

Biological invasions and natural colonisations: are they that different?

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Abstract

We argue that human-mediated invasions are part of the spectrum of species movements, not a unique phenomenon, because species self-dispersing into novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion as those assisted by people. Species changing their distributions by human-mediated and non-human mediated modes should be of identical scientific interest to invasion ecology and ecology. Distinctions between human-mediated invasions and natural colonisations are very valid for management and policy, but we argue that these are value-laden distinctions and not necessarily an appropriate division for science, which instead should focus on distinctions based on processes and mechanisms. We propose an all-encompassing framework of species range expansion. This does not detract from the importance of invasion biology as a discipline, but instead will help bring together research being conducted on multiple taxa, and by multiple disciplines, including epidemiology, that are often focused on an identical phenomenon: colonisation.

Keywords

Alien, biological invasion, colonisation, dispersal, exotic, invasion, introduction

Artificial distinctions don't aid science

Ecologists studying human-mediated biological invasions and those studying natural colonisations are essentially working on the same phenomenon (Johnstone 1986; Thompson et al. 1995). Yet, historically, ecological studies on biological invasions and on colonisations have been treated as distinct fields, with too few connections (Davis et al. 2001). Although we agree that the distinction between human-mediated invasions and natural colonisations is very valid for management and policy making, especially for species that have large ecological effects, we argue that this is a value-laden distinction and not necessarily an appropriate division for science, which instead should focus on distinctions based on processes and mechanisms. Current scientific divisions between invasion ecology and ecology is resulting in scientific synergies being inadvertently lost. Species naturally colonising novel environments necessarily go through the same stages of introduction, establishment and spread as species introduced by humans, because they are subject to the same barriers of survival, reproduction, dispersal and further range expansion, and therefore are identical from a scientific perspective (Ricklefs 2005; Jeschke et al. 2013; Rius and Darling 2014; Yek and Slippers 2014). In terms of understanding the processes, mechanisms, and consequences of colonisation, the means of access to new areas is inconsequential. Human-mediated transport merely allows more individuals and more species to arrive in new locations more often and more quickly, ultimately resulting in rates of colonisation being greater than what it is for natural colonisation. Instead what counts are the ecological constraints, the dynamics of species with no common, or a fragmented, evolutionary history, and the intrinsic suitability of the propagule to disperse to and survive in a novel environment. The current artificial polarisation of the respective sciences based on human mediation versus natural colonisation is hindering the progression of our understanding of the underlying mechanisms and processes of range expansions (Davis et al. 2001; Catford et al. 2009; Jeschke et al. 2013; Yek and Slippers 2014).

Following are four examples of the irrelevance of dispersal mode for the science of colonisation. The first is the Lessepsian migration: the dispersal of at least three hundred species from the Red Sea into the Mediterranean Sea following the opening of the Suez Canal. Most species have increased their distributions naturally, as the dominant currents and winds have dispersed their propagules northward (Mavruk and Avsar 2007), but some have also moved through shipping (Galil 2000). Although the ability for species to disperse and colonise was triggered by the removal of a geographical barrier through a human intervention, the act of dispersal has occurred both naturally and with further human assistance. Regardless of opinions about whether these are human-mediated range expansions or not, the science underpinning an understanding of the colonisations, and their ecological as well as evolutionary consequences, is identical.

The second example is the 2011 Tohoku tsunami, which carried about 1.5 million tonnes of debris, vegetation and fauna out to sea. The flotsam was carried across the Pacific where it was also colonised by other marine flora and fauna, and some reached North American coastlines nearly 8,000 kilometres away (Gewin 2013). On the larg-

est bits of flotsam, scientists have identified many Japanese species able to colonise the new continent, some of which may have negative environmental and economic consequences (Gewin 2013). Again, irrespective of opinions of whether these dispersals should be considered natural events to be accepted, or biological invasions to be managed, the science underpinning the understanding of their colonisation and potential effects is identical. Moreover, having two sets of scientific fields and experts to distinctively study colonisers and invaders in this scenario would make no more sense than in the previous example.

A more tangential and arguably extreme example would be the greatest colonisation in global history: humans. Ecologists now accept that people are not disconnected from the environment, and thus scientific understanding of our own spread across the globe cannot be isolated from that of all other species. However, it can certainly be argued that our own dispersal was human mediated, and caused great impact in new ecosystems, which would qualify as an invasion. Yet, certainly in pre-historic times our survival and further spread was fully compliant with, and restricted to, the rules of nature, which would qualify as a colonisation. So did humans naturally colonise the globe, or were we a biological invasion? We argue that the distinction is extraneous semantics: we were both, because both terms describe the same phenomenon.

The last example is the myriad of species undergoing range-shifts due to climate change, which is an issue that is set to result in even less clarity of what is an “exotic” species (Webber and Scott 2012) and what should be managed. One such species is the pine processionary moth, *Thaumetopoea pityocampa*, a major forest pest native to the Mediterranean Basin and now rapidly expanding its range towards higher latitudes and altitudes in response to climate change (Battisti et al. 2005, 2006). Where it becomes newly established should it be seen as an invasive pest or a problematic native species that has naturally and predictably shifted its range? Changes in species distributions are predicted to increase with time as climate change progresses (Thomas 2010), and this mass movement of biota will result in many novel combinations of species. These species will all interact based on the same mechanisms and restraints affecting anthropogenically-dispersed species, some with negative ecological impacts, and others without. Regardless of personal opinions of whether these are “invasions” or not, the science of the range changes is identical.

Arguments separating natural colonisations from human-mediated invasions

Despite several papers over multiple decades highlighting the lack of distinction between “invasions” and colonisations from an ecological perspective (Johnstone 1986; Thompson et al. 1995; Ricklefs 2005), there appears to be great resistance among invasion biologists to acknowledge this artificial separation (Davis et al. 2001). Here we focus on four main arguments that are often presented to argue why “invasions” are different, and we explain why we believe that these arguments are incorrect.

The first argument against ending the artificial separation between colonisation and invasion is that propagule pressure is greater for species dispersed by human mediation, and therefore this represents a difference in process. Propagule pressure consists of the number of individuals arriving in a new location at one time and the number of arrival times. Although we now have good data of accidental human-mediated propagule pressure from the likes of shipping ballast, and cargo freight, the same cannot be said for natural colonisation. As far as we are aware, no attempt has ever been made to compare propagule pressure in any location between natural dispersal events and human-mediated dispersal. But if such a comparison was made, we suspect that on a global-scale, propagule pressure would often be comparable for species dispersing naturally. For example, it has been estimated that 4.5 billion insects were dispersed over the North Sea each summer day from a 30 km coastal strip alone (Edwards 1986b; Heydemann 2008). Elsewhere, quantification of insects aerially deposited on snow-fields on 2500 m summit slopes found 24 insects per square metre annually (Edwards 1986a). Indeed, the prevalence of the arthropod fallout globally is so great that many animal communities are dependent upon it for survival, including on high mountains within alpine zones (Swan 1963), oligotrophic lakes, deserts, and deep oceans. Regardless, any difference between the two transport modes merely represents a change of rate, not a change of process.

The second argument is that colonisation pressure (the number of species introduced per colonisation event) is greater for species spread by human mediation, and therefore this is a difference in process. While we agree that such a discrepancy is likely for fauna that clearly cannot easily disperse biogeographically (e.g., lizards, land snails, frogs), the same may not necessarily be so for the bulk of species, the invertebrates, as detailed above. However, such a comparison may not necessarily be meaningful, because natural colonisations appear to occur over continuous periods, not necessarily just individual events (e.g., a cyclone). Just as for propagule pressure, as far as we are aware, there has never been an attempt to compare colonisation pressure in any one location from human-mediated dispersal versus natural dispersal, but disjunct data do exist for comparison. For example, for natural colonisations, within the first two years of the eruption of Mt. St. Helens, USA, in 1980, 43 spider species had ballooned in, including three European species (Edwards 1986b). Similarly, a decade of sampling of arthropod fallout on Mount Rainier, USA, found > 200 species from 17 orders and 140 families (Edwards 1986b; Edwards and Sugg 1993). Within three years of the formation of volcanic Long Island, Papua New Guinea, 20 invertebrate species were found (Thornton 2001). In comparison, meiobenthic assemblages found within residual sediment and ballast water of ships range from an unknown number of species from 6 Classes, including 12 nematode genera (Radziejewska et al. 2006), to 33 taxa from six ships (Gray et al. 2007) and 147 taxa from 32 ships (Duggan et al. 2005). The point we make is that there are no hard data to demonstrate that the number of species being dispersed by people is greater than that of species dispersing naturally, and such data would be highly beneficial. What may be clouding perspectives on this point is that in modern times there has no doubt been a dramatic increase in the rate of species

being moved by human mediation. But, just as for propagule pressure, any potential difference only represents a change of rate, not a change of process.

A third argument is that natural and human-mediated dispersal result in differences in genetic diversity that affect colonisation success, largely being that greater propagule pressure from human-mediated dispersal can result in greater genetic diversity. But there are many documented instances where invasions arose from a very small propagule. For example, the thousands of feral cats that now invade the Kerguelen Islands come from only 2 to 4 cats (Pascal 1980). In addition, although we agree that higher propagule pressure can give rise to greater genetic diversity which can result in a reduced chance of founder effects, species undergoing both natural and human-mediated transport can be successful with highly restricted or highly diverse genetics (Roman and Darling 2007). For both transport modes, where a single propagule (e.g., a queen ant or a seed) is either accidentally transported across a biogeographic barrier by human mediation, or naturally, the genetic restriction, and the Allee effects (Courchamp et al. 2008) potentially affecting colonisation are identical. Likewise, intentional introductions of multiple individuals to increase genetic diversity of the incipient population and natural colonisations that involve the dispersal of many individuals (e.g., a flock of birds in a pulse event or seasonal or continuous fallout of airborne arthropods) both potentially involve equivalent genetic variation that may or may not result in successful colonisation.

We agree that higher propagule pressure increases the likelihood of colonisation success (Blackburn et al. 2013) and also that more important than genetic diversity is the presence of genes suitable for movement to novel locations (Lee 2002; Winkler et al. 2008) and in some instances, genetic admixture (Rius and Darling 2014). Indeed, for species dispersed by either natural or human-mediated transport, and regardless of whether the dispersal is within a region or across a geographic barrier, often only a subset of a species' genetic pool can colonise new locations. This selectivity is a fundamental tenant of the taxon cycle which rightfully makes no distinction between species dispersed by human mediation or not (Ricklefs 2005). Interestingly it appears likely that humans have accidentally, as well as intentionally, acted as a selective filter on genetic-based traits that are suited to colonisation (Hufbauer et al. 2012). But again, such human influence is comparable to the natural selection of species with inherent capabilities for long-distance natural dispersal. Overall, irrespective of the dispersal mode, the distance of dispersal, and the mode by which genetic filtering or admixing occurs, the role of the numerous genetic characteristics to colonisation (Lee 2002) is identical for both dispersal modes.

Importantly for these three arguments, and possibly others, comparisons between species movement by human mediation and natural dispersal must be equivalent comparisons whereby only a single factor varies, but this is often not the case. For example, it is not valid to argue that there are genetic differences when comparing the deliberate introduction of a grass, whereby thousands of seeds with great genetic diversity are brought to an area, with the natural dispersal of a single seed because in this instance genetics is confounded with different levels of propagule pressure.

The fourth argument is that invasions, unlike colonisations, are drivers of mass-extinction. We have four issues with this argument. First, implicit in this argument is that natural colonisations don't have negative impacts, and they are not responsible for localised extinctions. We are unaware of a naturally dispersed species being reported as causing an extinction, but perhaps this is due to the difficulty of demonstrating that a species has indeed self-dispersed and not been spread by human means and then caused an extinction of a native species. Logically, however, throughout evolutionary time, as species have arisen and dispersed, and as species distributions have changed following climates and tectonic movements, they have outcompeted and replaced other biota. For example, placental mammals outcompeted marsupials throughout most of the world. This is particularly well studied in the multiple waves of migrations of mammals between North and South America as the Isthmus of Panama rose c. 3–10 Mio. years ago that resulted in the replacement of most of South America's mammals (Great American Interchange) (Leigh et al. 2014). Moreover, these extinctions would have occurred many more times than modern extinctions from human-mediated colonisations, albeit because of the greater timeframe. Second, although extinction is, arguably, the greatest impact a species can have on co-occurring biota, it remains that impact is a value-laden term that is controversial as a defining term for invasion biology (Blackburn et al. 2011; Jeschke et al. 2014), nor is it an underlying mechanism or processes of range expansion, and frequently species undergoing range expansion are passengers rather than drivers of change (Didham et al. 2005). Third, while it is clear that many species that disperse outside of their native range have significant negative impacts (Mack et al. 2000), with the (dramatic) exception of a few mammals, ants and pathogens, there is little evidence that exotic species induce species extinctions (Gurevitch and Padilla 2004), thus extinction is a relatively rare outcome. Better data are needed to make a conclusive comparison between extinction events resulting from human-mediated vs natural dispersal. Ultimately, this is a management and policy issue that should not make an artificial distinction between colonisation ecology and invasion biology.

A holistic, multi-disciplinary, framework

Many frameworks have been proposed that attempt to display the theoretical processes of biological invasions (Williamson 1996; Richardson et al. 2000; Catford et al. 2009; Saul et al. 2013). The framework for biological invasions proposed by Blackburn et al. (2011), we believe, presents the best effort yet to provide consensus for the processes associated with human-mediated species dispersal. This framework is particularly noteworthy for three reasons. First, it merged theoretical frameworks used by researchers and managers focusing on terrestrial plants and animals, thus the resulting synergy provides a more holistic picture of invasions. Second, nothing in the framework is based on the subjective criteria of impacts. Although we don't dispute that impacts can be very important, this subjectivity is an issue related to terminology, and not fun-

damental to the invasion process itself. Third, the framework excludes species within their native range that undergo population “explosions”, which have been inappropriately called invasions (see e.g., Blondel et al. 2013).

