboldtii*
Arisaema setosum	*Arisaema zhui*	*Arum purpureospathum*	*Caladium lindenii*
Arisaema siamicum	*Arisarum proboscideum*	*Arum rupicola var. rupicola*	*Caladium macrotites*
Arisaema siangense	*Arisarum simorrhinum*	*Arum rupicola var. virescens*	*Caladium picturatum*
Arisaema sikokianum	*Arisarum vulgare subsp. vulgare*	*Arum sintenisii*	*Caladium praetermissum*
Arisaema silvestrii	*Arisarum vulgare subsp. clusii*	*Asterostigma cryptostylum*	*Caladium schomburgkii*
Arisaema sinii	*Arisarum vulgare subsp. hastatum*	*Asterostigma cubense*	*Caladium smaragdinum*
Arisaema sizemoreae	*Arophyton buchetii*	*Asterostigma lividum*	*Caladium steyermarkii*
Arisaema smitinandii	*Arophyton crassifolium*	*Asterostigma lombardii*	*Caladium ternatum*
Arisaema somalense	*Arophyton humbertii*	*Asterostigma luschnathianum*	*Caladium tuberosum*
Arisaema souliei	*Arophyton pedatum*	*Asterostigma reticulatum*	*Calla palustris*
Arisaema speciosum var. speciosum	*Arophyton rhizomatosum*	*Asterostigma riedelianum*	*Callopsis volkensii*
Arisaema speciosum var. mirabile	*Arophyton simplex*	*Asterostigma tweedieanum*	*Carlephyton diegoense*
Arisaema speciosum var. ziroense	*Arophyton tripartitum var. tripartitum*	*Bakoa brevipedunculata*	*Carlephyton glaucophyllum*
Arisaema sukotaiense	*Arophyton tripartitum var. masoalaense*	*Bakoa lucens*	*Carlephyton madagascariense*
Arisaema taiwanense var. taiwanense	*Arum alpinariae*	*Bakoa nakamotoi*	*Cercestis afzelii*
Arisaema taiwanense var. brevipedunculatum	*Arum apulum*	*Biarum aleppicum*	*Cercestis camerunensis*
Arisaema tengtsungense	*Arum balansanum*	*Biarum angustatum*	*Cercestis congoensis*
Arisaema ternatipartitum	*Arum besserianum*	*Biarum auraniticum*	*Cercestis dinklagei*
Arisaema thunbergii subsp. thunbergii	*Arum byzantinum*	*Biarum bovei*	*Cercestis hepperi*
Arisaema thunbergii subsp. autumnale	*Arum concinnatum*	*Biarum carduchorum*	*Cercestis ivorensis*
Arisaema thunbergii subsp. geomundoense	*Arum creticum*	*Biarum carratracense*	*Cercestis kamerunianus*
Arisaema thunbergii subsp. urashima	*Arum cylindraceum subsp. cylindraceum*	*Biarum crispulum*	*Cercestis mirabilis*
Arisaema tortuosum subsp. tortuosum	*Arum cylindraceum subsp. pitsyllianum*	*Biarum davisii*	*Cercestis sagittatus*
Arisaema tortuosum var. neglectum	*Arum cyrenaicum*	*Biarum dispar*	*Cercestis taiensis*
Arisaema tortuosum subsp. sivadasanii	*Arum dioscoridis var. dioscoridis*	*Biarum ditschianum*	*Chlorospatha amalfiensis*
Arisaema tosaense	*Arum dioscoridis var. cyprium*	*Biarum eximium*	*Chlorospatha antioquiensis*
Arisaema translucens	*Arum dioscoridis var. philistaeum*	*Biarum fraasianum*	*Chlorospatha atropurpurea*
Arisaema triphyllum	*Arum dioscoridis var. syriacum*	*Biarum kotschyi*	*Chlorospatha besseae*
Arisaema tsangpoense	*Arum elongatum*	*Biarum marmarisense*	*Chlorospatha betancurii*
Arisaema tuberculatum	*Arum euxinum*	*Biarum mendax*	*Chlorospatha bogneri*
Arisaema ulugurense	*Arum gratum*	*Biarum olivieri*	*Chlorospatha callejasii*
Arisaema umbrinum	*Arum hainesii*	*Biarum pyramid var. pyrami*	*Chlorospatha castula*
Arisaema undulatifolium subsp. undulatifolium	*Arum hygrophilum*	*Biarum pyrami var. serotinum*	*Chlorospatha cogolloi*
Arisaema undulatifolium subsp. uwajimense	*Arum idaeum*	*Biarum rhopalospadix*	*Chlorospatha corrugata*
Arisaema utile	*Arum italicum subsp. italicum*	*Biarum straussii*	*Chlorospatha croatiana subsp. croatiana*
Arisaema vexillatum	*Arum italicum subsp. albispathum*	*Biarum syriacum*	*Chlorospatha croatiana subsp. enneaphylla*
Arisaema victoriae	*Arum italicum subsp. canariense*	*Biarum tenuifolium subsp. tenuifolium*	*Chlorospatha cutucuensis*
Arisaema wangmoense	*Arum italicum subsp. neglectum*	*Biarum tenuifolium subsp. abbreviatum*	*Chlorospatha dodsonii*
Arisaema wardii	*Arum jacquemontii*	*Biarum tenuifolium subsp. arundanum*	*Chlorospatha feuersteiniae*
Arisaema wattii	*Arum korolkowii*	*Biarum tenuifolium subsp. galianii*	*Chlorospatha gentryi*
Arisaema wilsonii	*Arum lucanum*	*Biarum tenuifolium subsp. idomenaeum*	*Chlorospatha hammeliana*
	Arum maculatum	*Biarum tenuifolium subsp. zelebori*	*Chlorospatha hastifolia*
		Bognera recondita	*Chlorospatha ilensis*
		Bucephalandra gigantea	*Chlorospatha kolbii*
			Chlorospatha kressii
			Chlorospatha lehmannii
			Chlorospatha longipoda
			Chlorospatha luteynii
			Chlorospatha macphersonii
			Chlorospatha mirabilis

Scientific name	Scientific name	Scientific name	Scientific name
Chlorospatha nicolsonii	*Cryptocoryne keei*	*Culcasia seretii*	*Dieffenbachia obscurinervia*
Chlorospatha planadensis	*Cryptocoryne lingua*	*Culcasia simiarum*	*Dieffenbachia oerstedii*
Chlorospatha ricaurtensis	*Cryptocoryne loeiensis*	*Culcasia striolata*	*Dieffenbachia olbia*
Colletogyne perrieri	*Cryptocoryne longicauda*	*Culcasia tenuifolia*	*Dieffenbachia paludicola*
Colocasia affinis	*Cryptocoryne mekongensis*	*Culcasia yangambiensis*	*Dieffenbachia panamensis*
Colocasia antiquorum	*Cryptocoryne minima*	*Cyrtosperma beccarianum*	*Dieffenbachia parlatorei*
Colocasia esculenta	*Cryptocoryne moehlmannii*	*Cyrtosperma bougainvillense*	*Dieffenbachia parvifolia*
Colocasia fallax	*Cryptocoryne nevillii*	*Cyrtosperma brassii*	*Dieffenbachia pittieri*
Colocasia gigantea	*Cryptocoryne noritoi*	*Cyrtosperma carrii*	*Dieffenbachia seguine*
Colocasia mannii	*Cryptocoryne nurii*	*Cyrtosperma cuspidispathum*	*Dieffenbachia shuttleworthiana*
Colocasia menglaensis	*Cryptocoryne pallidinervia*	*Cyrtosperma giganteum*	*Dieffenbachia standleyi*
Colocasia oresbia	*Cryptocoryne parva*	*Cyrtosperma gressittiorum*	*Dieffenbachia tonduzii*
Croatiella integrifolia	*Cryptocoryne pontederiifolia*	*Cyrtosperma hambalii*	*Dieffenbachia weberbaueri*
Cryptocoryne affinis	*Cryptocoryne pygmaea*	*Cyrtosperma johnstonii*	*Dieffenbachia weirii*
Cryptocoryne alba	*Cryptocoryne retrospiralis*	*Cyrtosperma kokodense*	*Dieffenbachia wendlandii*
Cryptocoryne albida	*Cryptocoryne schulzei*	*Cyrtosperma macrotum*	*Dieffenbachia williamsii*
Cryptocoryne annamica	*Cryptocoryne scurrilis*	*Cyrtosperma merkusii*	*Dieffenbachia wurdackii*
Cryptocoryne aponogetifolia	*Cryptocoryne sivadasanii*	*Dieffenbachia aglaonematifolia*	*Dracontioides desciscens*
Cryptocoryne auriculata	*Cryptocoryne spiralis var. spiralis*	*Dieffenbachia antioquensis*	*Dracontioides salvianii*
Cryptocoryne bangkaensis	*Cryptocoryne spiralis var. cognatoides*	*Dieffenbachia aurantiaca*	*Dracontium amazonense*
Cryptocoryne beckettii	*Cryptocoryne striolata*	*Dieffenbachia beachiana*	*Dracontium angustispathum*
Cryptocoryne bogneri	*Cryptocoryne tambraparaniana*	*Dieffenbachia bechiana*	*Dracontium asperispathum*
Cryptocoryne bullosa	*Cryptocoryne thwaitesii*	*Dieffenbachia bowmannii*	*Dracontium asperum*
Cryptocoryne ciliata	*Cryptocoryne uenoi*	*Dieffenbachia brittonii*	*Dracontium bogneri*
Cryptocoryne cognata	*Cryptocoryne undulata*	*Dieffenbachia burgeri*	*Dracontium croatii*
Cryptocoryne consobrina	*Cryptocoryne usteriana*	*Dieffenbachia cannifolia*	*Dracontium dubium*
Cryptocoryne cordata var. cordata	*Cryptocoryne versteegii*	*Dieffenbachia concinna*	*Dracontium gigas*
Cryptocoryne cordata var. diderici	*Cryptocoryne vietnamensis*	*Dieffenbachia copensis*	*Dracontium grandispathum*
Cryptocoryne cordata var. evae	*Cryptocoryne villosa*	*Dieffenbachia cordata*	*Dracontium grayumianum*
Cryptocoryne cordata var. grabowskii	*Cryptocoryne walkeri*	*Dieffenbachia costata*	*Dracontium guianense*
Cryptocoryne cordata var. zonata	*Cryptocoryne wendtii*	*Dieffenbachia crebripistillata*	*Dracontium iquitense*
Cryptocoryne coronata	*Cryptocoryne yujii*	*Dieffenbachia daguensis*	*Dracontium longipes*
Cryptocoryne crispatula var. crispatula	*Cryptocoryne zaidiana*	*Dieffenbachia davidsei*	*Dracontium margaretae*
Cryptocoryne crispatula var. balansae	*Cryptocoryne zukalii*	*Dieffenbachia duidae*	*Dracontium nivosum*
Cryptocoryne crispatula var. decus-mekongensis	*Culcasia angolensis*	*Dieffenbachia elegans*	*Dracontium peruvianum*
Cryptocoryne crispatula var. flaccidifolia	*Culcasia annetii*	*Dieffenbachia enderi*	*Dracontium pittieri*
Cryptocoryne crispatula var. planifolia	*Culcasia bosii*	*Dieffenbachia fortunensis*	*Dracontium plowmanii*
Cryptocoryne crispatula var. tonkinensis	*Culcasia brevipetiolata*	*Dieffenbachia fosteri*	*Dracontium polyphyllum*
Cryptocoryne crispatula var. yunnanensis	*Culcasia caudata*	*Dieffenbachia fournieri*	*Dracontium prancei*
Cryptocoryne cruddasiana	*Culcasia dinklagei*	*Dieffenbachia galdamesiae*	*Dracontium purdieanum*
Cryptocoryne decus-silvae	*Culcasia ekongoloi*	*Dieffenbachia gracilis*	*Dracontium soconuscum*
Cryptocoryne dewitii	*Culcasia falcifolia*	*Dieffenbachia grayumiana*	*Dracontium spruceanum*
Cryptocoryne edithiae	*Culcasia glandulosa*	*Dieffenbachia hammelii*	*Dracontium ulei*
Cryptocoryne elliptica	*Culcasia insulana*	*Dieffenbachia herthae*	*Dracunculus canariensis*
Cryptocoryne ferruginea	*Culcasia lanceolata*	*Dieffenbachia horichii*	*Dracunculus vulgaris*
Cryptocoryne fusca	*Culcasia liberica*	*Dieffenbachia humilis*	*Eminium albertii*
Cryptocoryne griffithii	*Culcasia linearifolia*	*Dieffenbachia imperialis*	*Eminium heterophyllum*
Cryptocoryne hudoroi	*Culcasia loukandensis*	*Dieffenbachia isthmia*	*Eminium intortum*
Cryptocoryne ideii	*Culcasia mannii*	*Dieffenbachia killipii*	*Eminium jaegeri*
Cryptocoryne jacobsenii	*Culcasia obliquifolia*	*Dieffenbachia lancifolia*	*Eminium koenenianum*
	Culcasia orientalis	*Dieffenbachia leopoldii*	*Eminium lehmannii*
	Culcasia panduriformis	*Dieffenbachia longispatha*	*Eminium rauwolffii var. rauwolffii*
	Culcasia parviflora	*Dieffenbachia lutheri*	*Eminium rauwolffii var. kotschyi*
	Culcasia rotundifolia	*Dieffenbachia macrophylla*	*Eminium regelii*
	Culcasia sanagensis	*Dieffenbachia meleagris*	*Eminium spiculatum*
	Culcasia scandens	*Dieffenbachia nitidipetiolata*	*Epipremnum amplissimum*
		Dieffenbachia obliqua	

