

Assessing the potential impacts of non-native small mammals in the South African pet trade

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Abstract

The pet trade is one of the most important pathways by which small mammals are introduced to non-native areas. To prevent the introduction and invasion of non-native pets, an impact assessment protocol is useful in understanding which pets might have potential negative impacts should they escape or be released from captivity. In this study, we used the Generic Impact Scoring System (GISS) to assess the potential effects associated with 24 non-native small mammal species sold in the South African pet trade. European rabbits *Oryctolagus cuniculus*, house mice *Mus musculus*, Norwegian rats *Rattus norvegicus* and eastern grey squirrels *Sciurus carolinensis* had the highest potential impacts for both socio-economic and environmental categories. We found no statistically significant difference between the overall environmental and socio-economic impact scores. Impacts on agricultural and animal production (livestock) were the main mechanisms in the socio-economic category, while the impacts on animals (predation), competition and hybridisation prevailed for environmental impacts. The non-native mammal pet species with high impacts should be strictly regulated to prevent the potential impacts and establishment of feral populations in South Africa.

Keywords

GISS, introduction pathways, invasions, impact assessment, policy implementation

Introduction

Different invasion pathways have been associated with the introduction and spread of non-native species (McNeely 2006; Hulme 2009). These pathways include accidental introductions (e.g. hitch-hikers or contaminants of transported goods) and intentional introductions through horticulture, biocontrol and pet trade (Padilla and Williams 2004; Hulme 2009; Keller et al. 2011). The latter has gained considerable attention over the past decades as the global trade in live animals increases (Keller and Lodge 2007; Faulkner et al. 2016; Ng et al. 2016; Lockwood et al. 2019). Some of the non-native pet species may establish self-sustaining populations through accidental escapes and intentional releases (Gaertner et al. 2015; da Rosa et al. 2017); for example, European rabbit *Oryctolagus cuniculus*, eastern grey squirrel *Sciurus carolinensis*, common marmoset *Callithrix jacchus* and the black tufted-ear marmoset *Callithrix penicillata* (Huynh et al. 2010; da Rosa et al. 2017; Measey et al. 2020).

Non-native pets have been associated with negative impacts on biodiversity, human health, the economy, and agriculture (Marbuah et al. 2014; Su et al. 2015; Shivambu et al. 2020). In Brazil, the common marmoset *C. jacchus* has been reported to negatively affect the population of vulnerable buffy-tufted marmosets *C. aurita* through hybridisation (Nogueira et al. 2011; Malukiewicz et al. 2014). An increase in the trade of non-native small mammal species is also associated with outbreaks of zoonotic diseases, e.g. Salmonellosis in 28 patients in the USA has been linked to pet rodents such as mice, rats and hamsters (Hargreaves 2007). The common marmoset has been implicated into transmitting rabies to humans in Brazil (Kotait et al. 2019). Economic impacts have also been reported for some non-native small mammals, e.g. the European rabbit *O. cuniculus* has been indicated to compete with livestock for pasture in Australia (Fleming et al. 2002). In addition, species such as the eastern grey squirrel, the Norwegian rat *Rattus norvegicus* and the house mouse *Mus musculus* have been reported to cause impacts on infrastructures and crops of economic importance (Signorile and Evans 2007; Almeida et al. 2013; Panti-May et al. 2017).

The negative impacts associated with any introduced species can be partly prevented by prohibiting the trade of those non-native species with known harmful impacts and invasive potential (Vaes-Petignat and Nentwig 2014; van der Veer and Nentwig 2015; da Rosa et al. 2018). In cases where non-native pet species have already been introduced but not yet established, possible impacts can be avoided by preventing their release or escape from captivity (da Rosa et al. 2018). In South Africa, the pet trade has been cited as an invasion pathway for different non-native animals through releases and accidental escapees, including species such as the mallard duck *Anas platyrhynchos* (Gaertner et al. 2015), the rose-ringed parakeet *Psittacula krameri* (Hart and Downs 2014), and the Australian red claw crayfish *Cherax quadricarinatus* (Nunes et al. 2017). The South African National Environmental Management: Biodiversity Act (No. 10 of 2004) (NEMBA) requires that impact and risk assessments are undertaken by either the issuing authority or the importer before issuing permits for non-native species being imported, sold, kept in captivity or released into the wild (van Wilgen et al. 2008).

Impact and risk assessment protocols are considered to be cost-effective and reliable methods that can be used to identify potential invasion impacts, enable ranking of them and support decision-making (Jeschke et al. 2014; da Rosa et al. 2018; Shivambu et al. 2020). Both impact and risk assessment protocols have been successfully used for fishes (van der Veer and Nentwig 2015), plants (Novoa et al. 2016) and for species in the pet trade (Bomford et al. 2005; Patoka et al. 2014; da Rosa et al. 2018; Weiperth et al. 2018) to investigate the potential invasion risks and impacts.

The present study focused on non-native small mammals sold as pets in South Africa. These non-native small mammal species include rodents, lagomorphs, primates, Eulipotyphla, carnivores, Afrosoricida, and Diprotodontia (Suppl. material 1, Table S1). These small mammal pets are traded on different platforms, including online, among breeders and in pet shops (Maligana et al. 2020). There is a relative paucity of information on the potential impacts associated with non-native small mammals sold as pets in South Africa. Non-native small mammal pets such as the sugar glider *Petaurus breviceps* (Heinsohn et al. 2015), the domesticated ferret *Mustela putorius furo* (Davison et al. 1999), the European rabbit (Fleming et al. 2002), the common and the black tufted-ear marmoset (Malukiewicz et al. 2014; Kotait et al. 2019) have been reported to cause impacts in their invaded areas. The aim of the present study was, therefore, to identify which non-native small mammal species sold as pets in South Africa have potentially high environmental and/or socio-economic impacts. We also investigated which impact mechanisms are associated with them. Given that previous studies found that non-native birds and mammals are associated with economic impacts (Kumschick and Nentwig 2010; Nentwig et al. 2010), we predicted that most of the non-native small mammal species traded as pets in South Africa would be more associated with socio-economic impacts rather than environmental impacts. In addition, some of the small mammal species, especially rodents, are associated with human habitation (Garba et al. 2014; Panti-May et al. 2017) and therefore, we expected them to cause more economic than environmental impacts.

Methods

Study species

In this study, pet shops were visited in South Africa to document the list of non-native small mammals sold. The list was complemented with data collated from the online trade. All pet shops and online websites were surveyed four times, once per season (spring, summer, autumn, and winter) between September 2018 and September 2019. During each visit, the numbers of each mammal species were recorded to determine the prevalence. We averaged the numbers of each species for both online and pet shop trade to indicate the most prevalent species. We carried out the impact assessments for 24 non-native small mammals sold in pet shops and online (Maligana et al. 2020; Suppl. material 1, Table S1).

Impact assessments

We conducted impact assessments using the Generic Impact Scoring System (GISS) (Nentwig et al. 2010). This tool depends on published evidence associated with environmental and socio-economic impacts of the studied species and allows comparisons and prioritisation. The environmental impacts (Kumschick and Nentwig 2010) were grouped into six impact categories, which included impacts on plants or vegetation (herbivory), impacts on animals (predation), competition, disease transmission, hybridisation, and impacts on ecosystems. The socio-economic impacts were also grouped into six categories, which included impacts on agricultural production, animal production (livestock), forestry production, human infrastructure, human health, and human social impacts (Kumschick and Nentwig 2010; Nentwig et al. 2010). The impact mechanism for each category under environmental and socio-economic impacts ranged from 0 to 5 (0: no impact or literature associated with scored species, 1–2: minor impacts, 3: medium impacts, and 4–5: major impacts) (Nentwig et al. 2010). The potential maximum scores for both environmental and socio-economic impacts is 60. Information on the impacts of the assessed species was retrieved by searching on Google Scholar and Web of Science (<https://clarivate.com/>) using the scientific and common names of the species in combination with each impact mechanism, for example, “*Oryctolagus cuniculus* impacts on plants or vegetation”, “*Callithrix jacchus* impacts on animals”, “house mouse impacts on agricultural production”, and “*Cebus capucinus* impacts on human social life”. In the present study, we only assessed the impacts associated with feral populations of non-native small mammals. We did not assess the reported impacts associated with non-native small mammals in captivity. The assessments of the impacts were based on the publication records entirely from areas outside South Africa.

Statistical analyses

We tested the similarity between the sum of the GISS environmental and socio-economic impact scores using the paired Wilcoxon’s signed-rank tests. We tested for significant differences between the mechanisms for environmental and socio-economic impacts using a Kruskal-Wallis test, and the Mann-Whitney pairwise tests were used to test for differences within the species and within the impact mechanisms. All statistical analyses were performed in R statistical software (version 3.4.4, R Core Team, 2018).

Results

Impact assessments

We found a total of 122 pet shops and seven online websites selling 24 non-native small mammals in South Africa. The European rabbit, the Norwegian rat, the house

mouse and the Guinea pig were the most prevalent species in both pet shops and online (Suppl. material 2, Table S2). The first three species and the eastern grey squirrel are established species in South Africa (Table 1). A total of 106 publications were found and used to rank the impacts of these species. Of the 24 non-native mammal species traded, we could only find published impacts for 10 species and therefore assessed those. The literature ranged between 1 to 23 publications for a single species, and for some of the species, the literature was identical (Suppl. material 2, Table S2). The total GISS scores ranged from 3 to 40, with environmental impact ranging from 0 to 18 and socio-economic impacts ranging from 0 to 22 (Table 1). The total score for environmental impact was 115 and for socio-economic impact was 81 (Table 1). When comparing the overall scores between the two impacts, there was no significant difference between overall environmental and socio-economic impact scores (Wilcoxon signed-rank test, $V = 23$, $P = 0.1022$). European rabbit, Norwegian rat and house mouse had the highest overall GISS scores (between 32 and 40) representing between 53% and 67% of the maximum impact assessment score (i.e. 60) (Table 1).

All the non-native mammal species assessed in the present study had environmental impacts, except for the Mongolian gerbil *Meriones unguiculatus* (Table 1, Fig. 1a). There was no significant difference between the potential environmental impacts of the non-native small mammal species assessed (Kruskal-Wallis test; $X^2 = 3.01$, $df = 9$, $P = 0.90$). The species with the highest environmental impact were the European rabbit, followed by the house mouse and the Norwegian rat (Table 1). These species represented between 50% and 60% of the maximum environmental impact score (i.e. 30).

Seven out of 10 of the non-native mammal species traded as pets had socio-economic impacts in the present study (Table 1, Fig. 1b). There was a significant difference between the socio-economic impact scores for the 10 non-native small mammals traded as pets (Kruskal-Wallis test, $X^2 = 22.27$, $df = 9$, $P = 0.003$, Fig. 1b). The European rabbit, the house mouse and the Norwegian rat had significantly higher socio-economic impacts when compared with the other seven species (Mann-Whitney pairwise test, Bonferroni corrected p values, $P < 0.001$, Table 1, Fig. 1b). They represented more than 50% of the maximum socio-economic impact score (i.e. 30).

Environmental impacts mechanisms

Between the environmental impact mechanisms, significant differences were found (Kruskal-Wallis test, $X^2 = 15.63$, $df = 5$, $P = 0.002$, Table 1). The only significant difference found was between the impact on animals (predation), disease transmission and the impact on the ecosystem (Mann-Whitney pairwise test, Bonferroni corrected p values, $P < 0.001$). The impact on animals (predation), competition, and hybridisation were the most common mechanisms followed by the impact on plants and vegetation (herbivory), impact on ecosystems, and disease transmission

Table 1. The GISS scores of 10 non-native small mammal species sold in the South African pet trade. The sum of each impact category is given, and the total impact indicates the overall sum of environmental and socio-economic impacts for each species. Detailed scores for each species and literature used are available in the Suppl. material 2, Table S2. An asterisk indicates species established in South Africa (see Picker and Griffiths 2017, and Measey et al. 2020).

| Species | Common names | Environmental impact | | | | | | | Socio-economic impact | | | | | | | Overall GISS impact scores | Number of literature used |
|--------------------------------|---------------------------|----------------------------------|---------------------|-------------|-----------------------|---------------|------------|------------------------------|-------------------------|-------------------------------|---------------------|----------------------|--------------|-------------------|-------------------------------|----------------------------|---------------------------|
| | | Plants or vegetation (Herbivory) | Animals (Predation) | Competition | Diseases transmission | Hybridisation | Ecosystems | Overall environmental scores | Agricultural production | Animal production (Livestock) | Forestry production | Human Infrastructure | Human health | Human social life | Overall socio-economic scores | | |
| <i>Callithrix jacchus</i> | Common marmoset | 0 | 3 | 5 | 0 | 5 | 0 | 13 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 16 | 10 |
| <i>Callithrix penicillata</i> | Black tufted-ear marmoset | 0 | 2 | 5 | 0 | 5 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 8 |
| <i>Cavia porcellus</i> | Guinea pig | 0 | 5 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 2 |
| <i>Meriones unguiculatus</i> | Mongolian gerbil | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 2 |
| <i>Mus musculus</i> * | House mouse | 3 | 5 | 2 | 0 | 3 | 3 | 16 | 5 | 4 | 0 | 4 | 3 | 0 | 16 | 32 | 23 |
| <i>Mustela putorius furo</i> | Domesticated ferret | 0 | 5 | 0 | 0 | 4 | 0 | 9 | 0 | 5 | 0 | 0 | 0 | 0 | 5 | 14 | 9 |
| <i>Oryctolagus cuniculus</i> * | European rabbit | 4 | 5 | 5 | 0 | 0 | 4 | 18 | 5 | 4 | 4 | 3 | 3 | 3 | 22 | 40 | 23 |
| <i>Petaurus breviceps</i> | Sugar glider | 0 | 5 | 5 | 0 | 2 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 7 |
| <i>Rattus norvegicus</i> * | Norwegian rat | 3 | 5 | 3 | 0 | 0 | 4 | 15 | 4 | 4 | 0 | 5 | 4 | 3 | 20 | 35 | 20 |
| <i>Sciurus carolinensis</i> * | Eastern grey squirrel | 5 | 3 | 3 | 3 | 0 | 0 | 14 | 4 | 0 | 5 | 3 | 0 | 0 | 12 | 26 | 10 |
| Overall scores | | 15 | 38 | 28 | 3 | 20 | 11 | 115 | 21 | 17 | 9 | 15 | 13 | 6 | 81 | 196 | 106 |

(Table 1). For each impact mechanism, different species had maximum scores, i.e., plants and vegetation (herbivory) (eastern grey squirrel), animals (predation) (Guinea pig, house mouse, domesticated ferret, the European rabbit, sugar glider and Norwegian rat), competition (common marmoset, black tufted-ear marmoset, European rabbit and sugar glider) and hybridisation (common marmoset and black tufted-ear marmoset) (Table 1).

Socio-economic impacts mechanisms

All assessed non-native small mammal species (n = 10) had socio-economic impacts except for the black tufted-ear marmoset, the Guinea pig and the sugar glider (Table 1). No significant differences between the impact mechanisms were found (Kruskal-Wallis test, $\chi^2 = 2.89$, df = 5, P = 0.54, Table 1). However, the most often mentioned impact mechanism was on agricultural production with a summed score of 21 (Table 1). Different species had maximum scores for each impact mechanism, namely, agricultural produc-

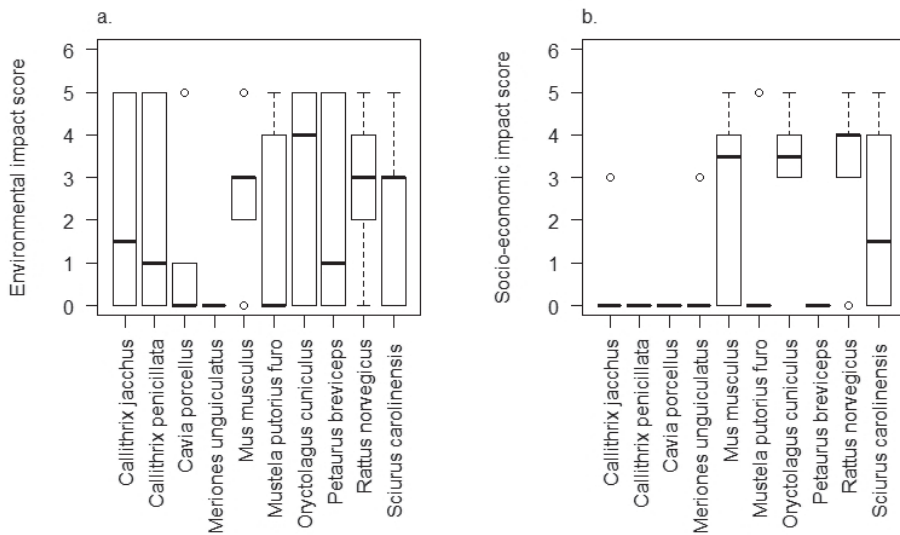


Figure 1. Box-plot showing **a** environmental and **b** socio-economic impact scores for the 10 non-native small mammals available in the South African pet trade. (Boxes show the 25th and 75th percentiles and whiskers (values below and above 5 and 4.5 for environmental and socio-economic respectively were considered as outliers) indicate maximum range, interquartile range, median, and the minimum range).

tion (house mouse and European rabbit), animal production (livestock) (domesticated ferret), forest production (eastern grey squirrel) and human infrastructure (Norwegian rat) (Table 1). Four out of 10 species had impacts on human health, and the Norwegian rat had the highest impact (Table 1). Only the European rabbit and the Norwegian rat had an impact on human social life, and these species had similar impact scores (Table 1).