Despite the advance provided by Blackburn’s invasion framework, we believe that it stops short of being more widely applicable for ecology because it solely considers species movements that are human-mediated, and therefore colonisation, even at the biogeographic scale, is excluded (Wilson et al. 2009; Blackburn et al. 2011; Gillespie et al. 2011). We believe that it would be far more scientifically logical and beneficial to consider all species movements under a single framework to provide a more holistic view of species movements, resulting in greater insights for invasion ecology, for ecology in general, island biogeography and for other sciences such as epidemiology. Here, we present such a framework that is slightly but distinctly modified from that proposed by Blackburn et al. (2011) to more holistically encapsulate the spectrum of species colonisations (Figure 1), and that can be utilised by many science disciplines.

Differences of our framework

The framework presented here differs from that in Blackburn et al. (2011) in five main ways. First and foremost, it incorporates natural range expansion as a dispersal mode, and acknowledges that any species in novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion, irrespective of how they got there. Second, Blackburn’s Transport and Introduction stages have been

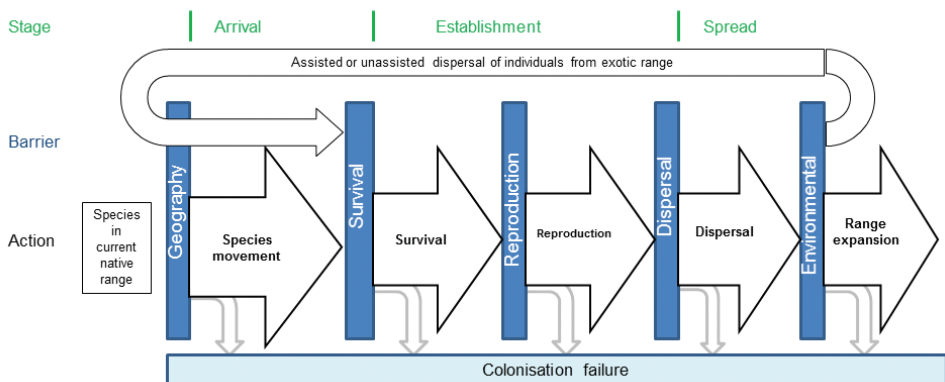


Figure 1. The colonisation framework. This framework considers both human-mediated dispersal and natural dispersal, and acknowledges that any species in novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion, irrespective of how they got there. This framework is relevant for epidemiology, simply by changing a few terms (e.g., species movement to infection, dispersal to transmission, invasion to disease spread).

merged into the Arrival stage, and within this the optional “Captivity or cultivation” barrier has been removed. Third, although acknowledged by Blackburn et al. (2011), we explicitly show that the process can be cyclical where the colonisation can be further initiated by dispersal from the exotic range, across another geographic barrier into a new biogeographic region, and can occur as both human mediated (e.g., the intentional introduction and establishment of salmonids into a country outside of its native range, followed by subsequent dispersal into additional aquatic systems (Crawford and Muir 2007)), or self-dispersal (e.g., Eurasian tree sparrows *Passer montanus* flying from Asia to Australia (Chapman 2000)). The fourth change is the use of simplified and descriptive categories. The use of codes to name the movements between the stages in the prior framework was slightly problematic in that these categories were non-descriptive and therefore were inefficient for communication, especially with the wider public. Additionally, from a scientific perspective, there is no need to have multiple categories between each barrier to describe each unique way that a species can move along the colonisation process. Thus we have replaced the many coded categories (e.g., Blackburn’s B1, B2, D1, D2) with single, all-encompassing descriptions between the barriers. Finally we incorporate many other, largely semantic, changes that eliminate focus from human-mediated dispersal. Additionally we have replaced “boom and bust” with “Colonisation failure” because this extreme population cycle does not always occur. The sole importance of this change in state is the extinction itself, not the greatly varying population dynamics that occur prior.

Advantages of the holistic framework

Both with and without the context of climate change, using the framework to detail colonisations overrides subjective issues defining exotics, such as distance away from a species’ historic distribution, recolonisation of extinct populations and colonisation without evolutionary history.

Blackburn’s framework was based on synergies of terrestrial plants and animals. Already the framework has proven applicable for marine animals (Jones et al. 2013). Similarly, our framework is applicable for any biotic phenomenon undergoing dispersal and subsequent range expansion. There is even scope for further synergies, such as with epidemiology, especially for emergent diseases. There appear to be very few frameworks for epidemiology, and those existing appear very rudimentary compared to frameworks for ecology (e.g., Gilligan 2002, but see Jeschke et al. 2013), despite both sciences operating with arguably equally complex environmental settings. Pathogens associated with human, animal and plant health must also disperse, establish within/on a host, reproduce, transmit to a new host and in some instances are able to continue to spread, even globally. Pathogenic spread can be incorporated within our framework with simple word changes for two colonisation *Actions* so that it reads: infection, survival, reproduction, transmission and epidemic (Figure 1). Indeed invasive species management has its roots with pathogen containment, so it is not surprising that the

process of species colonisation would follow an identical framework to that for epidemiology. Epidemiological examples include the accidental emergence and subsequent spread of swine and bird flues (Neumann et al. 2009), the intentional release of rabbit calicivirus in Australia (Bruce et al. 2004), the unintentional spread of pathogenic chytrid fungus affecting amphibians globally (Lips et al. 2006), and the recent epidemics of Ebola (Gire et al. 2014).

Finally, this framework more easily allows the exchange of research ideas and findings across biological disciplines (e.g., conservation biology, invasion ecology, island ecology and biogeography, epidemiology) and for different focal taxa or biomes (e.g., microorganisms, plants and animals, marine and terrestrial organisms) that are often focused on the same phenomenon – colonisation. In particular, for invasion biology, possibly more so than for other science disciplines, the isolation of researchers focused on different taxa or biomes, and researchers from managers, has resulted in the loss of clear definitions and vast inconsistencies in terminology (Heger et al. 2013; Kueffer and Larson 2014). Terminology clarifications and unifications are being repeatedly proposed (Colautti and MacIsaac 2004; Pyšek et al. 2004; Richardson et al. 2011), but they do not necessarily cover all biota, or are not being embraced by stakeholders, partly attributable to the fragmented nature of the science. We have made no attempt here to reconcile these terminological issues, aside from removing all synonyms from the framework. But considering colonisation as a holistic process may help alleviate some of invasion biology's terminology issues.

Concluding remarks: moving towards a holistic view

There is no doubt that dispersal mode greatly influences the opportunity for species to disperse (Wilson et al. 2009; Gillespie et al. 2011), and that human-mediated dispersal of species, both intentional and accidental, has greatly accelerated the rate that species cross biogeographic barriers and colonise novel environments, often with great consequences (Mack et al. 2000). Additionally, the species composition being moved by human assistance is substantially different to the composition that would otherwise move naturally. But we argue that any differences of colonisation seen between species dispersed by human-mediation or not, merely represent different configurations of the same process of colonisation. This is because post-arrival all propagules face the same barriers of survival, reproduction, dispersal and further range expansion. Similarly, irrespective of the dispersal mode, a colonising species may or may not have significant ecological impacts. Indeed species self-dispersing across biogeographic distances via natural dispersal represent some of the greatest biosecurity risks to human interests and environments (Yen et al. 2014), and therefore there is no valid scientific distinction to separate species movements based on dispersal mode.

We argue that climate change biologists, invasion biologists, restoration ecologists, island biogeography biologists, community assembly ecologists and epidemiologists are unnecessarily conducting research in isolation from each other despite essentially

studying the same phenomenon – colonisation. Biological invasions do not represent a distinctly different or change in process, just an acceleration of the colonisation process through multiple mechanisms. The major difference between invasion and colonisation stands, we believe, on ethical ground. This difference should not dictate the science, only management and policy making. For biological invasions, we believe that predictive understanding would benefit most greatly from focusing on (1) determining why so many more species do not manage to successfully colonise new areas (Zenni and Nuñez 2013), and (2) for successful colonisers, determining why some species can establish with a single propagule, whereas others require many propagules. For all of the above sciences, we argue that they would mutually benefit from each other by holistically considering colonisations.

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Beasts or beauties? Laypersons' perception of invasive alien plant species in Switzerland and attitudes towards their management

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Abstract

This study investigated laypersons' perception of invasive alien plant species (IAPS) and attitudes towards their management with the help of a written questionnaire in the cities of Zurich, Geneva, and Lugano, Switzerland. Survey participants (n = 720) judged attractiveness from certain species on visual contact (eight IAPS were shown as photographs). *Trachycarpus fortunei* and *Ludwigia grandiflora* were liked most, while *Ambrosia artemisiifolia* was clearly disliked most. With the exception of *Trachycarpus fortunei*, all plant species were perceived as rather ordinary, familiar and native to Switzerland, and feelings of ordinarieness, familiarity and nativeness were positively correlated. Few participants could correctly identify the species depicted. Knowledge of an IAPS (ability to identify it) and desire to have it around were negatively correlated. Participants agreed most with the eradication of IAPS that cause serious costs and problems. However, people were rather unwilling to remove *Buddleja davidii*, *Solidago canadensis*, and *Trachycarpus fortunei* which are already widely established ornamentals in settlement areas or gardens. Overall, willingness to remove an IAPS and to report it to the authorities decreased with increasing desirability (and thus beauty) of a species.

Keywords

Invasive alien plant species, Switzerland, public perception, public attitudes, management

Introduction

Invasive alien species (IAS) are often considered a major threat to the world's biodiversity (MEA 2005, Vilà et al. 2011, Simberloff et al. 2013). They occur in all taxonomic groups and can affect all types of ecosystems (CBD 2009). IAS can be defined as species which establish outside their natural past range and dispersal potential and, once established, rapidly extend their range in the new region, causing significant harm to biological diversity, ecosystem functioning, socio-economic values, and/or human health in the invaded region (Vilà et al. 2011, Hulme et al. 2013). The strong increase in human travel, trade, and transportation has led to the introduction of many species to areas where they would not have been present without human assistance (Keller et al. 2011). As humans take an active part in the introduction, establishment, and spread of IAS, it is necessary to understand human perceptions and choices regarding the use and management of invasive species (Bardsley and Edwards-Jones 2007). However, research on biological invasions has focused more often on the ecological aspects of IAS than on social perceptions and attitudes of people (but see, e.g., García-Llorente et al. 2008, Andreu et al. 2009, Selge et al. 2011, Sharp et al. 2011, van der Wal et al. 2015). The present study is one of the first to investigate laypersons' perception of invasive alien plant species (IAPS) and attitudes towards their management in Switzerland.

Designing policies which prevent the introduction and release of IAS, and the management of species already established have become priority goals in many European countries (Commission of the European Communities 2008). About ten years ago, the Swiss Federal Office for the Environment (FOEN) commissioned an inventory of alien species in its country (Wittenberg 2005). Similar to other Central European countries, the assessment came up with about 800 alien species. Most of the aquatics and terrestrial invertebrates and diseases were accidental arrivals, whereas most of the vertebrates and plants were deliberate introductions. Plant species introduced as ornamentals are by far the largest group worldwide from which potential invasive ones emerge (Mack 2001). In Switzerland, for instance, 15 of the 23 IAPS on the Black List¹ have been deliberately introduced as ornamentals (Wittenberg 2005). However, as they cause substantial damage, prevention, control, and eradication measures are needed.

The general public's support and participation can be a key to success or failure of prevention, control, and eradication measures regarding IAS (Bertolino and Genovesi 2003, Bremner and Park 2007). However, the public's knowledge about IAS may be very limited. Several studies indicate that laypersons, at least in highly industrialized countries, know little about (local) plant and animal species, their diversity, and their ecological importance (e.g., Hunter and Brehm 2003, Pilgrim et al. 2007, Lindemann-Matthies and Bose 2008). Moreover, the discussion about IAS management and species conservation often neglects values which people attach to certain organisms (overview in

¹ The "Black List" includes invasive alien plants of Switzerland that cause damage in the areas of biodiversity, health, and/or economy. The establishment and the spread of these species must be prevented (FOEN 2007).

Heink and Jax 2014). Perceptions of laypersons on species conservation might strongly differ from those of ardent conservationists and natural resource managers, especially when the lethal removal of charismatic mammals is discussed (Minteer and Collins 2005, Lundberg 2010). However, laypersons might also not support the removal of “beautiful” IAPS, i.e., plants which are typically used as ornamentals (Veitch and Clout 2001, Lindemann-Matthies 2005). They might be perceived as a local enrichment to cities, gardens, banquettes, and even industrial zones (McKinney 2006). In consequence, public attention might be drawn away from problems related to the invasiveness of certain species. It is therefore important to know how people perceive and respond to IAS, as this facilitates the design of environmental management policies and communication strategies that are more likely to find acceptance among the general public (Fischer and van der Wal 2006).

This study investigated the perception of IAPS by more than 700 laypersons in Switzerland and their attitudes towards species management. The study contributes to international research on public perception of IAS and attitudes towards management strategies (e.g., Fischer and van der Wal 2006, Bremner and Park 2007, García-Llorente et al. 2008, Sharp et al. 2011), on stakeholders' perception of alien plant species in Switzerland (Humair et al. 2014a), and, more generally, on biodiversity perception (e.g., Colton and Alpert 1998, Fischer and Young 2007, Lindemann-Matthies and Bose 2008). It also provides baseline data for conservation activities that build upon the existing perceptions and attitudes of laypersons in Switzerland.

Main objectives were to investigate laypersons' (1) characterization of eight IAPS shown on paper, (2) ability to identify them, and (3) attitudes towards certain types of management. It was also investigated whether laypersons' perception of IAPS and attitudes towards certain types of management were influenced by socio-demographic variables and study location.

Methods

Study design and data collection

The study was carried out in three cities Zurich, Geneva, and Lugano, which are situated in three different regions and cantons (= administrative divisions) of Switzerland. Zurich in the north of the country belongs to the canton of Zurich (German-speaking part of Switzerland), Geneva in the southwest to the canton of Geneva (French-speaking part), and Lugano in the very south to the canton of Ticino (Italian-speaking part). Data were collected at the lake-sides of the three cities, as people are likely to be there during leisure time, and willing to take their time to answer the questions. Randomly selected passers-by (18 years and older) were asked, always in a similar way, to participate in a study about plants. In summer 2009, 720 persons filled out the questionnaire (240 in each city) in the local language. Data collection exercises required approximately 15 minutes time, and anonymity was guaranteed to the participants.