Scientific name	Scientific name	Scientific name	Scientific name
Epipremnum aureum	*Heteropsis salicifolia*	*Homalomena kiahii*	*Homalomena steenisiana*
Epipremnum carolinense	*Heteropsis spruceana*	*Homalomena korthalsii*	*Homalomena stollei*
Epipremnum ceramense	*Heteropsis steyermarkii*	*Homalomena kualakohensis*	*Homalomena striatieopetiolata*
Epipremnum dahlii	*Heteropsis tenuispadix*	*Homalomena kvistii*	*Homalomena subcordata*
Epipremnum falcifolium	*Holochlamys beccarii*	*Homalomena lancea*	*Homalomena symplocarpifolia*
Epipremnum giganteum	*Homalomena adiensis*	*Homalomena lancifolia*	*Homalomena tenuispadix*
Epipremnum meeboldii	*Homalomena aeneifolia*	*Homalomena latifrons*	*Homalomena terajaensis*
Epipremnum moluccanum	*Homalomena agens*	*Homalomena lauterbachii*	*Homalomena treubii*
Epipremnum moszkowskii	*Homalomena ardua*	*Homalomena lindenii*	*Homalomena truncata*
Epipremnum nobile	*Homalomena argentea*	*Homalomena longipes*	*Homalomena vagans*
Epipremnum obtusum	*Homalomena aromatica*	*Homalomena magna*	*Homalomena vietnamensis*
Epipremnum papuanum	*Homalomena asmae*	*Homalomena major*	*Homalomena vittifolia*
Epipremnum pinnatum	*Homalomena asperifolia*	*Homalomena matangae*	*Homalomena vivens*
Epipremnum silvaticum	*Homalomena atroviridis*	*Homalomena megalophylla*	*Homalomena wallichii*
Filarum manserichense	*Homalomena atrox*	*Homalomena melanesica*	*Homalomena wallisii*
Furtadoa mixta	*Homalomena batoeensis*	*Homalomena metallica*	*Homalomena wendlandii*
Furtadoa sumatrensis	*Homalomena bellula*	*Homalomena minor*	*Homalomena wongii*
Gearum brasiliense	*Homalomena burkilliana*	*Homalomena minutissima*	*Homalomena zollingeri*
Gonatopus angustus	*Homalomena clandestina*	*Homalomena moffleriana*	*Incarum pavonii*
Gonatopus boivinii	*Homalomena cochinchinensis*	*Homalomena monandra*	*Jasarum steyermarkii*
Gonatopus clavatus	*Homalomena confusa*	*Homalomena montana*	*Lagenandra bogneri*
Gonatopus marattioides	*Homalomena consobrina*	*Homalomena nigrescens*	*Lagenandra dewitii*
Gonatopus petiolulatus	*Homalomena cordata*	*Homalomena nutans*	*Lagenandra erosa*
Gorgonidium beckianum	*Homalomena corneri*	*Homalomena obovata*	*Lagenandra gomezii*
Gorgonidium bulbostylum	*Homalomena crinipes*	*Homalomena obscurifolia*	*Lagenandra jacobsenii*
Gorgonidium cardenasianum	*Homalomena cristata*	*Homalomena occulta*	*Lagenandra keralensis*
Gorgonidium intermedium	*Homalomena curtisii*	*Homalomena ovalifolia*	*Lagenandra koenigii*
Gorgonidium mirabile	*Homalomena curvata*	*Homalomena ovata*	*Lagenandra lancifolia*
Gorgonidium striatum	*Homalomena davidiana*	*Homalomena padangensis*	*Lagenandra meeboldii*
Gorgonidium vargasii	*Homalomena debilicrista*	*Homalomena palawanensis*	*Lagenandra nairii*
Gorgonidium vermicidum	*Homalomena distans*	*Homalomena peekelii*	*Lagenandra ovata*
Gymnostachys anceps	*Homalomena doctersii*	*Homalomena peltata*	*Lagenandra praetermissa*
Hapaline appendiculata	*Homalomena elegans*	*Homalomena pendula*	*Lagenandra thwaitesii*
Hapaline benthamiana	*Homalomena elegantula*	*Homalomena philippinensis*	*Lagenandra toxicaria*
Hapaline brownii	*Homalomena erythropus subsp. erythropus*	*Homalomena picturata*	*Lagenandra undulata*
Hapaline celatrix	*Homalomena erythropus subsp. allenii*	*Homalomena pineodora*	*Lasia concinna*
Hapaline colaniae	*Homalomena expedita*	*Homalomena pontederifolia*	*Lasia spinosa*
Hapaline ellipticifolia	*Homalomena gadutensis*	*Homalomena producta*	*Lasimorpha senegalensis*
Hapaline kerrii	*Homalomena gaudichaudii*	*Homalomena pseudogeniculata*	*Lemna aequinoctialis*
Hapaline locii	*Homalomena giamensis*	*Homalomena pulleana*	*Lemna disperma*
Helicodiceros muscivorus	*Homalomena gillii*	*Homalomena punctulata*	*Lemna gibba*
Hestia longifolia	*Homalomena griffithii*	*Homalomena pyrospatha*	*Lemna japonica*
Heteropsis boliviana	*Homalomena hainanensis*	*Homalomena robusta*	*Lemna minor*
Heteropsis croatii	*Homalomena hammelii*	*Homalomena roezelii*	*Lemna minuta*
Heteropsis duckeana	*Homalomena hanneae*	*Homalomena rostrata*	*Lemna obscura*
Heteropsis ecuadorensis	*Homalomena hastata*	*Homalomena rubescens*	*Lemna perpusilla*
Heteropsis flexuosa var. flexuosa	*Homalomena havilandii*	*Homalomena rusdii*	*Lemna tenera*
Heteropsis flexuosa var. maguirei	*Homalomena hendersonii*	*Homalomena sarawakensis*	*Lemna trisulca*
Heteropsis linearis	*Homalomena hooglandii*	*Homalomena saxorum*	*Lemna turionifera*
Heteropsis longispathacea	*Homalomena humilis*	*Homalomena schlechteri*	*Lemna valdiviana*
Heteropsis macrophylla	*Homalomena impudica*	*Homalomena scortechinii*	*Lemna yungensis*
Heteropsis melinonii	*Homalomena insignis*	*Homalomena sengkenyang*	*Lorenzia umbrosa*
Heteropsis oblongifolia	*Homalomena jacobsiana*	*Homalomena silvatica*	*Lysichiton americanus*
Heteropsis peruviana	*Homalomena josefii*	*Homalomena singaporensis*	*Lysichiton camtschatcensis*
Heteropsis rigidifolia	*Homalomena kalkmanii*	*Homalomena soniae*	*Mangonia tweedieana*
Heteropsis robusta	*Homalomena kelungensis*	*Homalomena speariae*	*Mangonia uruguaya*
			Monstera acacoyaguensis

Scientific name

Monstera acuminata
Monstera adansonii var. adansonii
Monstera adansonii var. klotzschiana
Monstera adansonii var. laniata
Monstera amargalensis
Monstera aureopinnata
Monstera barrieri
Monstera buseyi
Monstera cenepensis
Monstera costaricensis
Monstera deliciosa
Monstera dissecta
Monstera dubia
Monstera epipremnoides
Monstera filamentosa
Monstera florescanoana
Monstera glaucescens
Monstera gracilis
Monstera kessleri
Monstera lechleriana
Monstera lentii
Monstera luteynii
Monstera maderaverde
Monstera membranacea
Monstera minima
Monstera molinae
Monstera obliqua
Monstera oreophila
Monstera pinnatipartita
Monstera pittieri
Monstera planadensis
Monstera praetermissa
Monstera punctulata
Monstera siltepecana
Monstera spruceana
Monstera standleyana
Monstera subpinnata
Monstera tenuis
Monstera tuberculata var. tuberculata
Monstera tuberculata var. brevinoda
Monstera vasquezii
Monstera xanthospatha
Montrichardia arborescens
Montrichardia linifera
Nephthytis afzelii var. afzelii
Nephthytis afzelii var. graboensis
Nephthytis bintuluensis
Nephthytis hallaei
Nephthytis mayombensis
Nephthytis poissonii var. poissonii
Nephthytis poissonii var. constricta
Nephthytis swainei

Scientific name

Ooia grabowskii
Ooia kinabaluensis
Orontium aquaticum
Pedicellarum paiei
Peltandra sagittifolia
Peltandra virginica
Philodendron acreanum
Philodendron acuminatissimum
Philodendron acutifolium
Philodendron adamantinum
Philodendron adhatodifolium
Philodendron advena
Philodendron aemulum
Philodendron alatum
Philodendron albisuccus
Philodendron alliodorum
Philodendron alternans
Philodendron alticola
Philodendron altomacaense
Philodendron amargalense
Philodendron ampamii
Philodendron amplisinum
Philodendron ampullaceum
Philodendron anaadu
Philodendron ancuashii
Philodendron angustialatum
Philodendron angustilobum
Philodendron angustisectum
Philodendron anisotomum
Philodendron annulatum
Philodendron antonioanum
Philodendron appendiculatum
Philodendron applanatum
Philodendron appunii
Philodendron aristeguietae
Philodendron aromaticum
Philodendron asplundii
Philodendron atabapoense
Philodendron aurantiifolium subsp. aurantiifolium
Philodendron aurantiifolium subsp. calderense
Philodendron aurantispadix
Philodendron aureimarginatum
Philodendron auriculatum
Philodendron auritum
Philodendron auyantepuiense
Philodendron avenium
Philodendron azulitense
Philodendron bahiense
Philodendron bakeri
Philodendron balaoanum
Philodendron barbourii
Philodendron barrosoanum
Philodendron basii
Philodendron basivaginatum
Philodendron baudoense

Scientific name

Philodendron beniteziae
Philodendron bernardopazii
Philodendron billietiae
Philodendron bipennifolium
Philodendron bipinnatifidum
Philodendron biribiriense
Philodendron blanchetianum
Philodendron bogotense
Philodendron borgesii
Philodendron brandii
Philodendron brandtianum
Philodendron brasiliense
Philodendron breedlovei
Philodendron brenesii
Philodendron brent-berlinii
Philodendron brevispathum
Philodendron brewsterense
Philodendron brunneicaule
Philodendron buchtienii
Philodendron buntingianum
Philodendron burgeri
Philodendron burle-marxii
Philodendron calatheifolium
Philodendron callosum subsp. callosum
Philodendron callosum subsp. ptarianum
Philodendron campii
Philodendron camposportoanum
Philodendron canaimae
Philodendron canicaule
Philodendron cardonii
Philodendron cardosoi
Philodendron carinatum
Philodendron cataniapoense
Philodendron caudatum
Philodendron chimantae
Philodendron chimboanum
Philodendron chinchamayense
Philodendron chiriquense
Philodendron chirripoense
Philodendron chrysocarpum
Philodendron cipoense
Philodendron clarkei
Philodendron clewellii
Philodendron colombianum
Philodendron coloradense
Philodendron condorcanquense
Philodendron conforme
Philodendron consanguineum
Philodendron consobrinum
Philodendron copense
Philodendron corcovadense
Philodendron cordatum
Philodendron coriaceum
Philodendron correae
Philodendron cotapatense

Scientific name

Philodendron cotobrusense
Philodendron cotonense
Philodendron craspedodromum
Philodendron crassinervium
Philodendron crassispathum
Philodendron crassum
Philodendron cremersii
Philodendron cretosum
Philodendron croatii
Philodendron cruentospathum
Philodendron cruentum
Philodendron cuneatum
Philodendron curvilobum
Philodendron daniellii
Philodendron danteanum
Philodendron dardanianum
Philodendron davidsei
Philodendron davidsonii subsp. davidsonii
Philodendron davidsonii subsp. bocatoranum
Philodendron deflexum
Philodendron delascioi
Philodendron delinksii
Philodendron deltoideum
Philodendron densivenium
Philodendron devansayanum
Philodendron devianum
Philodendron dioscoreoides
Philodendron discretivenium
Philodendron distantilobum
Philodendron divaricatum
Philodendron dodsonii
Philodendron dolichophyllum
Philodendron dominicalense
Philodendron dressleri
Philodendron dryanderae
Philodendron duckei
Philodendron dunstervilleorum
Philodendron dussii
Philodendron dwyeri
Philodendron dyscarpium var. dyscarpium
Philodendron dyscarpium var. ventuarianum
Philodendron eburneum
Philodendron ecordatum
Philodendron edenudatum
Philodendron edmundoi
Philodendron effusilobum
Philodendron elaphoglossoides
Philodendron elegans
Philodendron elegantulum
Philodendron englerianum subsp. englerianum
Philodendron englerianum subsp. duidae
Philodendron ensifolium subsp. ensifolium