Discussion

The non-native small mammals traded as pets and assessed in the present study had no significant differences between the overall environmental and socio-economic impact categories. However, a related study on feral mammal species by Hagen and Kumschick (2018) found a difference between environmental and socio-economic impacts where environmental impacts were significantly higher when compared with socio-economic impacts. An explanation for this difference could be that different domesticated non-native species were scored, and only three species were identical between the studies (Hagen and Kumschick 2018). Three species, the European rabbit, Norwegian rat, and house mouse were estimated to have the highest overall impact. Previous studies have also shown that these species have relatively high impacts in both environmental and socio-economic impact categories (Nentwig et al. 2010; Hagen and Kumschick 2018).

The environmental impacts of these three species with high scores were related to their impacts on other animals (predation) and competition, because they have caused the extinction of native species or generally compete with several species of high conservation concern. For example, the extinction of the Laysan crake *Porzana palmeri* in Hawaii has been linked to the introduction of Guinea pigs and European rabbits, and in Australia, rabbits outcompete the vulnerable rufous hare-wallaby *Lagorchestes hirsutus* for food and space (Lees and Bell 2008; Hume 2017). The house mouse and the Norwegian rat are associated with the reduction of native species and are also responsible for the extinction of several bird, insect and reptile species on different islands (Atkinson 1985; Marris 2000; Cuthbert and Hilton 2004; Zeppelini et al. 2007; Jones et al. 2008; Dagleish et al. 2017). These three species represent the most popular species in the South African pet trade industry (Maligana et al. 2020; Suppl. material 1, Table S1). In addition, the European rabbit is regarded as invasive on South African offshore islands, while the Norwegian rat and the house mouse are invasive on the mainland and offshore islands (Picker and Griffiths 2017; Measey et al. 2020). Consequently, these species may likely have higher impacts than other species scored in this study, given their establishment status in South Africa. There is also a lack of studies on the actual environmental and socio-economic impacts of these small mammals recorded in South Africa (Hagen and Kumschick 2018). It is also possible that most of the impacts reported elsewhere for these non-native mammals have already taken place in South Africa but are not yet documented. The results for the present study were different when compared with a study on non-native invertebrate pets in South Africa which found that popular species had minimal impacts (Nelufule et al. 2020). This difference may be explained by the fact that invertebrates are generally not well studied when compared with mammal species (Nentwig et al. 2010; Kumschick et al. 2015; Hagen and Kumschick 2019; Nelufule et al. 2020). Some popular mammal species in the pet trade, such as the sugar glider, have previously been reported to have relatively high potential ecological risk (da Rosa et al. 2018). This species can survive in the wild and has been reported to cause negative impacts on biodiversity by preying on the critically endangered swift parrot *Lathamus discolor* in Tasmania, Australia (Campbell et al. 2018). If this species is released from captivity, it can cause similar impacts in South Africa, as it is also popular in the pet trade, especially in the online trade (Suppl. material 1, Table S1).

The common marmoset and the black tufted-ear marmoset were the only species scoring high impacts through hybridisation. These two species have been reported to threaten the vulnerable populations of buffy-tufted marmosets *C. aurita* and Wied's marmosets *C. kuhlii* in Brazil (Nogueira et al. 2011; Cezar et al. 2017; Moraes et al. 2019). The hybrids of these two primates have been reported in the wild, and they are also fertile (Ruiz-Miranda et al. 2006; Oliveira and Grelle 2012; Malukiewicz et al. 2014). It is evident that these primates are a threat to populations of other marmosets in their introduced ranges. However, it is unlikely that these species will threaten the populations of other primates in South Africa as there are no native marmoset species. However, this does not suggest that these species will not cause impacts through other mechanisms as there is evidence of impacts on other animals through predation (Alexandrino et al. 2012).

The only species which recorded maximum impact on forestry production and plants or vegetation (herbivory) in the present study was the eastern grey squirrel. This species scored a maximum potential impact because it has been reported to cause impacts to endangered plant species, and its impacts have also resulted in major economic losses. For example, Lawton et al. (2007) reported that economic damage caused by eastern grey squirrels to beech *Fagus sylvatica*, sycamore *Acer pseudoplatanus* and ash *Fraxinus excelsior* (listed as near threatened by IUCN, (Khela 2013)) woodlands in the UK was estimated to be ~£10 million (Williams et al. 2010; Merrick et al. 2016). This species has also been reported to damage *Populus × euroamericana* plantations (Signorile and Evans 2007). Given that this species thrives in the urban and commercial areas in South Africa, it is likely to cause impacts on forestry production, nut, fruit and vegetable crops, and also telecommunication cables (Measey et al. 2020).

Several non-native mammal species assessed in the present study are regarded as agricultural pests (Reid et al. 2007; Girling 2013). Therefore, the impact on agriculture was high when compared with other impact mechanisms. The species responsible for the maximum potential impact under this mechanism were the house mouse and the European rabbit. These species scored high because their impacts were mostly associated with major economic losses on agriculture, and also their eradication plans required the application of pesticides which are expensive and have negative impacts (Twigg et al. 2002; Williams et al. 2010; Haniza et al. 2015; Capizzi 2020; Mill et al. 2020). In developing countries, invasive rats and mice compete with humans for food (Stenseth et al. 2003), targeting various crops such as cereals, rice, palm oil, fruits, cocoa, and sugarcane, which results in a significant economic loss and affects food security (Tobin and Fall 2004; Varnham 2006). The United Nations reported that in 1982 rats and mice damaged ~42 million tons of food globally, worth ~US \$30 billion worldwide (Almeida et al. 2013). Even though there is lack of information on the impacts associated with non-native invasive rats and mice in South Africa, these species are likely to be causing socio-economic impacts. Studies in South Africa indicated that pesticides are used to control rats and mice in different households in urban areas (Balme et al. 2010; Rother 2012; Roomaney et al. 2012). This may suggest that these rodents may be problematic, but little attention has been given to the economic losses associated with control measures and other socio-economic impacts in general.

Domesticated ferrets were responsible for the highest impact through the animal production (livestock) mechanism. In New Zealand, they have been reported to host the *Bovine tuberculosis* disease that has been transmitted to livestock and threatens production of beef, dairy and venison markets (Ragg et al. 1995; Byrom 2002; de Lisle et al. 2008). Domesticated ferrets might also pose the risk of transmitting *B. tuberculosis* in South Africa, given that they are kept as pets and have become invasive after accidental escapes in New Zealand (Byrom 2002). The Norwegian rat had the highest score for infrastructural impact. Their damage to infrastructure includes gnawing of electric cables, burrowing, and contaminating water and food through droppings and urine (Johnson 2008; Garba et al. 2014; Panti-May et al. 2017). Their gnawing on communication cable and wires has further resulted in fires; as a result, repellents/rodenticides

are generally used to control them (Shumake et al. 2000). The Norwegian rat also had a high potential impact on human health in the present study because they carry pathogens that are transmittable and fatal to humans such as *Bartonella*, *Echinococcosis* and *Seoul* virus (Firth et al. 2014; Abdel-Moein and Hamza 2016). This rat has also been reported to bite humans, causing wounds which require medical attention (Donoso et al. 2004; Garba et al. 2014; Panti-May et al. 2017). It is possible that non-native invasive rats may threaten the health of humans in South Africa, given their wide distribution in the urban landscapes and having been found to carry zoonotic agents such as helminths, toxoplasmosis and leptospirosis (Taylor et al. 2008; Julius et al. 2018).

Only the European rabbit and the Norwegian rat had an impact on human social life, and these species had the same impact scores. Rabbit burrows cause damage to gardens and golf courses (Brown 2012). Norwegian rats also make damaging burrows, for example, in cities, especially under concrete sidewalks and in backyards (Sullivan 2004; van Adrichem et al. 2013). In South Africa, the Norwegian rat would likely cause severe human social life impacts when compared with the European rabbit given that it is distributed in urban areas and rabbits are present on the offshore islands only (Bastos et al. 2011; Julius et al. 2018; Measey et al. 2020). However, impacts associated with the European rabbit may be severe on the offshore islands where the species is known to reduce vegetation (Sherley 2016). Should species with high impacts be released or escape from captivity and establish feral populations, impacts reported in the present study may occur and results in reduction of biodiversity and economic loss during eradication and the repairing of damages caused.

Conclusions and recommendations

The present study showed that several of the South African non-native small mammal pets that are traded and were assessed pose either potentially high environmental and/or socio-economic impacts as documented in other countries. But of great concern are the following species: the European rabbit, the house mouse, the Norwegian rat and the eastern grey squirrel which have been reported as established in South Africa and its offshore islands (Picker and Griffiths 2017; Measey et al. 2020). The establishment of the European rabbit and the eastern grey squirrel in South Africa is associated with escapees from captivity (Measey et al. 2020). It is likely that these species are causing similar impacts in South Africa but unreported. We recommend that established species with high impacts should be prioritised for eradication and management. The trade for those species with significantly higher environmental and socio-economic impacts should be stopped and monitored, prioritised in policy development and regulations implemented so that their potential impacts in South Africa may be prevented. Regulations on the trade of non-native species exist, but these regulations are not implemented in many countries, and furthermore in South Africa, there is an increased demand for non-native pets and ongoing illegal trade (van Wilgen et al. 2008; Martin et al. 2018; Siriwat and Nijman 2018). To prevent impacts by non-native pet species, countries may need to document alien species traded, and do impact or risk assessments to identify invasive species, which may require management.

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Supplementary material I

Table S1

Authors: Ndivhuwo Shivambu, Tinyiko C. Shivambu, Colleen T. Downs

Data type: pet trade data

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Link: <https://doi.org/10.3897/neobiota.60.52871.suppl1>

Supplementary material 2

Table S2

Authors: Ndivhuwo Shivambu, Tinyiko C. Shivambu, Colleen T. Downs

Data type: impact assessment detailed scores

Explanation note: Assessment of non-native mammalian species sold in the pet trade in South Africa.

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Please don't mow the Japanese knotweed!

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We welcome Martin et al.'s (2020) significant contributions toward advancing understanding of *Reynoutria japonica* var. *japonica* (Japanese knotweed) clonal growth strategies and resource allocation in response to environmental heterogeneity; understanding knotweed ecophysiology is essential to inform and enhance large-scale invasive knotweed management. However, we strongly disagree that mowing should be recommended for the landscape management of invasive knotweeds on the grounds of limited efficacy, practicality and environmental and economic sustainability. To achieve the successful control and long-term management of invasive rhizome-forming plants, we should do more with less, as the evidence guides us (Jones et al. 2018).

Invasive Knotweed Management

As Martin et al. (2020) state, Japanese knotweed is very difficult to control (Child 1999; Skibo 2007; Delbart et al. 2012; Jones et al. 2018). Mature invasive knotweeds (Japanese knotweed *s.l.* taxa) are physically large plants (above and belowground biomass regularly exceeds several kilograms per m², respectively) with extensive belowground growth (several metres in diameter and depth; Fennell et al. 2018; Jones et al. 2018). Depth and extent of belowground biomass affect management strategy by enabling

the plant to recover from many physical, herbicide-based and integrated control treatments, even when applied over relatively long time periods (>3 years; Jones et al. 2018).

While we acknowledge that mowing is a widely applied vegetation management method for infrastructure maintenance, cutting as a management method for established invasive knotweeds has been reported as ineffective in the medium to long-term at a range of spatial scales throughout the academic and grey literature in Europe and North America (Seiger 1997; Brabec and Pyšek 2000; Child and Wade 2000; Green 2003; CEH 2004; Soll 2004; Gover et al. 2005; Kabat et al. 2006; Rennocks 2007; Skibo 2007; Bashtanova et al. 2009; Macfarlane 2011; Delbart et al. 2012), though native species diversity may increase during active management (Adler 1993; Hartwig and Kiviat 2009).

Historically, where cutting was proposed as a management method in the UK and North America, it was suggested that Japanese knotweed stems were cut down to ground level at least every 2 to 3 weeks through the growing season to deplete belowground rhizomes (Child and Wade 2000; McHugh 2006; EA 2013). Yet, to our knowledge, there are no examples of successful long-term invasive knotweed management using this treatment programme, despite the application of approximately 20 cuts per year. While the 3 cuts per year proposed by Martin et al. is more economically sustainable than 20 applications, if the more intensive programme has not demonstrated efficacy at the field scale, it would seem unlikely that 3 cuts per year will deplete the rhizome sufficiently to achieve short-term control, let alone effective long-term management. Hujerová et al. (2013) and Van Evert et al. (2020) reported that aboveground cutting of taproot-forming *Rumex* spp. (Docks; also members of the Polygonaceae) three times per year did not eliminate these species from grassland, or result in plant death. This is despite Docks being smaller and less vigorous than any of the invasive knotweeds. Consequently, on the grounds of treatment efficacy alone, we do not recommend mowing as an effective management method for Japanese knotweed.

Aside from limited efficacy, consideration of practicality and the risk of further spread of Japanese knotweed in the environment should inform the application of mowing. Accessing large swathes of invaded riparian or roadside habitat with heavy equipment is frequently problematic, and it is crucial to ensure that stem and rhizome fragments created by cutting methods do not result in wider dispersal of knotweed into the environment (Sieger 1997; Child and Wade 2000; Soll 2004; McHugh 2006; Skibo 2007; Bashtanova et al. 2009; Macfarlane 2011; Delbart et al. 2012; EA 2013, Jones 2015). Minimising dispersal at the landscape scale is unfeasible, considering that leaf (Brabec 1997), stem (De Waal 2001) and rhizome fragments (weighing as little as 0.06 g; McFarlane 2011) may give rise to new plants. Further, Scott (1988), Beerling (1990) and Beerling et al. (1994) highlight direct lateral expansion of rhizome in response to cutting, exacerbating local spread. Causing the dispersal and/or exacerbating the spread of invasive knotweeds in the UK may be in contravention of national biodiversity legislation (e.g. The Wildlife and Countryside Act 1981, UK).

Parsimony as a principle for invasive plant management

There are strong environmental, ecological and economic arguments for the management of invasive alien plants (IAPs) to minimise their negative environmental and economic impacts (Pergl et al. 2020). However, limited empirical evidence underpinning the ecology and management of rhizome-forming invasive plants can lead to the application of ineffective and labour-intensive physical control treatments, and/or unnecessary/excessive herbicide use. This undermines the sustainability of long-term control programmes for these species, resulting in further spread and dispersal in the environment with no discernible management benefit (i.e. '*the cure is worse than the disease*'; Kettenring and Adams 2011; Jones et al. 2018; Jones and Eastwood 2019).

In short, to achieve the successful control and long-term management of invasive rhizome-forming plants, we should do more with less, as the evidence guides us (Jones et al. 2018). While we welcome Martin et al.'s significant contributions toward advancing understanding of Japanese knotweed belowground, in particular clonal growth strategies and resource allocation in response to environmental heterogeneity, we strongly disagree that mowing should be recommended for the landscape management of invasive knotweeds on the grounds of limited efficacy, practicality and environmental and economic sustainability.

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Multi-taxa inventory of naturalized species in Chile

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Abstract

Here we present a multi-taxa inventory of naturalized alien species recorded on continental Chile and adjacent marine habitats, including eight taxonomic groups. We identified 1,122 species. These comprise 790 vascular plants (terrestrial and aquatic); 31 nonvascular plants [Bryophyta (mosses), Marchantiophyta (liverworts) and Anthocerotophyta (hornworts)]; 18 marine and freshwater macro and micro algae; 71 fungi; 39 terrestrial vertebrates (amphibians, reptiles, mammals and birds); 108 insects; 37 marine and freshwater invertebrates and vertebrates (6 polychaetes, 3 mollusks and 28 Pisces); and 28 terrestrial gastropods. For all taxonomic groups, naturalized species were found to mainly be distributed in regions with Mediterranean and temperate climates, with few at either extreme of the country. The invasion curves show that naturalized species first underwent a positive increment, followed by an apparent plateau phase,

mainly in vascular plants, insects and vertebrates. In fungi, marine and freshwater macro and microalgae, vertebrates and invertebrates, the cumulative number of naturalized species increased sharply starting in the early 20th century; the lack of collections before 1900 is also evident. When considering naturalized species as a whole, this inventory highlights that the rate of new naturalizations consistently increased after 1950, especially for some taxonomic groups such as insects, fungi, and vascular plants. This multi-taxa inventory of naturalized species provides a platform for national reporting on biodiversity indicators and highlights areas where Chile must invest resources to manage biological invasions.

Keywords

alien species, Chile, database, invasion periods, rate of introduction

Introduction

Inventories of naturalized alien species are not only fundamental to elucidate the causes and consequences of the invasion phenomenon (Mack et al. 2000; Pimentel et al. 2005; van Kleunen et al. 2015; Seebens et al. 2017), but also because of their relevance in nature conservation, ecosystem functioning, human health and economy (Hulme 2009; Pyšek and Richardson 2010). Currently, there is an urgent need for inventories of naturalized species, since they reflect these species' local patterns and provide critical information about invasive species distribution (van Kleunen et al. 2015; Seebens et al. 2017). However, in developing countries, naturalized species distribution is still poorly documented and understood (Gardener et al. 2012; Speziale et al. 2012; but see Castilla et al. 2005; Moreno et al. 2006; Castilla and Neill 2009 for marine non-native species; Fuentes et al. 2013 for plants). These species have been neglected in collections and studies due to a historical bias that found no scientific value in studying the naturalized component (Pauchard et al. 2004; Fuentes et al. 2013). Thus, a national Chilean naturalized species inventory is now essential for the early detection and potential eradication or control of invasive species through risk assessment protocols (Moreno et al. 2006; Fuentes et al. 2010, 2013). Additionally, naturalized species inventories provide datasets suitable for the analysis of temporal patterns of biological invasions, in contrast with the current pattern that reflects geographical biases in information on invasion patterns (Pyšek et al. 2008; Núñez and Pauchard 2010).