Questionnaire approach

The questionnaire consisted of two parts, which were printed on two separate sheets of paper to avoid influences of the second part, in which information about IAPS was provided, on the first part (Suppl. material 2). Participants were instructed to ask for the second sheet after finishing the first one. The first part investigated laypersons' perception of eight IAPS and their ability to identify them (objectives 1 and 2). Seven of these species were on the Black List (*Ambrosia artemisiifolia*, *Buddleja davidii*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Ludwigia grandiflora*, *Senecio inaequidens*, and *Solidago canadensis*) and one was on the Watch List (*Trachycarpus fortunei*). Species were chosen by impact (*A. artemisiifolia*, *H. mantegazzianum* and *I. glandulifera* are among the 100 worst alien terrestrial plant species in Europe (<http://www.europe-aliens.org/speciesTheWorst.do>)), popularity (*B. davidii* and *S. canadensis* are typical garden plants), threats to human health (*H. mantegazzianum* produces sap that causes skin lesions upon contact and pollen of *A. artemisiifolia* is highly allergenic), and regional importance, e.g., *S. canadensis* in Zurich, *L. grandiflora* in Geneva and *T. fortunei* in Lugano (FOEN 2006). Moreover, *A. artemisiifolia*, *H. mantegazzianum*, *I. glandulifera*, *L. grandiflora*, *S. inaequidens*, and *S. canadensis* are included in the "Swiss Ordonnance on Organism Dissemination in the Environment (ODE) RS 814.911" (2008) and may therefore not be introduced into the environment in Switzerland.

All plants were presented as photographs and their invasive status was not revealed. Each species had to be characterized by five opposing attributes (ugly-beautiful, extraordinary-ordinary, exotic-indigenous, unfamiliar-familiar, unwanted-wanted) on 7-step scales (e.g., very ugly, ugly, rather ugly, neither/nor, rather beautiful, beautiful, very beautiful). After the characterization exercise, participants had to identify as many species as they could and write down their common names. A plant was regarded as correctly identified if its common name was provided at the genus or species level.

The second part investigated laypersons' attitudes towards different types of management (objective 3). A short introduction provided information about IAPS and also clarified that all species shown in the first part were invasive. Participants had to choose among four different types of management (no intervention, no removal of aesthetically pleasing plants, but removal of less appealing ones, removal of only those invasive plants that provoke serious problems and costs, removal of all invasive plants in order to conserve unique habitats and species) to find the one type of management they considered most suitable. To investigate whether the choice of a certain management type depends on the species involved, a brief portrait of one of the IAPS used in the picture test was included in each questionnaire. Eight different versions of the second questionnaire part were thus prepared (varying in portraits, but being otherwise identical). The questionnaires were handed out to the 240 participants (30 persons per version) in each city which overall amounted to 720 questionnaires being filled out. Participants had to select among three types of management (no intervention, surveillance without taking immediate action, removal), and choose the one they considered

to be most fitting for the IAPS presented. In case they had chosen the latter type, they were asked where the species should be removed (from nature reserves, natural areas, forests or farmland, settlement areas, cities, and gardens). Moreover, they were asked whether they would report the species if they detected it, and whether they would remove it from their own garden.

Finally, participants were asked about their age, sex, level of formal education, professional expertise (profession related to biology, ecology or landscape topics), and environmental commitment (membership in an environmental organization). These variables were found influential in studies on biodiversity perception (e.g., Lindemann-Matthies and Bose 2008, Junge et al. 2011), and on attitudes towards invasive species (e.g., Fischer and van der Wal 2006, Bremner and Park 2007, García-Llorente et al. 2008).

Participants and data analysis

Participants (52% women) were between 18 and 79 years old (mean age = 32 years). About 68% of participants had a high school degree, 9% a profession related to biology, ecology, or landscape topics, and 22% were members in an environmental organization. Similar numbers were found in a large representative Swiss study on landscape perception (Junge et al. 2011).

Linear regressions were used to test for influences of socio-demographic variables and study location on participants' characterizations of eight IAPS and number of IAPS correctly identified. The final minimum adequate models were obtained by backward elimination of non-significant ($p > 0.05$) variables. As this type of analysis does not allow strong correlations between explanatory variables ($r > 0.35$), Pearson correlations between binomial and metric explanatory variables were tested first (Crawley 2005). The following variables and factors were initially included in the models: age, sex, level of education (high-school degree or not), professional experience (profession related to biology/ecology/landscape topics or not), environmental commitment (membership in an environmental organization or not), and study location (dummy coded with Geneva and Lugano tested versus Zurich).

Ordinal regression was used to test for influences on participants' attitudes towards certain types of management (as outlined in Figure 2). The four different types were reduced to three, i.e., no intervention, partial intervention (combination of answers "removal of IASP that provoke serious problems and costs" and "removal of aesthetically less appealing ones") and total removal of IAPS, and treated as an ordered dependent variable (from low to high intervention intensity). The following variables and factors were initially included in the model: age, sex, level of education, professional experience, environmental commitment, study location (dummy coded), and "taxonomic knowledge" (number of species correctly identified). All analyses were carried out with SPSS for Windows 20.0.

Results

Characterization of eight IAPS (objective 1)

Almost all plants were perceived as beautiful and wanted. On average, *Ludwigia grandiflora* was considered most beautiful, *Trachycarpus fortunei* most extraordinary, exotic and wanted, *Senecio inaequidens* most ordinary, indigenous and familiar, *Solidago canadensis* most unfamiliar, and *Ambrosia artemisiifolia* most ugly and unwanted (Figure 1). Aesthetic appeal and desirability of a species (attributed scores on the “ugly-beautiful” and “unwanted-wanted” scale, respectively) were positively correlated as were perceived nativeness, familiarity and ordinariness (scores on the “exotic-indigenous”, “unfamiliar-familiar” and “extraordinary-ordinary” scale, all correlation coefficients between 0.15 and 0.46, all $p < 0.001$). Moreover, perceived nativeness and desirability (scores on the “exotic-indigenous” and “unwanted-wanted” scale) were positively correlated (all correlation coefficients between 0.14 and 0.22, all $p < 0.002$). Only in case of *T. fortunei*, no significant correlation was found between nativeness and familiarity or nativeness and desirability ($p > 0.906$).

Study location influenced characterizations (Table 1, see Figure 1). Compared with Zurich, most plant species were less wanted by participants in Lugano, and some also less wanted by participants in Geneva. Moreover, several plants were considered more ordinary, but less indigenous in Lugano than in the other two locations (especially *T. fortunei*). Age especially influenced how beautiful and extraordinary a plant was perceived to be (see Table 1). Sex-related differences were always due to higher ratings by women (on the 7-step scales), and occurred especially in case of beauty and familiarity. Level of formal education and professional expertise hardly influenced ratings, while environmental organization members considered *L. grandiflora*, *H. mantegazzianum* and *I. glandulifera* less extraordinary, and the latter two also more indigenous than did non-members.

Identification of the eight IAPS (objective 2)

Only 75 participants could correctly identify at least one of the plant species presented (1 species: 41 persons, 2–3 species: 27 persons, 4–7 species: 7 persons, 8 species: nobody). *B. davidii* and *H. mantegazzianum* were most often and *S. inaequidens* and *L. grandiflora* least often correctly identified (see numbers in brackets in Table 2).

In the model ($r^2 = 0.16$), age, professional experience, membership in an environmental organization and study location influenced participants’ “taxonomic” knowledge. With increasing age, individuals were more able to identify species correctly ($b = 0.01$, $t = 6.29$, $p < 0.001$), as were participants with professional expertise ($b = 0.39$, $t = 4.54$, $p < 0.001$) and environmental organization members ($b = 0.23$, $t = 3.74$, $p < 0.001$). Participants in Lugano were less able than the others to identify species correctly ($b = -0.16$, $t = -3.08$, $p = 0.002$).

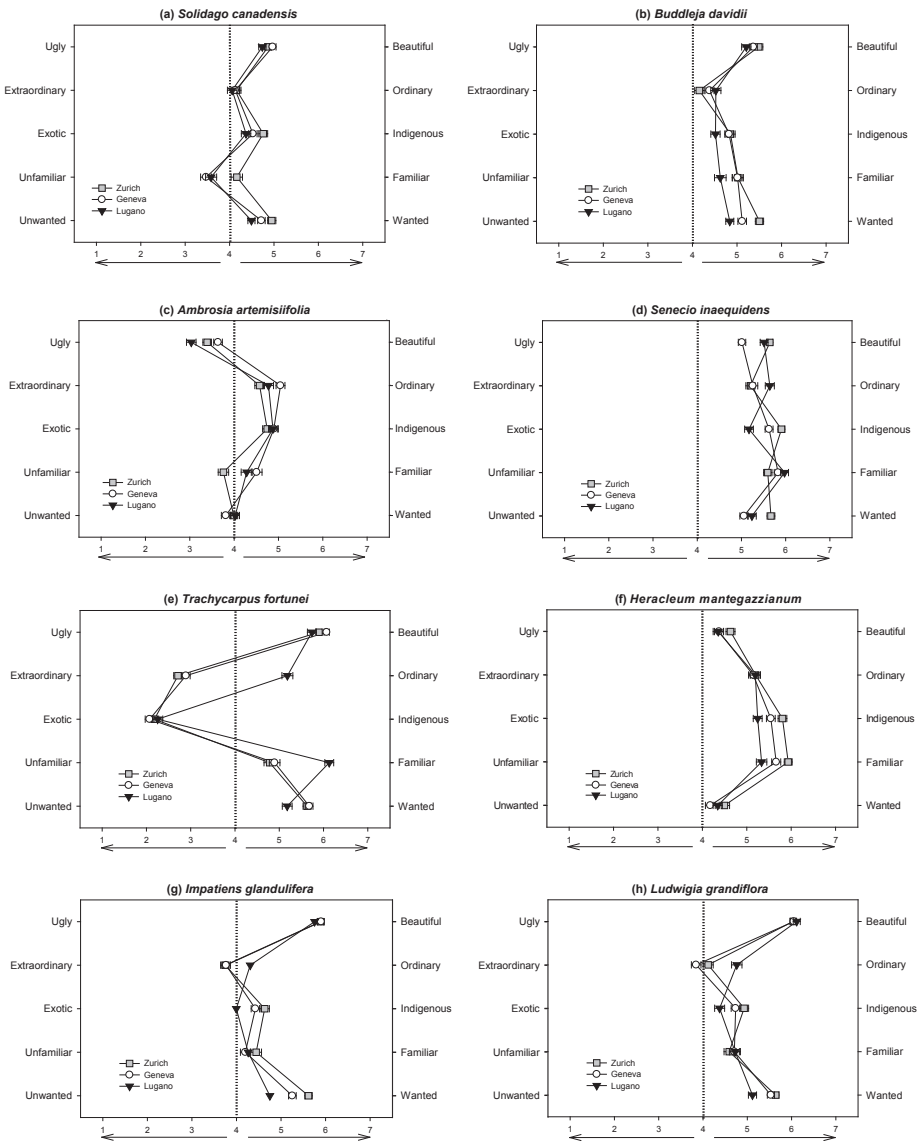


Figure 1. Characterization of eight invasive alien plant species in Zurich, Geneva and Lugano. Participants ($n = 720$) had to characterize each species by five opposing attributes (ugly-beautiful, extraordinary-ordinary, exotic-indigenous, unfamiliar-familiar, unwanted-wanted) on 7-step scales (e.g., very ugly, ugly, rather ugly, neither/nor, rather beautiful, beautiful, very beautiful). Mean rating scores and standard errors of means are shown.

Knowledge of an IAPS (ability to identify it on paper) and desire to have it around (attributed score on the “unwanted-wanted” scale) were negatively correlated. An IAPS was considered (rather) unwanted by those participants who knew it, and (rather) wanted by those who did not. Only with *B. davidii* was this not the case (see Table 2).

Table 1. Influence of socio-demographic variables and study location on laypersons' (n = 720) characterization of eight invasive alien plant species of Switzerland that were shown to them on photos. All characterizations were done with the help of 7-step rating scales, anchored on both sites with five dichotomous attributes (e.g., very ugly-very beautiful; see Figure 1). Data were analyzed by multiple regressions (backward selection). Only significant effects (t- and p-values) are shown (*: p < 0.05; **: p < 0.01; ***: p < 0.001). P-values were adjusted by Bonferroni-correction for multiple testing.