Scientific name

Philodendron ensifolium subsp. campanense

Philodendron ensifolium subsp. colonense

Philodendron ernestii

Philodendron erubescens

Philodendron escuintlense

Philodendron exile

Philodendron eximium

Philodendron fendleri

Philodendron ferrugineum

Philodendron fibrillosum

Philodendron fibrosum

Philodendron findens

Philodendron flumineum

Philodendron follii

Philodendron folsomii

Philodendron fortunense

Philodendron fragile

Philodendron fragrantissimum

Philodendron fraternum

Philodendron furcatum

Philodendron giganteum

Philodendron gigas

Philodendron glanduliferum subsp. glanduliferum

Philodendron glanduliferum subsp. camiloanum

Philodendron glaziovii

Philodendron gloriosum

Philodendron goeldii

Philodendron gonzalezii

Philodendron grandifolium

Philodendron grandipes

Philodendron granulare

Philodendron graveolens

Philodendron grayumii

Philodendron grazielae

Philodendron grenandii

Philodendron guaiquinimae

Philodendron gualeanum

Philodendron guianense

Philodendron guttiferum

Philodendron hammelii

Philodendron hastatum

Philodendron hatschbachii

Philodendron hebetatum

Philodendron hederaceum var. hederaceum

Philodendron hederaceum var. kirkbridei

Philodendron hederaceum var. oxycardium

Philodendron heleniae subsp. heleniae

Philodendron heleniae subsp. amazonense

Philodendron henry-pittieri

Philodendron herbaceum

Philodendron herthae

Philodendron heterocraspedon

Scientific name

Philodendron heterophyllum

Philodendron heteropleurum

Philodendron holstii

Philodendron hooveri

Philodendron hopkinsianum

Philodendron houlletianum

Philodendron huanucense

Philodendron huashikatii

Philodendron huaynacapacense

Philodendron humile

Philodendron hylaeae

Philodendron ichthyoderma

Philodendron immixtum

Philodendron inaequilaterum

Philodendron inconcinnum

Philodendron inops

Philodendron insigne

Philodendron jacquinii

Philodendron jefense

Philodendron jodavisianum

Philodendron jonkerorum

Philodendron juninense

Philodendron kautskyi

Philodendron killipii

Philodendron knappiae

Philodendron krauseanum

Philodendron kroemeri

Philodendron krugii

Philodendron lacerum

Philodendron laticiferum

Philodendron latifolium

Philodendron lazorii

Philodendron leal-costae

Philodendron lechlerianum

Philodendron lehmannii

Philodendron lemae

Philodendron lentii

Philodendron leucanthum

Philodendron leyvae

Philodendron liesneri

Philodendron ligulatum var. ligulatum

Philodendron ligulatum var. heraclioanum

Philodendron ligulatum var. ovatum

Philodendron lindenianum

Philodendron lindenii

Philodendron linguifolium

Philodendron lingulatum

Philodendron linnaei var. linnaei

Philodendron linnaei var. rionegrense

Philodendron llanense

Philodendron loefgrenii

Philodendron longilaminatum

Philodendron longilobatum

Scientific name

Philodendron longipedunculatum

Philodendron longipes

Philodendron longirrhizum

Philodendron longistilum

Philodendron lundii

Philodendron lupinum

Philodendron macroglossum

Philodendron macropodum

Philodendron maculatum

Philodendron madronense

Philodendron maguirei

Philodendron malesevichiae

Philodendron mamei

Philodendron marahuacae

Philodendron maroae

Philodendron martianum

Philodendron martini

Philodendron mathewsii

Philodendron mawarinumae

Philodendron maximum

Philodendron mayoi

Philodendron mcphersonii

Philodendron megalophyllum

Philodendron melanochrysum

Philodendron melinonii

Philodendron mello-barretoanum

Philodendron membranaceum

Philodendron merenbergense

Philodendron meridense

Philodendron mesae

Philodendron mexicanum

Philodendron micranthum

Philodendron microstictum

Philodendron millerianum

Philodendron minarum

Philodendron misahualliense

Philodendron missionum

Philodendron modestum

Philodendron monsalveae

Philodendron montanum

Philodendron moonenii

Philodendron morii

Philodendron multinervum

Philodendron multispadiceum

Philodendron muricatum

Philodendron musifolium

Philodendron myrmecophilum

Philodendron nadruzianum

Philodendron nanegalense

Philodendron narinoense

Philodendron nebulense

Philodendron ninoanum

Philodendron niqueanum

Philodendron nullinervium

Philodendron oblanceolatum

Philodendron obliquifolium

Scientific name

Philodendron oblongum

Philodendron obtusilobum

Philodendron ochrostemon

Philodendron oligospermum

Philodendron opacum

Philodendron orionis

Philodendron ornatum

Philodendron pachycaule

Philodendron pachyphyllum

Philodendron palaciosii

Philodendron paludicola

Philodendron panamense

Philodendron panduriforme var. panduriforme

Philodendron panduriforme var. reichenbachianum

Philodendron parvilobum

Philodendron pastazanum

Philodendron patriciae

Philodendron paucinervium

Philodendron paxianum

Philodendron pedatum

Philodendron pedunculum

Philodendron peperomioides

Philodendron peraiense

Philodendron perplexum

Philodendron phlebodes var. phlebodes

Philodendron phlebodes var. kermesinum

Philodendron pimichinense

Philodendron pinnatifidum

Philodendron pinnatilobum

Philodendron pipolyi

Philodendron pirrense

Philodendron placidum

Philodendron planadense

Philodendron platypetiolatum

Philodendron platypodum

Philodendron pogonocaule

Philodendron polliciforme

Philodendron popenoei

Philodendron populneum

Philodendron prominulinervium

Philodendron propinquum

Philodendron pseudauriculatum

Philodendron pseudoundulatum

Philodendron pteropus

Philodendron pterotum

Philodendron puhuangii

Philodendron pulchellum

Philodendron pulchrum

Philodendron purpureoviride

Philodendron purulhense

Philodendron pusillum

Philodendron quinquelobum

Philodendron quinquenervium

Philodendron quitense

Scientific name	Scientific name	Scientific name	Scientific name
Philodendron radiatum var. radiatum	*Philodendron seguine subsp. lingua-bovis*	*Philodendron tuerckheimii*	*Piptospatha burbidgei*
Philodendron radiatum var. pseudoradiatum	*Philodendron senatocarpium*	*Philodendron tweedieanum*	*Piptospatha elongata*
Philodendron rayanum	*Philodendron serpens*	*Philodendron tysonii*	*Piptospatha impolita*
Philodendron recurvifolium	*Philodendron silverstonei*	*Philodendron ubigantupense*	*Piptospatha insignis*
Philodendron remifolium subsp. remifolium	*Philodendron simmondsii*	*Philodendron uleanum*	*Piptospatha manduensis*
Philodendron remifolium subsp. sabulosum	*Philodendron simonianum*	*Philodendron uliginosum*	*Piptospatha marginata*
Philodendron renauxii	*Philodendron simsii*	*Philodendron undulatum*	*Piptospatha perakensis*
Philodendron reticulatum	*Philodendron simulans*	*Philodendron urraoense*	*Piptospatha remiformis*
Philodendron rhizomatosum	*Philodendron smithii*	*Philodendron ushanum*	*Piptospatha repens*
Philodendron rhodoaxis subsp. rhodoaxis	*Philodendron solimoesense*	*Philodendron utleyanum*	*Piptospatha ridleyi*
Philodendron rhodoaxis subsp. lewisii	*Philodendron sonderianum*	*Philodendron validinervium*	*Piptospatha truncata*
Philodendron rhodospathiphyllum	*Philodendron sousae*	*Philodendron vargealtense*	*Piptospatha viridistigma*
Philodendron ricardoi	*Philodendron sparreorum*	*Philodendron variifolium*	*Pistia stratiotes*
Philodendron rigidifolium subsp. rigidifolium	*Philodendron speciosum*	*Philodendron venezuelense*	*Podolasia stipitata*
Philodendron rigidifolium subsp. sanctae-ritae	*Philodendron sphalerum*	*Philodendron venosum*	*Pothoidium lobbianum*
Philodendron rimachii	*Philodendron spiritus-sancti*	*Philodendron ventricosum*	*Pothos armatus*
Philodendron riparium	*Philodendron splitgerberi*	*Philodendron venulosum*	*Pothos atropurpurascens*
Philodendron robustum	*Philodendron spruceanum*	*Philodendron venustifoliatum*	*Pothos barberianus*
Philodendron rodrigueziae	*Philodendron squamicaule*	*Philodendron venustum*	*Pothos beccarianus*
Philodendron roezlii	*Philodendron squamiferum*	*Philodendron verapazense*	*Pothos brassii*
Philodendron rojasianum	*Philodendron squamipetiolatum*	*Philodendron verrucapetiolum*	*Pothos brevistylus*
Philodendron romeroi	*Philodendron standleyi*	*Philodendron verrucosum*	*Pothos brevivaginatus*
Philodendron roraimae var. roraimae	*Philodendron stenolobum*	*Philodendron victoriae*	*Pothos chinensis*
Philodendron roraimae subsp. aracamuniense	*Philodendron stenophyllum*	*Philodendron vinaceum*	*Pothos clavatus*
Philodendron roseocataphyllum	*Philodendron steyermarkii*	*Philodendron viride*	*Pothos crassipedunculatus*
Philodendron roseopetiolatum	*Philodendron straminicaule*	*Philodendron wadedavisii*	*Pothos curtisii*
Philodendron roseospathum var. roseospathum	*Philodendron striatum*	*Philodendron wallisii*	*Pothos cuspidatus*
Philodendron roseospathum var. angustilaminatum	*Philodendron strictum*	*Philodendron warszewiczii*	*Pothos cylindricus*
Philodendron rothschuhianum	*Philodendron suberosum*	*Philodendron weberbaueri*	*Pothos dolichophyllus*
Philodendron rubrocinctum	*Philodendron subhastatum*	*Philodendron wendlandii*	*Pothos dzui*
Philodendron rubromaculatum	*Philodendron subincisum*	*Philodendron werkhoveniae*	*Pothos englerianus*
Philodendron rudgeanum	*Philodendron sucrense*	*Philodendron wilburii var. wilburii*	*Pothos falcifolius*
Philodendron rugosum	*Philodendron sulcatum*	*Philodendron wilburii var. longipedunculatum*	*Pothos gigantipes*
Philodendron ruizii	*Philodendron sulcicaule*	*Philodendron williamsii*	*Pothos gracillimus*
Philodendron ruthianum	*Philodendron surinamense*	*Philodendron wittianum*	*Pothos grandis*
Philodendron sagittifolium	*Philodendron swartiae*	*Philodendron woronowii*	*Pothos hellwigii*
Philodendron samayense	*Philodendron tachirense*	*Philodendron wullschlaegelii*	*Pothos hookeri*
Philodendron santodominguense	*Philodendron tarmense*	*Philodendron wurdackii*	*Pothos inaequilaterus*
Philodendron saxicola	*Philodendron tatei subsp. tatei*	*Philodendron xanadu*	*Pothos insignis*
Philodendron scalarinerve	*Philodendron tatei subsp. melanochlorum*	*Philodendron yavitense*	*Pothos junghuhnii*
Philodendron scherberichii	*Philodendron tenue*	*Philodendron yutajense*	*Pothos keralensis*
Philodendron schottianum	*Philodendron tenuipes*	*Philodendron zhuanum*	*Pothos kerrii*
Philodendron schottii subsp. schottii	*Philodendron tenuispadix*	*Philonotion americanum*	*Pothos kingii*
Philodendron schottii subsp. talamancae	*Philodendron teretipes*	*Philonotion bolivaranum*	*Pothos lancifolius*
Philodendron scitulum	*Philodendron thalassicum*	*Philonotion spruceanum*	*Pothos laurifolius*
Philodendron scottmorianum	*Philodendron thaliifolium*	*Phymatarum borneense*	*Pothos leptostachyus*
Philodendron seguine subsp. seguine	*Philodendron tortum*	*Pichinia disticha*	*Pothos longipes*
	Philodendron toshibae	*Pinellia cordata*	*Pothos longivaginatus*
	Philodendron traunii	*Pinellia fujianensis*	*Pothos luzonensis*
	Philodendron triangulare	*Pinellia integrifolia*	*Pothos macrocephalus*
	Philodendron tricostatum	*Pinellia pedatisecta*	*Pothos mirabilis*
	Philodendron tripartitum	*Pinellia peltata*	*Pothos motleyanus*
	Philodendron triplum	*Pinellia polyphylla*	*Pothos oliganthus*
	Philodendron trojitense	*Pinellia ternata*	*Pothos ovatifolius*
	Philodendron trujilloi	*Pinellia tripartita*	*Pothos oxyphyllus*
		Pinellia yaoluopingensis	*Pothos papuanus*
			Pothos parvispadix