Approaches such as invasion curves and variations in the rate of naturalized species introductions allow us to identify invasion periods as well as the temporal dynamics of species accumulations (Fuentes et al. 2008; Seebens et al. 2017). Pyšek and Prach (1993) prepared invasion curves methods for reconstructing the propagation history of four alien species in the Czech Republic. They adjusted an exponential model to the accumulated number of locations against time. The slope of the corresponding regression line was used as a measure of the invasion rate (Mihulka and Pyšek 2001). Abrupt inflexions on the invasion curve indicate expansion periods

of the alien species involved (Pyšek and Prach 1993). In this context, whether different taxa show similar invasion curves in a given region is an open question, hence, comparing invasion curves can reveal differences in the invasion process. Seebens et al. (2017) proposed that differences in the pathways and distribution of species introductions suggest that the chronology of invasion could vary among taxonomic groups. This approach allows us to infer whether the increase in numbers of naturalized species shows any sign of saturation, or whether we can expect biological invasions to continue increasing (Seebens et al. 2017).

A substantial part of Chile has been recognized as a hotspot of world biodiversity (Ormazabal 1993; Myers et al. 2000; Mittermeier et al. 2005) due to its remarkably high levels of endemism and the biogeographic isolation of several taxonomic groups (Armesto et al. 1998; Habit et al. 2006; Vidal and Díaz-Páez 2012; Rodríguez et al. 2018), raising concerns regarding its susceptibility to invasions (Arroyo et al. 2000; Fuentes et al. 2015; Seebens et al. 2017). The extraordinary biogeographic characteristics of Chile make it ideal for understanding biological invasion patterns and have great potential for inferring future invasion trends. However, the study of biological invasions in Chile has been addressed mainly in the last decade, both in terrestrial (Quiroz et al. 2009), and marine systems (Castilla and Neill 2009; Villaseñor-Parada et al. 2017). Therefore, the few inventories that exist of naturalized species have been created for only certain taxonomic groups (e.g., boring polychaetes, Moreno et al. 2006; vascular plants, Fuentes et al. 2013; ascidians, Turon et al. 2016; aquatic plants, Urrutia et al. 2017; marine seaweed, Villaseñor-Parada et al. 2018), with no comprehensive inventory of naturalized species, which would allow for the identification of invasion patterns at the multi-taxa level. To address this knowledge gap, the Project GEF/MMA/PNUD, aimed to develop the first national inventory of naturalized species, including eight taxonomic groups recorded on continental Chile and adjacent marine habitats (PNUD 2017). In this paper, we have updated these lists with current taxonomic status and the full dataset has been included as supplementary material. Here, we present a comprehensive inventory of naturalized species in Chile and analyze the distributional and temporal trends of biological invasions in the country in order to identify priority responses to the growing threat from biological invasions.

Methods

Continental Chile extends over 38.5 degrees of latitude (17.5°–56°S; 4300 km), and administratively, the country is divided into 16 regions (which range from 15,403 to 132,291 km² in size) and 56 provinces, sequentially ordered from north to south. This arrangement is closely correlated with increasing precipitation and decreasing temperatures with increasing latitude (di Castri and Hajek 1976; Luebert and Plischoff 2006). This establishes a smooth gradient in climatic conditions

and a sequence of biomes, from hyperdesert in the north, a Mediterranean climate region in the center and temperate rain forest and cold sub-Antarctic wetlands in the south. In this physical pattern, most of the human population, which is associated with greater environmental alterations, is distributed mainly in the Mediterranean area. In relation to marine systems, the oceanographic conditions of the Chilean coast are strongly influenced by the Humboldt Current System and the Cape Horn Current (Camus 2001; Thiel et al. 2007). To the north of 42°S, the Chilean coast is virtually a line, with few geographical features, but strongly influenced by diverse factors, such as upwelling and El Niño Southern Oscillation (ENSO). On the contrary, south of 42°S is characterized by the high occurrence of geographical accidents, and low salinities due to the influence of fjords (Camus 2001, 2008; Thiel et al. 2007).

We performed an exhaustive bibliographic revision and used herbarium and zoological collections to identify all the species recorded as naturalized in continental Chile and adjacent marine habitats for each of the eight taxonomic groups: a) vascular plants (terrestrial and aquatic); b) nonvascular plants [Bryophyta (mosses), Marchantiophyta (liverworts), and Anthocerotophyta (hornworts)]; c) marine and freshwater macro and micro algae; d) fungi; e) terrestrial vertebrate fauna (amphibians, reptiles, birds and mammals); f) insects; g) marine and freshwater vertebrates (Pisces) and invertebrates (polychaetes and mollusks); and h) terrestrial gastropods. For each taxonomic group, we used the most accepted and comprehensive definition of naturalized species (see Table 1 for details). In general terms, naturalized species were considered as those that are not native to Chile (i.e. nonindigenous) and whose presence is due to intentional or accidental introduction as a result of human activities. We considered all organisms that are naturalized or invasive, but not those that survive only with human assistance (Richardson et al. 2000). The preliminary list of each taxonomic group was then verified by experts (local and international). Thus, we had a second opinion regarding the inclusion or rejection of naturalized species in the database. For each species, we made a substantial effort to compile and organize a database integrating both species characteristics and spatial distribution information (see Table 2 for details). We checked all records for their scientific names and spatial distributions.

To construct the invasion curves of naturalized species we modified the procedure in Pyšek and Prach (1993), following Fuentes et al. (2008). We plotted the cumulative number of species collected/recorded in Chile against time in 20-year periods. Data on the first-year records were gathered from various sources (including online databases, scientific peer-reviewed publications, reports and books) and analyzed for 20-year periods. For invasion curves and the annual rate of first records, we only included species that were first reported in a known year. Thus, terrestrial gastropods, as well as marine and freshwater vertebrates, were excluded from these analyses.

Table 1. Definitions of naturalized alien species for each taxonomic group included in the inventory.

| Taxonomic group | Definition |
|---|---|
| Naturalized vascular plants (terrestrial and aquatic) | We included all naturalized alien species <i>sensu</i> Richardson et al. (2000). Additionally, we used expert criteria when the status of the plant species was ambiguous or not supported by publications. Due to a lack of knowledge regarding the native ranges of several species in southern South America (i.e. among Chile, Argentina, Perú, and Bolivia) and to avoid problems in relation to their status (i.e. naturalized or native), we deliberately excluded plants whose natural distribution range fell within the neighboring regions and shared an immediate border with Chile. For this group, the database was constructed on the most recent research by Fuentes et al. (2013), and updated to include new records and spatial information. |
| Naturalized nonvascular plants (Bryophyta (mosses), Marchantiophyta (liverworts) and Anthocerotophyta (hornworts)) | To classify naturalized species in this group we utilized six criteria following Crundwell (1985): 1) absence of subfossil record, 2) evidence of a change in geographical distribution, 3) anomalous geographical distribution, on a world scale or locally, 4) association with some means of introduction e.g. botanic garden or ports, 5) less than the normal amount of genetic variation in populations. Sometimes in dioecious species only one sex is present, and 6) association with open, disturbed or temporary habitats. |
| Naturalized marine and freshwater macro and microalgae | For both marine and freshwater environment, we included all naturalized species referring to organisms that have established a self-sustaining population, but have not necessarily been involved in an invasion process (Richardson et al. 2000; Falk-Petersen et al. 2006). We considered 12 criteria proposed by different authors to identify species introduced into marine systems worldwide (Chapman and Carlton 1991; Cranfield et al. 1998; Ribera and Boudouresque 1995; Boudouresque and Verlaque 2002), and these were: 1) new report in one area, 2) geographical discontinuity in its worldwide distribution, 3) expansion of its distribution range in the invaded area from its point of introduction following a logical pattern (e.g. gradual decrease in abundance from its point of introduction, colonization of new sites following a spatio-temporal pattern), 4) very localized distribution in the introduced region, restricted when compared with similar native species (for example, of the same genus, of the same functional group, with similar life histories), 5) proximity to the probable source of introduction (e.g. ports, cultivation centers), 6) association (or dependence) with other introduced species, 7) association (or dependence) with anthropic activities (e.g. colonizes docks or other artificial substrates), 8) no native evolutionary origin (e.g. absence of congeners in the variable range), 9) tendency to generate massive proliferations (at least seasonally), 10) is identified as naturalized or invasive in other parts of the world, 11) life stories that infer a high invasive power, and 12) genetically identical distant populations. |
| Naturalized fungi | For this group, the concept of naturalized species is not easily handled due to the lack of larger inventories of Chilean fungi before 1945. Also, the deficient knowledge in terms of the biogeography of fungi can make it difficult to determine what is a naturalized species. Priority was given to published records of biotrophic and saprotrophic specialists associated to allochthonous plants (trees), apart from collection specimens (CONC-F, Universidad de Concepción) recorded between 2004 and 2017 for the first time in Chile. The preliminary list was revised and completed by external experts. |
| Naturalized terrestrial vertebrates (mammals, birds, amphibians and reptiles) | In this taxonomic group, we included all naturalized species based on the definition proposed by the United Nations Development Program (UNDP). This definition includes all naturalized alien species that were introduced intentionally or accidentally by humans, establishing a self-sustaining population, without intervention by humans. This general definition was complemented by specific literature for this taxonomic group (e.g. Daniels and Corbett 2003; Lever 1994). |
| Naturalized insects | For this group, we included all naturalized alien species, referring to organisms that have established a self-sustaining population, but not necessarily ended up in an invasion process (Falk-Petersen et al. 2006; Carvallo 2009). |
| Naturalized marine and freshwater vertebrates and invertebrates (polychaetes and mollusks) and terrestrial gastropoda | We used the criteria proposed by Orensanz et al. (2002), Castilla et al. (2005) and Castilla and Neill (2009), which states the following: 1) status determined by scientific literature or expert criteria, 2) anomalous geographical distribution, on a world scale or locally, 3) species with wide geographic distribution, including cosmopolitan species, 4) species described as nonindigenous in Chile, and 5) species that are abundant near to ports or aquaculture centers, but rare or not present in other areas of the country. |

Table 2. Species traits, descriptions, and traits level included in the inventory of naturalized species present in Chile.

| | Plant traits | Description |
|-----------------------|---|---|
| Taxonomic information | Family, genus, scientific name and author | Text |
| Distribution | Native range | Name of the countries, continents or bioclimatic zones |
| | Administrative Regions occupied by the naturalized species in Chile | 15= AYP, Arica y Parinacota 1= TAR, Tarapacá 2= ANT, Antofagasta 3= ATA, Atacama 4= COQ, Coquimbo 5= VAL, Valparaíso 13= RME, Región Metropolitana 6= LBO, Libertador Bernardo O'Higgins 7= MAU, Maule 8= BIO, Biobío 9= ARA, La Araucanía 14= LRI, Los Ríos 10= LLA, Los Lagos 11 AIS, Aisén 12= MAG, Magallanes ND = no data. |
| Introduction | First year report | The year (or range) of the first report in Chile |
| | Type of introduction | Accidental / Intentional / Other |
| Impacts | Description of impacts | The known impacts produced by the species around the world. |

Results

We identified 1,122 species, which we consider as naturalized at least in some parts of continental Chile and adjacent marine habitats (Table 3). These comprise 790 vascular plants (terrestrial and aquatic); 31 nonvascular plants (Bryophyta, Marchantiophyta and Anthocerotophyta); 18 marine and freshwater macro and micro algae; 71 fungi; 39 terrestrial vertebrates (amphibians, reptiles, birds and mammals); 108 insects; 37 marine and freshwater vertebrates and invertebrates (6 polychaetes, 3 mollusks and 28 Pisces); and 28 terrestrial gastropods (Table 3). For most taxonomic groups, the highest numbers of naturalized species were found mainly in the Mediterranean and rainy climatic zones (Table 3, Fig. 1A, B). Terrestrial vertebrates also showed a significant number of species in the cold steppe zone (Table 3), as did insects, and vascular plants in the semi-arid zone (Table 3, Fig. 1A, B).

The cumulative number of naturalized species collected in Chile over time (i.e. invasion curves) has shown a consistent increment in all taxonomic groups during the 19th and 20th century (Fig. 2). Despite the temporal differences among taxonomic groups in their first records, slopes of invasion curves for naturalized species did differ among taxonomic groups, suggesting different rates of species accumulations. While vascular plants, nonvascular plants, and terrestrial vertebrates showed a slight, but steady increase in the number of naturalized species over the last 150 years (Fig. 2A, B, F), the cumulative number of naturalized species in the remaining four taxa increased steeply at the beginning of the 20th century (Fig. 2C, D, E, G). The total rate of first records remained low between 1850 and 1950 (on average 2.8 first records annually, Fig 3A). Since 1951, first records have increased steeply (on average 5.9 first records annually, Fig 3A). During this period, the continuous increment in first record rates has been consistent in vascular plants, insects and fungi (Fig. 3B). On the contrary, nonvascular plants, terrestrial vertebrates, algae, and marine invertebrates have shown markedly low first record rates over the last 160 years (less than 1 first record annually, Fig. 3B).

Table 3. Number of naturalized species by climatic zones in continental Chile and adjacent marine habitats. The total number of species within each taxonomic group is given in parentheses. Marine organisms are present in the coastal area in front of each climatic zones.

| Climatic zones | Vascular plants (790) | Non-vascular plants (31) | Marine & freshwater macro- & microalgae (18) | Fungi (71) | Terrestrial vertebrates (39) | Insects (108) | Marine & freshwater vertebrates & invertebr. (37) | Terrestrial gastropods (28) |
|-----------------|-----------------------|--------------------------|--|------------|------------------------------|---------------|---|-----------------------------|
| Desert | 192 | 0 | 4 | 1 | 13 | 38 | 6 | 1 |
| Semi-arid | 318 | 8 | 5 | 1 | 15 | 61 | 10 | 6 |
| Mediterranean | 636 | 29 | 11 | 55 | 31 | 108 | 25 | 9 |
| Temperate rainy | 463 | 14 | 13 | 41 | 20 | 78 | 12 | 10 |
| Cold steppe | 255 | 8 | 6 | 1 | 23 | 24 | 14 | 2 |

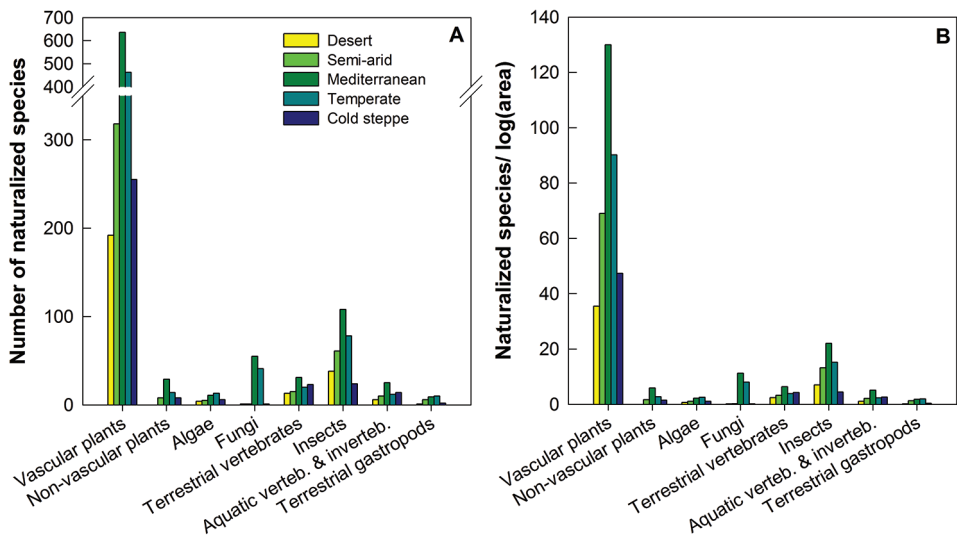


Figure 1. Total number of naturalized species (**A**) and number of naturalized species per log(area) (**B**) by climatic zones of continental Chile and adjacent marine habitats.