Attributes and species	Age	Women vs. men	Prof. related to ecology	NGO member	Geneva vs. Zurich	Lugano vs. Zurich
Beautiful						
<i>S. canadensis</i>	6.11***					
<i>B. davidii</i>	3.09*	4.56***	3.01*			
<i>A. artemisiifolia</i>	6.53***				3.27*	
<i>S. inaequidens</i>	2.87*	2.97*			-5.95***	
<i>H. mantegazzianum</i>	4.45***	3.19**				
<i>I. glandulifera</i>		3.25**				
<i>L. grandiflora</i>		3.31**				
Ordinary						
<i>B. davidii</i>			2.97*			
<i>S. inaequidens</i>	-4.38***					
<i>T. fortunei</i>	-2.78*					17.88***
<i>H. mantegazzianum</i>				-2.84*		
<i>I. glandulifera</i>				-2.99*		4.14***
<i>L. grandiflora</i>	-3.09*					5.06***
Indigenous						
<i>B. davidii</i>		3.84***				
<i>S. inaequidens</i>						-5.51***
<i>H. mantegazzianum</i>				3.42*		-3.63***
<i>I. glandulifera</i>	3.33**					-3.87***
<i>L. grandiflora</i>						-3.51***
Familiar						
<i>S. canadensis</i>	3.98***				-3.77***	
<i>B. davidii</i>		4.52***	5.54***			
<i>A. artemisiifolia</i>					4.38***	3.07*
<i>T. fortunei</i>		3.20*		2.83*		9.12***
<i>H. mantegazzianum</i>		3.59***	3.38**			-3.81***
<i>I. glandulifera</i>	4.53***					
<i>L. grandiflora</i>		3.03*				
Wanted						
<i>S. canadensis</i>	3.30**					-2.76*
<i>B. davidii</i>		3.56***			-2.90*	-5.06***
<i>S. inaequidens</i>	3.66***				-4.50***	
<i>T. fortunei</i>						-4.07***
<i>I. glandulifera</i>		3.80***			-3.00*	-7.08***
<i>L. grandiflora</i>						-4.68***

Table 2. Relationship between knowledge of IAPS (measured as the ability to identify them) and degree of their desirability (measured on a 7-step scale with 1: very unwanted, 2: unwanted; 3: rather unwanted; 4: neither unwanted nor wanted; 5: rather wanted, 6: wanted, 7: very wanted). The number of participants (overall 720 persons) who could correctly identify the species is shown in brackets. Data were analyzed only when more than ten participants could identify the species. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Species	Desirability (mean rating scores)		Test statistics	
	Unable to identify	Able to identify	F-value	P-value
<i>Solidago canadensis</i>	4.7 \pm 0.05	4.0 \pm 0.27 (25)	6.76	0.009
<i>Buddleja davidii</i>	5.2 \pm 0.06	5.1 \pm 0.20 (51)	0.08	0.781
<i>Ambrosia artemisiifolia</i>	4.0 \pm 0.06	2.1 \pm 0.33 (19)	31.45	<0.001
<i>Senecio inaequidens</i>	5.3 \pm 0.06	2.0 (1)	-	-
<i>Trachycarpus fortunei</i>	5.5 \pm 0.06	3.2 \pm 0.60 (6)	-	-
<i>Heracleum mantegazzianum</i>	4.4 \pm 0.07	3.6 \pm 0.32 (28)	5.38	0.021
<i>Impatiens glandulifera</i>	5.2 \pm 0.05	3.2 \pm 0.45 (9)	-	-
<i>Ludwigia grandiflora</i>	5.4 \pm 0.05	2.5 \pm 0.91 (2)	-	-

Opinion on types of management (objective 3)

In view of participants, for IAPS that cause serious costs and problems, removal was clearly the best type of management and thus most often chosen (Figure 2). Results of the ordinal regression analysis showed that only “taxonomic” knowledge (number of IAPS correctly identified) significantly influenced a person's decision for a certain type of management. With increasing knowledge, the likelihood increased that one of the stricter types of management (partial or total removal of IAPS) was opted for (Wald = 12.73, $p < 0.001$).

When asked how to proceed with the individual species presented in the second questionnaire sheet, participants more often opted for removal than surveillance, only with *T. fortunei* and *B. davidii* was this not the case (Figure 3).

Participants who had opted for the removal of a species were asked where they wanted a species to be removed. Especially in case of *S. canadensis*, *B. davidii*, *T. fortunei* and *I. glandulifera*, a removal from nature reserves, natural areas and forests or farmland received more support than one from settlement areas, cities, and gardens (Table 3). In case of *A. artemisiifolia* and *H. mantegazzianum*, however, a removal from participants' own gardens was indicated most often, although participants were not sure that they would actually recognize these two species. Relatively few participants would announce IAPS to the authorities, especially not *B. davidii* and *T. fortunei*.

The overall determination to remove an IAPS from the environment (mean proportion of agreement to removal of species in the seven locations, see Table 3) was negatively correlated to its attributed desirability (mean score per species on the unwanted-wanted scale). With increasing desirability (and thus beauty) of an IAPS, the proportion of agreement to remove it from the environment decreased ($r = -0.75$, p

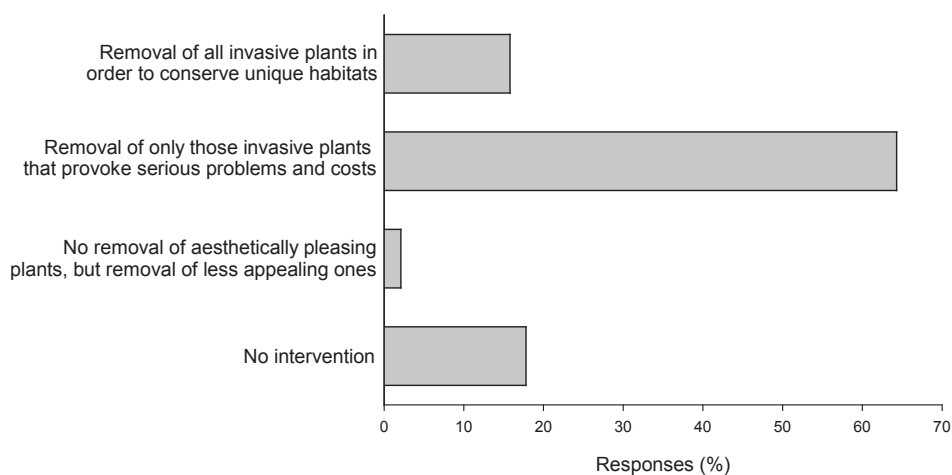


Figure 2. Preference for certain types of management in Zurich, Geneva and Lugano. Participants ($n = 720$) had to choose among four management types the one they considered most suitable.

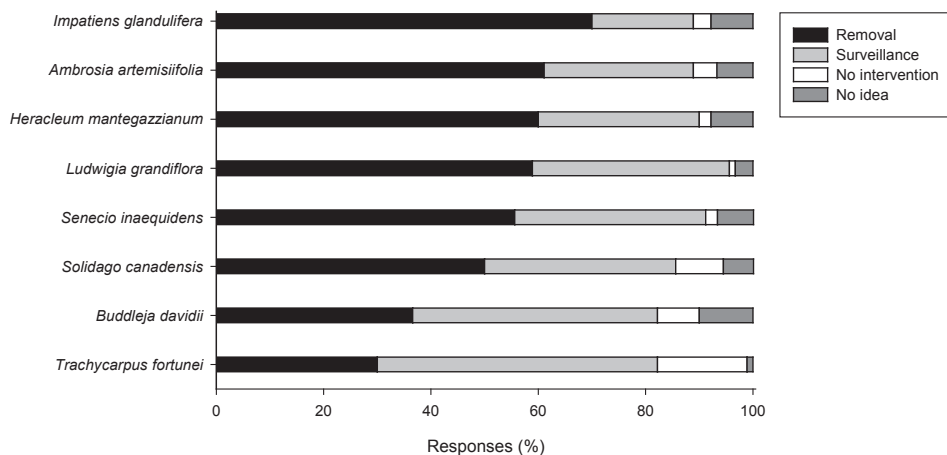


Figure 3. Proportion of people choosing various types of management for eight invasive alien plant species. Each species was introduced to 90 participants who then had to select the one type they considered most suitable for the species presented.

= 0.034). Analyzed separately, with increasing desirability of an IAPS, agreement to its removal from settlement areas ($r = -0.85$, $p = 0.034$), cities ($r = -0.81$, $p = 0.015$), gardens ($r = -0.76$, $p = 0.029$) and own gardens ($r = -0.71$, $p = 0.048$) decreased. Desirability and willingness to report an IAPS to the authorities were negatively correlated ($r = -0.76$, $p = 0.029$).

Table 3. Willingness of participants to remove IAPS in certain locations and to report these species to the authorities. Only participants who had previously opted for a removal of these species in Switzerland (numbers provided in brackets) were included.

Species	Removal of species (agreement in %)						Reporting of species (%)		
	Nature reserves	Natural areas	Forests or farmland	Settlement areas	Cities	Gardens	Own garden	Overall mean	
<i>Solidago canadensis</i> (n = 45)	75.6	66.7	60.0	24.4	20.0	24.4	64.4	47,9	46.7
<i>Buddleja davidii</i> (n = 33)	69.7	60.6	39.4	24.2	27.3	27.3	45.5	42,0	30.3
<i>Ambrosia artemisiifolia</i> (n = 55)	52.7	45.5	58.2	76.4	69.1	63.6	85.5	64,4	49.0
<i>Senecio inaequidens</i> (n = 50)	54.0	58.0	66.0	36.0	30.0	46.0	78.0	52,6	56.0
<i>Trachycarpus fortunei</i> (n = 27)	59.3	70.4	55.6	11.1	14.8	18.5	33.3	37,6	33.4
<i>Heracleum mantegazzianum</i> (n = 54)	66.7	63.0	46.3	53.7	37.0	55.6	87.0	58,5	48.1
<i>Impatiens glandulifera</i> (n = 63)	68.3	68.3	55.6	19.0	14.3	17.5	54.0	42,4	46.0
<i>Ludwigia grandiflora</i> (n = 53)	77.4	67.9	64.2	39.6	35.8	37.7	60.4	54,7	45.2

Discussion

Almost all plants were perceived as beautiful and wanted (first part of the questionnaire). Moreover, perceived beauty and desirability (high scores on the “beautiful” and “wanted” side of the rating scales) were positively correlated. It should be noted that participants’ characterizations were unaffected by information about the invasive status of these species, this information was provided only in the second part of the questionnaire. As most participants did not recognize the species presented anyway, the results reflect unbiased feelings and preferences. Encounters with IAPS might thus evoke pleasurable (aesthetic) feelings, at least in laypersons, and a desire to keep them where they are. Participants’ aesthetic feelings were hardly influenced by education or expertise, but were more prominent in women and increased with age. Women are generally more in favor than men of visually appealing plants (Strumse 1996, Lindemann-Matthies and Bose 2007), while older people might have developed a gardener’s view on plants. Experiences with plants through garden work or other leisure-time activities are likely to increase with age, which might find their expressions in stronger feelings for the beauty and uniqueness of plants - even when it comes to *Ambrosia artemisiifolia*. This might also explain the increase in “taxonomic” knowledge with age.

Plants with bright flower colors, large sizes, and fragrance were found to be highly attractive to humans (Mack 2001, Lindemann-Matthies 2005, Lindemann-Matthies and Bose 2007). A preference for showy flowers was also evident in the present study. *Ludwigia grandiflora*, the largeflower (sic) primrose-willow, with its single large yellow flower was considered most beautiful and wanted, while *Ambrosia artemisiifolia* with its inconspicuous appearance was considered most ugly and unwanted. On several Mediterranean islands, the widespread invasive Bermuda buttercup (*Oxalis pes-caprae*), an herbaceous annual plant, was also perceived as highly attractive for its yellow flowers and many people were surprised that it was not a native species (Bardsley and Edwards-Jones 2007).

With exception of the Chinese windmill palm (*Trachycarpus fortunei*), all species were perceived as rather ordinary, familiar and indigenous. Feelings of familiarity, ordinariness and nativeness were positively correlated. Such feelings paired with a lack in “taxonomic” knowledge might severely bias laypersons’ perception of IAPS. Perceived familiarity with an IAPS has been found to have a mitigating effect on risk perception, and perceptions of risk increased if a species was perceived to be non-native (Humair et al. 2014b). Inexperienced laypersons may also be victims of a confusing use of terms. Alien species are often called “exotic”, “foreign” or “introduced” (see McNeely 2001, p. 3, Colautti and MacIsaac 2004). In consequence, laypersons might expect IAPS to be exactly like that: exotic in appearance like the Chinese windmill palm. However, it should be noted that in Lugano, compared to the other two places, several plant species, and especially *T. fortunei*, were considered more ordinary, familiar, and less wanted (although still strongly on the “wanted” side of the scale). This reflects reality as *T. fortunei* is indeed common in the Ticino (FOEN 2006), and also indicates that despite their obvious lack of “taxonomic” knowledge, participants in Lugano had a feeling for IAPS in their environment.

Level of formal education did not influence participants' attitudes towards certain management types (but see Fischer and van der Wal 2006, García-Llorente et al. 2008), while knowledge of IAPS did. Participants who were able to identify IAPS from photos and might thus be able to recognize them outdoors, considered these species much more unwanted than those who were not. Correspondingly, support for a total removal of IAPS was much higher among "taxonomic experts", who were significantly more often individuals with a profession related to biology/ecology or landscape planning and members in an environmental organization. Due to their (professional) expertise and interest in environmental issues, they might know more about IAPS, be more sensitized about their negative impacts, and thus react accordingly in their choice of management types.

Participants agreed most with the proposal to eradicate only IAPS that cause serious problems and costs. A preference for the eradication of only economically damaging species instead of eradication of all IAS was also found in other studies (Bardsley and Edward-Jones 2007, Bremner and Park 2007, García-Llorente et al. 2008). This result was thus not unexpected and may reflect a greater concern of the public for the negative economic rather than ecological effects of IAPS. In case of *A. artemisiifolia* and *H. mantegazzianum*, agreement for species removal in almost all locations was high (note that this was the case after information about these species was presented). This supports the notion that it is not the threat to the environment, but the threat to the well-being of people that is of central concern in the invasive plant discussion (Fransson and Gärling 1999). However, when it came to attractive and already widely established ornamentals such as *B. davidii*, *S. canadensis* and *T. fortunei*, participants were much less willing to remove these species from settlement areas or gardens. Overall, willingness to remove an IAPS and to report it to the authorities decreased with increasing desirability (and thus beauty) of a species. This indicates that laypersons, even when they have information about IAPS and the problems they can cause, still think that the beauty of some invasive plants may in settlement areas more than outweigh the damage they may cause. In other words: beauties do not easily become beasts.

As seen in this study, invasive species management might get in conflict with a public unwilling to support eradication of appealing plants. *Ludwigia grandiflora* and *Trachycarpus fortunei* (both with strong invasive potential in Switzerland, e.g., Walther et al. 2007, Nehring and Kolthoff 2011) were perceived as beautiful and wanted. However, taxonomic knowledge of these (and other) species diminished the wish to have them around. In contrast to the above mentioned species, *Ambrosia artemisiifolia* was already perceived as rather ugly and unwanted. Nevertheless, there is also no reason to hope that populations of ragweed will be detected, reported to the authorities, or eradicated by laypersons as only few persons knew what the species actually looks like.

There are certain limitations to the present study. Younger people were over-represented as they were much more willing to participate than older ones. Moreover, higher qualified and environmentally engaged individuals were also overrepresented. Similar results were found in other comparable studies (e.g., Colton and Alpert 1998, Bremner and Park 2007). Participants are thus a convenience sample, and results can-

not be generalized to the public in Switzerland. In the questionnaire, participants' perceptions of the eight IAPS were examined with conceptually-related attributes using semantic differentials. The positive correlations between, e.g., aesthetic appeal and desirability of a species as well as between familiarity and nativeness could thus be due to overlaps of these concepts. However, these characteristics covered a spectrum of relevant attributes used in the discussion about IAS and in previous research (e.g., Fischer and van der Wal 2007). In the description of the eight invasive plant species (Suppl. material 1), negative effects of the invasive species were explained to the participants. This information may have influenced participants' choice of certain types of management, but was considered to be necessary background information for laypersons.