Scientific name	Scientific name	Scientific name	Scientific name
Pothos philippinensis	*Rhaphidophora formosana*	*Rhaphidophora talamauana*	*Schismatoglottis bauensis*
Pothos pilulifer	*Rhaphidophora fortis*	*Rhaphidophora tenuis*	*Schismatoglottis bifasciata*
Pothos polystachyus	*Rhaphidophora geniculata*	*Rhaphidophora ternatensis*	*Schismatoglottis bogneri*
Pothos remotiflorus	*Rhaphidophora glauca*	*Rhaphidophora tetrasperma*	*Schismatoglottis brevicuspis*
Pothos repens	*Rhaphidophora gorokensis*	*Rhaphidophora teysmanniana*	*Schismatoglottis calyptrata*
Pothos roxburghii	*Rhaphidophora guamensis*	*Rhaphidophora todayensis*	*Schismatoglottis canaliculata*
Pothos salicifolius	*Rhaphidophora hayi*	*Rhaphidophora tonkinensis*	*Schismatoglottis ciliata*
Pothos scandens	*Rhaphidophora hongkongensis*	*Rhaphidophora typha*	*Schismatoglottis clarae*
Pothos tener	*Rhaphidophora hookeri*	*Rhaphidophora ustulata*	*Schismatoglottis clausula*
Pothos thomsonianus	*Rhaphidophora intonsa*	*Rhaphidophora versteegii*	*Schismatoglottis clemensiorum*
Pothos touranensis	*Rhaphidophora intrusa*	*Rhaphidophora waria*	*Schismatoglottis confinis*
Pothos versteegii	*Rhaphidophora jubata*	*Rhodospatha acosta-solisii*	*Schismatoglottis conoidea*
Pothos volans	*Rhaphidophora kokodensis*	*Rhodospatha arborescens*	*Schismatoglottis convolvula*
Pothos zippelii	*Rhaphidophora koordersii*	*Rhodospatha badilloi*	*Schismatoglottis corneri*
Protarum sechellarum	*Rhaphidophora korthalsii*	*Rhodospatha bolivarana*	*Schismatoglottis crinitissima*
Pseudohydrosme buettneri	*Rhaphidophora laichauensis*	*Rhodospatha boliviensis*	*Schismatoglottis cyria*
Pseudohydrosme gabunensis	*Rhaphidophora lancifolia*	*Rhodospatha brachypoda*	*Schismatoglottis decipiens*
Pycnospatha arietina	*Rhaphidophora latevaginata*	*Rhodospatha brent-berlinii*	*Schismatoglottis dilecta*
Pycnospatha palmata	*Rhaphidophora liukiuensis*	*Rhodospatha cardonae*	*Schismatoglottis dulosa*
Remusatia hookeriana	*Rhaphidophora lobbii*	*Rhodospatha densinervia*	*Schismatoglottis ecaudata*
Remusatia pumila	*Rhaphidophora luchunensis*	*Rhodospatha dissidens*	*Schismatoglottis edanoi*
Remusatia vivipara	*Rhaphidophora maingayi*	*Rhodospatha falconensis*	*Schismatoglottis elegans*
Remusatia yunnanensis	*Rhaphidophora megaphylla*	*Rhodospatha forgetii*	*Schismatoglottis erecta*
Rhaphidophora acuminata	*Rhaphidophora megasperma*	*Rhodospatha guasareensis*	*Schismatoglottis eximia*
Rhaphidophora africana	*Rhaphidophora megastigma*	*Rhodospatha herrerae*	*Schismatoglottis eymae*
Rhaphidophora angustata	*Rhaphidophora microspadix*	*Rhodospatha katipas*	*Schismatoglottis ferruginea*
Rhaphidophora araea	*Rhaphidophora mima*	*Rhodospatha kraenzlinii*	*Schismatoglottis gamoandra*
Rhaphidophora australasica	*Rhaphidophora minor*	*Rhodospatha latifolia*	*Schismatoglottis gillianiae*
Rhaphidophora balgooyi	*Rhaphidophora moluccensis*	*Rhodospatha monsalveae*	*Schismatoglottis glauca*
Rhaphidophora banosensis	*Rhaphidophora montana*	*Rhodospatha moritziana*	*Schismatoglottis grabowskii*
Rhaphidophora beccarii	*Rhaphidophora monticola*	*Rhodospatha mukuntakia*	*Schismatoglottis hainanensis*
Rhaphidophora bonii	*Rhaphidophora neoguineensis*	*Rhodospatha oblongata*	*Schismatoglottis harmandii*
Rhaphidophora brevispathacea	*Rhaphidophora nicolsonii*	*Rhodospatha pellucida*	*Schismatoglottis hayana*
Rhaphidophora burkilliana	*Rhaphidophora okapensis*	*Rhodospatha perezii*	*Schismatoglottis hayi*
Rhaphidophora calophylla	*Rhaphidophora oligosperma*	*Rhodospatha piushaduka*	*Schismatoglottis hottae*
Rhaphidophora chevalieri	*Rhaphidophora ovoidea*	*Rhodospatha robusta*	*Schismatoglottis ifugaoensis*
Rhaphidophora conica	*Rhaphidophora pachyphylla*	*Rhodospatha statutii*	*Schismatoglottis inculta*
Rhaphidophora conocephala	*Rhaphidophora parvifolia*	*Rhodospatha steyermarkii*	*Schismatoglottis jelandii*
Rhaphidophora corneri	*Rhaphidophora peepla*	*Rhodospatha venosa*	*Schismatoglottis jepomii*
Rhaphidophora crassicaulis	*Rhaphidophora peeploides*	*Rhodospatha wendlandii*	*Schismatoglottis jitinae*
Rhaphidophora crassifolia	*Rhaphidophora perkinsiae*	*Sauromatum brevipes*	*Schismatoglottis josefii*
Rhaphidophora cravenschoddeana	*Rhaphidophora pertusa*	*Sauromatum brevipilosum*	*Schismatoglottis kurzii*
Rhaphidophora cretosa	*Rhaphidophora petrieana*	*Sauromatum diversifolium*	*Schismatoglottis lancifolia*
Rhaphidophora cryptantha	*Rhaphidophora philippinensis*	*Sauromatum gaoligongense*	*Schismatoglottis latevaginata*
Rhaphidophora cylindrosperma	*Rhaphidophora pilosa*	*Sauromatum giganteum*	*Schismatoglottis linae*
Rhaphidophora dahlii	*Rhaphidophora puberula*	*Sauromatum hirsutum*	*Schismatoglottis lingua*
Rhaphidophora decursiva	*Rhaphidophora sabit*	*Sauromatum horsfieldii*	*Schismatoglottis longispatha*
Rhaphidophora discolor	*Rhaphidophora sarasinorum*	*Sauromatum tentaculatum*	*Schismatoglottis luzonensis*
Rhaphidophora dulongensis	*Rhaphidophora schlechteri*	*Sauromatum venosum*	*Schismatoglottis maelii*
Rhaphidophora elliptica	*Rhaphidophora schottii*	*Scaphispatha gracilis*	*Schismatoglottis matangensis*
Rhaphidophora elliptifolia	*Rhaphidophora spathacea*	*Scaphispatha robusta*	*Schismatoglottis mayoana*
Rhaphidophora elmeri	*Rhaphidophora spuria*	*Schismatoglottis acutifolia*	*Schismatoglottis merrillii*
Rhaphidophora falcata	*Rhaphidophora stenophylla*	*Schismatoglottis adoceta*	*Schismatoglottis mindanaoana*
Rhaphidophora floresensis	*Rhaphidophora stolleana*	*Schismatoglottis ahmadii*	*Schismatoglottis mira*
Rhaphidophora foraminifera	*Rhaphidophora sulcata*	*Schismatoglottis ardenii*	*Schismatoglottis modesta*
	Rhaphidophora sylvestris	*Schismatoglottis asperata*	*Schismatoglottis monoplacenta*
		Schismatoglottis barbata	

132

Scientific name	Scientific name	Scientific name	Scientific name
Schismatoglottis moodii	*Scindapsus geniculatus*	*Spathiphyllum lanceifolium*	*Stenospermation latifolium*
Schismatoglottis motleyana	*Scindapsus glaucescens*	*Spathiphyllum lechlerianum*	*Stenospermation longifolium*
Schismatoglottis multiflora	*Scindapsus grandifolius*	*Spathiphyllum maguirei*	*Stenospermation longipetiolatum*
Schismatoglottis multinervia	*Scindapsus hederaceus*	*Spathiphyllum matudae*	*Stenospermation longispadix*
Schismatoglottis nervosa	*Scindapsus javanicus*	*Spathiphyllum mawarinumae*	*Stenospermation maguirei*
Schismatoglottis niahensis	*Scindapsus latifolius*	*Spathiphyllum minor*	*Stenospermation majus*
Schismatoglottis nicolsonii	*Scindapsus longipes*	*Spathiphyllum monachinoi var. monachinoi*	*Stenospermation marantifolium*
Schismatoglottis patentinervia	*Scindapsus longistipitatus*	*Spathiphyllum monachinoi var. perangustum*	*Stenospermation mathewsii var. mathewsii*
Schismatoglottis pectinervia	*Scindapsus lucens*	*Spathiphyllum montanum*	*Stenospermation mathewsii var. stipitatum*
Schismatoglottis penangensis	*Scindapsus maclurei*	*Spathiphyllum neblinae*	*Stenospermation monsalvae*
Schismatoglottis petri	*Scindapsus mamilliferus*	*Spathiphyllum ortgiesii*	*Stenospermation multiovulatum*
Schismatoglottis platystigma	*Scindapsus marantifolius*	*Spathiphyllum patinii*	*Stenospermation nebulense*
Schismatoglottis plurivenia	*Scindapsus officinalis*	*Spathiphyllum patulinervum*	*Stenospermation olgae*
Schismatoglottis puberulipes	*Scindapsus perakensis*	*Spathiphyllum perezii*	*Stenospermation parvum*
Schismatoglottis pudenda	*Scindapsus pictus*	*Spathiphyllum phryniifolium*	*Stenospermation peripense*
Schismatoglottis pumila	*Scindapsus roseus*	*Spathiphyllum pygmaeum*	*Stenospermation pittieri*
Schismatoglottis pusilla	*Scindapsus rupestris*	*Spathiphyllum quindiuense*	*Stenospermation popayanense*
Schismatoglottis pyrrhias	*Scindapsus salomoniensis*	*Spathiphyllum schlechteri*	*Stenospermation pteropus*
Schismatoglottis retinervia	*Scindapsus schlechteri*	*Spathiphyllum schomburgkii*	*Stenospermation robustum*
Schismatoglottis roseospatha	*Scindapsus scortechinii*	*Spathiphyllum silvicola*	*Stenospermation rusbyi*
Schismatoglottis samarensis	*Scindapsus splendidus*	*Spathiphyllum solomonense*	*Stenospermation sessile*
Schismatoglottis sarikeensis	*Scindapsus subcordatus*	*Spathiphyllum tenerum*	*Stenospermation spruceanum*
Schismatoglottis schottii	*Scindapsus suffruticosus*	*Spathiphyllum uspanapaensis*	*Stenospermation subellipticum*
Schismatoglottis scortechinii	*Scindapsus sumatranus*	*Spathiphyllum wallisii*	*Stenospermation ulei*
Schismatoglottis sejuncta	*Scindapsus treubii*	*Spathiphyllum wendlandii*	*Stenospermation velutinum*
Schismatoglottis silamensis	*Spathantheum fallax*	*Spirodela oligorrhiza*	*Stenospermation wallisii*
Schismatoglottis simonii	*Spathantheum orbignyanum*	*Spirodela polyrhiza*	*Stenospermation zeacarpium*
Schismatoglottis subundulata	*Spathicarpa gardneri*	*Spirodela punctata*	*Steudnera assamica*
Schismatoglottis tahubangensis	*Spathicarpa hastifolia*	*Spirodela sichuanensis*	*Steudnera capitellata*
Schismatoglottis tecturata	*Spathicarpa lanceolata*	*Stenospermation adsimile*	*Steudnera colocasiifolia*
Schismatoglottis tessellata	*Spathiphyllum atrovirens*	*Stenospermation ammiticum*	*Steudnera colocasioides*
Schismatoglottis thelephora	*Spathiphyllum barbourii*	*Stenospermation amomifolium*	*Steudnera discolor*
Schismatoglottis trifasciata	*Spathiphyllum bariense*	*Stenospermation ancuashii*	*Steudnera gagei*
Schismatoglottis trivittata	*Spathiphyllum blandum*	*Stenospermation andreanum*	*Steudnera griffithii*
Schismatoglottis trusmadiensis	*Spathiphyllum brent-berlinii*	*Stenospermation angosturense*	*Steudnera henryana*
Schismatoglottis turbata	*Spathiphyllum brevirostre*	*Stenospermation angustifolium*	*Steudnera kerrii*
Schismatoglottis ulusarikeiensis	*Spathiphyllum buntingianum*	*Stenospermation arborescens*	*Stylochaeton angolense*
Schismatoglottis unifolia	*Spathiphyllum cannifolium*	*Stenospermation archeri*	*Stylochaeton bogneri*
Schismatoglottis venusta	*Spathiphyllum cochlearispathum*	*Stenospermation benavidesae*	*Stylochaeton borumense*
Schismatoglottis viridissima	*Spathiphyllum commutatum*	*Stenospermation brachypodum*	*Stylochaeton crassispathum*
Schismatoglottis wahaiana	*Spathiphyllum cuspidatum*	*Stenospermation crassifolium*	*Stylochaeton cuculliferum*
Schismatoglottis wallichii	*Spathiphyllum diazii*	*Stenospermation densiovulatum*	*Stylochaeton euryphyllum*
Schismatoglottis warburgiana	*Spathiphyllum dressleri*	*Stenospermation dictyoneurum*	*Stylochaeton grande*
Schismatoglottis wongii	*Spathiphyllum floribundum*	*Stenospermation ellipticum*	*Stylochaeton hypogeum*
Schismatoglottis zonata	*Spathiphyllum friedrichsthalii*	*Stenospermation escobariae*	*Stylochaeton kornasii*
Schottariella mirifica	*Spathiphyllum fulvovirens*	*Stenospermation flavescens*	*Stylochaeton lancifolium*
Scindapsus alpinus	*Spathiphyllum gardneri*	*Stenospermation flavum*	*Stylochaeton malaissei*
Scindapsus altissimus	*Spathiphyllum gracile*	*Stenospermation gentryi*	*Stylochaeton milneanum*
Scindapsus beccarii	*Spathiphyllum grandifolium*	*Stenospermation glaucophyllum*	*Stylochaeton natalense subsp. natalense*
Scindapsus carolinensis	*Spathiphyllum grazielae*	*Stenospermation gracile*	*Stylochaeton natalense subsp. maximum*
Scindapsus coriaceus	*Spathiphyllum humboldtii*	*Stenospermation hilligii*	*Stylochaeton natalense subsp. obliquinerve*
Scindapsus crassipes	*Spathiphyllum jejunum*	*Stenospermation interruptum*	*Stylochaeton oligocarpum*
Scindapsus curranii	*Spathiphyllum juninense*	*Stenospermation laevis*	
Scindapsus cuscuaria	*Spathiphyllum kalbreyeri*		
Scindapsus cuscuarioides	*Spathiphyllum kochii*		
Scindapsus falcifolius	*Spathiphyllum laeve*		