Discussion

Unlike previous studies that have provided a database of naturalized species in Chile (e.g., Fuentes et al. 2013 vascular plants; Moreno et al. 2006 boring polychaetes; Turon et al. 2016 ascidians; Urrutia et al. 2017 aquatic plants, Villaseñor-Parada et al. 2018 marine seaweed and Castilla et al. 2005; Moreno et al. 2006; Castilla and Neill 2009 for marine non-native species), here, we present the first multi-taxa dataset of naturalized species for the whole country. Unfortunately, there are biases in creating this type of inventory because vascular plants are over-represented compared to other taxa, probably because they are more conspicuous, stationary and hence more easily discovered (DAISIE 2009). This plant bias occurred in the present study, where 74.1 % of

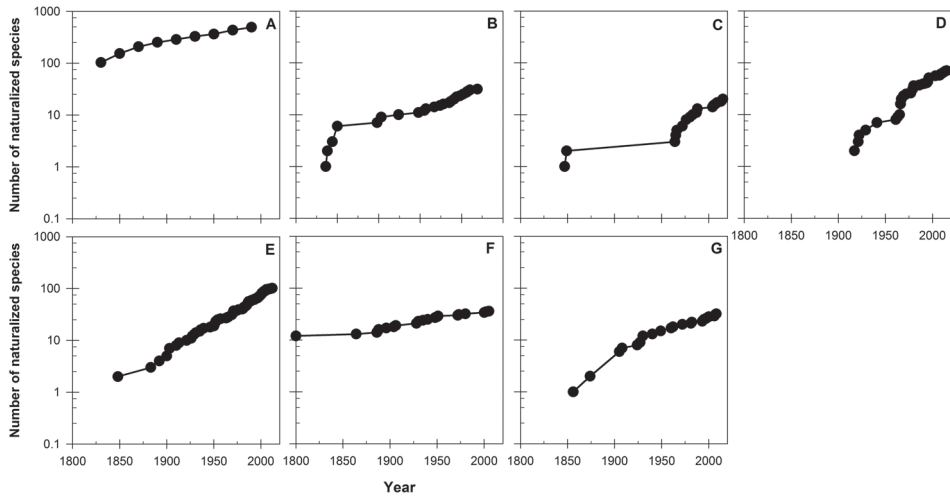


Figure 2. Temporal trends in the invasion of naturalized species in continental Chile and adjacent marine habitats, for each taxonomic group for which data on introduction dates were available (terrestrial gastropods are not shown due to lack of data). The cumulative number of recorded species is shown over the last 200 years. **A** vascular plants **B** nonvascular plants **C** marine and freshwater macro and micro algae **D** fungi **E** insects **F** terrestrial vertebrate fauna and **G** marine and freshwater vertebrates and invertebrates.

the naturalized species recorded in Chile are vascular plants. Most of the naturalized species in this database came from herbarium records and zoological collections, while few came from literature. Regarding fauna, there were also some biases in the data sources, e.g. while vertebrates were well represented in museum collections, records of naturalized insects came mainly from literature. The use of natural history collections as the primary source of information highlights their role in naturalized species studies at large spatial and temporal scales in Chile (e.g. see Fuentes et al. 2015 for vascular plants). The present study integrates data in a unique inventory to obtain a more realistic pattern of naturalized species richness and distributions. One major issue came up; when the number of records for certain naturalized species was still particularly low, we could not be completely certain whether these species had naturalized in the area (e.g., nonvascular plants which were poorly sampled before 1950). Nonetheless, the more than 1,100 well-checked species reported in this study should be sufficient to diagnose the situation in Chile in the past and evaluate future risks.

For all taxonomic groups, naturalized species were found to be mainly distributed in Mediterranean and temperate climate regions (central and central-southern Chile), with few species recorded in the far north and south of the country. In the case of vascular plants, several authors have shown similar distribution patterns for naturalized species (Castro et al. 2005; Fuentes et al. 2008; Fuentes et al. 2013). The high concentration of naturalized species in these two climate zones can be related to the fact that since Spanish colonization, most Chileans have lived in this area (ca. 80 % of the population) (Fuentes et al. 2013). Consequently, this area has been strongly trans-

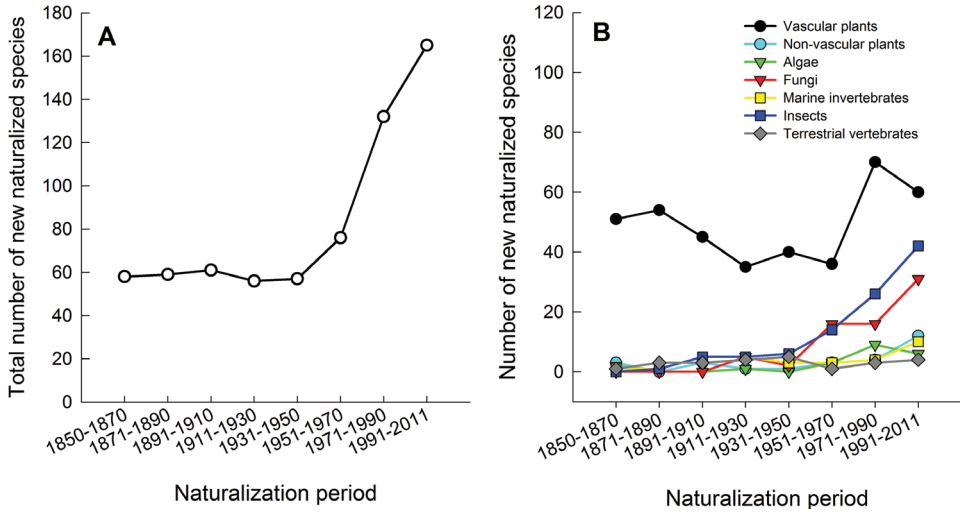


Figure 3. Total temporal trends in first record rates for all species (A) and seven taxonomic groups (B) in Chile. Terrestrial gastropods, as well as marine and freshwater vertebrates are not shown due lack of data.

formed by human activities and land-use changes, while the northern and southern areas have been relatively isolated, mainly due to their climatic conditions and remoteness from the main cities in central-southern Chile (Arroyo et al. 2000; Fuentes et al. 2008, 2015). In marine systems, ship traffic, ballast water and activities associated with aquaculture have been identified as the main introduction vectors for naturalized species (Naylor et al. 2001; Hewitt et al. 2009). In Chile, the main ports are located on the south-central coast (e.g. Valparaíso 33°S, San Antonio 33°35'S, Lirquén 36°42'S, Talcahuano 36°43'S, San Vicente 36°44'S, Coronel 37°01'S and Corral 39°52'S), which increases the susceptibility of these ecosystems to be invaded by naturalized species. Paradoxically, this sector of the Chilean coast has been one of the least studied in terms of biological invasions (Villaseñor-Parada et al. 2017), and even though the number of reports of naturalized species was found to be high, this number could be underestimated due to the lack of information available (Camus 2005; Carlton 2009; Castilla and Neill 2009; Villaseñor-Parada et al. 2017). The few naturalized species recorded in the extreme north and south of the country, could be associated with sampling efforts in these areas, the fact that naturalized species have not yet arrived to these areas due to low propagule pressure or introduction effort, and/or the fact that some species may have arrived, but not thrived because such habitats were incompatible with their ecological niches (Garrido 1985; Jaksic 1998; Fuentes et al. 2015; Villaseñor-Parada et al. 2017, 2018). For vascular plants in particular, the low species density in the Atacama Desert may be attributable to the harsh climatic conditions there, while the lack of naturalized plants in the far south may be the result of a combination of inaccessibility and lower levels of anthropization (Fuentes et al. 2008, 2015). In the case of insects, the highest presence of naturalized species was found to be concentrated in

Chile's central zone, which could be explained by the higher concentration of seaports, border crossings and airports, and the import of biological control agents (Parra and González 2007), pollinators (Montalva et al. 2008), and products of plant or animal origin that, in turn, are contaminated with foreign insects (Estay 2016). Thus, a more comprehensive inventory of naturalized species in these areas will help to identify priority responses to the growing threats from biological invasions.

Thorough documentation of the accumulation of naturalized species, allows us to assess the accumulation process and the dynamics of the establishment and expansion of naturalized species in Chile. We identified invasion periods in Chile based on bibliographic revisions, herbarium and zoological collections for each of the eight taxonomic groups analyzed. Comparatively, the invasion curves show that naturalized species first underwent a positive increment, followed by an apparent plateau phase, mainly in vascular plants, nonvascular plants, and terrestrial vertebrates. In the remaining four taxonomic groups (fungi, insects, marine and freshwater vertebrates and invertebrates, macro and microalgae), the cumulative number of naturalized species increased abruptly at the beginning of the 20th century. The lack of collections before 1900 is also evident for most of the taxonomic groups. In marine systems, the first reports of marine flora and fauna date back to the end of the 18th century, as a result of scientific expeditions that were limited to enumerating the different taxa collected, with few and brief descriptions (Etcheverry 1958; Ramírez 2010). In 1940, the first publications by resident Chilean taxonomists who ratified and added information on the presence of the aforementioned taxa started to appear (Ramírez 2010). Therefore, although the results observed when analyzing the temporal trend of marine invasions show a growing increase since 1900 (Fig. 2C, G), these results are biased due to a lack of prior information before this date. Since the Spanish colonization, an important number of species has been introduced in the drier central Mediterranean climate area, associated with landscape transformations (Aronson et al. 1998). Additionally, in the 19th century there was an important increase in the number of biodiversity records in Chile associated with the inventories developed by naturalists, such as Claudio Gay (Gay 1845, 1854). For vascular plants, there were sustained increments in the collection of weeds from 1894 to 1934, associated with wheat imports (Matthei 1995), whereas the increase of naturalized fungal species, especially macromycetes, is strongly correlated with the fast and extensive spread of naturalized timber plantations, mainly pine and eucalyptus, during the late decades of the 20th century (Palfner and Casanova 2019). The latter authors observed an almost threefold increase in allochthonous, and ubiquitous fungi associated with *Pinus radiata* plantations in central-southern Chile within the last 40 years. For other taxonomic groups, such as terrestrial vertebrates, the record of introduced species is relatively more complete and the relative lower rate of increase may be due to control measures implemented by government services (Iriarte et al. 2005). Specific phytosanitary regulations and other laws related to the introduction of naturalized species have most likely worked in these cases.

Considering naturalized species as a whole, this inventory highlights the consistent increase in the rate of new naturalizations since 1950, especially for some taxonomic groups, such as insects, fungi, and vascular plants. Even where rates of establishment

did not prove to be rising for nonvascular plants, algae, marine, and terrestrial vertebrates, the cumulative number of naturalized taxa did show a consistent increase for these taxonomic groups. Our results are consistent with the fact that the annual rate of first records worldwide has increased during the last 200 years, with 37% of all first records reported recently (1970–2014) (Seebens et al. 2017). Continuous increases in the rates of naturalized species first records in Chile, stress the need to improve the implementation of national legislation and international agreements that aim to reduce the threats that naturalized alien species pose to biodiversity, particularly in the case of insects and fungi. Additionally, the above pattern suggests that the number of new naturalized species will most likely continue to increase because current tools to prevent biological invasions are not effective enough to slow down the increment in the number of naturalized species (Seebens et al. 2017). This inventory is a basis for future studies that analyze more detailed biological patterns and mechanisms that explain invasion processes in many taxa that have been understudied (*sensu*, Capdevila-Argüelles and Zillett 2005). In this context, to effectively assess consequences and risks, in terms of the spread and invasion of individual species, documentation with an efficient combination of species records requires a coordinated effort across multiple government agencies and research institutions, in addition to well-designed and specifically oriented sampling and monitoring programs.

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Supplementary material I

A comprehensive inventory of naturalized species in Chile

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Australia's wish list of exotic pets: biosecurity and conservation implications of desired alien and illegal pet species

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Abstract

Globalisation of the live pet trade facilitates major pathways for the transport and introduction of invasive alien species across longer distances and at higher frequencies than previously possible. Moreover, the unsustainable trade of species is a major driver for the over-exploitation of wild populations. Australia minimises the biosecurity and conservation risk of the international pet trade by implementing highly stringent regulations on the live import and keeping of alien pets beyond its international CITES obligations. However, the public desire to possess prohibited alien pets has never been quantified and represents a number of species that could be acquired illegally or legally under different future legislative conditions. As such, highly desirable species represent an ongoing conservation threat and biosecurity risk via the pet-release invasion pathway.

We aimed to characterise the Australian desire for illegal alien pets and investigate potential sources of external information that can be utilised to predict future desire. Using public live import enquiry records from the Australian Commonwealth Department of Agriculture, Water and the Environment as a proxy for alien pet desire, we tested for differences in the proportion of species with threatened listings and records of invasions, after accounting for taxonomy. Additionally, we used a United States of America (U.S.) live imports dataset to infer pet demand in another Western market with less stringent regulations and determined whether species highly desired in Australia had higher U.S. trade demand than would be expected by chance.

The Australian public desire for alien pets is heavily and significantly biased towards species threatened with extinction, species popular in the U.S. trade and species with a history of successful invasions. Not only does this indicate the potential impacts of pet desire on invasion risk and the conservation of threatened species, but we also highlight the potential role of the U.S. trade as an effective predictor for Australian desire. Our research emphasises the value of novel datasets in building predictive capacity for improved biosecurity awareness.

Keywords

alien, invasive species, non-native, smuggling, wildlife trade

Introduction

Globalisation of trade and tourism has led to substantial changes in the international trade of live pets (Bush et al. 2014). Rapid information sharing, particularly via social media, has increased public awareness of traded species, potentially leading to subsequent increases in pet demand (Clarke et al. 2019; Kitson and Nekaris 2017). Additionally, the use of e-commerce platforms such as international classifieds has facilitated the acquisition of pets in greater numbers and from a greater diversity of regions than previously possible (Bergin et al. 2018; Morgan and Chng 2018; Siriwat et al. 2019), including species with highly restricted distributions (Shepherd et al. 2019). As such, the proliferation of the pet trade has the potential to exacerbate its existing detrimental impacts, including the over-exploitation of wildlife, the violation of animal welfare and both the transport and introduction of invasive alien species (IAS) via the pet-release pathway (Ashley et al. 2014; Auliya et al. 2016; Baker et al. 2013; Lockwood et al. 2019).

Australia has experienced an increased rate of IAS incursions over the last two decades, particularly from species prominent in the international pet trade, such as rose-ringed parakeets (*Psittacula krameri*), corn snakes (*Pantherophis guttatus*) and red-eared sliders (*Trachemys scripta elegans*) (Henderson et al. 2011; McFadden et al. 2017; Toomes et al. 2019; Vall-Iloera et al. 2017). These trends are of concern for Australian biosecurity, as establishment success of IAS is dependent on propagule pressure, which is influenced by the number of individuals smuggled in and their probability of release/escape from captivity (Cassey et al. 2018; García-Díaz et al. 2015; Stringham and Lockwood 2018). Given the cost and difficulty of eradicating IAS from large landmasses (García-Díaz et al. 2017; Holmes et al. 2016; Jardine and Sanchirico 2018; Rout et al. 2014), the interception of IAS earlier in the invasion pathway is necessary for efficient management of biosecurity in Australia.

Australia implements wildlife trade restrictions beyond its' CITES obligations (Department of the Environment and Energy 2019). This stringent regulatory framework has played a major part in mitigating the threat of IAS to date, as highlighted by fewer IAS established in Australia compared with the U.S. (Capinha et al. 2017;

Smith et al. 2008; Strecker et al. 2011), a country with less stringent pet trading and keeping regulations (Eskew et al. 2019; Smith et al. 2017). However, a challenge associated with Australia's regulatory system is the lack of consistent surveillance of alien pets held, legally or otherwise, within Australia. There are a number of species that are not permitted for live import, yet are legal to domestically trade within Australia (Fredberg and McNeil 2010). Additional species have been acquired illegally, either from international smuggling or from domestic captive breeding (Toomes et al. 2019). Therefore, an unquantified proportion of pet keepers have the capacity to legally or illegally acquire desired pets if they are not accessible through importation. Anticipating which species are likely to be desired, acquirable and subsequently pose a biosecurity risk through deliberate/accidental releases, is essential to mitigating the cost of IAS.

While it is important to consider Australia's acquisition of alien pets from the perspective of biosecurity risk, there are also potentially serious conservation implications. The unsustainable harvest and trade of species at rates exceeding their reproductive output can be a major driver of biodiversity loss (Mandimbihasina et al. 2020; Natusch and Lyons 2012; Siriwat and Nijman 2018; Shepherd 2010). Threatened species and those with low fecundity are especially susceptible to this threatening process, due to the effect of perceived rarity on market value (Holden and McDonald-Madden 2017; Siriwat et al. 2019). Even when captive breeding is established to supply a given market, harvesting can still take place in order to increase genetic diversity of captive populations from 'founder stock' (Brooks et al. 2010; Lyons and Natusch 2011) or to introduce a new subpopulation/breed/locality into the market with higher perceived value (Auliya et al. 2016). These issues are particularly apparent in illegal trade, as there are no licensing systems in place to promote sustainable practice. As such, the demand for and acquisition of alien pets within Australia may be contributing to a leading global threatening process.

Quantifying and characterising public demand for alien wildlife is extremely difficult given that the keeping of most alien pets in Australia is illegal or unregulated by any domestic permit system (Toomes et al. 2019). Specifically, to date, there has been no attempt to quantify or elucidate public preference for exotic alien pets. Here, we seek to generate insights about potential demand for alien vertebrates by analysing a novel dataset on the public 'desire' for alien species. We obtained records of anonymous public enquiries to the Australian Commonwealth Department of Agriculture, Water and the Environment (DAWE; formerly the Department of Environment and Energy) relating to the legality of importation of various alien taxa. We aimed to investigate whether species desired in Australia (i.e. species present in DAWE enquiries) were biased towards being threatened by extinction, as indicated by broader research on pet demand (Holden and McDonald-Madden 2017; Siriwat et al. 2019) or towards being invasive species elsewhere, which would indicate trade-related biosecurity risks (Toomes et al. 2019). Furthermore, we compared Australian desire with that of a Western nation with less stringent pet-keeping regulations (the U.S.) in order to identify a potential source of data to predict future desire. The U.S. plays a leading role in the

global exotic pet trade, importing millions of live animals annually to be kept as pets (Harfoot et al. 2018; Smith et al. 2009). Thus, we considered the species imported into the U.S. to represent the total diversity of traded pets and their quantity as a proxy for ‘Western’ demand for pets.

Methods

Australian phone enquiries

The Australian Department of Agriculture, Water and the Environment (DAWE) maintains a hotline for people to enquire about the legality of importing or owning a particular species in Australia. A DAWE policy officer answers and responds to the enquiry and records non-identifiable information about each request. The information recorded by the officer, if supplied by the caller, includes: (i) the date the enquiry occurred; (ii) the location of the enquirer (city or State/Territory); (iii) the species enquired about; (iv) the action (importing, keeping/owning, breeding); and (v) whether the action was for private or commercial reasons. We acquired this dataset for all enquiries lodged from October 2017 to April 2019, which contained a total of 150 phone calls. We acknowledge that the sample size of this dataset is relatively small; however, as we are using the data to identify broad-scale biases, we assumed the data to be sufficiently representative of highly-desired alien pets. Moreover, as enquiries are free and anonymous, we assumed the set of anonymous callers to be an unbiased representation of pet keepers/traders with an interest in importing alien pets.