Conclusions

Public support is seen as crucial for the prevention and successful management of IAS in Switzerland (Wittenberg 2005). The present results highlight the importance of understanding the values and attitudes held by the general public with respect to IAS management support (see also Bremner and Park 2007). Participants' intuitive perception of the eight IAPS presented was one of "desirable native (or in case of *T. fortunei* exotic) beauties". Taking into account that only few participants had prior knowledge of IAPS due to their profession or personal interest, the results exemplify the need to help laypersons understand the threats (beautiful) IAPS can pose. Otherwise, they may question and rather not support eradication or control programmes, especially of species that are considered attractive.

The present results also highlight that public information should focus more on impact-related criteria of IAPS than on species' origin (see also van der Wal et al. 2015). With the exception of *T. fortunei*, all IAPS were perceived as native. Without actually knowing species (and participants were lacking "taxonomic" knowledge) a distinction by "origin" is hard to make as one cannot tell whether a species is native by just looking at it. It might thus be advisable to skip the native-alien distinction in public information and education and to concentrate instead on the actual risks a species might cause (Selge et al. 2011, Boonman-Berson et al. 2014, van der Wal et al. 2015). Perceived abundance and damage to nature and the economy, rather than non-nativeness, influenced attitudes towards species management (van der Wal et al. 2015).

In general, participants were rather supportive of a removal of IAPS. However, information about negative effects does not change beauties into beasts. The present results highlight that laypersons may ignore the damage attractive IAPS can cause, and thus not support their removal in settlement areas and gardens, especially when these species do not affect human health. Information on IAPS should thus not only focus on their general impact, but rather on reasons for the eradication and control in particular locations. First attempts in this direction have already been made in Switzerland. Cantonal authorities and NGOs have published a number of information sheets about IAPS for garden owners, and flyers about, e.g., *Solidago canadensis* have

been distributed to garden owners who live close to conservation areas (for an example see DGS 2015).

The present results highlight also the importance of taxonomic knowledge. Although taxonomic knowledge of laypersons may be irrelevant for the effective management of IAPS, it is still an important proxy for people's reaction to IAPS. Six out of the eight IAPS in the present study are included in the "Swiss Ordonnance on Organism Dissemination in the Environment 814.911" and may therefore not be introduced in the environment in Switzerland. However, a lack of knowledge of these species is likely to limit the efficiency of this legal obligation. If laypersons are unable to identify these IAPS, they are also unable to detect them and report them to the authorities. One way to counteract this lack of "taxonomic" knowledge could be to directly engage the public in eradication projects. Nationwide "root-out-days" are yearly events in Switzerland where the public receives information about the IAPS in focus (in 2015 *Solidago canadensis*, <http://www.arten-ohne-grenzen.ch/>). Personal experience and direct involvement in the root-out-event might foster the understanding of the public of the damage caused by IASP and the necessity of measures to control even beautiful invasive plants.

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Supplementary material 1

Short description of the eight invasive alien plant species

Authors: Petra Lindemann-Matthies

Data type: species description

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Supplementary material 2

English translation of the questionnaire

Authors: Petra Lindemann-Matthies

Data type: text translation

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Collapse of a reproducing population of non-native African jewelfish (*Hemichromis letourneuxi*) in a Florida lake

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Abstract

Established populations of non-natives may collapse without a clear causal mechanism. Hypothetically, fluctuations in habitat structural complexity may influence dynamics of invaders and the biotic resistance offered by predators. Herein I report observations of the collapse of a reproducing population of the non-native African jewelfish (*Hemichromis letourneuxi*) in a Florida lake concurrent with an unusual low-water period. I test the hypothesis that predation may have played a key role in the collapse using a combination of field surveys of habitat and fish abundance and predator-prey experiments. Habitat complexity was high before and after the low water period but virtually nonexistent during low water. The abundance of African jewelfish and native juvenile bluegill (*Lepomis macrochirus*) and eastern mosquitofish (*Gambusia holbrooki*) declined concurrently with decreasing complexity but the native species rebounded when lake levels increased. Large-bodied natives such as largemouth bass (*Micropterus salmoides*) and adult bluegill showed no pattern of fluctuation related to habitat complexity. African jewelfish survival was 1.6 times greater at high versus low complexity and over 7 times higher versus no complexity in the presence of largemouth bass. Conversely, eastern mosquitofish, a species that exerts strong effects on small-bodied fishes in structurally complex habitats had no effect on African jewelfish survival. Predation effects on susceptible non-natives should be considered as a potential control action. Population collapse is understudied but may provide insights into long-term dynamics of invaders and information useful for management of problematic species.

Keywords

Population collapse, habitat complexity, drought, biotic resistance, predation, invasive, Cichlidae

Introduction

Established populations of non-native species may decline or collapse without human intervention (Simberloff and Gibbons 2004). Some populations eventually rebound though others may remain at low levels or decline to extinction. Pathogens, small-population demographics, or stochastic events are frequent explanations for such fluctuations; however, the cause of the decline is unknown in many cases (Simberloff and Gibbons 2004). Boom-and-bust population cycles have been observed with non-native freshwater fishes in Florida, USA. Some declines are related to cold weather events impacting populations of non-natives of tropical origin (Snodgrass 1991, Trexler et al. 2000, Call et al. 2013). Nevertheless, reasons behind other examples are less clear (Loftus and Kushlan 1987, Fury and Morello 1994, Trexler et al. 2000, Shafland et al. 2008). Hypothetically a variety of abiotic and biotic factors might influence patterns of non-native fish abundance. Evaluating causes of observed population decline or collapse may provide insights into long-term dynamics of invaders and useful information for management of problematic species.

Predators, pathogens, or competitors can prevent establishment of non-natives, reduce their range or abundance, or eliminate local populations (Baltz and Moyle 1993, Byers 2002, Harvey et al. 2004). The influence of biotic resistance should vary spatially and temporally depending on changes in habitat features that mediate interactions among resident species and non-natives, potentially resulting in fluctuating abundance or population collapse of non-natives. Habitat structural complexity is an important factor influencing predator-prey dynamics and hence fish community structure (Savino and Stein 1982, MacRae and Jackson 2001). For example, large-bodied predatory fishes such as largemouth bass (*Micropterus salmoides* Lacepede) limit the use of open waters by small-bodied fishes (Werner and Hall 1988). Conversely, structurally complex habitat such as dense stands of aquatic macrophytes or other habitats that limit access of large-bodied species (e.g., shallows) reduce the effectiveness of predatory fishes and provide predation refuges for vulnerable species (Werner et al. 1983, Gotceitas and Colgan 1989, DeVries 1990). Differential vulnerability in structurally complex versus simple habitats may lead to the common observation of higher abundance of small-bodied fishes in complex habitats (Werner et al. 1978, Barrientos and Allen 2008). Decline in the density or area of structurally complex habitat generally results in reduced abundance of small-bodied fishes (Ware and Gasaway 1976, Bettoli et al. 1993, Colle and Shireman 1994, Sass et al. 2006) and should increase biotic resistance to susceptible invaders.

Little is known about the impact of biotic resistance on non-native freshwater fish abundance in Florida. Predation has been implicated anecdotally in the severe decline of only one reproducing non-native fish in the state, the silver dollar (*Metynnis* sp.), where elimination of dense stands of the submersed macrophyte *Hydrilla verticillata* was thought to have facilitated predation by largemouth bass (Shafland et al. 2008). Despite the lack of data on the influence of biotic resistance on field populations of non-native fishes in Florida, experimental evidence shows that predation and aggres-

sive competition from natives offer resistance against establishment of many small-bodied (<150 mm total length [TL]) non-natives (Hill et al. 2011, Thompson et al. 2012). Such resistance is hypothesized to result in an overall lack of successful small-bodied invaders despite strong introduction pathways (Thompson et al. 2012). Additional investigation into the general importance of biotic resistance as an influence on invasion success is warranted.

Herein I report observations of the collapse of a reproducing population of the non-native African jewelfish (*Hemichromis letourneuxi* Sauvage) in a lake in west-central Florida concurrent with an unusual low-water period. A proposed mechanism of the collapse is predation facilitated by the loss of structurally complex refuge habitat. A combination of field observations and experiments were used to test this hypothesis. My objectives were to (1) document changes in habitat complexity in the littoral zone, (2) estimate the relative abundance of African jewelfish and select native fishes using visual sampling to document trends associated with changing habitat, and (3) experimentally investigate the hypothesis that predation may play a key role in the population collapse.

Methods

Study species

The small-bodied (75–100 mm TL) African jewelfish (Cichlidae) was first introduced near Miami, Florida in the early 1960s (Rivas 1965) with reports from the Tampa Bay region in west-central Florida since 1974 (Courtenay et al. 1974, USGS 2015). The African jewelfish is of increasing interest in fish sampling and environmental DNA monitoring by management agencies (Kline et al. 2013, Diaz-Ferguson et al. 2014, Moyer et al. 2014). Its recent spread in south, southwest, and west-central Florida (Langston et al. 2010), including expansion into environmentally sensitive protected areas (Kline et al. 2013), is of management concern because of potential impacts on native invertebrates and small-bodied fishes by this aggressive predator (Rehage et al. 2014, Schofield et al. 2014).

Study site

Observations were made from 2003 to 2013 at Lake St. Clair, Hillsborough County, Florida, a 23.5-ha suburban borrow lake within the Bullfrog Creek basin of the Tampa Bay watershed (lake center near 27°46'23"N, 82°21'57"W). The water was relatively clear, with mean Secchi disk depths of 203 cm ($n = 3$, $SD = 3$) in 2012. Substrates in the littoral zone consisted mostly of sand. The littoral zone had emergent vegetation (mostly *Hydrocotyle* sp. [in 2003 only], *Panicum repens*, *Pontederia cordata*, and *Sagittaria lancifolia*), with submersed vegetation intermixed (mostly *Luziola fluitans*,

with small patches of *Potamogeton illinoensis*) and a few small areas with filamentous algae. Rising water levels occasionally inundated terrestrial vegetation. Most of the lake was deep (~4–6.5 m) outside the littoral zone with a steep drop-off and little habitat complexity. Soft sediments dominated the open water zone substrate. A water control structure in the north end of the lake maintains pool level and discharges via underground pipe to the Bullfrog Creek basin.

Water levels fluctuated more than 2 m during the study period. An unusual low-water period occurred in the lake for six to seven months in 2007 as a result of an extended drought during 2005–2007. Whole-lake visual surveys showed that the water level had dropped below the littoral zone such that almost no aquatic vegetation was submerged. An area of *Scirpus* sp. (~100 m long × 4 m wide) remained inundated in the northwest portion of the lake. Other structures such as docks were completely or nearly above the water level. Shorelines during low water were typically bare sand with a thin margin of shallow water rapidly dropping off into the deepest zone.

Field observations

Quantitative field observations were done in three 25-m littoral zone transects along the southeastern ($n = 60$ samples; 2003 to 2012) and southern shoreline (two transects; $n = 41$ samples each; 2005–2012). Sample numbers by year were 2003 = 2, 2004 = 2, 2005 = 16, 2006 = 24, 2007 = 27, 2008 = 14, 2009 = 14, 2010 = 4, 2011 = 8, 2012 = 15, and 2013 = 16. The two southernmost transects included the public access area with the lake's only boat ramp. The transect locations were fixed because of constraints regarding legal property access along the private lake shore. Habitat complexity, number of African jewelfish, abundance of other small fish, specifically juvenile bluegill (*Lepomis macrochirus* Rafinesque) and eastern mosquitofish (*Gambusia holbrooki* Girard), and abundance of larger fish, specifically adult bluegill (>100 mm TL) and largemouth bass were noted during each sample.

The complexity of aquatic macrophytes or inundated terrestrial vegetation in each transect was estimated using a ranked, categorical scale. Complexity was assigned a score of 0 if absent, 1 if sparse cover (<33% areal coverage), 2 if moderate cover (33–66% areal coverage), and 3 if dense cover (>66% areal coverage). These data estimate trends in refuge availability during the study.

Visual surveys for fish were made during daylight hours with the aid of polarized sunglasses and high water clarity. These surveys were done by slowly walking along the shoreline during daylight hours. Fish occasionally responded by moving away into vegetation or deeper water, but generally did not overtly react to the observer. Surveys were not conducted during the brief, cold winter periods (usually December through February) or during windy weather.

African jewelfish were counted. Though small-bodied, this species is active and brightly colored which facilitated observations. In practice, counting large numbers of small-bodied native fishes was difficult and inaccurate. Therefore, estimates of juve-

nile bluegill (<100 mm TL) and eastern mosquitofish abundance were made using a ranked, categorical scale. These species were scored according to the number observed, 0 if none were observed, 1 for 1–19, 2 for 20–99, and 3 for ≥ 100 . Estimates of largemouth bass and adult bluegill (>100 mm TL) were made using a ranked, categorical scale where 0 was assigned if the species was absent, 1 if 1–5 individuals were observed, and 2 if more than 5 were observed. Category ranges were chosen based on preliminary observations in the case of small fishes and frequencies observed during the study for larger species. Largemouth bass was the main predatory species in the lake. Bluegill habitat use frequently differs with body size, with juveniles closely associated with structurally complex habitat in the presence of predatory fishes and less vulnerable adults capable of using more open water habitats (Mittelbach 1981, Werner and Hall 1988, Paukert and Willis 2002). The small-bodied eastern mosquitofish is strongly associated with structurally complex habitat, especially in the presence of predators (Chick and McIvor 1997), and seldom occurs in open water habitats (Werner et al. 1978). I expected that juvenile bluegill and eastern mosquitofish would follow a similar pattern to African jewelfish and decline considerably due to a reduction in refuge habitat associated with the drought. Eastern mosquitofish also is a known aggressive competitor and predator of small-bodied fishes and might influence African jewelfish survival (Meffe 1985, Thompson et al. 2012; see also *Predation experiments*, below).