Scientific name	Scientific name	Scientific name	Scientific name
Stylochaeton pilosum	*Theriophonum infaustum*	*Typhonium sagittariifolium*	*Xanthosoma baguense*
Stylochaeton puberulum	*Theriophonum manickamii*	*Typhonium saraburiensis*	*Xanthosoma bayo*
Stylochaeton salaamicum	*Theriophonum minutum*	*Typhonium sinhabaedyae*	*Xanthosoma belophyllum*
Stylochaeton shabaense	*Theriophonum sivaganganum*	*Typhonium smitinandii*	*Xanthosoma bilineatum*
Stylochaeton tortispathum	*Typhonium acetosella*	*Typhonium stigmatilobatum*	*Xanthosoma bolivaranum*
Stylochaeton zenkeri	*Typhonium adnatum*	*Typhonium subglobosum*	*Xanthosoma brasiliense*
Symplocarpus egorovii	*Typhonium albidinervium*	*Typhonium taylorii*	*Xanthosoma brevispathaceum*
Symplocarpus foetidus	*Typhonium albispathum*	*Typhonium trifoliatum*	*Xanthosoma caladioides*
Symplocarpus nabekuraensis	*Typhonium alismifolium*	*Typhonium trilobatum*	*Xanthosoma caracu*
Symplocarpus nipponicus	*Typhonium angustilobum*	*Typhonium tubispathum*	*Xanthosoma caulotuberculatum*
Symplocarpus renifolius	*Typhonium bachmaense*	*Typhonium varians*	*Xanthosoma conspurcatum*
Synandrospadix vermitoxicus	*Typhonium baoshanense*	*Typhonium vermiforme*	*Xanthosoma contractum*
Syngonium angustatum	*Typhonium blumei*	*Typhonium violifolium*	*Xanthosoma cordatum*
Syngonium armigerum	*Typhonium bognerianum*	*Typhonium watanabei*	*Xanthosoma cordifolium*
Syngonium atrovirens	*Typhonium brownii*	*Typhonium weipanum*	*Xanthosoma cubense*
Syngonium auritum	*Typhonium bulbiferum*	*Typhonium wilbertii*	*Xanthosoma daguense var. daguense*
Syngonium castroi	*Typhonium circinnatum*	*Typhonodorum lindleyanum*	*Xanthosoma daguense var. amargalense*
Syngonium chiapense	*Typhonium cochleare*	*Ulearum donburnsii*	*Xanthosoma dealbatum*
Syngonium chocoanum	*Typhonium conchiforme*	*Ulearum sagittatum var. sagittatum*	*Xanthosoma eggersii*
Syngonium crassifolium	*Typhonium cordifolium*	*Ulearum sagittatum var. viridispadix*	*Xanthosoma exiguum*
Syngonium dodsonianum	*Typhonium digitatum*	*Urospatha angustiloba*	*Xanthosoma flavomaculatum*
Syngonium erythrophyllum	*Typhonium echinulatum*	*Urospatha antisylleptica*	*Xanthosoma fractum*
Syngonium foreroanum	*Typhonium eliosurum*	*Urospatha caudata*	*Xanthosoma granvillei*
Syngonium gentryanum	*Typhonium filiforme*	*Urospatha edwallii*	*Xanthosoma guttatum*
Syngonium harlingianum	*Typhonium flagelliforme*	*Urospatha friedrichsthalii*	*Xanthosoma hebetatum*
Syngonium hastiferum	*Typhonium fultum*	*Urospatha loefgreniana*	*Xanthosoma helleborifolium*
Syngonium hastifolium	*Typhonium gagnepainii*	*Urospatha meyeri*	*Xanthosoma herrerae*
Syngonium hoffmannii	*Typhonium gallowayi*	*Urospatha riedeliana*	*Xanthosoma hylaeae*
Syngonium laterinervium	*Typhonium glaucum*	*Urospatha sagittifolia*	*Xanthosoma latestigmatum*
Syngonium llanoense	*Typhonium griseum*	*Urospatha somnolenta*	*Xanthosoma longilobum*
Syngonium macrophyllum	*Typhonium hayatae*	*Urospatha wurdackii*	*Xanthosoma lucens*
Syngonium mauroanum	*Typhonium huense*	*Wolffia angusta*	*Xanthosoma mafaffoides*
Syngonium meridense	*Typhonium hunanense*	*Wolffia arrhiza*	*Xanthosoma mariae*
Syngonium neglectum	*Typhonium inopinatum*	*Wolffia australiana*	*Xanthosoma maroae*
Syngonium oduberi	*Typhonium jinpingense*	*Wolffia borealis*	*Xanthosoma maximiliani*
Syngonium podophyllum var. podophyllum	*Typhonium johnsonianum*	*Wolffia brasiliensis*	*Xanthosoma mendozae*
Syngonium podophyllum var. peliocladum	*Typhonium jonesii*	*Wolffia columbiana*	*Xanthosoma mexicanum*
Syngonium rayi	*Typhonium laoticum*	*Wolffia cylindracea*	*Xanthosoma narinoense*
Syngonium sagittatum	*Typhonium liliifolium*	*Wolffia elongata*	*Xanthosoma nitidum*
Syngonium salvadorense	*Typhonium lineare*	*Wolffia globosa*	*Xanthosoma obtusilobum*
Syngonium schottianum	*Typhonium listeri*	*Wolffia microscopica*	*Xanthosoma orinocense*
Syngonium sparreorum	*Typhonium medusae*	*Wolffia neglecta*	*Xanthosoma paradoxum*
Syngonium standleyanum	*Typhonium mirabile*	*Wolffiella caudata*	*Xanthosoma pariense*
Syngonium steyermarkii	*Typhonium neogracile*	*Wolffiella denticulata*	*Xanthosoma peltatum*
Syngonium triphyllum	*Typhonium nudibaccatum*	*Wolffiella gladiata*	*Xanthosoma pentaphyllum*
Syngonium wendlandii	*Typhonium orbifolium*	*Wolffiella hyalina*	*Xanthosoma platylobum*
Syngonium yurimaguense	*Typhonium pedatisectum*	*Wolffiella lingulata*	*Xanthosoma plowmanii*
Taccarum caudatum	*Typhonium pedunculatum*	*Wolffiella neotropica*	*Xanthosoma poeppigii*
Taccarum crassispathum	*Typhonium peltandroides*	*Wolffiella oblonga*	*Xanthosoma pottii*
Taccarum peregrinum	*Typhonium penicillatum*	*Wolffiella repanda*	*Xanthosoma puberulum*
Taccarum ulei	*Typhonium pottingeri*	*Wolffiella rotunda*	*Xanthosoma pubescens*
Taccarum warmingii	*Typhonium praecox*	*Wolffiella welwitschii*	*Xanthosoma pulchrum*
Taccarum weddellianum	*Typhonium praetermissum*	*Xanthosoma acutum*	*Xanthosoma riedelianum*
Theriophonum dalzellii	*Typhonium pusillum*	*Xanthosoma akkermansii*	*Xanthosoma riparium*
Theriophonum danielii	*Typhonium reflexum*	*Xanthosoma aristeguietae*	*Xanthosoma robustum*
Theriophonum fischeri	*Typhonium roxburghii*	*Xanthosoma auriculatum*	
	Typhonium russell-smithii		

Scientific name	Scientific name	Scientific name	Scientific name
Xanthosoma sagittifolium	*Xanthosoma trichophyllum*	*Zantedeschia aethiopica*	*Zantedeschia valida*
Xanthosoma saguasense	*Xanthosoma trilobum*	*Zantedeschia albomaculata subsp. albomaculata*	*Zomicarpa pythonium*
Xanthosoma seideliae	*Xanthosoma ulei*	*Zantedeschia albomaculata subsp. macrocarpa*	*Zomicarpa steigeriana*
Xanthosoma stenospathum	*Xanthosoma undipes*	*Zantedeschia elliottiana*	*Zomicarpella amazonica*
Xanthosoma striatipes	*Xanthosoma viviparum*	*Zantedeschia jucunda*	*Zomicarpella maculata*
Xanthosoma striolatum	*Xanthosoma weeksii*	*Zantedeschia odorata*	
Xanthosoma syngoniifolium	*Xanthosoma wendlandii*	*Zantedeschia pentlandii*	
Xanthosoma taioba	*Xanthosoma yucatanense*	*Zantedeschia rehmannii*	
Xanthosoma tarapotense	*Zamioculcas zamiifolia*		