We categorised the stated use of the animal into six categories: (i) pet (private use); (ii) zoo (commercial use for display in a zoo/wildlife park); (iii) exhibitor (commercial use for exhibition/show); (iv) breeding pets (commercial use to breed as pet); (v) breeding food (commercial use to breed as food); (vi) other (not otherwise specified). If an enquirer specified multiple intended uses, all use types were recorded. We referenced species and common names against the Global Biodiversity Information Facility (GBIF 2019) to resolve species identification to the most specific possible taxonomic level. If multiple species were discussed in a single call, we recorded each species as an independent enquiry ($n = 198$). For our analyses, we only considered enquiries relating to vertebrate pets ($n = 168$). We categorised cartilaginous fishes (Chondrichthyes) and ray-finned fishes (Actinopterygii) into one clade (Fish).

U.S. imports of live animals

The U.S. maintains a database of imports/exports of live organisms and wildlife products, called the Law Enforcement Management Information System (LEMIS), which is maintained by the U.S. Fish and Wildlife Service (see Romagosa (2014) and Eskew

et al. (2019) for more details). We acquired the LEMIS dataset for records from 1999 to 2016. We excluded records of exported animals, records that did not specify the quantity of individuals imported, records that were not categorised as live imports and all non-vertebrate records. We only considered import records that were deemed relevant to the pet trade (i.e. commercial or personal use designation). This dataset resulted in 3083 species, resolved using GBIF. For analysis, we derived the popularity of each species in the U.S. import records by ranking the species by total number of individuals imported from 1999 to 2016.

Comparison datasets

We compared four metrics between species in DAWE enquiries and U.S. imports: (i) popularity in the trade; (ii) the proportion of threatened taxa; (iii) the proportion of taxa with international trade restrictions; and (iv) the proportion of species known to be invasive species elsewhere. To compare the proportion of threatened taxa, we matched each species from DAWE enquiries and LEMIS imports to their IUCN Red List designations: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) (IUCN 2019). For the purpose of our analysis, we re-categorised the Red List designation into a binary variable: Not Threatened (LC and NT) and Threatened (VU, EN and CR). Species listed as “Data Deficient” were excluded from our analysis. We created a binary variable because we had small sample sizes for some IUCN designations. To compare proportions of trade-restricted taxa, we recorded whether species were listed in the Appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UNEP-WCMC 2019). Finally, we used the Global Invasive Species Database (GISD) to determine if a species has a history of successful invasions (ISSG 2019). We supplemented this dataset to include species known to the authors as being considered invasive in peer-reviewed scientific literature, for example, established populations of Argentine black and white tegus (*Salvator merianae*) in Florida (Johnson et al. 2017). For enquiries involving hybrids, we took a conservative precautionary approach and categorised them as GISD-listed if at least one parent species has a history of invasions.

Analysis

We performed four analyses comparing the species in the phone enquiries with the species in exotic pet trade at large (i.e. species from U.S. imports). First, we compared the popularity (see *U.S. imports of live animals*) of the species in the phone enquiries to the overall popularity of species in the exotic pet trade at large. Next, we compared whether the proportion of threatened species (i.e. species listed in the IUCN Red List)

in the phone enquiries differs from the proportion of threatened species in the exotic pet trade at large. Then, we tested whether the proportion of species with trade restrictions (i.e. species listed in CITES appendix) in the phone enquiries differs from the proportion of species with trade restrictions in the exotic pet trade at large. Finally, we tested whether the proportion of species known to be invasive species elsewhere (whether or not in a GISD database) in the phone enquiries differs from the proportion of species known to be invasive species elsewhere in the exotic pet trade at large.

To test these hypotheses, we performed a series of empirical hypothesis tests (analogous to two-tailed t-tests but for ranked data; also known as bootstrap hypothesis testing) by randomly sampling from the U.S. imports dataset and comparing this to what was observed in the DAWE phone enquiries. To obtain the popularity of pets in the overall exotic pet trade, we uniformly randomly sampled species from the U.S. import records and calculated their collective median rank. To obtain the proportion of species threatened, with trade restrictions or invasive in the overall exotic pet trade, we randomly sampled species from the U.S. import records and recorded their collective proportions (respectively). The sample size of this sampling procedure was set to the total number of phone enquiries and was stratified by taxonomic class to account for taxonomic bias. For example, for the species popularity test, there was a total of 79 phone enquiries corresponding to species or subspecies, of which 42 enquiries were mammals (class Mammalia), 24 were birds (class Aves), 14 were reptiles (class Reptilia) and nine were fish (class Actinopterygii or Chondrichthyes). Therefore, for each iteration of sampling, we randomly sampled from the U.S. imports 42 mammals, 24 birds, 14 reptiles and nine fish. We repeated this sampling for 10,000 iterations for each analysis, with replacement. The sample size, stratified by taxonomic class, differed slightly for the proportion threatened (IUCN) test since some species are not yet evaluated by the IUCN or designated as Data Deficient and therefore excluded from analysis. We then compared the phone enquiry median rank or proportion (i.e. observed rank/proportion) with the resulting distribution of rank or proportions from sampling of the U.S. imports. P-values were calculated as the proportion of sampling iterations that were more extreme than the observed rank or proportion. For these analyses, we only considered taxa that were resolved to the taxonomic level of species (i.e. no genus, family etc.).

Results

Summary statistics

In total, there were 196 enquiries from 150 phone calls. Most enquiries were related to the private keeping of pets ($n = 180$), followed by breeding for food ($n = 11$; Fig. 1). Across all uses, there were 126 unique taxa (subspecies, species, genus, family etc.) and 84 unique species (including subspecies), of which 114 unique taxa and 73 unique species pertained to pet enquiries (Fig. 2a, b). Mammals received the most enquiries ($n = 83$) followed by birds ($n = 27$), then reptiles ($n = 25$; Fig. 3a). Carnivora was the order with the most en-

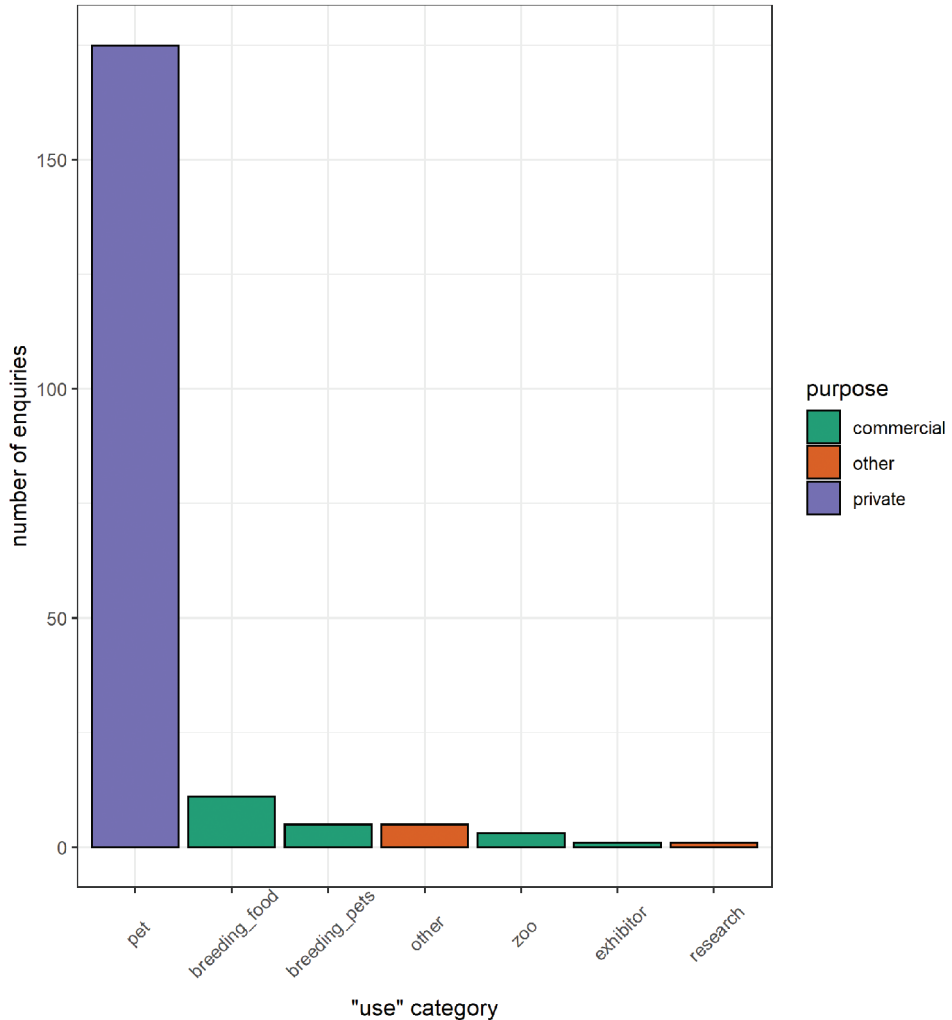


Figure 1. The stated use and purpose of public import enquiries recorded by the Australian Government Department of Agriculture, Water and the Environment. Use was categorised using enquiry notes (Pet = private use of the animal as a pet; breeding food = commercial use of the animal to be bred as food; breeding pets = commercial use of the animal to breed and sell as pets; zoo = commercial use for display in a zoo/wildlife park; exhibitor = commercial use for exhibitions/shows; research = use of the animal for scientific research; other = use not stated).

quiries, followed by parrots (Psittaciformes), then hedgehogs (Erinaceomorpha; Fig. 3b). Overall, the most enquired taxa were hedgehogs (Erinaceinae), fennec fox (*Vulpes zerda*), African grey parrot (*Psittacus erithacus*), monkeys (Simiiformes) and pygmy marmoset (*Cebuella pygmaea*; Fig. 3c). The two most commonly enquired non-vertebrate taxa were tarantula spiders (Theraphosidae, $n = 14$) and freshwater atyid shrimp (*Caridina*, $n = 5$). All remaining non-vertebrate taxa ($n = 3$) had a single enquiry each.

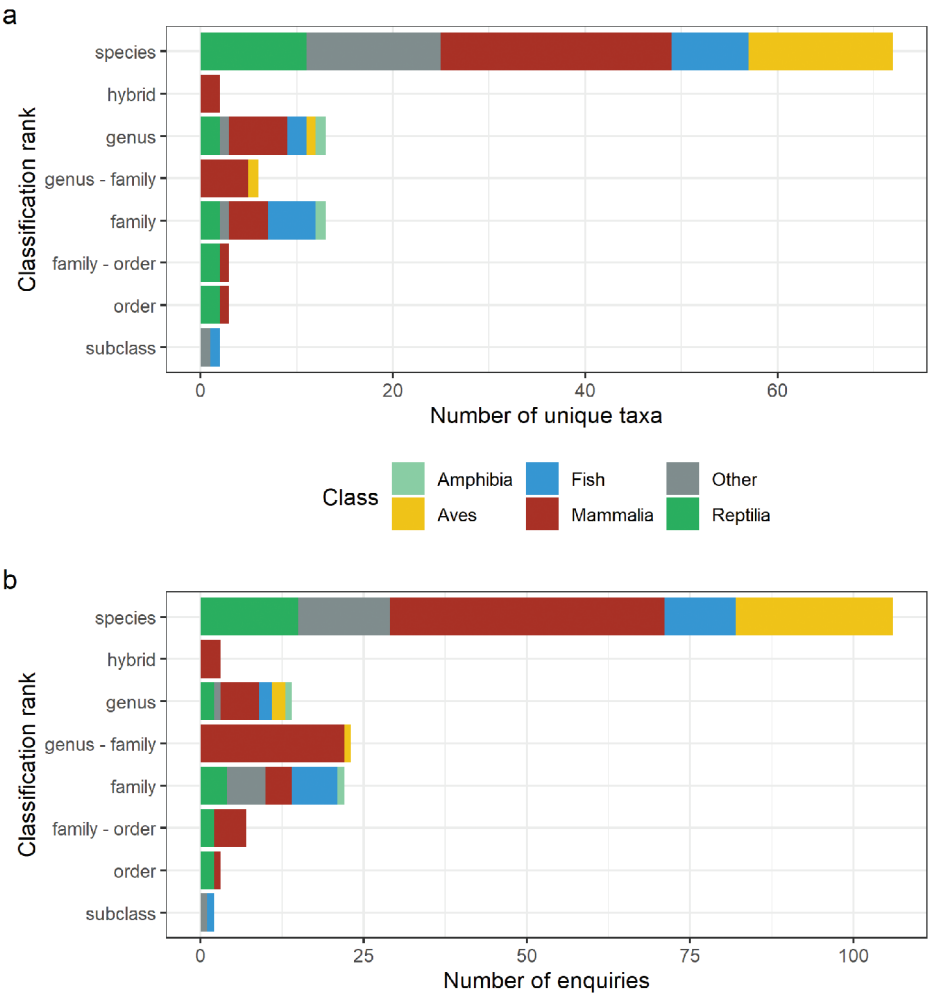


Figure 2. The number of unique taxa (a) and total enquiries (b) according to taxonomic classification rank for enquiries relating the private use of keeping or importing pets. We resolved the species or common names mentioned by the enquirers to the most specific possible taxonomic rank. Here, species refers to both species and subspecies. Genus – family corresponds to taxonomic ranks in between genus and family (i.e. tribe, subfamily) and family – order corresponds to taxonomic ranks in between family and order (i.e. infra-order). Colours correspond to the taxonomic class, where fish includes Chondrichthyes and Actinopterygii. Other taxonomic class refers to taxa not in vertebrate (Vertebrata) classes.

Comparative analysis

We found that enquired species were more popular than expected by chance compared to species in the U.S. exotic pet trade ($p = 0.007$, Fig. 4a). We found that the proportion of enquired species threatened by extinction (IUCN listed) is higher than the

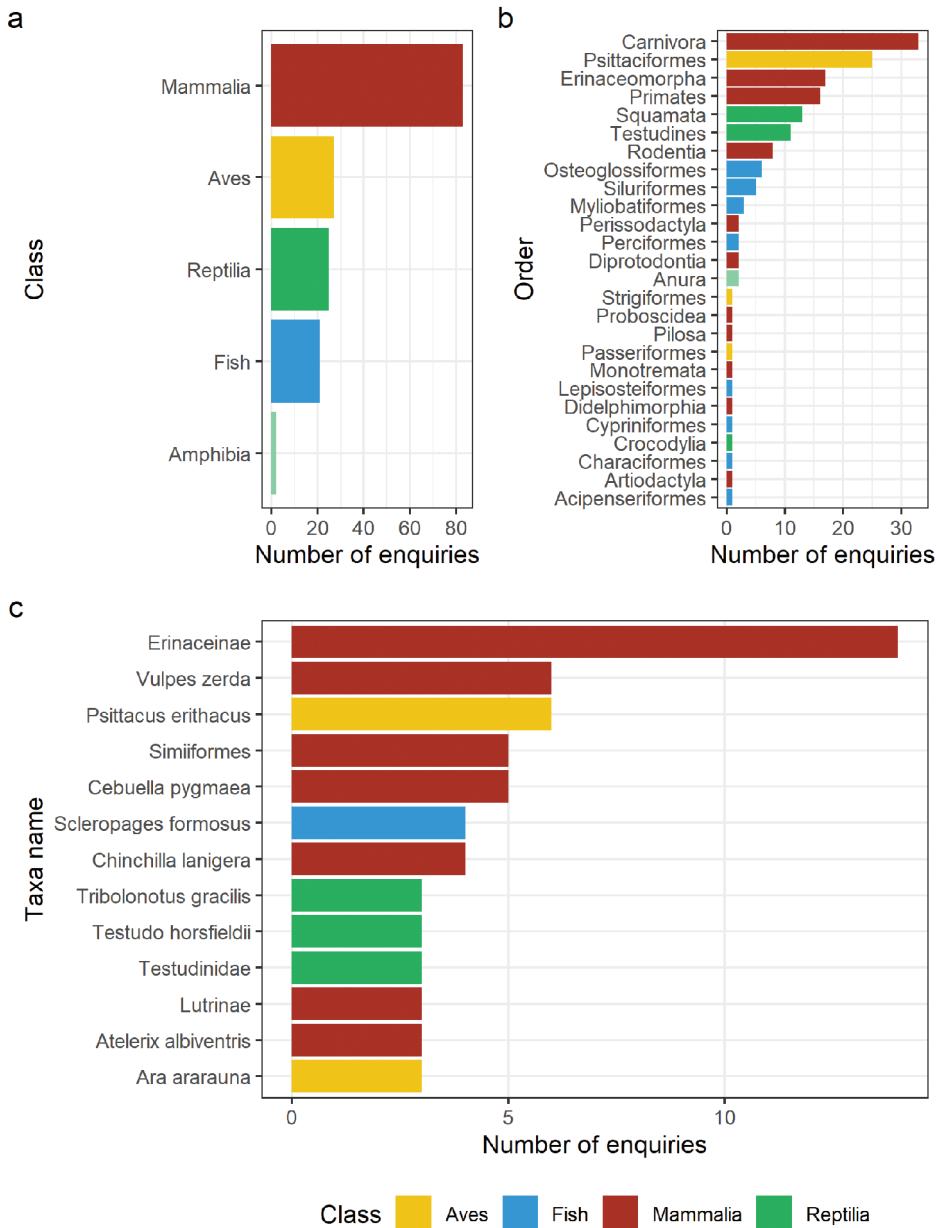


Figure 3. The number of enquiries by taxonomic class (a) and order (b) and highest taxa specified (c), excluding invertebrates. The subfamily Erinaceinae includes hedgehogs, *Vulpes zerda* is the fennec fox, *Psittacus erithacus* is the African grey parrot, order Simiiformes refers to monkeys, *Cebuella pygmaea* is the pygmy marmoset, *Scleropages formosus* is the Asian arowana, *Chinchilla lanigera* is the long-tailed chinchilla, *Tribolonotus gracilis* is the red-eyed crocodile skink, *Testudo horsfieldii* is the Russian tortoise, the family Testudinidae includes tortoises, the family Lutrinae include otters, *Atelerix albiventris* is the four-toed hedgehog and *Ara ararauna* is the blue-and-yellow macaw.