Whole-lake presence/absence surveys were done for African jewelfish to determine the spatial distribution of the species during the study. These surveys included the entire littoral zone (~3,370 m of shoreline) and were made from a slow-moving kayak. Eight surveys were completed prior to the lowest water levels of 2007 (5 surveys in 2005, 2 in 2006, and 1 in early 2007). Seven surveys were done during the low water in 2007. The 25 post-drought surveys included 5 in 2008, 4 in 2009, 2 in 2010, 4 in 2011, 6 in 2012, and 4 in 2013. Two whole-lakeshore boat electrofishing surveys (Smith-Root GPP 9.0; Smith-Root, Vancouver, WA) were done during daylight hours in 2013 (July and August) to survey for African jewelfish and to attempt to collect additional fish species to those observed during visual sampling if present.

Predation experiments

Two tank experiments were done to test the hypothesis that predation may have played a key role in the collapse of African jewelfish abundance in Lake St. Clair. The first experiment tested for differences in survival of African jewelfish under predation threat from largemouth bass across a range of habitat complexity (largemouth bass challenge). The other experiment tested the effects of eastern mosquitofish on African jewelfish (eastern mosquitofish challenge). Largemouth bass and eastern mosquitofish are common native species in Florida, are thought to resist invasion by non-native fishes (Hill et al. 2011, Thompson et al. 2012), and present non-native fishes with differing challenges (Hill et al. 2011). Largemouth bass is a large-bodied (up to > 500 mm TL) gape-limited predator that often restricts the use of open waters by small-bodied fishes

(Werner et al. 1983, Hambright et al. 1991, Hill et al. 2006). Eastern mosquitofish is small-bodied (~60 mm TL) predator and aggressive competitor (Meffe 1985, Hill et al. 2011) that influences use of structured habitats by small fishes (Thompson et al. 2012). Fish were collected from research ponds at the UF/IFAS Tropical Aquaculture Laboratory, Ruskin, Florida. Fish were used only once during the experiments.

The largemouth bass challenge had three treatments that varied by the strength of the predation refuge provided by habitat—(1) strong which simulated conditions prior to the low-water period when thick stands of submersed and emergent aquatic macrophytes were present, (2) weak which simulated a transitional period when most complex habitat was stranded but some vegetation remained underwater, and (3) none which simulated low-water conditions where virtually no complex habitat remained inundated. The strong refuge treatment had artificial vegetation (645 stems/m²) consisting of black plastic strips tied to a plastic lighting grate that covered 50% of the tank bottom (Savino and Stein 1982) and a vertical barrier consisting of netting (3.8-cm mesh) fitted 8 cm outside the artificial vegetation. Largemouth bass were excluded from the vegetation by the barrier but African jewelfish could freely swim through the barrier into open water. The barrier functioned to restrict the movement of largemouth bass and their access to prey, mimicking thick vegetation (Engel 1987). The weak refuge treatment had the artificial vegetation but lacked the barrier. The remaining treatment had no habitat refuge for the African jewelfish.

The experiment was done in concrete tanks (221 cm × 79 cm × 58 cm; water depth 30 cm) on a re-circulating system in a greenhouse at the UF/IFAS Tropical Aquaculture Laboratory, Ruskin, Florida. Water parameters were: dissolved oxygen = > 8 ppm, temperature = 24–30 °C, pH = 7.9–8.1, total ammonia nitrogen < 1.0 ppm, nitrite < 0.02 ppm, total alkalinity = 188 ppm, and total hardness = 342 ppm. Four replicates of each treatment were randomly assigned to tanks in the system. Ten African jewelfish (mean TL ± SD = 64 ± 12 mm) were stocked into each tank and a single largemouth bass (205 ± 21 mm TL) was stocked 3 days later. The African jewelfish were morphologically vulnerable to the largemouth bass based on prey body depth and predator gape size (Hill et al. 2006). African jewelfish were fed a commercial feed at a rate of 5% body weight per day to simulate food resources in natural water bodies (Thompson et al. 2012). Experiments lasted 4 days after which all African jewelfish were removed and counted. Additional tanks (n = 4 without artificial vegetation and n = 4 with artificial vegetation; duration of 4 days each) stocked only with African jewelfish were run prior to and following the experiment to determine if there was a loss rate of the prey in the absence of predators; no African jewelfish were lost or died during these trials. Differences in survival were tested using analysis of variance (ANOVA) on arcsine-square root transformed data using SAS v9.3 (SAS Institute, Cary, NC, USA). Tukey's HSD multiple comparison procedure was used to determine which treatments differed following a statistically significant ANOVA.

The eastern mosquitofish challenge was done in oval polyethylene tanks with an area of about 1.2 m² at the base and 1.4 m² at the water surface (water depth 25 cm). Tanks were on a flow-through system receiving aerated well water. Water parameters

were: dissolved oxygen = 7–8 ppm, temperature = 26–28 °C, pH = 8.0, unionized ammonia nitrogen undetectable, nitrite < 0.05 ppm, total alkalinity = 170 ppm, and total hardness = 459 ppm. Artificial vegetation (216 stems/m²) was centrally located to cover 49% of the tank bottom (Savino and Stein 1982; Thompson et al. 2012). Four replicates of two treatments were done—(1) 50 eastern mosquitofish (30 ± 6 mm TL) stocked on day 1 or (2) mosquitofish-free controls. Five African jewelfish (57 ± 6 mm TL) were stocked into each tank on day 1. These densities were within the range of densities observed in the lake prior to the low water period (see also Thompson et al. 2012). Fish were fed a commercial feed at a rate of 5% body weight per day to simulate food resources in natural water bodies (Thompson et al. 2012). Fish were removed and counted after 10 days. All surviving African jewelfish were scored for caudal fin damage, a common sign of eastern mosquitofish attack (Meffe 1985, Hill et al. 2011).

Results

Field observations

Habitat complexity within the littoral zone was high before and after the low water period and was low during the drought (Fig. 1). Decline in complexity was evident near the end of 2006 with the main low water period of 2007 having values of 0 for 60% of samples. Complexity increased during 2008 (Fig. 1). Some variation occurred as higher lake levels returned due to flooding of terrestrial vegetation and re-growth of aquatic macrophytes.

African jewelfish were observed in quantitative samples each year from 2003 until the low-water period of 2007 (Fig. 1a). The mean (±SD) number observed for 47 samples prior to spring 2007 was 17.7 (±7.9). Only 3 individuals were observed in 3 samples during the low water period. Following the drought, no African jewelfish was observed in any transect until 2012. An average of 0.7 (±1.0) African jewelfish per transect was noted in 15 samples in 2012 and 2.3 (±1.6) per transect in 16 samples in 2013. The small number of observed African jewelfish in 2003 was related to the presence of dense surface mats of *Hydrocotyle*; observations in other areas of the lake suggested that they were common.

Abundance of small-bodied native fishes declined substantially during the low water period but rebounded quickly following increases in water levels and habitat complexity (Fig. 1b). Eastern mosquitofish was generally abundant whenever vegetation was present but also extensively used shallow waters along the lake edge. The abundance of larger-bodied species such as largemouth bass and adult bluegill had no apparent pattern of fluctuation related to habitat complexity (Fig. 1c).

Whole lake presence/absence surveys revealed African jewelfish throughout the littoral zone prior to the drought, but none were observed post-drought until 2012. Presence of small numbers of African jewelfish was noted in the south and southeast portions of the lake in five of six surveys in 2012 and in the south, southeast, and

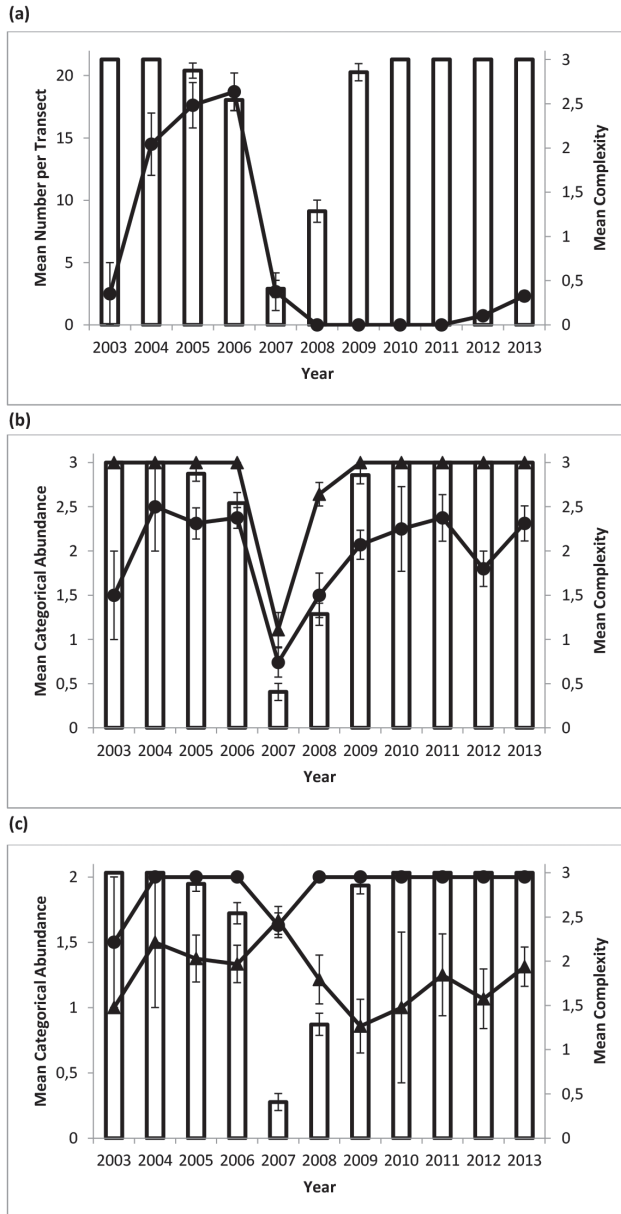


Figure 1. Trends in habitat complexity and fish abundance in Lake St. Clair. Abundance (\pm SE) of **a** African jewelfish (circles), **b** juvenile bluegill (circles) and eastern mosquitofish (triangles), and **c** adult bluegill (circles) and largemouth bass (triangles) in visual transects across years in Lake St. Clair, Florida. Scales for fish abundance vary by panel. Mean habitat complexity (\pm SE; bars) across years is on the secondary y-axis (0 = absent, 1 = <33% coverage, 2 = 33–66% coverage, and 3 = >66% coverage). African jewelfish abundance is number per transect. Abundance for juvenile bluegill and eastern mosquitofish is on a categorical scale (0 = absent, 1 = 1–19, 2 = 20–99, and 3 = 100 or more observed per transect). Abundance for adult bluegill and largemouth bass is on a categorical scale (0 = absent, 1 = 1–5, and 2 = 6 or more observed per transect)

southwest portions in all surveys in 2013. No African jewelfish were noted in other sections of the lake post-drought. Native bluegill, eastern mosquitofish, and largemouth bass were noted in all sections of the lake in all surveys.

Native fishes observed during this study, in relative order of abundance, were eastern mosquitofish, bluegill, largemouth bass, channel catfish (*Ictalurus punctatus* Rafinesque), golden shiner (*Notemigonus crysoleucas* Mitchell), warmouth (*Lepomis gulosus* Cuvier), black crappie (*Pomoxis nigromaculatus* Lesueur), and golden topminnow (*Fundulus chrysotus* Gunther). Non-native fishes besides African jewelfish were not observed during visual sampling but walking catfish (*Clarias batrachus* Linnaeus; $n = 2$) and Asian swamp eel (*Monopterus albus* Zuiew; $n = 1$) were collected by boat electrofishing in 2013. Of these species, channel catfish likely exerted considerable predation pressures on small fishes during the low water period (Hill personal observations) but was uncommon in surveys. Channel catfish individuals were frequently observed near docks and along shorelines when lake residents provided feed and were common in angler catches (Hill personal observations).

Predation experiments

African jewelfish survival varied with habitat in the largemouth bass challenge and positively correlated with habitat complexity ($F_{2,11} = 27.93$, $P = 0.0001$; Fig. 2). Mean survival in the strong habitat refuge treatment was 1.6 times higher than in the weak refuge treatment and over 7 times higher than in the treatment lacking a habitat refuge from predation. African jewelfish survival was 100% in all tanks in the eastern mosquitofish challenge. No caudal fin damage was observed for any African jewelfish.

Discussion

The collapse of African jewelfish abundance in Lake St. Clair was dramatic and rapid. African jewelfish were common in visual surveys for 4 years but were not observed for nearly 5 years following a major low-water event where virtually all structurally complex habitat was stranded above the water level. Abundance of native small-bodied fishes showed a similar though less dramatic pattern of decline as habitat complexity decreased. However, these species rapidly rebounded following a return of complex habitat. Larger-bodied natives showed little pattern relative to changing habitat complexity. The main predatory species in open waters, largemouth bass, was common throughout the study period. Predation experiments showed that the vulnerability of African jewelfish to a large-bodied, open-water predator increased with decreasing habitat complexity. Conversely, African jewelfish survival was not affected by a small-bodied native species within complex habitats. These results support the hypothesis that habitat-related changes in predation dynamics contributed to a marked decline in African jewelfish abundance in Lake St. Clair.

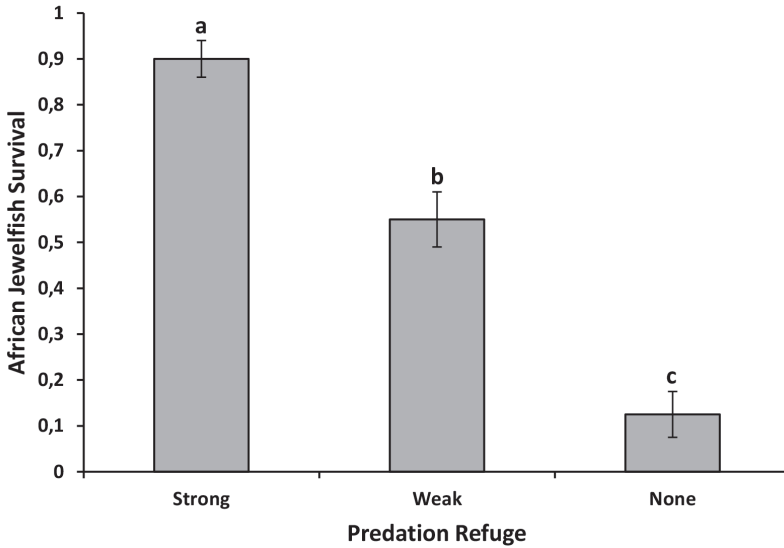


Figure 2. African jewelfish survival across habitat types in an experiment with largemouth bass as a predator. Mean survival (\pm SE) across strong, weak, or no predation refuge. Different letters denote statistically different treatment means ($P < 0.05$).