Appendix 3. Fitted function plots produced from the boosted regression tree models for species categorised in the (A) introduction, (B) naturalization and (C) invasion stages.
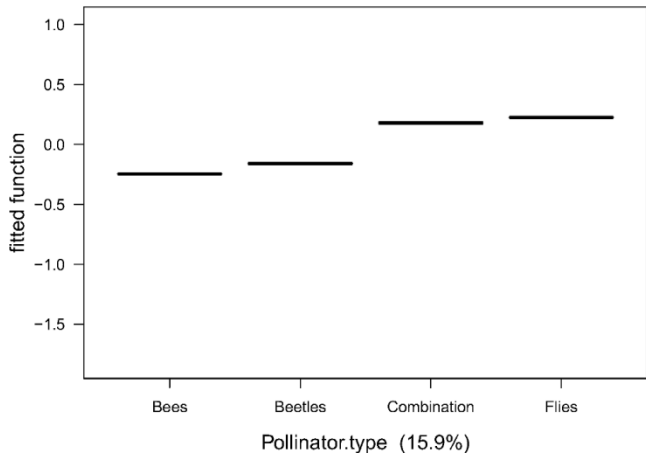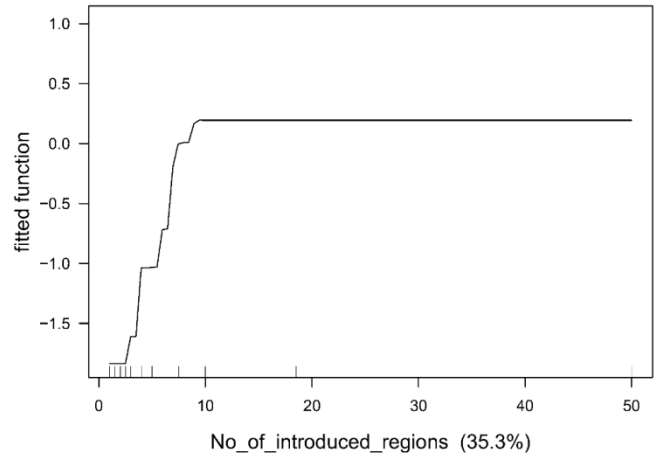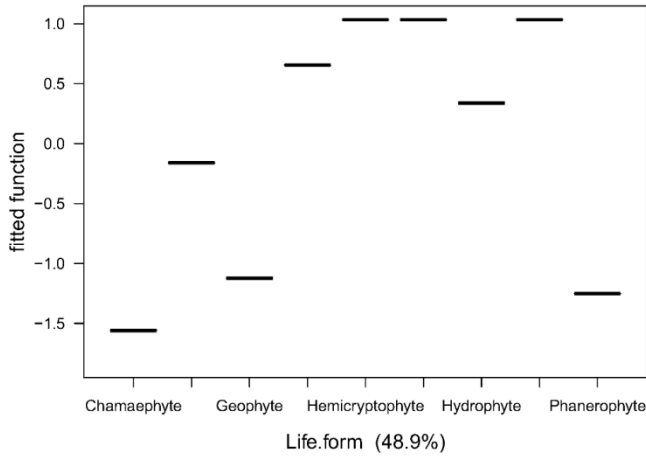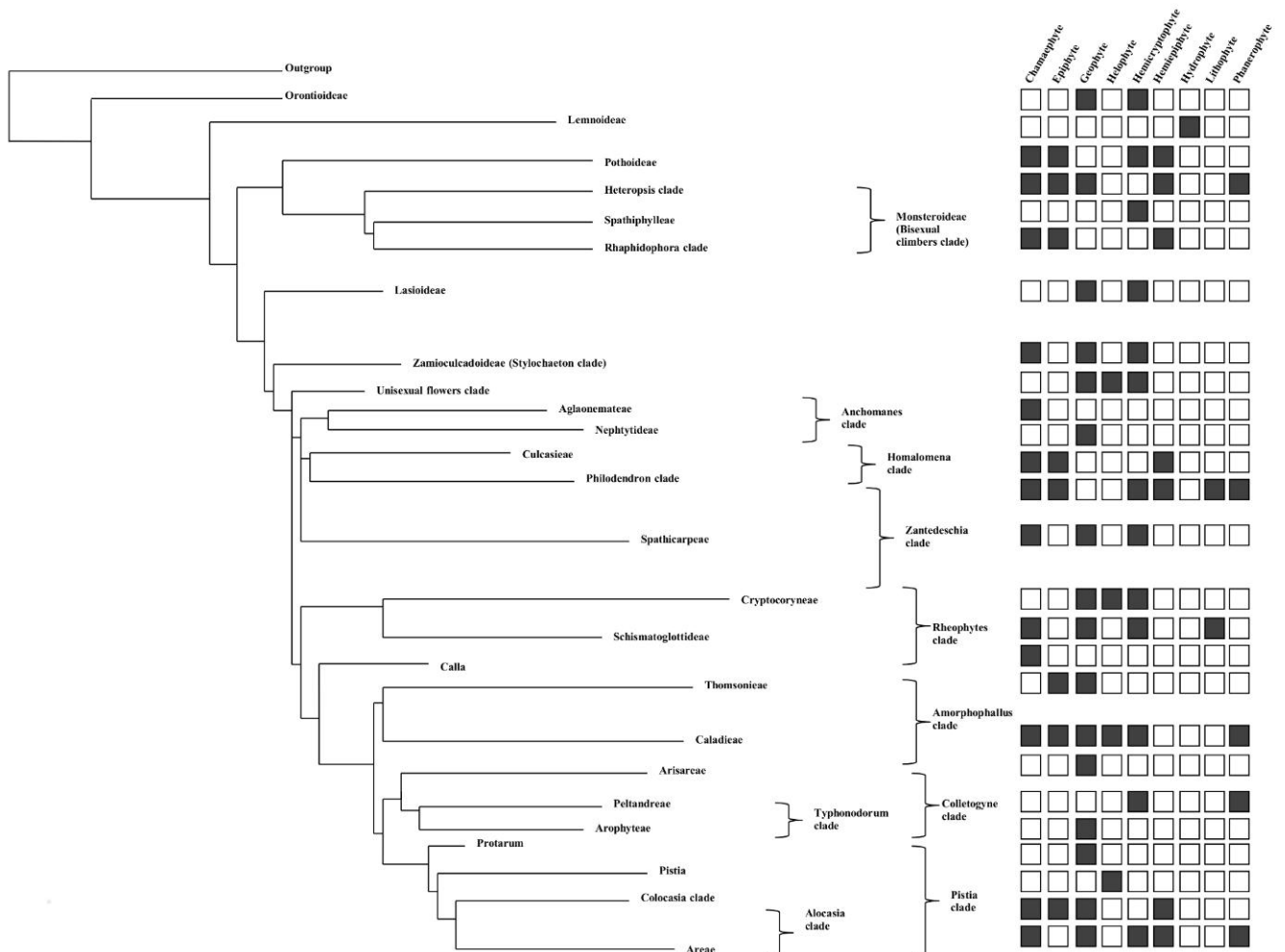
A)
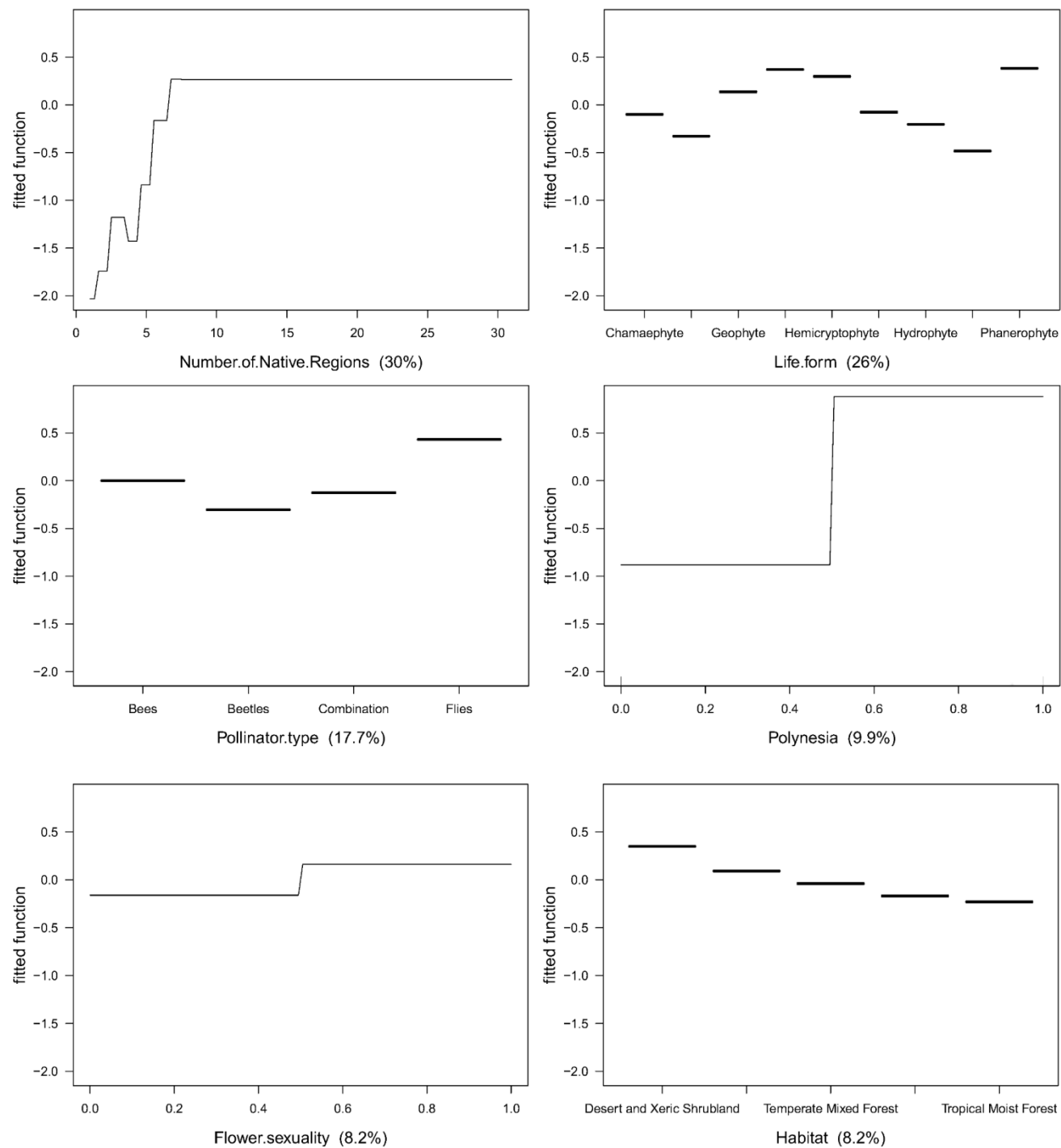
B)
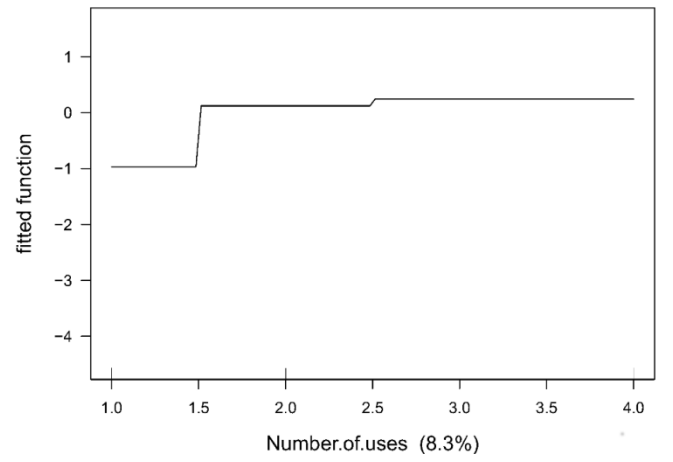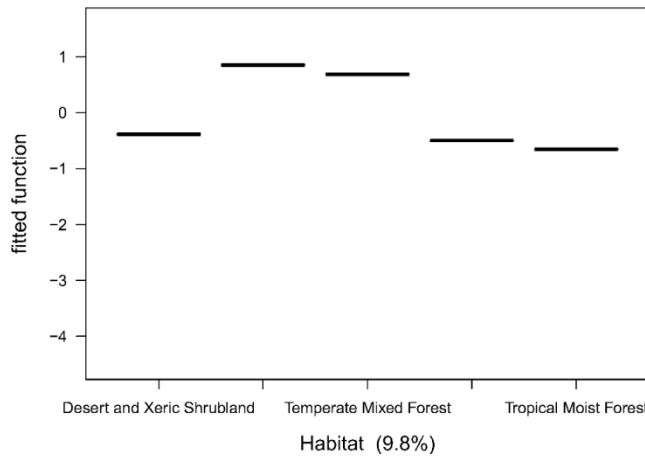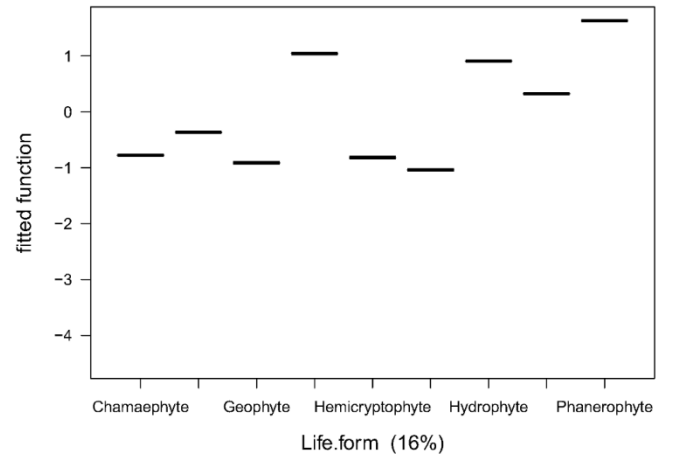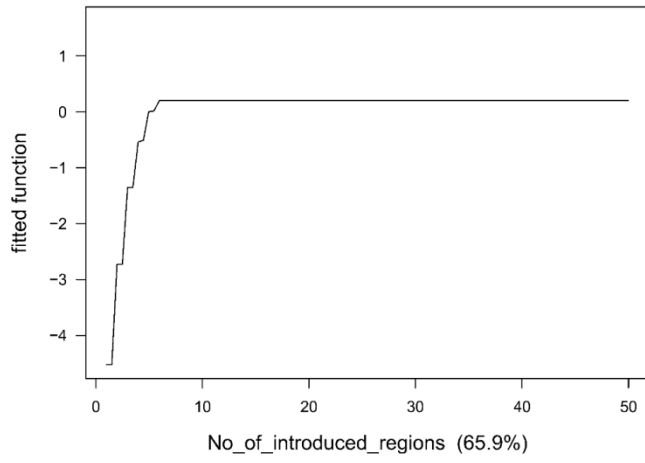
C)

Appendix 4. Stick phylogeny of Araceae lineages. Black squares correspond to each clade and their associated life form(s). For further details on the phylogeny see (Cusimano *et al.*, 2011). The tree reveals that life-forms are spread across the phylogeny.

Appendix 5. Phenograms illustrating species that have a potential to become invasive based on shared traits within the following monophyletic groups: (A) Lemnoideae, (B) *Alocasia*, (C) *Amydrium*, (D) *Ariopsis*, (E) *Arum*, (F) *Caladium,* (G) *Cryptocoryne,* and (H) *Gymnostachys*.

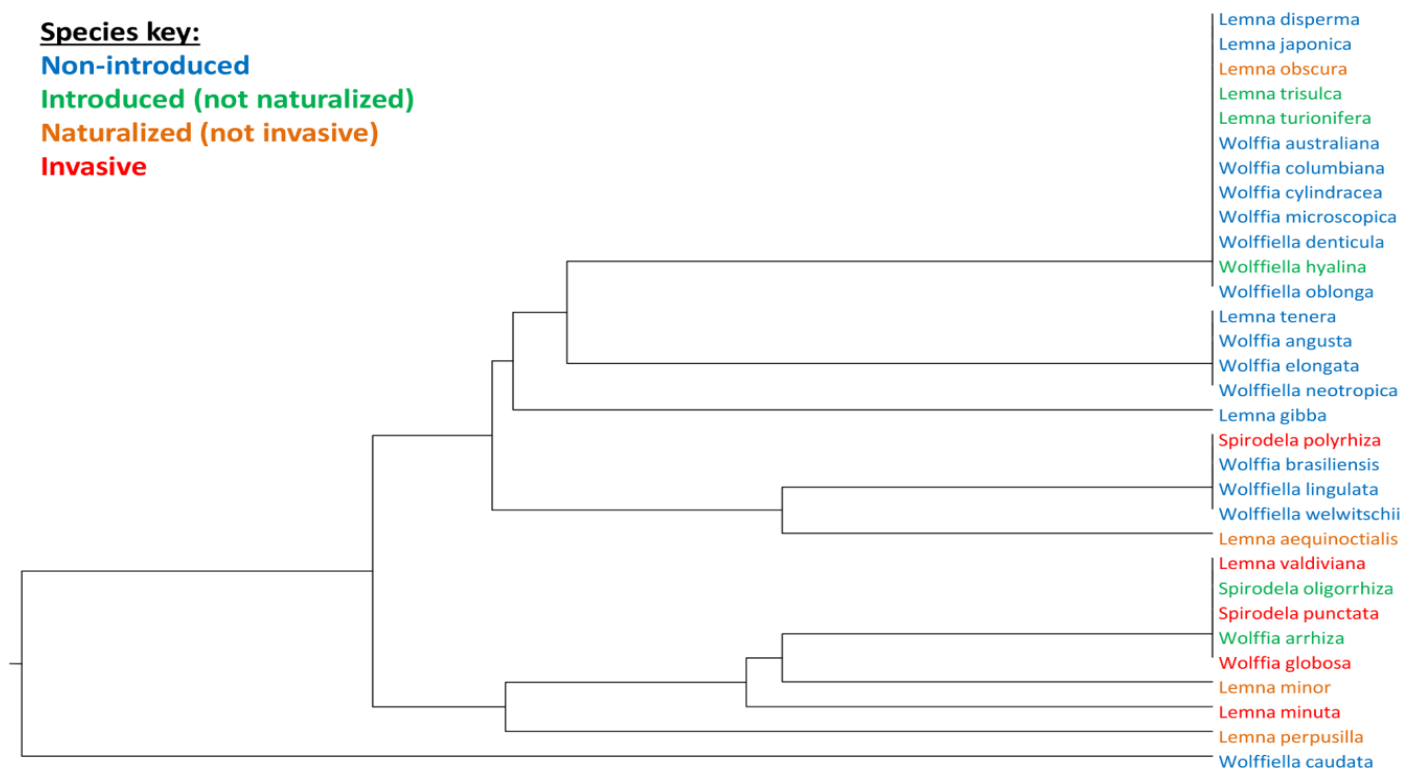**A)**

B)