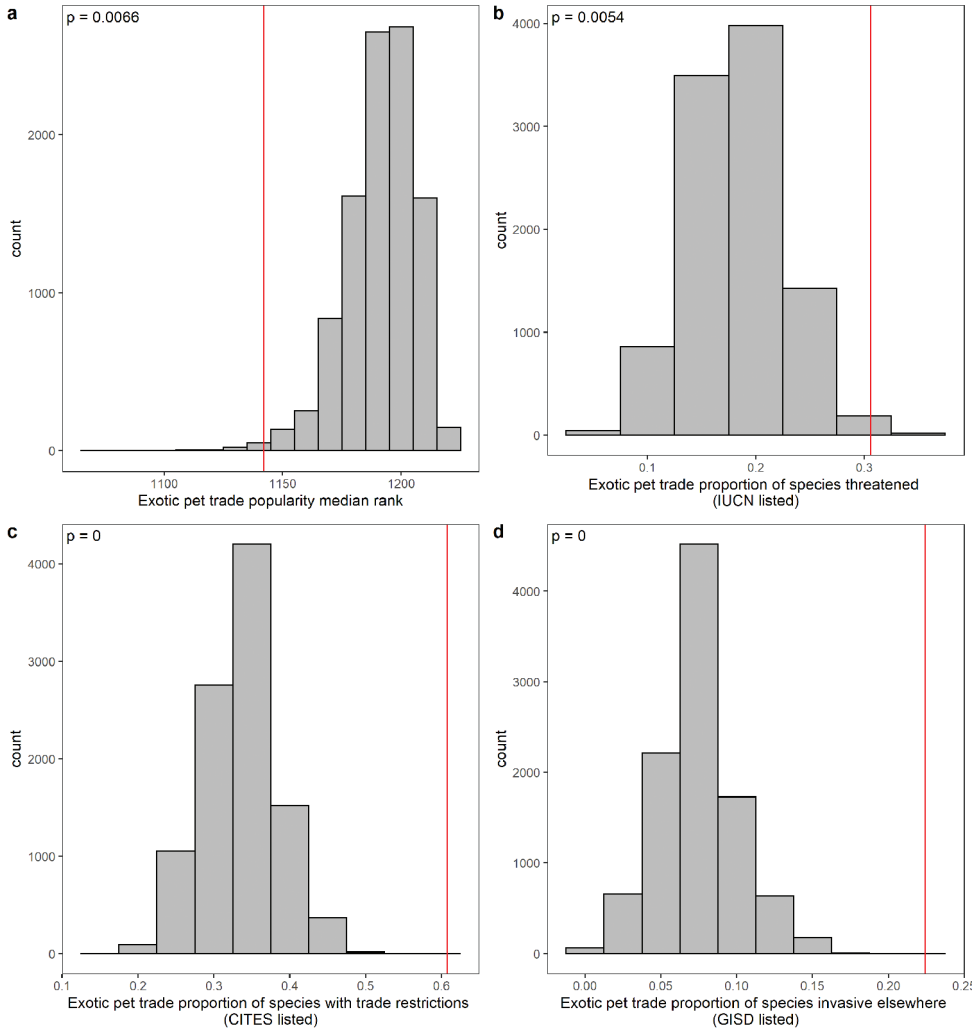


Figure 4. Empirical hypothesis tests comparing: (a) enquired species popularity; (b) proportion of threatened species; (c) proportion of international trade-restricted species; and (d) proportion of invasive species, to the overall exotic pet trade. Each histogram represents 10,000 iterations of random sampling from the U.S. Fish and Wildlife imports dataset from 1999–2016 (representative of the Western exotic pet trade), stratified by taxonomic class. Red lines correspond to the ‘observed’ median rank or proportion from the enquired species. P-values are calculated as the proportion of sampling iterations that fall to the left or right of the observed rank or proportion. Non-vertebrate taxa were not included in these analyses.

proportion in overall pet trade ($p = 0.005$, Fig. 4b). Additionally, we found that the proportion of enquired species with trade restrictions (CITES listed) is higher than the proportion in overall pet trade ($p < 0.005$, Fig. 4c). Finally, we found that the proportion of enquired species that are invasive species elsewhere (GISD listed) is higher than the proportion found in overall pet trade ($p < 0.005$, Fig. 4d).

Discussion

Australia imposes strict legislation to prevent the importation of alien vertebrate species (Henderson and Bomford 2011), yet the continual rise in illegally smuggled pets suggests that biosecurity efforts are being undermined (Toomes et al. 2019). Here, we characterised the attributes of desirable alien species. In the absence of direct information on which illegal alien species are most desirable, our approach serves as a reasonable first step to identify the characteristics of species that can be a future and conservation biosecurity threat. We revealed that the Australian desire for illegal alien pets is biased towards species threatened with extinction, species with global trade restrictions in place, species with a history of successful invasions and species frequently imported into the U.S., a western market with less stringent pet-trade regulations. In addition, we show a taxonomic bias towards a desire for mammal species. This knowledge is easily interpretable and can be used to anticipate future trends in illegal animal imports and to focus biosecurity surveillance efforts.

Our findings that desired species were more likely to be IUCN-listed and CITES-listed compared to overall trade are consistent with the Anthropogenic Allee Effect, a process in which the trade and harvest of a species increases with rarity due to its effect on perceived value (Courchamp et al. 2006; Holden and McDonald-Madden 2017). Specifically, our results show a bias towards CITES-listed primates, some of which have previously been seized from illegal captivity in Australia, such as the pygmy marmoset (*Cebuella pygmaea*) (Toomes et al. 2019). In Thailand, Siriwat et al. (2019) found a high number of primates for sale in various social media groups, as well as price-rarity dynamics consistent with the Anthropogenic Allee Effect.

In addition to conservation indicators, we found that desired species were much more likely to be invasive than expected by chance. Unlike the Anthropogenic Allee Effect, we are not aware of any study that shows a correlation between desirability of a species and their invasion status. This novel finding is of great concern for biosecurity agencies because it suggests that a filtering process is occurring where illegally smuggled animals may already be “pre-selected” to have the characteristics that are correlated with invasive species. For instance, traits closely associated with successful invasions include high fecundity and broad climatic tolerances (Herrel and van der Meijden 2014; Capellini et al. 2015; Howeth et al. 2016). In addition, the most desired taxa (mammals and birds) are considered ‘charismatic’, meaning people prefer them due to their appearance, behaviour or function (Beeves et al. 2019). These charismatic taxa may present an additional challenge to biosecurity because, if they become introduced or established, the general public may oppose eradication efforts (e.g. free-roaming horses in Australia, monk parakeets in the U.S. (Crowley et al. 2017; Knight 2019; Pruett-Jones et al. 2012)). Some examples of enquired species, which have yet to be detected in Australia but have established invasive species elsewhere, include the Argentine black and white tegu (*S. merianae*) (Johnson et al. 2017) and raccoon dogs (*Nyctereutes procyonoides*) (Kauhala and Kowalczyk 2011), representing potential future biosecurity risks for Australia. However, we emphasise that the probability of establishment of alien

species, as well as the scale of potential impacts, should be considered alongside public desire in determining high-priority biosecurity threats (Bacher et al. 2018; Blackburn et al. 2014; Bomford et al. 2009; Cassey et al. 2014; Davidson et al. 2016).

Our analysis relied on information collected in the style of a self-selecting survey from people interested in acquiring alien species, particularly pets. This does not necessarily represent actual intentions to illegally acquire alien pets and it remains unknown how desirability and introduction efforts are correlated. Given the records of illegally smuggled animals and illegally kept pets in Australia (Toomes et al. 2019), it is clear that there are people in Australia intent on acquiring illegal-alien pets. Whether the enquirers' desired pets are aligned with people who illegally acquire pets has not been tested. Therefore, one future avenue of research would be to interview people involved in the illicit trade. However, this is a problem with illegal activities in general; it is difficult to acquire information as people are unwilling to disclose or admit to illicit actions (Gnambs and Kaspar 2015). Following survey methodologies developed in the field of criminology may be useful to acquire information about the species in the illicit trade and the motives behind the want to acquire these species (Kleck and Roberts 2012). Similarly, these methods could be used to contact existing Australian wildlife breeders/traders and acquire a list of desired species that would be traded if legalised. Such a dataset would provide a representative sample of Australian wildlife traders and would help verify the extent to which anonymous enquiries are representative.

The legislative framework surrounding the import of alien pets, to which our enquiry data pertain, has a number of shortcomings that need to be addressed in order for the threat of alien imports to be reduced. In particular, there are discrepancies between what can be legally imported into Australia and what can be legally kept in domestic captivity as part of the national permitted list (Part 13A of the EPBC 1999) or State/Territory legislation. A large number of species are not permitted for live import, yet possession of live individuals within Australia is not necessarily a prosecutable offence unless evidence can be provided that the individuals have an illegal origin (Ciavaglia et al. 2015). Such evidence, requiring forensic analysis of provenance (e.g. Campbell et al. (2019)) is rarely available and costly to acquire. Thus, the purportedly captive-bred trade of species which potentially pose high biosecurity risks to Australia and which potentially originated from illegal import, continues unabated. We recommend renewed priority in addressing this legislative gap, including a national audit of alien species currently traded, in order to increase synergy between permitted imports and legal captive keeping.

Using U.S. import frequency, we have demonstrated that Australian import enquiries are heavily biased towards species popular in an overseas western market. The underlying process behind this observation deserves more investigation. We hypothesise that both U.S. legal trade and Australian demand for alien pets are driven by the same underlying processes, facilitated by the emergent role of social media in providing access to and awareness of available pets (Clarke et al. 2019; Harrington et al. 2019; Kitson and Nekaris 2017). Under this hypothesis, DAWE enquiries would represent a random sample of desire for species in the U.S. trade weighted by their popularity. This suggests the U.S. import data may have considerable utility for Australian biosecurity in predict-

ing species that are likely to either be illegally present yet undetected, or arrive illegally in the short-term future. This is exemplified by the fact that the vast majority (98.7%) of the 75 alien reptile species detected in Australia are present in the U.S. trade (Toomes et al. 2019). Further research aims to test these hypotheses with a comparative analysis between U.S. imports and the interception records collated by Toomes et al. (2019).

Conclusions

Invasive alien species have the potential to be introduced into Australia despite substantial investment in border and post-border biosecurity. We characterised a subset of domestic desire for alien pets via public import enquiries and identified several biases pertinent to both biosecurity and the conservation of threatened species. Specifically, desired species are more likely to be threatened by extinction and be invasive species elsewhere compared to species in the overall pet trade. Moreover, we emphasise the need for modifications to Australia's live import list in order to maintain relevance with a rapidly changing international pet trade. Finally, the utility of the U.S. pet demand as a predictor of Australian desire for alien pets needs to be investigated further and for other regional pet markets, in order to foster greater biosecurity preparedness.

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Into the great wide open: do alien plants spread from rivers to dry savanna in the Kruger National Park?

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Abstract

Protected areas play an important role as refuges from invasive species impacts on biodiversity. Within the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project, plant species were recorded in a representative set of 60 plots, 50 × 50 m in size, across the entire KNP, distributed so as to cover a range of savanna habitats, i.e. perennial rivers, seasonal rivers and dry crests, and two main bedrock types (granite and basalt). The data were used to assess the role of rivers in the dispersal of alien plants and study whether the alien plant species spread from rivers to open dry savanna. The resulting dataset provided the first thorough information on the spatial distribution of naturalised alien plants in KNP. In total, we recorded 20 plant species that are alien to the park, four of them considered invasive: *Parthenium hysterophorus*, *Opuntia stricta*, *Xanthium strumarium* and *Zinnia peruviana*. The most widespread species in KNP was *Tridax procumbens*, recorded in 11 plots (i.e. 18% of all sampled), four other species were found in > 10% of the plots. One species, *Bidens bipinnata*, was not previously reported from the park and represents a new record. The majority of aliens were concentrated along perennial rivers (60% of all occurrences), but some were repeatedly recorded at seasonal rivers as well and two of the most invasive species in KNP, *Opuntia stricta* and *Parthenium hysterophorus*, occurred also on dry crests away from water.

The average number of alien species per plot was low (1.6), as was their mean percentage contribution to all species in a plot (2.2%), but some plots harboured as many as seven species and contributed up to 11.9%. Moreover, only 21 plots (35%) were alien-species free. In terms of the total species number per habitat, perennial rivers had significantly more aliens than crests and were marginally significantly richer than seasonal rivers. By recording all naturalised alien species occurring in the plots – many of them are not invasive but may become so in the future – and by using the GloNAF database of global distribution of naturalised species, we assessed the invasion potential of the recorded species.

Keywords

alien species richness, crest, habitat, perennial river, plant invasion, protected area, savanna, seasonal river

Introduction

The majority of protected areas worldwide are vulnerable to invasions, with very few completely free of alien species (Foxcroft et al. 2017; Moodley et al. 2020) and many suffering various impacts at the species and community levels. These impacts include the alteration of habitats, ecosystem regime shifts and losses to native species abundance, diversity and richness (Foxcroft et al. 2013; Hulme et al. 2014; Pyšek et al. 2020). In a global assessment, De Poorter (2007) found there were 487 protected areas where invasive alien species posed a serious threat to biodiversity. Along these lines, invasive plants are almost universally regarded as a major threat by managers of protected areas (Pyšek et al. 2013). However, the situation is not improving over time, as shown by Shackleton et al. (2020). These authors compared how the threat by and management of invasive species have changed in a representative set of 21 protected areas that were included in the international SCOPE programme on biological invasions in the mid-1980s (Drake et al. 1989). Amongst the taxonomic groups analysed, invasive plants pose the greatest continued threat, as documented by increased numbers in 31% of the protected areas over ~30 years from 1980s to the present (Shackleton et al. 2020).

One of the iconic protected areas included into the SCOPE programme is the Kruger National Park (KNP) in South Africa. Established in 1898, it is the largest game reserve in South Africa and one of the oldest national parks in the world (Caruthers 1995). It covers an area of ~20,000 km², the majority in a subtropical climate with the Tropic of Capricorn crossing the park in the North. Several large, mostly perennial, rivers flow through the park in a west-east direction, including Sabie, Olifants, Crocodile, Letaba, Shingwedzi, Luvuvhu and Limpopo (Fig. 1, MacFadyen et al. 2018). Environmental heterogeneity is generated by a mosaic of geological conditions (granitoid bedrock in the western vs. basalt and gabbro in the eastern part), altitude (140–780 m a.s.l.), climate (450–750 mm of annual precipitation) and character of vegetation (dominant woody species, proportional representation of woody cover vs. open grassland; du Toit et al. 2003; MacFadyen et al. 2016).

There are about 360 alien plant species currently recorded in KNP (Foxcroft et al. 2017), of which only a few are considered noxious invaders (Jarošík et al. 2011).

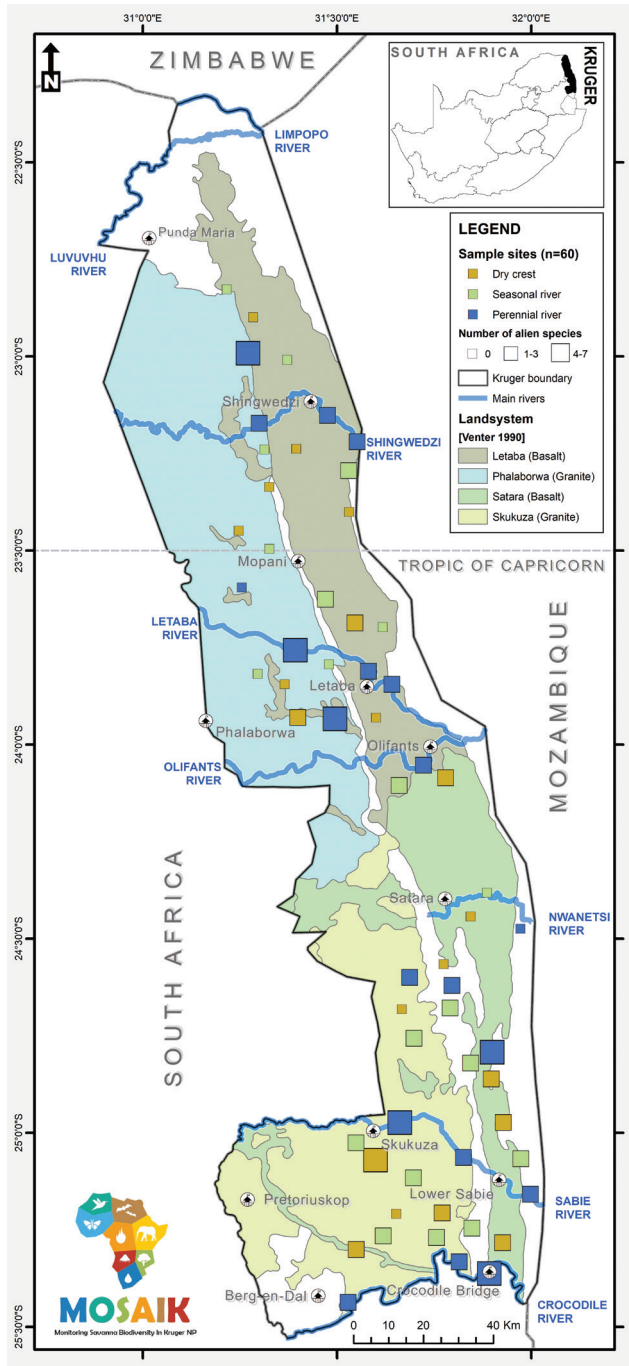


Figure 1. The Kruger National Park situated between latitudes 22°19'40"S to 25°31'44"S and longitudes 30°53'18"E to 32°01'59"E, with location of the 60 sampled sites, separated according to habitat and distributed across the four land systems. The size of the symbols indicates the number of alien plant species recorded in the plot.