Prey persist in the environment because some portion of the population is invulnerable to predation at any one time (Matter and Mannan 2005). Morphological vulnerability of African jewelfish (Hill et al. 2006) suggests that this species must exploit behavioral or habitat refuges to escape predation. Structurally complex habitat limits access of large-bodied predators to smaller prey (Engle 1987), reduces the efficiency of predators (Savino and Stein 1982), and decreases the proportion of fish in predator's diets (Bettolli et al. 1992). African jewelfish is highly associated with structurally-complex habitats such as aquatic macrophytes (Shafland 1996, Hill personal observations) and has declined dramatically in some south Florida canals concurrent with the near elimination of aquatic vegetation by water managers (Shafland et al. 2008, Hill unpublished data). African jewelfish in experimental tanks largely remained within the artificial vegetation and behind the barrier when these habitat features were available, an effective strategy to reduce vulnerability and increase survival. African jewelfish without effective cover were highly vulnerable to predation, suggesting the need for refuge habitat for persistence in the presence of open water predators. Normal water levels in Lake St. Clair provide considerable refuge habitat. Low water levels removed virtually all structurally complex habitat and exposed African jewelfish to open water predators.

Structurally complex habitat may not be sufficient refuge from predators for some fish species (MacRae and Jackson 2001). Research suggests that eastern mosquitofish harass and consume small-bodied non-native fishes and reduce refuge quality of shallows and structurally complex habitat via agonistic interactions (Hill et al. 2011,

Thompson et al. 2012). Eastern mosquitofish had no effect on adult African jewelfish survival in experimental tanks and no observations suggest that eastern mosquitofish attack or displace African jewelfish from refuge habitat. These results imply little influence of eastern mosquitofish on biotic resistance against this non-native species, perhaps contributing to the nearly unique success among small-bodied fishes of African jewelfish as a widespread, established invader in Florida (see Thompson et al. 2012). Conversely, eastern mosquitofish and the highly similar western mosquitofish (*Gambusia affinis* Baird & Girard) frequently reduce the survival of larval or juvenile fishes by predation (Meffe 1985, Taylor et al. 2001, Thompson et al. 2012); eastern mosquitofish effects on early life stages of African jewelfish require additional investigation.

Unlike African jewelfish, small native fishes rapidly rebounded from their reduced abundance. Eastern mosquitofish were able to refuge from larger fishes during the low water period by exploiting the shallow lake margins (see DeVries 1990, Paterson and Whitfield 2000). This live-bearing fish has high reproductive output with sexual maturity at 1–2 months, gestation periods of 2–3 weeks, and brood sizes averaging up to 100 offspring (Pyke 2005). Reproduction is nearly year-round in Florida (Hill personal observations). Juvenile bluegills never disappeared entirely and were replenished by multiple yearly breeding cycles accomplished by relatively large, and therefore less vulnerable, adults which are capable of using open water habitats (Paukert and Willis 2002). Despite being robust and generally successful as an invader (Langston et al. 2010), the small and brightly colored adult African jewelfish were vulnerable to predators with the loss of refuge habitat and despite frequent spawning bouts and parental care their life history strategy apparently proved inadequate to maintain their abundance.

The results of the present study do not exclude other hypotheses that might partly explain the observed population collapse. Nevertheless, other factors potentially reducing African jewelfish abundance were not evident. Population size was fairly large and the species was distributed throughout the entire littoral zone where vegetation was present, suggesting that Allee effects and stochasticity of small population demographics were not important (Dennis 2002). Cold winter temperatures may eliminate this species from small, shallow aquaculture ponds in this region, though populations in nearby lakes of smaller surface area and lesser depth than Lake St. Clair persisted through a major cold event of the winter of 2009–2010 (Hill personal observations; see also Schofield et al. 2010). Moreover, African jewelfish were present in surveys done in early 2007 (late winter) prior to the extreme low-water conditions. Besides low water levels, no unusual water conditions were observed nor were fish kills of African jewelfish or any other species. African jewelfish is hardy and adaptable to a wide range of environmental conditions (Schofield et al. 2007, Langston et al. 2010) and occurs commonly in waters receiving road, residential, and agricultural runoff (Hill personal observations). Some unobserved disease might have affected the population, but, as recommended by Simberloff and Gibbons (2004), an unidentified pathogen is only an “explanation of last resort.”

Recovery of collapsed populations of non-natives is of as much interest as the collapse itself. Unfortunately, the origin of the African jewelfish observed in 2012

is unknown. A slow increase in abundance and spatial range of African jewelfish is evident since this time (present study, Hill personal observations). Re-colonization of Lake St. Clair from regional water bodies is unlikely because there are no direct water connections except for the overflow structure and pipe discharging into a small tributary stream. Access via this route is highly unlikely due to intermittent flow in both the discharge pipe and receiving stream, the large gap between lake levels and the overflow structure during the time period (usually 60–90 cm or more), and the large elevation difference between the structure and the outlet. Release by humans is a probable cause of re-establishment in the lake, especially at the public access area (e.g., Copp et al. 2005). Fishing for largemouth bass is common on the lake and live African jewelfish collected from other regional waters have been used as bait (illegally) in Lake St. Clair during the period between low water and their subsequent detection in surveys (2007–2012; Hill personal observations). It is also possible that some African jewelfish survived the low-water period and persisted at such low abundance that they were missed in surveys until 2012. Periodic monitoring would determine if African jewelfish returns to its former abundance or remains a minor component of the lake's fish fauna. Similarly, surveys of regional waters with historic records would yield insights into the commonality of collapse in African jewelfish populations.

Management options may be few once non-native fishes establish (Kolar et al. 2010). For situations where non-natives are confined to small, closed water bodies, use of rotenone or other chemical treatments may be effective (e.g., Hill and Cichra 2005). Removals using active or passive capture techniques are seldom effective at eradication (Kolar et al. 2010, but see Hill and Sowards 2015). Predatory fishes are stocked in some situations to control non-native fishes (e.g., Shafland 1995), though eradication is not typical. Partial de-watering to strand structurally-complex refuge habitat or removal of aquatic vegetation could increase the effectiveness of resident or stocked predatory fishes in controlling or eliminating susceptible non-natives. For example, habitat simplification has been shown experimentally to increase the predatory effects of largemouth bass and other common predators (Savino and Stein 1982, Alexander et al. 2015). Elimination of aquatic vegetation may additionally remove preferred habitat and thus reduce abundance of vegetation-dependent species (e.g., Schofield and Nico 2007). Vegetation removal is a typical preliminary step to chemical application (Finlayson et al. 2010) and might be a sufficient action if the risk of the spread of the species is not unacceptable relative to the cost, collateral kill, and public relations challenge that may accompany fish toxicant application (Britton et al. 2011). The potential for effective control or eradication by predators also should be considered for water bodies where fish toxicant application is impractical. Use of manipulation of habitat complexity as a control measure for non-native fishes, just as with other control methods, would require a plan to monitor the water body for non-native persistence, taking into account the characteristics of the water body and the non-native species, and to reduce or eliminate re-introduction of the non-native from local dispersal or human activities.

Simberloff and Gibbons (2004) found little directed research investigating collapse of non-native species populations and concluded that this phenomenon is of little importance to invasion biology. However, since 2004 additional examples of population collapse have been observed in non-native taxa as diverse as ants (Cooling et al. 2012), crayfish (Sandstrom et al. 2014), and mammals (Sheehy and Lawton 2014). Few additional fish examples have been published but spontaneous collapse for unknown reasons has been noted for the widespread, invasive topmouth gudgeon (*Pseudorasbora parva* Temminck and Schlegel) in Europe (Copp et al. 2007). Predation by native species is seldom thought to be the cause of these newer examples (but see Sheehy and Lawton 2014). Boom-and-bust cycles and spontaneous population collapse for non-native fishes in Florida are mentioned in the literature but accounts are largely anecdotal (but see Harrison et al. 2013 and Boucek and Rehage 2014 for cold effects). Although cichlids are among the most numerous and successful established non-native fishes in Florida (Shafland et al. 2008), population abundance and range of several species have fluctuated considerably and some species have disappeared from the state, generally with no known cause (Shafland 1996, Shafland et al. 2008, USGS 2015). One of the most prevalent mechanisms to explain boom-and-bust cycles of native fishes is the effect of the interaction of environmental factors and life history traits on annual recruitment (e.g., Lobon-Cervia 2009, Matthews and Marsh-Matthews 2011). This is likely a rich area of future research investigating population fluctuations of Florida non-natives (e.g., the influence of major cold events; Schofield et al. 2010, Harrison et al. 2013, Boucek and Rehage 2014). As suggested by the present study, biotic resistance through predation likewise may prove an important mechanism. If population collapse is indeed as common, yet understudied, as suggested by a casual review of the literature for Florida, much additional research is warranted. A parallel can be drawn between population collapse and failed invasions, a more widely acknowledged yet similarly understudied phenomenon in the literature (Zenni and Nunez 2013). Greater attention to these occurrences can give insight into processes linked to invasion success, thus providing a more complete picture of the importance of population collapse and its potential use in risk analysis and non-native species management.

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Invasive *Acacia mearnsii* De Wilde in Kunming, Yunnan Province, China: a new biogeographic distribution that Threatens Airport Safety

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Abstract

Acacia mearnsii De Wilde is on the top 100 of the world's most invasive alien species and has successfully invaded many areas around the world. However, its distribution and expansion is seldom reported in China. This study for the first time conducted a survey on the new distribution of *A. mearnsii* at the Kunming Changshui Airport (Yunnan Province, China), through monitoring on population characteristics (number, density, height and ground diameter) and spatial distribution (spread distance). Our survey results show that *A. mearnsii* has spread rapidly across the airport. This study discusses three factors of environmental factors, human disturbance and weed characteristics behind this successful invasion. The species invasion has a strong potential to change the local vegetation structure, enhances the probability of bird strikes at the airport, and is vulnerable to invade new biogeographic regions if it is not controlled. Currently, eradication combined with mechanical control is considered to be the best option for control. Our study helps improve awareness about the potential risk of *A. mearnsii* invasion in other airports around China and the world.

Keywords

Acacia mearnsii, plant invasion, new distribution, birdstrike prevention, management strategy

Introduction

Invasive plant species are increasingly threatening biodiversity and ecosystem functioning around the world. They are often referred to as naturalized alien (exotic or non-native) plants that establish and maintain their population by self-reproduction and self-diffusion at considerable distances from the parent plants, and have become harmful species, to some extent, or have had a negative influence on humans (Lamarque et al. 2011; Pyšek et al. 2004; Richardson et al. 2000). These species are characterized by easy establishment, fast growth and high propagule pressure (Dodet and Collet 2012).

Acacia mearnsii De Wilde (black wattle) is native to Australia, and is listed as being among “100 of the world’s worst invasive alien species” by the World Conservation Union (Lowe et al. 2000; Luque et al. 2014). The species has already been disseminated globally for more than 150 years owing to its multiple uses (e.g., leather, resins, fuel, paper, medical applications, etc.) (Castro-Dièz et al. 2011; Richardson et al. 2011). The Global Invasive Species Database (GISD) reported the species has become an invasive problem in France, India, Israel, Italy, New Zealand, Portugal, Reunion, South Africa, Spain, Uganda and United States. Its invasiveness threatens the native environment by competing with indigenous vegetation, replacing grass populations, and reducing native biodiversity, which causes large economic losses to these regions (<http://www.issg.org/database>).

In the 1950s, *A. mearnsii* was first introduced into China for afforestation and commercial forestry (Fu 2005; Griffin et al. 2011). However, after that, the expansion of this species was seldom reported in China. In recent years, a few studies reported that 10 provinces in China have already recorded *A. mearnsii* (including Yunnan Province) (Cai et al. 2009; Feng et al. 2010; Fu 2005; Ke et al. 2010; Li et al. 2007). However, there is not sufficient evidence to show *A. mearnsii* has turned into an invasive species in these provinces.

At the Kunming Changshui international airport (here after referred to as Changshui airport), Yunnan, China, we discovered that *A. mearnsii* populations have appeared by self-renewal in recent years. The trees attract many birds to rest on them, which increases the opportunities for bird strike at the airport (Gallagher et al. 2011; Gibson et al. 2011; Li 2014; Li et al. 2011; Xu et al. 2011). We undertook an *A. mearnsii* invasion survey, which is the first time in China that a detailed monitoring investigation of this species has been performed. The aims of this study were thus to determine: (1) could *A. mearnsii* become an invasive species in China, especially in areas with similar climates (such as Kunming); (2) what are the potential risks of *A. mearnsii* invasion at the airport where bird strike prevention measures are needed to ensure flight safety; (3) which effective management options can be adopted for the treatment of *A. mearnsii* invasion?

Materials and methods

Acacia mearnsii

Acacia mearnsii belongs to the Mimosaceae (affiliated to the Leguminosae), and is a heliophile, evergreen, nitrogen fixing, fast growing tree species. A detailed description is provided by De Wit et al. (2001) and Sherry (1971). The species grows in disturbed, mesic habitats and thrives in a range of climates, including warm temperate dry climates and moist tropical climates (<http://www.issg.org/database>). Duke (1983) reported that it can tolerate an annual precipitation of between 660–2280 mm, an annual mean temperature of 14.7–27.8 °C, and a pH of 5.0–7.2. The GISD says that it does not grow well on very dry or poor soils, however, Crous et al. (2012) reported that it is highly drought-tolerant, able to withstand low minimum water potentials, and can utilize a large proportion of soil water.