Species key:
Non-introduced
Introduced (not naturalized)
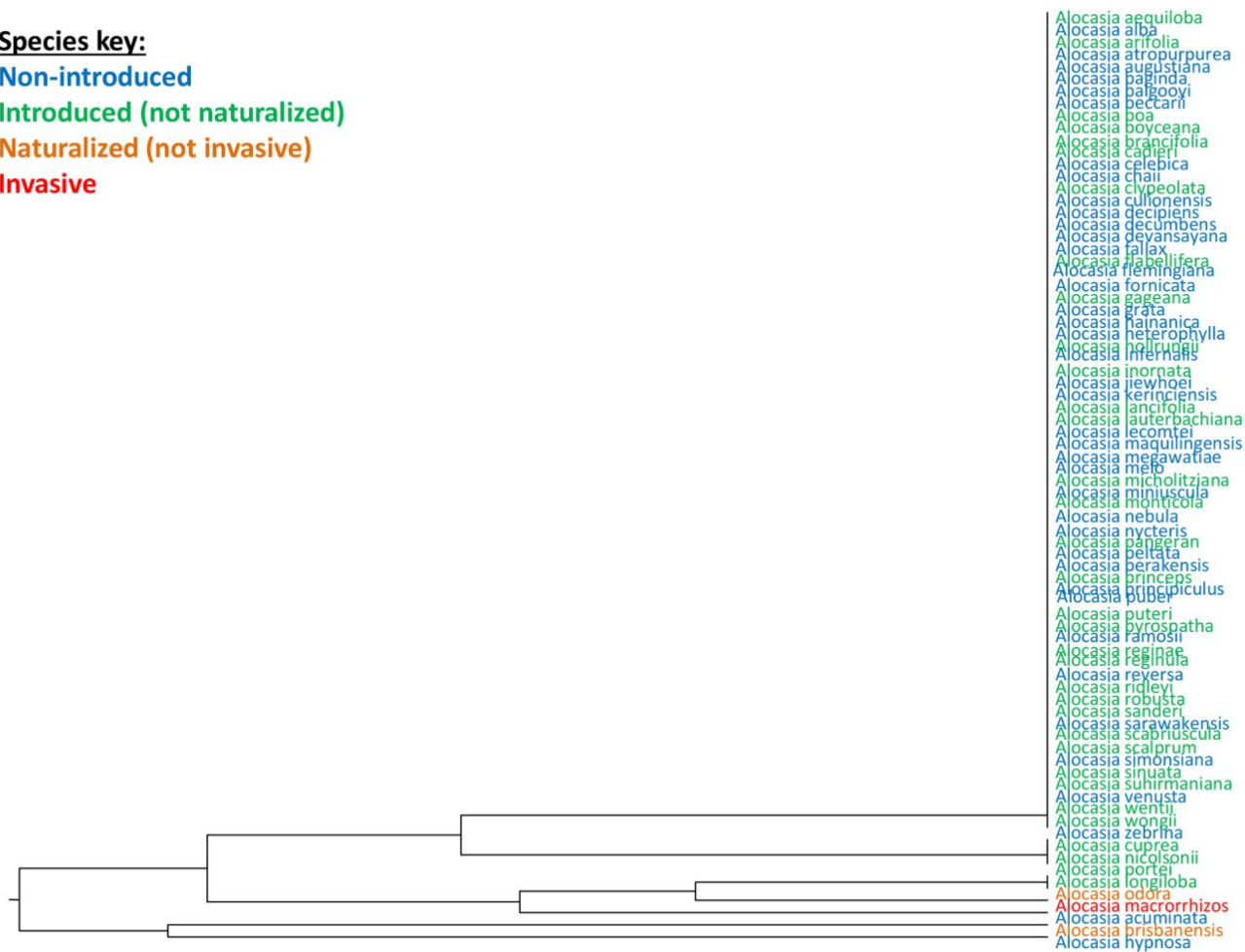Naturalized (not invasive)
Invasive

C)

Species key:
Non-introduced
Introduced (not naturalized)
Naturalized (not invasive)
Invasive

D)

Species key:
Non-introduced
Introduced (not naturalized)
Naturalized (not invasive)
Invasive

Ariopsis peltata
Colocasia mannii
Colocasia oresbia
Steudnera assamica
Steudnera capitellata
Steudnera colocasioides
Steudnera discolor
Steudnera gagei
Remusatia hookeriana
Remusatia pumila
Colocasia affinis
Colocasia esculenta
Ariopsis protanthera
Colocasia antiquorum
Colocasia fallax
Colocasia gigantea
Colocasia menglaensis
Steudnera henryana
Steudnera kerrii
Remusatia vivipara

E)

F)

G)

Species key:
Non-introduced
Introduced (not naturalized)
Naturalized (not invasive)
Invasive

Cryptocoryne affinis
Cryptocoryne alba
Cryptocoryne annamica
Cryptocoryne aponogetifolia
Cryptocoryne auriculata
Cryptocoryne bangkaensis
Cryptocoryne beckettii
Cryptocoryne bogneri
Cryptocoryne bullosa
Cryptocoryne cordata
Cryptocoryne coronata
Cryptocoryne cruddasiana
Cryptocoryne decus-silvae
Cryptocoryne dewitii
Cryptocoryne edithiae
Cryptocoryne elliptica
Cryptocoryne ferruginea
Cryptocoryne fusca
Cryptocoryne griffithii
Cryptocoryne hudoroi
Cryptocoryne ideii
Cryptocoryne jacobsenii
Cryptocoryne keei
Cryptocoryne lingua
Cryptocoryne loeiensis
Cryptocoryne longicauda
Cryptocoryne mekongensis
Cryptocoryne minima
Cryptocoryne moehlmannii
Cryptocoryne nevillii
Cryptocoryne noritoi
Cryptocoryne nurii
Cryptocoryne pallidinervia
Cryptocoryne parva
Cryptocoryne pontederiifolia
Cryptocoryne pygmaea
Cryptocoryne retrospiralis
Cryptocoryne schulzei
Cryptocoryne scurrilis
Cryptocoryne sivadasanii
Cryptocoryne spiralis
Cryptocoryne striolata
Cryptocoryne tambraparaniana
Cryptocoryne thwaitesii
Cryptocoryne uenoi
Cryptocoryne undulata
Cryptocoryne usteriana
Cryptocoryne versteegii
Cryptocoryne vietnamensis
Cryptocoryne villosa
Cryptocoryne walkeri
Cryptocoryne wendtii
Cryptocoryne yujii
Cryptocoryne zaidiana
Cryptocoryne zukalii
Lagenandra dewitii
Lagenandra erosa
Lagenandra gomezii
Lagenandra jacobsenii
Lagenandra keralensis
Lagenandra koenigii
Lagenandra lancifolia
Lagenandra ovata
Lagenandra praetermissa
Lagenandra thwaitesii
Lagenandra undulata
Cryptocoryne albida
Cryptocoryne ciliata
Cryptocoryne crispatula
Cryptocoryne cognata
Cryptocoryne consobrina
Lagenandra nairii
Lagenandra toxicaria

H)

Species key:
Non-introduced
Introduced (not naturalized)
Naturalized (not invasive)
Invasive

Symplocarpus egorovii
Symplocarpus foetidus
Symplocarpus nabekuraensis
Symplocarpus nipponicus
Symplocarpus renifolius
Lysichiton americanus
Lysichiton camtschatcensis
Orontium aquaticum

Appendix 6. Specimens of *Epipremnum aureum* in the KwaZulu-Natal herbarium.

Record number	Accession number	Locality	GPS coordinates
1322	1230365	Kwambonambi, Marche Hotel garden	28.59972° S 32.08361° E
120	1250948	Pinetwon, Japanese Garden	29.83556° S 30.87028° E

Appendix 7. *Epipremnum aureum* pamphlets distributed for additional sightings.

Appendix 8. *Epipremnum aureum* in the KwaZulu-Natal province, South Africa. The geographical distribution contains 321 unsurveyed (i.e. cultivated) and 78 surveyed (i.e. naturalized) populations.
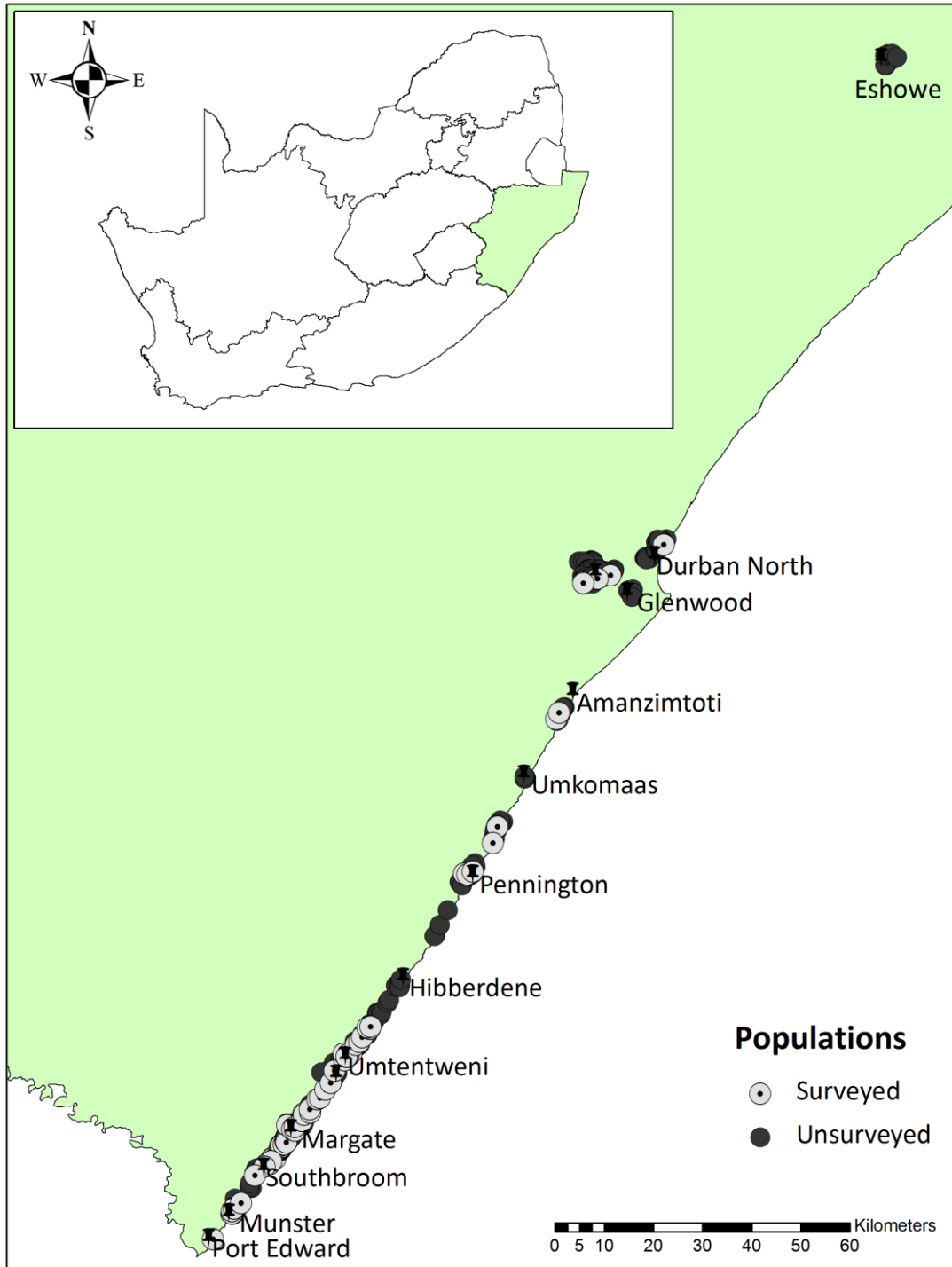
Appendix 9. Raw data of all introduced Monsteroideae and their associated traits that were analysed.

Scientific Name	Introduced	Naturalized	Invasive	Status	Minimum residence time (2016-x)	Minimum residence time_References	Continent of origin	Number of Introduced Regions	Number of Introduced Regions_References
Amydrium humile Schott	1			0	30	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	Asia	1	(Randall, 2007)
Amydrium zippelianum (Schott) Nicolson	1			0	NA		Asia & Oceania	1	(Randall, 2007)
Anadendrum microstachyum (de Vriese & Miq.) Backer & Alderw.	1			0	41	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	Asia	1	(Randall, 2007)
Epipremnum amplissimum (Schott) Engl.	1			0	49	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	1	Atlas of Living Australia

Epipremnum aureum (Linden & André) G.S.Bunting	1		1	1	58	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	20	eMonocot
Epipremnum falcifolium Engl.	1			0	33	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	1	GBIF
Epipremnum pinnatum (L.) Engl.	1		1	1	152	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia & Oceania	3	eMonocot; USDA, 2011; HEAR
Monstera acuminata K.Koch	1			0	NA		North America	1	GBIF
Monstera adansonii Schott *var. adansonii*	1			0	35	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	2	eMonocot, 2010
Monstera deliciosa Liebm.	1	1		1	45	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	6	eMonocot, 2010; USDA, 2011; GBIF; Randall, 2007

Monstera obliqua Miq.	1	0	NA		North & South America & Oceania	1	Randall, 2007
Monstera punctulata (Schott) Schott ex Engl.	1	0	30	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	1	Randall, 2007
Monstera standleyana G.S.Bunting	1	0	37	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	1	Randall, 2007
Monstera subpinnata (Schott) Engl.	1	0	NA		South America	1	Randall, 2007
Monstera tenuis K.Koch	1	0	22	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	1	Randall, 2007
Rhaphidophora australasica F.M.Bailey	1	0	35	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	1	GBIF
Rhaphidophora conica Engl.	1	0	63	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	1	GBIF