The boundaries of KNP were shown to act as a barrier to invasions from the surrounding intensively-used agricultural landscape or urbanised areas (Foxcroft et al. 2011), in accordance with the role protected areas play in other parts of the world by offering refuges from invasive species (Pyšek et al. 2003; Gallardo et al. 2017). For KNP, it has been shown that the best human-related predictors of the number of alien invasive plants inside the park were the amount of water bringing propagules from adjacent densely populated areas, together with density of major roads (Foxcroft et al. 2011) and human settlements in the park surroundings (Spear et al. 2013). A study of invasive species across South African National Parks identified ornamental planting and rivers as the primary pathways of invasion (Foxcroft et al. 2019) – a large number of alien ornamental species and alien species occurring along rivers are reported for KNP (Foxcroft et al. 2008). Therefore, a great threat from alien plant invasions to KNP is associated with rivers that act as the most efficient pathways for propagules from adjacent areas. However, while these indicators represent the potential for introduction of alien plants into KNP, the context dependence of the invasion process requires study at finer scales to determine which alien species may become naturalised and invade within KNP.

In response to the escalating importance of plant invasions, KNP has initiated a number of programmes aimed at preventing and mitigating incursions of alien species (van Wilgen et al. 2017). These efforts have yielded data on the distribution of major invaders through long-term monitoring (Foxcroft et al. 2009) and species-specific studies on the ecology of particular invaders (Foxcroft et al. 2004; Hui et al. 2011). However, as is often the case in plant invasion research, the data collection focused on alien species hotspots, such as human-disturbed habitats or rivers and, to date, none of the projects in KNP has systematically investigated the distribution of alien plants across the entire park or assessed how successfully they persist across a range of different habitats.

To contribute to closing this gap, we use our data collected by the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project aimed at studying biodiversity across the entire KNP, within four distinct land systems with variable supply of water and contrasting geologies. Here we aim to (i) describe the distribution of alien plant species, (ii) assess to what extent alien plants are confined to rivers as the main introduction pathways and dispersal vectors, versus how commonly they occur in drier habitats away from rivers and (iii) identify potentially invasive species of the future.

Methods

Data collection

The data analysed in this paper were collected within the MOSAIK project between 2018 and 2020. MOSAIK's primary objective is to sample plant and animal (mammals, birds, bats and moths) biodiversity in habitats across different land systems in

KNP (as defined by Venter 1990). To this purpose, we established triplets of 50×50 m plots, each triplet including a site (i) near a perennial river or another permanent source of water, such as a dam or pool (the criterion being water present all year round), (ii) near a seasonal river, defined as a river or stream where water is only present in the rainy season and (iii) on a dry crest at least 5 km from any source of water (Fig. 2). The plots within each triplet were selected to capture the different habitats in a similar landscape context within a reasonable distance of ~7–13 km between plots. There were 20 triplets distributed so as to cover the four land systems (five triplets in each), giving a total of 60 plots (Fig. 1). Consequently, each of the three habitats was sampled by 20 plots and each of the two bedrock types by 30 plots.

Plants were sampled during two rainy seasons, 16 January to 4 February 2019 and 17 January to 3 February 2020. All vascular plant species were recorded in each 2500 m² plot and their abundance estimated visually using the Braun-Blanquet cover-abundance seven-grade scale (Mueller-Dombois and Ellenberg 1974). To quantify the occurrence of species in plots, the Braun-Blanquet scores were transformed to percentage values as follows: 5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2 = 15%, 1 = 2.5%, + = 1.0%, r = 0.02% (van der Maarel 1979). The time spent to sample a plot ranged from 1 to 7 hours, with an average of $2:15 \pm 1:01$ hour (mean \pm S.D.).

Species that are alien to South Africa were selected for analyses in this paper. To assign species an alien status, we followed geographical criteria broadly accepted in the invasion literature, referring to species introduced by humans to regions outside their native range (see Pyšek et al. 2004; Essl et al. 2018 for definitions). Further, to classify which of the recorded alien species are naturalised (forming self-sustainable populations in the wild) or invasive (subgroup of naturalised species rapidly spreading in the invaded area), we followed the definition proposed by Richardson et al. (2000) and Blackburn et al. (2011). This classification of species was based on previous publications relevant to the study area (Foxcroft et al. 2017). For each species, we recorded the region of origin and life history information.

To assess the invasion potential of the alien species recorded in KNP, we extracted information on their global naturalisation success from the GloNAF (Global Naturalized Alien Flora) database (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). This database includes information on the occurrence of naturalised plant species in 843 regions of the world (at the level of countries, states and provinces in case of large countries and islands) and summarises the distributions of almost 14,000 taxa. For each species recorded in our plots, we extracted the number of GloNAF records globally and in Africa.

Statistical analysis

Differences amongst habitats and bedrock in the mean numbers of alien species in plots were tested by using a Linear Mixed-Effects Model (LMM) (R Development Core Team 2013; Bates et al. 2015). The square-root of the number of alien species

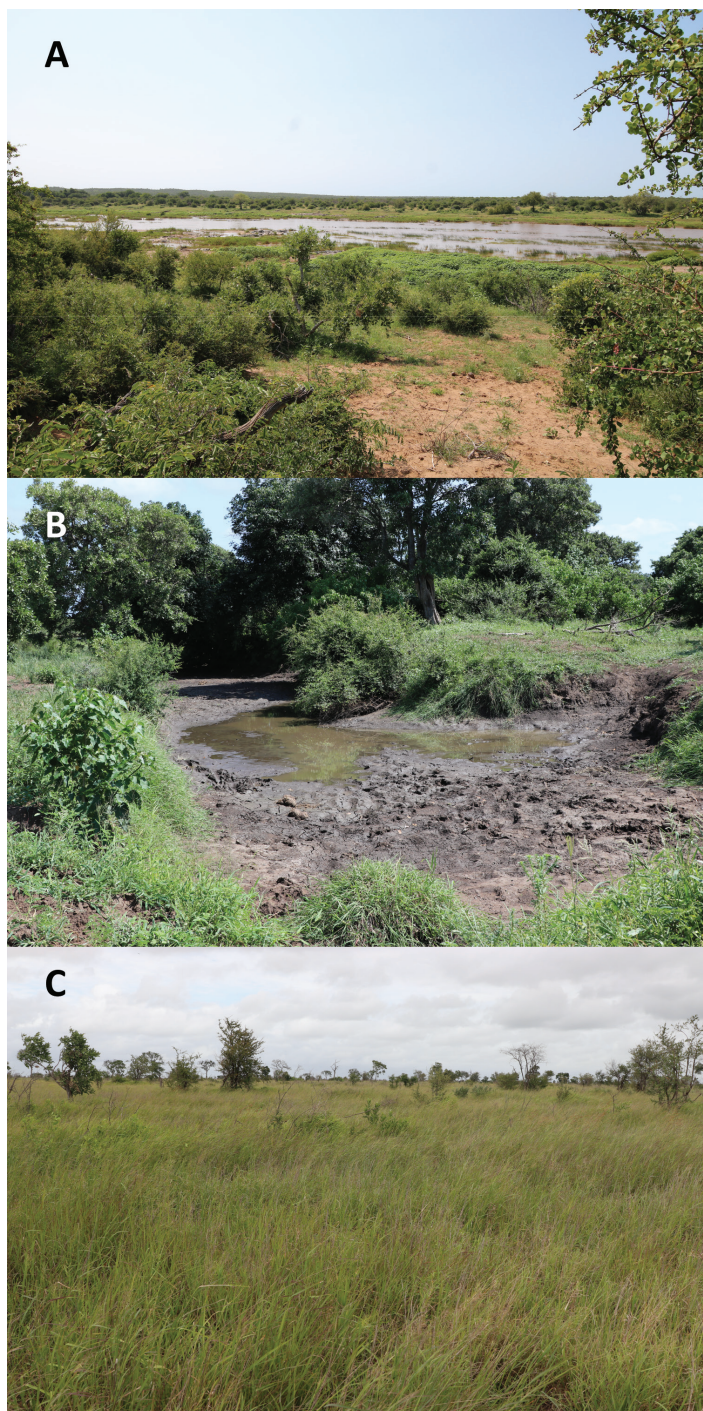


Figure 2. Images of habitats that were considered in the Kruger National Park study: **A** perennial river, **B** seasonal river and **C** dry crest. The plots were located in the vicinity of the rivers, near the river beds and within the crest.

was the response variable and the type of bedrock (granite vs. basalt), habitat (seasonal rivers, perennial rivers, crests) and their interactions were the predictors. The triplets of plots were set as the random effect factor (grouping variable). Possible autocorrelations, based on the distances between individual triplets, were modelled as a continuous function, using the “cor” parameter. The significances of different predictors (bedrock, habitat, bedrock \times habitat interaction) were tested using deletion tests, by comparing the explanatory power of models with and without a particular term (Crawley 2007). The quality of models was checked visually, by plotting standardised residuals against fitted values. Possible deviations from normality were inspected using probability plots. The data on the percentages of aliens amongst all species in plots were arcsin-transformed.

A log-linear model (Crawley 2007) was used to test the differences in the total numbers of aliens amongst different habitats and bedrocks. In this model, the total number of aliens was the response variable and habitat (seasonal rivers, perennial rivers, crests), bedrock (granite, basalt) and their interaction were the predictors. The significance of individual terms was tested using deletion tests, by comparing the explanatory power of models with and without that particular main effect or interaction (Crawley 2007). All models were created in the R software (R Development Core Team 2013).

Results

Structure of alien flora: effects of habitat and bedrock on species' occurrence patterns

In total, we recorded 20 plant species that are classified as naturalised aliens to KNP (Table 1). Family Asteraceae was most represented with nine species, followed by Amaranthaceae with four species, Cactaceae with two species and the remaining five species in five other families. There are 13 species that occur as annuals (50%), 10 as perennials (39%), two as shrub or semi-shrub (*Malvastrum coromandelianum* and *Datura innoxia*, respectively). Four of the species recorded are considered invasive in KNP: *Parthenium hysterophorus* (recorded in nine plots, i.e. 15% of all sampled), *Xanthium strumarium* (three plots), *Opuntia stricta* (three plots) and *Zinnia peruviana* (two plots). The remaining species are considered naturalised, except *Bidens bipinnata* that was not previously reported from the park and represents a new record; for this species, the status remains to be confirmed.

The most widespread species in KNP was *Tridax procumbens*, recorded in 11 plots (i.e. 18%), other species recorded in more than 10% of plots being *Bidens biternata*, *Malvastrum coromandelianum*, *Parthenium hysterophorus* and *Alternanthera pungens* (Table 1; Fig. 3). The majority of alien species recorded in our KNP plots have successfully naturalised in various parts of the world, with 11 of them occurring in more than 100 regions globally (*Portulaca oleracea* and *Chenopodium album* with 311 and 298 regions, respectively, are the most widespread). These data indicate the overall potential of recorded alien plants to spread; the majority of them have also successfully

Table 1. Overview of alien plant species recorded in savanna habitats in the Kruger National Park. Total number of records, separately for basalt and granite bedrock, frequency of occurrence in plots (n = 60) and the range of covers are given (one cover value indicates that the species occurred in plots with the same cover). Species that are currently considered as invasive in KNP are marked with * (based on Foxcroft et al. 2017). The naturalisation success is expressed as the number of regions in the GloNAF 1.1 database (n = 843, van Kleunen et al. 2015, 2019; Pyšek et al. 2017) in which the species is recorded as naturalised, shown globally and for Africa. Life history: a – annual herb, p – perennial herb, ss – subshrub. Species are ranked by decreasing frequency in KNP.

| Species | Family | Life history | Origin | Occurrences | Frequency (%) | Basalt | Granite | Cover (%) | Naturalised globally/in Africa |
|-----------------------------------|---------------|--------------|--------------------------------|-------------|---------------|--------|---------|-----------|--------------------------------|
| <i>Tridax procumbens</i> | Asteraceae | a | central America | 11 | 18.3 | 3 | 8 | 0.1 | 146/55 |
| <i>Bidens biternata</i> | Asteraceae | a | East Asia (Himalayas) | 10 | 16.7 | 4 | 6 | 0.1–15.0 | 31/29 |
| <i>Malvastrum coromandelianum</i> | Malvaceae | a, p, ss | North America | 10 | 16.7 | 5 | 5 | 0.1 | 161/29 |
| <i>Parthenium hysterophorus</i> * | Asteraceae | p | North America | 9 | 15.0 | 4 | 5 | 0.1 | 119/13 |
| <i>Alternanthera pungens</i> | Amaranthaceae | p | tropical America | 8 | 13.3 | 5 | 3 | 0.1–2.5 | 124/35 |
| <i>Bidens bipinnata</i> | Asteraceae | a | Asia, North America | 6 | 10.0 | 2 | 4 | 0.1–15 | 88/26 |
| <i>Gomphrena celosioides</i> | Amaranthaceae | a, p | tropical South America | 6 | 10.0 | 2 | 4 | 0.1 | 94/43 |
| <i>Acanthospermum hispidum</i> | Asteraceae | a | tropical America | 5 | 8.3 | 3 | 2 | 0.1–2.5 | 128/49 |
| <i>Portulaca oleracea</i> | Portulacaceae | a | Eurasia | 4 | 6.7 | 3 | 1 | 0.1 | 311/56 |
| <i>Melanthera scandens</i> | Asteraceae | p | tropical to subtropical Africa | 4 | 6.7 | 3 | 1 | 0.1 | 12/12 |
| <i>Litogyne gariepina</i> | Asteraceae | p | obscure | 3 | 1.7 | 2 | 1 | 0.1 | – |
| <i>Xanthium strumarium</i> * | Asteraceae | a | America ¹ | 3 | 5.0 | 2 | 1 | 0.1 | 147/18 |
| <i>Opuntia stricta</i> * | Cactaceae | p | North America | 3 | 5.0 | 0 | 3 | 0.1 | 84/10 |
| <i>Achyranthes aspera</i> | Amaranthaceae | a, p | Mediterranean | 2 | 3.3 | 2 | 0 | 0.1 | 160/52 |
| <i>Zinnia peruviana</i> * | Asteraceae | a | North to South America | 2 | 3.3 | 1 | 1 | 0.1 | 45/9 |
| <i>Opuntia ficus-indica</i> | Cactaceae | p | North America | 1 | 1.7 | 0 | 1 | 0.1 | 139/40 |
| <i>Argemone ochroleuca</i> | Papaveraceae | a | North America | 1 | 1.7 | 1 | 0 | 0.1 | 96/15 |
| <i>Chenopodium album</i> agg. | Amaranthaceae | a | Eurasia | 1 | 1.7 | 1 | 0 | 0.1 | 298/28 |
| <i>Datura innoxia</i> | Solanaceae | p, ss | North America | 1 | 1.7 | 1 | 0 | 0.1 | 126/29 |
| <i>Verbesina encelioides</i> | Asteraceae | a | South America | 1 | 1.7 | 0 | 1 | 0.1 | 88/12 |

¹some sources give Eurasia as the region of origin

naturalised in Africa. In particular, *Portulaca oleracea* (56 regions), *Tridax procumbens* (55), *Achyranthes aspera* (52), *Acanthospermum hispidum* (49) and *Gomphrena celosioides* (43) are species that are most widely naturalised in this continent (Table 1).

In terms of distribution of the recorded species by habitats, the majority were concentrated at perennial rivers. Some species, for example, *Alternanthera pungens*, *Gomphrena celosioides* and *Acanthospermum hispidum*, occurred almost exclusively in this habitat, whilst others, for example, *Bidens biternata*, *Malvastrum coromandelianum* and *Parthenium hysterophorus*, were repeatedly recorded also at seasonal rivers and *Opuntia stricta*, *Parthenium hysterophorus* and *Tridax procumbens* on the crests, too (Fig. 3).

The majority of species did not prefer any particular bedrock, with the exception of four species occurring more frequently on granites: *Tridax procumbens* (eight records on granites vs. three on basalts), *Bidens bipinnata*, *Gomphrena celosioides* (four vs. two) and *Opuntia stricta* (three records exclusively on granite). The species occurring more often on basalt bedrock were *Alternanthera pungens* (three vs. five) and *Melanthera scandens* (three vs. one) (Table 1).