Study area

Changshui airport is located in the north-eastern part of Kunming (the capital city of Yunnan Province) (Fig. 1a, b). It is the fourth largest airport in China. It handles 20 million passengers each year and has 275 routes to 134 cities, such as Beijing,

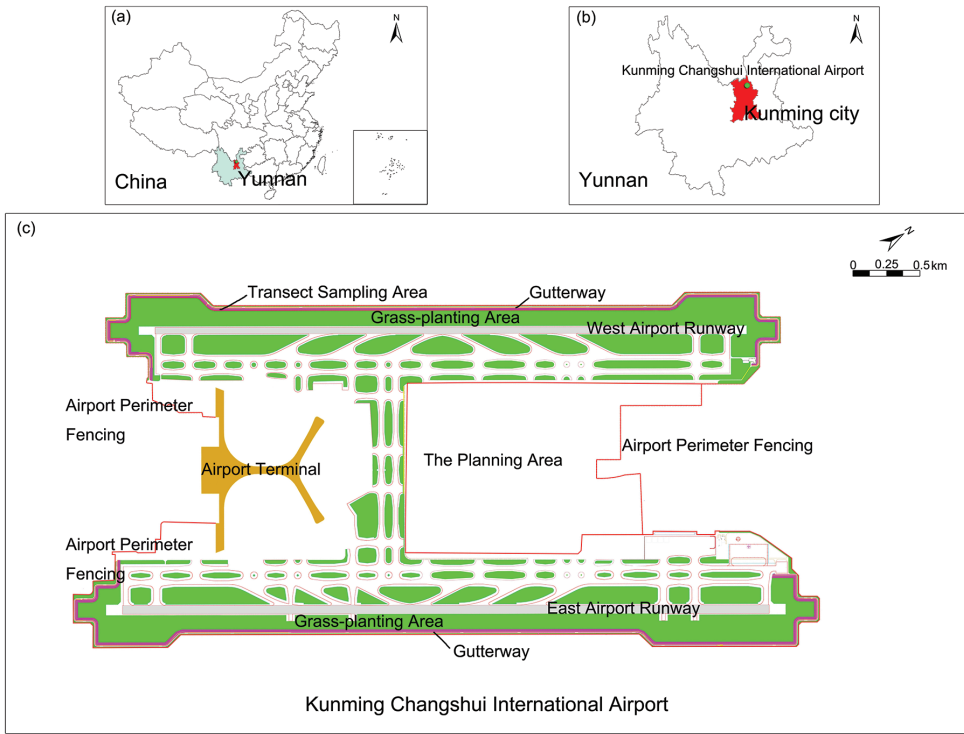


Figure 1. Location map (a, b) and the main functional units of the Changshui airport (c).

Shanghai, Singapore and Paris. The total area of Changshui airport is 22.97 km², its functional units are composed of an airport terminal, two runways (East and West), grass-planting area and the planning area (area for future development) (Fig. 1c). The grass-planting area of the airport was established in 2012 where grassy herbaceous plants (mainly graminoid) are cultivated. The airport is surrounded by farmland, secondary forest and villages. It is located in a subtropical semi-humid monsoon climate zone, with an average temperature of 15 °C and an average precipitation of 1035 mm. The climate features are quite similar to the original habitats of *A. mearnsii* in Australia (Duke 1983; Fu 2005; Gao and Ren 1989; <http://www.issg.org/database>).

Survey method

The pilot survey in early 2013 showed that *A. mearnsii* seedlings mostly had appeared in the grass-planting area near two gutterways and the planning area within the airport. Considering flight safety, the airport authority approved the use of the grass area around the west gutterway as our sample area. In this context, we conducted 12 surveys, twice a month, in the sample area from June 2013 to November 2013. Two line transects along the gutterway (6.2 km long, see Fig. 1c) in west grass-planting area were established. Quadrat plots (5 × 5 m) were used as the secondary unit for surveys, with a 100 m interval between each plot. The number, height and ground diameter of *A. mearnsii* were recorded in each plot. The dispersal rate was also estimated by measuring the diffusion distance of new seedlings of *A. mearnsii* along two transects during the survey period.

Results

Invasion of *A. mearnsii*

The *A. mearnsii* populations first appeared in the south side of the west gutterway in May 2013 and spread slowly. In the following months when rainfall became abundant (i.e., July and August), the spread of *A. mearnsii* increased rapidly and most of them formed into relatively dense populations. They then also appeared in the north side of the west gutterway in August. Fig. 2 shows the extent of *A. mearnsii* invasion within the grass-planting area near the west gutterway. In the south side of gutterway, there were 400 m of *A. mearnsii* populations through the initial measurement in June. The diffusion rate was fastest in August, and the distance increased up to 1100 m with 400 m of these new seedlings. The diffusion continued to the west of the gutterway with 200, 300 and 200 m, respectively, from September to November. During the whole study period, the black wattle seedlings had totally spread to 1800 m with an average rate of 300 m per month. In the north side of gutterway, the new population distribution of *A. mearnsii* with 200 m was measured in August, and spread with 150 m to both ends of the gutterway in September. The last increase with 100 m in east side of the gutterway was found in October.

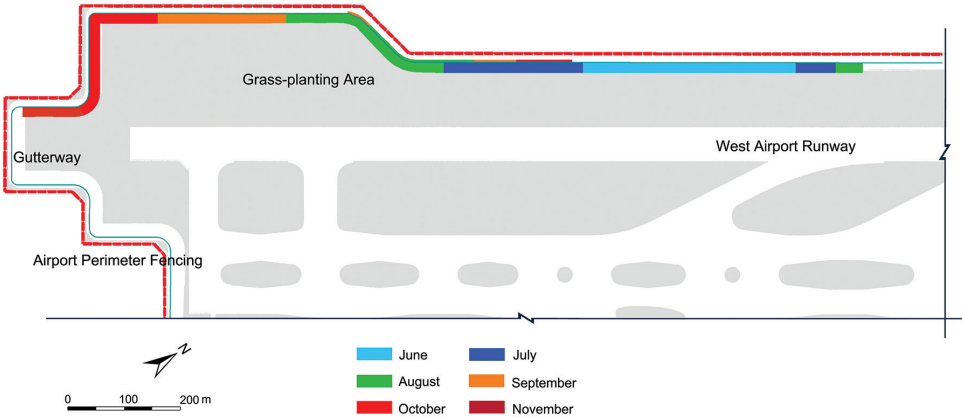


Figure 2. The distribution of *A. mearnsii* in the grass-planting area near the west gutterway at Changshui airport (June–November 2013).

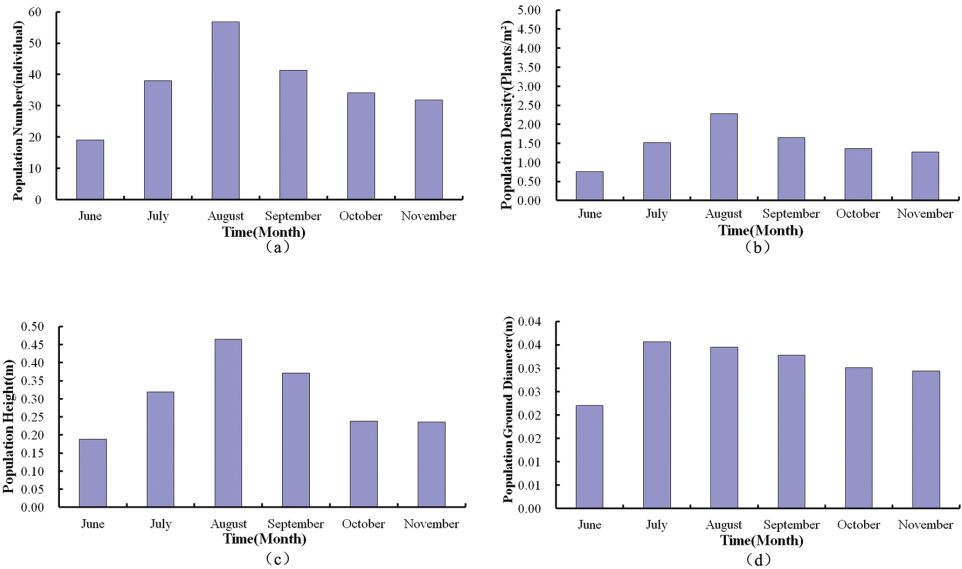


Figure 3. The population characteristics of *A. mearnsii* on mean population number (a), mean population density (b), mean population height (c) and mean population ground diameter (d) for plots in the west transect sampling area at Changshui airport.

Population characteristics of *A. mearnsii*

Plot-average data are shown in Fig. 3. Fig. 3(a) shows the average number of *A. mearnsii* species each month during the survey period. The population number reached a maximum in August, and the average number of trees per plot was 37 and the maximum number was 268. Fig. 3(b) shows the average sample density. Similarly, In

August it reached the highest density peak. The average density of *A. mearnsii* was 1–3 plants/m². In the denser areas, it was up to 10 plants/m², and the area had begun to resemble a wood. Fig. 3(c) shows the average sample heights were 19–47 cm. Most of the trees in the survey area were over 1 m high and the maximum height of *A. mearnsii* was up to 1.35 m in August. Fig. 3(d) reflects the mean diameter (ground diameter) of *A. mearnsii*, which ranges from 2.2 cm to 3.56 cm, and some seedlings increased their diameter more than 10 cm.

Discussion

Local invasion rate

Our investigation clearly demonstrates a successful invasion of *A. mearnsii* in the grass-planting area near the west gutterway at Changshui airport. The invasions have also appeared in other sites of the airport, such as in the grass-planting area near east gutterway and in the planning area of the airport. The data also show that the black wattle had an extraordinary pace of expansion at the survey area, which was reflected in the diffusion distance and in the population characteristics. The population overall diffused to 1800 m in the south side of the gutterway from June to November and 450 m in the north side of the gutterway from August to November. Population features (such as number, density, height and ground diameter) showed that the species had a very high growth rate. They increased dramatically in June and reached the peak in August, then decreased after 3 months, which exactly corresponds to the pattern of local rainfall. It should be noted that these increased growths are partially flattened or slowed down by human disturbance. In order to prevent bird strikes, the frequent pruning works are practiced by airport staff and they clean up the larger and higher plants artificially at the airport, including many *A. mearnsii* seedlings in our survey area. However, despite this pruning, *A. mearnsii* populations still showed a rapid diffusion over the grass-planting area near the gutterway of the airport. With such a trend, *A. mearnsii* would become woodland in the near future and the whole grass-planting area of airport would be threatened.

Possible factors affecting invasion success

Explanations for *A. mearnsii* invasions have received attention in some studies (Dodet and Collet 2012; Donaldson et al. 2014; Lamarque et al. 2011; Low 2012). We identify a number of factors that are possible for the successful invasion by *A. mearnsii* at the Changshui airport, and group them into environmental factors, human disturbance and weed characteristics. Dodet and Collet (2012) highlighted that invasion may become effective only when environmental conditions allow the species to express their potential for invasion. In this case study, the land claimed as the airport were villages, farmland and planted forests (including planted black wattle forests) prior to the con-

struction of the airport in 2007, which probably resulted in extensive *A. mearnsii* seed banks that were spread and concentrated in the grass-planting area and in the planning area. Secondly, the species is highly adapted to the habitat because it has similar climate conditions to its natural habitat, which leads to high growth performance and an ability to become the dominant population. Thirdly, the on-going flight activities can take more seeds of *A. mearnsii* into the airport environment, either by flight flows or human/plane attachments. Meanwhile, interference by construction activities enhances invasion ability of *A. mearnsii*, because it can help break seed dormancy underground. Finally, the weedy characteristics are also key drivers of invasive success (Gibson et al. 2011; Low 2012), such as long-lasting inflorescences, a variety of dispersal pathways, the ability to re-sprout and germinate in abundance following disturbance, and high growth rates. All result in the emergence of a large number of tree seedlings after environmental adaptation in grass-planting area at the airport. However, uncertainty still remains as to the relative importance of environmental factors and species traits when determining the propensity of *A. mearnsii* at the Changshui airport to become invasive, and this needs to be further studied.

Risk assessment and management implications

Acacia mearnsii grows quickly and spreads rapidly in our study area. The species can radically change local vegetation structure, such as converting grass-planting area into woodland, or even forest (if there are no control measures) with this single dominant species. In addition, woodland or forest could enhance bird abundance and increase the probability of bird strike events (Li et al. 2010; Liao et al. 2012; Sandström et al. 2006; Tilghman 1987; Xu et al. 2011), which have been upgraded to an “A” class air disaster risk by the FAI (Federation Aéronautique Internationale). The detailed study of bird abundance for Changshui airport in 2013 showed there were 34 bird species often stay on or around the *A. mearnsii* trees, including *Passer montanus*, *Carduelis ambigua*, *Alauda gulgula*, *Motacilla alba*, and *Ardeola bacchus* (Bird Strike Prevention Office of Kunming Changshui International Airport 2013; Li 2014). In this context, invasions by *A. mearnsii* species will pose a potential threat to bird strikes at the airport.

The whole grass environment at the airport is vulnerable to invasion by the current population of black wattle if it is not controlled, and the populations will continue to spread or invade new biogeographic regions. Therefore precautionary risk assessment and adaptive management towards this species in the study area should be undertaken so that the negative impact and harm can be limited. At the airport, the *A. mearnsii* populations are in the early stages of invasion, and appropriate mix of available management methods should be employed to maximize their effect. So eradication combined with mechanical control is an effective option at current stage (van Wilgen and Richardson 2014). This is helped by the fact that the tree populations are localized and the trees themselves are kept in small. For the stages when trees grow up, mechanical control before flowering and seed maturity should be adopted to eliminate

their further dispersal. Finally, promoting education and awareness of the dangers of *A. mearnsii* invasion is also needed to prevent further expansion of this species in the region (van Wilgen and Richardson 2014).

Conclusions

This study has shown that *A. mearnsii* has successfully invaded areas inside Changshui airport. The populations continue to spread at a rapid rate, and may invade new areas and change local ecosystem. Furthermore, the rapid distribution of *A. mearnsii* poses an increased threat to airport flights. These results imply that eradication, combined with an education program, need to be proposed. The rapid invasion of *A. mearnsii* at the study area highlights the potential risks to other airports in tropical and warm temperate areas of China or around the world. We therefore suggest detailed monitoring and assessment of *A. mearnsii* species should be carried out in these regions.

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