Rhaphidophora decursiva (Roxb.) Schott	1	0	44	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	3	GBIF
Rhaphidophora korthalsii Schott	1	0	NA		Asia & Oceania	1	Randall, 2007
Rhaphidophora megaphylla H.Li	1	0	11	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	1	GBIF
Rhaphidophora pachyphylla K.Krause	1	0	44	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Oceania	1	Atlas of Living Australia
Rhaphidophora pertusa (Roxb.) Schott	1	0	47	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	2	GBIF
Rhaphidophora schottii Hook.f.	1	0	21	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	1	GBIF
Rhaphidophora versteegii Engl. & K.Krause	1	0	NA		Oceania	1	Randall, 2007

Rhodospatha moritziana Schott	1	0	15	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North & South America		
Rhodospatha venosa Gleason	1	0	11	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	South America	1	GBIF
Scindapsus pictus Hassk.	1	0	58	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	Asia	3	GBIF
Spathiphyllum blandum Schott	1	0	26	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	1	Randall, 2007
Spathiphyllum cannifolium (Dryand. ex Sims) Schott	1	0	8	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	South America & Oceania	3	GBIF
Spathiphyllum cochlearispathum (Liebm.) Engl.	1	0	27	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	2	GBIF

Spathiphyllum commutatum Schott	1	0	NA		Asia & Oceania	1	Randall, 2007
Spathiphyllum floribundum (Linden & André) N.E.Br.	1	0	12	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	South America	2	GBIF
Spathiphyllum friedrichsthalii Schott	1	0	76	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North & South America	1	GBIF
Spathiphyllum kochii Engl. & K.Krause	1	0	54	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	South America	2	GBIF
Spathiphyllum lanceifolium (Jacq.) Schott	1	0	NA		South America	1	GBIF
Spathiphyllum ortgiesii Regel	1	0	17	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	North America	1	GBIF
Spathiphyllum patinii (R.Hogg) N.E.Br.	1	0	44	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	South America	2	Randall, 2007; GBIF

Spathiphyllum phryniifolium Schott	1	0	11	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	North & South America	1	Randall, 2007
Spathiphyllum wallisii Regel	1	0	40	GBIF (2016). Global Biodiversity Information Facility, http://www.gbif.org/, Accessed 26/09/2016	South America	4	GBIF; eMonocot, 2010; HEAR
Stenospermation amomifolium (Poepp.) Schott	1	0	6	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	South America	1	GBIF
Stenospermation multiovulatum (Engl.) N.E.Br.	1	0	20	Tropicos.org. 2016. Missouri Botanical Garden, St. Louis, MO, USA. http://www.tropicos.org, Accessed 26/09/2016	North & South America	1	Randall, 2007
Stenospermation popayanense Schott	1	0	NA		South America	1	Randall, 2007

Appendix 10. The outcome of the weed risk assessment of *M. deliciosa* in South Africa.

Family:	Araceae	**Date assessed:**	15/09/2016
Taxon:	*Monstera deliciosa* Liebm.	**Assessor:**	D. Moodley
Common name:	Swiss Cheese Plant	**AWRA score:**	7
Synonyms:	*Monstera borsigiana* K.Koch *Monstera deliciosa var. borsigiana* Engl. *Monstera deliciosa var. sierrana* G.S.Bunting *Monstera lennea* K.Koch *Monstera tacanaensis* Matuda *Philodendron anatomicum* Kunth	**Recommendation:**	Reject

Refer to:

Pheloung *et al.* (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57, pp 239-251.

Gordon *et al.* (2010) Guidance for addressing the Australian Weed Risk Assessment questions. *Plant Protection Quarterly* 25, pp 56-74.

Question	Answer	Score	Possible scores
1.01 Is the species highly domesticated?	y	-3	0 or -3
1.02 Has the species become naturalized where grown?	y	1	-1 or 1
1.03 Does the species have weedy races?	n	-1	-1 or 1
2.01 Species suited to South African climates	2	2	0, 1 or 2
2.02 Quality of climate match data (0-low; 1-intermediate; 2-high)	2	2	0, 1 or 2
2.03 Broad climate suitability (environmental versatility)	n	0	0, 1 or 2
2.04 Native or naturalized in regions with tropical or subtropical climates	y	1	0 or 1
2.05 Does the species have a history of repeated introductions outside its natural range?	y	2	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.01 Naturalized beyond native range	y	2	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.02 Garden/amenity/disturbance weed	y	2	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.03 Weed of agriculture/horticulture/forestry	n	0	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.04 Environmental weed	n	0	Refer to "lookup" table (Appendix 2) from Pheloung *et al.*, 1999
3.05 Congeneric weed	n	0	Refer to "lookup" table (Appendix 2)

			from Pheloung *et al.*, 1999
4.01 Produces spines, thorns or burrs	n	0	0 or 1
4.02 Allelopathic	n	0	0 or 1
4.03 Parasitic	n	0	0 or 1
4.04 Unpalatable to grazing animals			-1 or 1
4.05 Toxic to animals	y	1	0 or 1
4.06 Host for recognised pests and pathogens	y	1	0 or 1
4.07 Causes allergies or is otherwise toxic to humans	y	1	0 or 1
4.08 Creates a fire hazard in natural ecosystems	n	0	0 or 1
4.09 Is a shade tolerant plant at some stage of its life cycle	y	1	0 or 1
4.10 Grows on infertile soils	y	1	0 or 1
4.11 Climbing or smothering growth habit	y	1	0 or 1
4.12 Forms dense thickets	n	0	0 or 1
5.01 Aquatic	n	0	0 or 5
5.02 Grass	n	0	0 or 1
5.03 Nitrogen fixing woody plant	n	0	0 or 1
5.04 Geophyte	n	0	0 or 1
6.01 Evidence of substantial reproductive failure in native habitat	n	0	0 or 1
6.02 Produces viable seed	y	1	-1 or 1
6.03 Hybridises naturally			-1 or 1
6.04 Self-fertilisation	n	-1	-1 or 1
6.05 Requires specialist pollinators	n	0	0 or -1
6.06 Reproduction by vegetative propagation	y	1	-1 or 1
6.07 Minimum generative time (years)	3.0	0	-1, 0, or 1
7.01 Propagules likely to be dispersed unintentionally	y	1	-1 or 1
7.02 Propagules dispersed intentionally by people	y	1	-1 or 1
7.03 Propagules likely to disperse as a produce contaminant	n	-1	-1 or 1
7.04 Propagules adapted to wind dispersal	n	-1	-1 or 1
7.05 Propagules buoyant			-1 or 1

7.06 Propagules bird dispersed			-1 or 1
7.07 Propagules dispersed by other animals (externally)	n	-1	-1 or 1
7.08 Propagules dispersed by other animals (internally)			-1 or 1
8.01 Prolific seed production	n	-1	-1 or 1
8.02 Evidence that a persistent propagule bank is formed (>1 yr)	n	-1	-1 or 1
8.03 Well controlled by herbicides			-1 or 1
8.04 Tolerates or benefits from mutilation, cultivation or fire	y	1	-1 or 1
8.05 Effective natural enemies present in South Africa			-1 or 1

Notes and References:

1.01	"a popular foliage houseplant"; "common ornamental climber throughout the world"	http://floridata.com/Plants/Araceae/Monstera+deliciosa/794; Mayo, S. 1985. Araceae. In: R. Polhill (ed.). Flora of Tropical East Africa. 71 pp.
1.02	Florida; New Zealand and Galapagos	http://regionalconservation.org/ircs/database/plants/PlantPage.asp?TXCODE=Monsdeli; http://www.hear.org/gcw/species/monstera_deliciosa/
1.03	"Although its been around for ages, there are still very few cultivars you can buy". There is no evidence that cultivars are weedy	http://www.ourhouseplants.com/plants/monstera-deliciosa; http://keyserver.lucidcentral.org/weeds/data/media/Html/monstera_deliciosa.htm
2.01	Bioclimatic model	Current study
2.02	Bioclimatic model	Current study
2.03	Suited to tropical and warm subtropical climates	http://www.gbif.org/species/2868241
2.04	"Occasionally naturalised in	http://keyserver.lucidcentral.org/weeds/data/media/Html/monstera_deliciosa.htm

	the warmer temperate, sub-tropical and tropical regions of eastern Australia"	
2.05	"It was introduced into cultivation in England in 1752; reached Singapore in 1877 and India in 1878. Specimens of the fruit were exhibited by the Massachusetts Horticultural Society in 1874 and 1881. It has become familiar as an ornamental in most of the warm countries of the world and is widely used in warm and temperate regions"	Morton, J. 1987. Ceriman. p. 15–17. In: Fruits of warm climates. Julia F. Morton, Miami, FL.
3.01		http://www.hear.org/gcw/species/monstera_deliciosa/
3.02	"This very common garden plant has become a weed of riparian areas and urban bushland, particularly in the warmer parts of eastern Australia. It is relatively common in coastal areas, usually growing where garden refuse has been dumped"	http://keyserver.lucidcentral.org/weeds/data/media/Html/monstera_deliciosa.htm
3.03	No evidence	

3.04	Not known to be invasive	
3.05	No evidence	
4.01	Species does not have these traits	
4.02	No evidence	
4.03	No evidence	
4.04	Unknown	
4.05	"The oxalic acid, and possibly other unidentified principles, in the unripe fruit, the floral remnants of the ripe fruit, and all parts of the plant, cause oral and skin irritation"	Morton, J. 1987. Ceriman. p. 15–17. In: Fruits of warm climates. Julia F. Morton, Miami, FL.
4.06	"The following diseases have been recorded in Florida: leaf spot caused by Leptosphaeria sp., Macrophoma philodendri, Phytophthora sp., and Pseudomonas cichorri; anthracnose from Glomerella cingulata; bacterial soft rot from infection by Erwinia carotovora; and root rot caused by Pythium splendens and Rhizoctonia	Morton, J. 1987. Ceriman. p. 15–17. In: Fruits of warm climates. Julia F. Morton, Miami, FL.

	solani"	
4.07	"The oxalic acid, and possibly other unidentified principles, in the unripe fruit, the floral remnants of the ripe fruit, and all parts of the plant, cause oral and skin irritation"	Morton, J. 1987. Ceriman. p. 15–17. In: Fruits of warm climates. Julia F. Morton, Miami, FL.
4.08	Lush evergreen foliage	
4.09	"Plant grows in the shade"	http://hort.ufl.edu/database/documents/pdf/shrub_fact_sheets/mondela.pdf
4.10	"Soil tolerances: slightly alkaline; clay; sand; acidic; loam"	http://hort.ufl.edu/database/documents/pdf/shrub_fact_sheets/mondela.pdf
4.11	"Vigorous vine which quickly climbs up any shaded tree trunk"	http://hort.ufl.edu/database/documents/pdf/shrub_fact_sheets/mondela.pdf
4.12	No evidence	
5.01	Epiphytic	
5.02	Vine	
5.03	Araceae family	
5.04	Climber	
6.01	Reproduction is usually by vegetative spread	http://www.terrain.net.nz/friends-of-te-henui-group/weeds/fruit-salad-plant-monstera-deliciosa.html
6.02	"Due to recalcitrant nature of	http://www.tropilab.com/swisscheeseplant.html

	the seeds, they have a short viable life"	
6.03	Unknown	
6.04	"The stigma is receptive before the ripening of the stamens, thus avoiding the self-fertilization"	Madison, M. 1977. A revision of Monstera (Araceae). Gray Herbarium of Harvard University. 100pp.
6.05	Bees and Insects	http://tropical.theferns.info/viewtropical.php?id=Monstera+deliciosa
6.06	"From leaf cuttings, herbaceous stem cuttings, and softwood cuttings"	http://davesgarden.com/guides/pf/go/1204/#b
6.07	"Suckers will fruit in 2 to 4 years, cuttings in 4 to 6 years"	
7.01	"It is mainly found growing where garden waste has been dumped along roadsides and waterways"	http://keyserver.lucidcentral.org/weeds/data/media/Html/monstera_deliciosa.htm
7.02	"Fruit salad plant has a long history as a popular houseplant throughout the world"	Martin, T.J. 2002. A Mexican migrant the naturalisation of *Monstera deliciosa* (fruit salad plant) in New Zealand. Auckland Botanical Society Journal, 57: 151-154
7.03	No evidence	
7.04	No evidence	
7.05	Unknown	
7.06	Unknown, but likely, since berries are edible	
7.07	No evidence, but fruits have no means for attachment	
7.08	Unknown	

8.01	"Generally there are no seeds, but sometimes, pale-green, hard seeds the size of large peas, may occur in a dozen or so of the segments"; "Seeds are occasionally produced but seedlings take a long time to develop fully"	Morton, J. 1987. Ceriman. p. 15–17. In: Fruits of warm climates. Julia F. Morton, Miami, FL.; http://www.dpi.nsw.gov.au/__data/assets/pdf_file/0003/119775/monsterosa-deliciosa.pdf
8.02	Seeds must be sown immediately	Mustafin, A. M. (1983) Monstera propagation by seed. Byulleten' Gosudarstvennogo Nikitskogo Botanicheskogo Sada, 1983, No.51, pp.29-33, 8
8.03	Unknown. In New Zealand they recommend cut and treat stump using Triclopyr	-
8.04	"I sometimes chop the stem into 3 inch pieces, let them harden off for a day or two, then lay with nodes down on top of the soil. You don't even need leaves to do this. These things will practically propagate themselves"	http://forums.gardenweb.com/discussions/1689993/propagating-monstera-deliciosa
8.05	Unknown	

Appendix 11. Response curves demonstrating the relationship between the environmental variables and the probability of *M. deliciosa* presence. The environmental variables comprise Bio 1 (annual mean temperature), Bio 7 (temperature annual range (i.e. maximum temperature of the warmest month – minimum temperature of the coldest month)), Bio 12 (annual precipitation), and Bio 15 (precipitation seasonality). Temperature variables are measured in degrees Celsius and precipitation variables in mm. Rug lines on the lower x-axes represents values of *M. deliciosa* occurrences, and pseudo-absence values are shown on the upper x-axes.