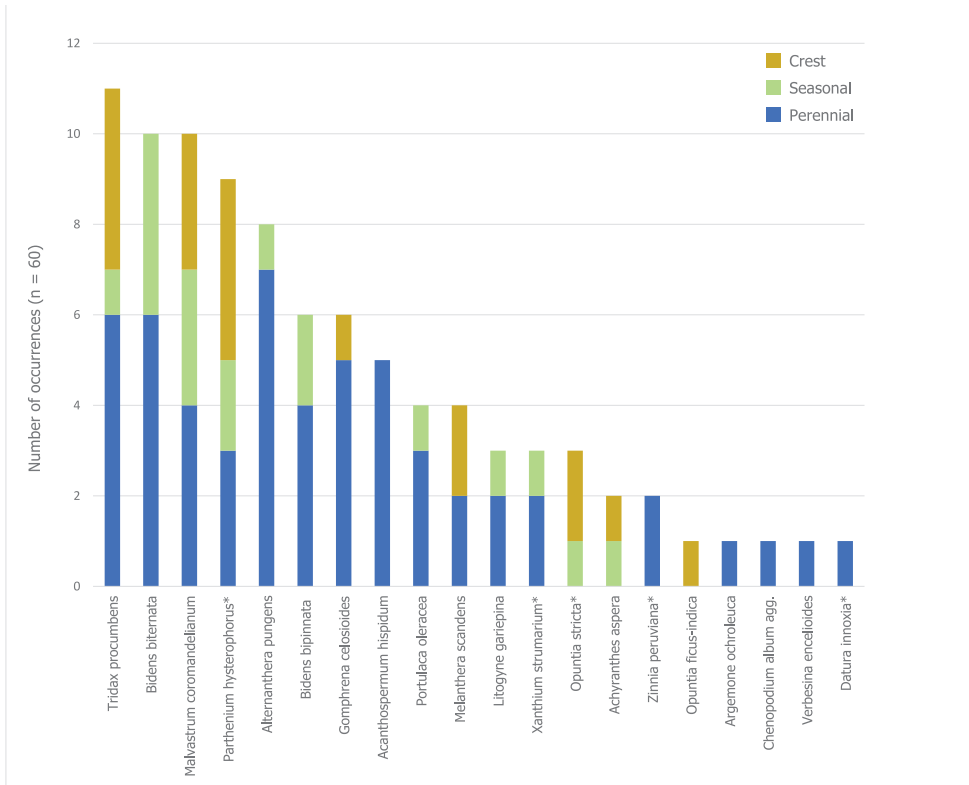


Figure 3. Distribution of alien species in the Kruger National Park according to the savanna habitats delimited within the MOSAIK project (perennial rivers, seasonal rivers, dry crest). Numbers of occurrences (n = 20 per habitat) are shown. Species with * are considered invasive in KNP.

Levels of invasion in savanna habitats: rivers and beyond

The average number of alien species per plot was relatively low, 1.6 ± 1.7 (mean \pm S.D.), but only 21 plots out of 60 were alien free, meaning that 65% of plots harboured some alien species. The maximum number of alien species per plot was seven. On average, the alien species made up 2.2% (range 0–11.9%) of all species in a plot. The numbers of alien and native species in plots were not correlated ($r = 0.067$, $DF_{\text{resid}} = 58$, $p = 0.609$).

Testing the average number of aliens per plot (Fig. 4A) revealed a significant effect of habitat (LMM: deletion test, $DF_{\text{model}} = 5$ vs. 7, L-ratio = 22.175, $p < 0.001$), with perennial rivers being significantly richer than seasonal rivers and crests (LMM: $DF_{\text{error}} = 36$, $T = -2.751$, $p = 0.0092$; $DF_{\text{error}} = 36$, $T = -3.662$, $p = 0.0008$, respectively).

In total, there were 17, 11 and 8 species recorded at perennial rivers, seasonal rivers and on the crest, respectively, and the total numbers of alien species in a habitat (Fig. 4B) significantly differed (log-linear model: deletion test, $DF_{\text{resid}} = 2$ vs. 4, Dev. = -10.76, $p = 0.005$). Perennial rivers had significantly more aliens than crests ($z = -2.842$, $p = 0.0125$).

and seasonal rivers ($z = 2.361$, $p = 0.048$). Only three species (*Tridax procumbens*, *Malvastrum coromandelianum* and *Parthenium hysterophorus*) occurred in all three habitats. Perennial rivers had six species occurring exclusively in this habitat and another six they share with seasonal rivers (see Fig. 3), one species was found exclusively on crests (*Opuntia ficus-indica*) and none only at seasonal-river sites (Fig. 5). In terms of the number of occurrences (defined as the sum of the numbers of records over all alien species), the importance of the perennial rivers was even more pronounced. The 55 occurrences at perennial rivers

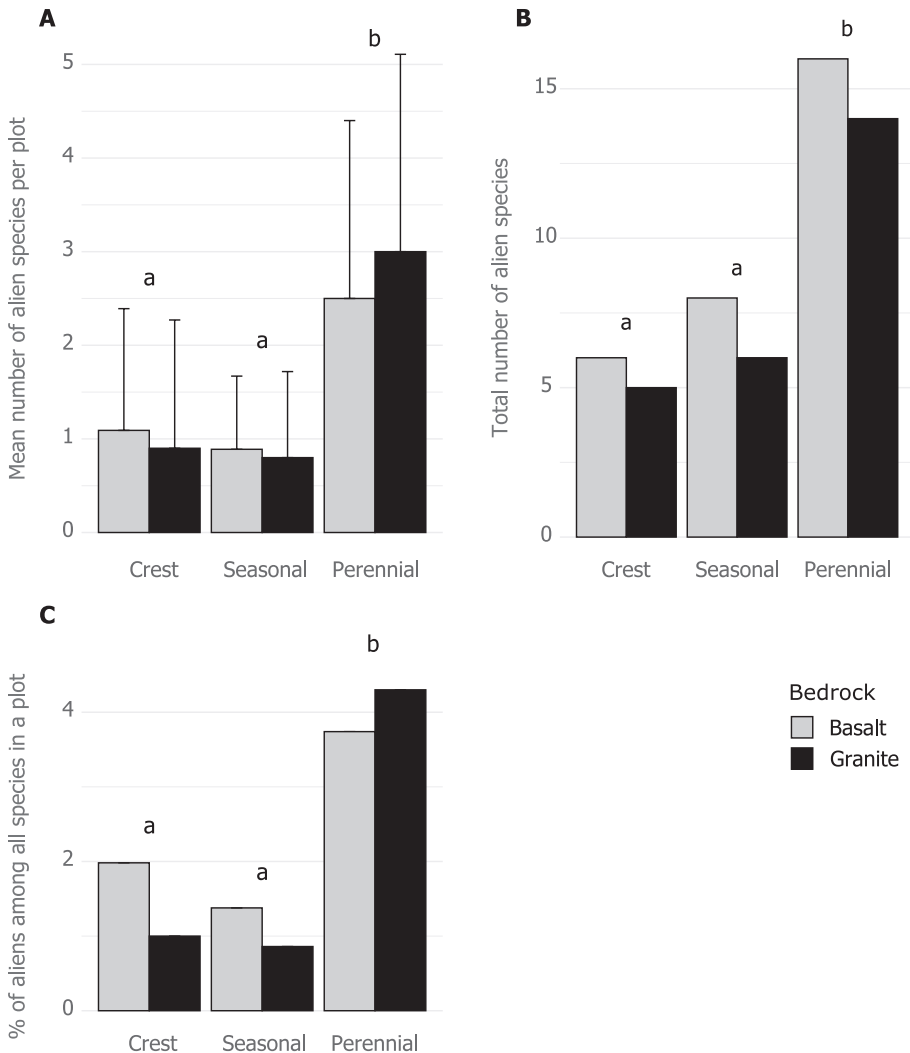


Figure 4. Level of invasion by bedrock and habitat. **A** Mean numbers \pm S. D. of species per plot ($n = 20$ per habitat) **B** total species numbers and **C** percentage of alien species amongst all species in a plot are shown for particular factors. The habitats bearing the same letter were not significantly different in the respective characteristics; the effect of bedrock was not significant.

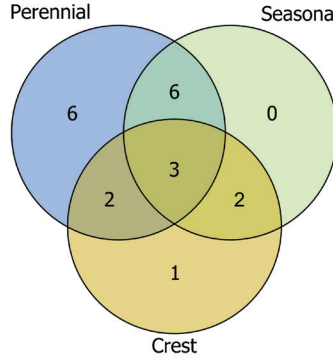


Figure 5. Venn diagram showing the sharing of alien species by habitats in the Kruger National Park. *Tridax procumbens*, *Malvastrum coromandelianum* and *Parthenium hysterophorus* were the species recorded at all three habitats.

(compared to 18 at seasonal rivers and 18 in crest plots) means that 60.4% of all alien species' occurrences were associated with the former habitat.

The percentage of alien species per plot (Fig. 4C) differed amongst habitats (LMM: deletion test, $DF_{\text{model}} = 5$ vs. 7, L-ratio = 7.884, $p = 0.005$), with perennial rivers being marginally significantly richer than crests (LMM: $DF_{\text{error}} = 36$, $T = -2.004$, $p = 0.053$) and significantly richer than seasonal rivers (LMM: $DF_{\text{error}} = 36$, $T = -2.218$, $p = 0.033$).

Levels of invasion: no effect of bedrock

Of the 20 alien species recorded in total, 16 were found on granites and 17 on basalts, with corresponding averages per plot 1.6 ± 1.9 and 1.5 ± 1.5 , respectively. Neither the main effect of bedrock, nor the bedrock \times habitat interaction had significant effects on the mean number of aliens per plot (LMM: deletion test, $DF_{\text{model}} = 6$ vs. 7, L-ratio = 0.895, $p = 0.344$, and $DF_{\text{model}} = 7$ vs. 9, L-ratio = 0.294, $p = 0.634$, respectively; Fig. 4A), the total number of aliens in a given category (log-linear model: deletion test, $DF_{\text{resid}} = 2$ vs. 3, Dev. = -4.55, $p = 0.5$; and $DF_{\text{resid}} = 0$ vs. 2, Dev. = -0.056, $p = 0.972$, respectively; Fig. 4B) and the percentage of aliens amongst all species per plot (LMM: deletion test, $DF_{\text{resid}} = 6$ vs. 7, L-ratio = 1.242, $p = 0.537$; and $DF_{\text{resid}} = 5$ vs. 7, L-ratio = 1.355, $p = 0.322$, respectively; Fig. 4C).

Discussion

It has been suggested that the negative impacts of plant invasions in protected areas in African savannas are less dramatic than in the savanna regions and ecosystems in the Neotropics and Australia. Foxcroft et al. (2010) reviewed this issue and concluded that

the rather low levels of savanna invasions are in part due to lower rates of intentional plant introductions to Africa, for example, less widespread planting of large numbers of grass species, the key role of large mammalian herbivores in these ecosystems, historical and biogeographical issues related to the regions of origin of introduced species and the adaptation of African ecosystems to fire. Most of these factors are especially relevant in large protected areas, such as KNP, where the above constraints to invasion are strengthened by the fact that the protected areas act as barriers to colonisation of alien species from the outside (Pyšek et al. 2003; Foxcroft et al. 2011). They also act as refuges protecting native species against combined effects of invasion and climate change, as shown for European protected areas (Gallardo et al. 2017).

Due to research conducted mostly in the temperate areas, rivers have long been recognised as major pathways of alien plant introduction to new regions; they are highly prone to invasion by alien plants, largely because of their dynamic hydrology that makes them conduits for efficient dispersal of propagules (Planty-Tabacchi et al. 1996; Hood and Naiman 2000; Sibiya 2019). Fluctuating water levels provide space for new species by removing vegetation and increasing resources by making nutrients and light available (Richardson et al. 2007; Sibiya 2019). As most rivers flow through human settlements, there are multiple opportunities for the introduction of alien propagules into riparian zones and there is quantitative evidence that alien plants concentrate in riparian sites (e.g. Chytrý et al. 2008; Pyšek et al. 2010). While some species invading riparian habitats remain restricted to the vicinity of the river, other plants spread away from the river often after a considerable time lag spanning decades (Čuda et al. 2020). This represents a major threat to vegetation beyond the riparian ecosystems and can start new invasions into habitats previously not affected.

However, we found that the threat of invasion beyond the main perennial rivers and adjacent floodplain areas, where the major invaders are concentrated (Jarošík et al. 2011), is currently relatively minor in KNP. The majority of aliens recorded by our survey still occur at plots located near perennial rivers – but not all (Fig. 1). Some of the species not confined to rivers are amongst the most widespread, for example, *Bidens biternata*, *Malvastrum coromandelianum* and *Parthenium hysterophorus* and were repeatedly recorded also at seasonal-river plots. More importantly, two of the most invasive plants in the park, *Opuntia stricta* and *Parthenium hysterophorus*, were also found on the crest plots. Apparently, despite the successful biological control of *Opuntia stricta* in KNP in 1980s–1990s (Foxcroft et al. 2004), this invasive species is still present in dry areas of the savanna and could potentially start a new invasion. In addition, almost all of the alien plants we recorded in KNP have successfully naturalised in many regions of the world, half of them in more than 100 regions, which needs to be taken as a warning of the potential for many species to become serious invaders in KNP in the future. That these alien species successfully persist in subtropical and tropical climates is evident from all of them having naturalised in many other African regions, too, and five being distributed in more than 40 regions on this continent (*Portulaca oleracea*, *Tridax procumbens*, *Achyranthes aspera*, *Acanthospermum hispidum* and *Gomphrena celosioides*). None of these most widely naturalised species in

Africa is currently considered invasive in KNP, but attention should be paid by park management, especially in surveillance programmes.

It needs to be pointed out, however, that alien species recorded in our plots mostly occur in low abundance. *Bidens bipinnata* occasionally reached up to 15% of cover and *Alternanthera pungens* and *Acanthospermum hispidum* ~5%. Aliens also account for a rather small proportion of the total plant richness; on average, there were less than two alien species per plot, with maximum of seven and contribute less than 3% to the total plot richness. However, in two plots at perennial rivers, alien species contributed 11.9% and 9.2% and additional seven plots harboured more than 5% of aliens. This, together with the fact that almost three quarters of all sampled plots had at least one alien species, indicates that KNP needs to monitor the occurrence of these species, ideally on a regular and systematic basis. Our detailed survey covered, in cumulative terms, 15 hectares and, extrapolating the figures to the total park area, implies that alien plant species are already a fairly common phenomenon throughout the whole park.

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Germination of the invasive legume *Lupinus polyphyllus* depends on cutting date and seed morphology

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Abstract

In semi-natural grasslands, mowing leads to the dispersal of species that have viable seeds at the right time. For invasive plant species in grasslands, dispersal by mowing should be avoided, and information on the effect of cutting date on the germination of invasive species is needed. We investigated the germination of seeds of the invasive legume *Lupinus polyphyllus* Lindl. depending on the cutting date. We measured seed traits associated with successful germination that can be assessed by managers for an improved timing of control measures. To this end, we sampled seeds of *L. polyphyllus* on six cutting dates and analyzed the germination of these seeds in climate chambers and under ambient weather conditions. We collected information on seed morphology (color/size/hardseededness) for each cutting date to identify seed traits associated with successful germination. Observed germination patterns were highly asynchronous and differed between seeds cut at different dates. Seeds cut early, being green and soft, tended to germinate in autumn. Seeds cut late, being dark and hard, were more prone to germinate the following spring, after winter stratification. This allows the species to utilize germination niches throughout the year, thus indicating a bet-hedging strategy. Seed color and the percentage of hard seeds were good predictors of germination percentage, but not of mean germination time and synchrony. Managers should prevent the species producing black and hard seeds, while cutting plants carrying green and soft seeds is less problematic. Furthermore, germination patterns differed between climate chambers and the common garden, mainly because germination of dormant seeds was lower in climate chambers. More germination experiments under ambient weather conditions should be carried out, as they can give information on the germination dynamics of invasive species.

Keywords

dormancy, grassland management, lupine, phenology, seed traits

Introduction

The timing of germination determines which environmental conditions the seedling will experience and thereby influences a variety of plant characteristics (Casas et al. 2012). Consequently, the germination ecology of a species largely decides in which habitats and under which climates it may establish. The introduction of species to new ranges often leads to new germination conditions (Kudoh et al. 2007), and the ability to germinate successfully under a variety of environmental conditions is a characteristic of many successful and widespread invasive species (Baker 1974; Wainwright and Cleland 2013). Whether seeds are viable depends largely on their development stage, which is influenced by the timing of seed set and seed ripening.

In semi-natural grasslands, the mowing date is the environmental factor that most strongly determines the timing of seed release. Furthermore, mowing is a way of seed dispersal for species that have viable seeds at the right time. In most cases, the dispersal of mature seeds after mowing is a desirable process, as it is responsible for sustaining a high plant diversity in semi-natural grasslands (Auffret 2011; Humbert et al. 2012). In other cases, such as weeds or non-native invasive species, dispersal of ripe seeds by mowing is not wanted (Wilson et al. 2009) and shifts in grassland management and the time of cutting may create opportunities for invasives to establish in these ecosystems. Consequently, understanding the germination ecology of invasive plants is essential for their management and control and for limiting their spread to new sites.

Established invasive species are often more challenging to manage than newly arrived species (Simberloff 2003). Ideally, control measures would take place before seed formation, but time windows for adequate management can be short in areas where different conservation goals have to be matched. In the case of species invading mountain grasslands, e.g., mowing of areas critical for the protection of ground-nesting birds has to be postponed until nesting is finished, which means that invasive species may have produced viable seeds by the time of mowing. Consequently, managers are looking for information on the relationships between cutting dates, seed morphology, and seed germinability. *Lupinus polyphyllus* Lindl. is a widespread perennial legume originating from North-America. It is widely found as an ornamental plant (Fremstad 2010) and commonly used for soil stabilization and soil melioration (Rehfuess et al. 1991). Due to its many uses, the species is naturalized in different regions all over the world, e.g. in Europe (Fremstad 2010; Hejda 2013), New Zealand (Holdaway and Sparrow 2006) and Chile (Meier et al. 2013). Invaded habitats include road verges (Valtonen et al. 2006), riparian terraces (Meier et al. 2013), and mountain grasslands (Klinger et al. 2019). Due to its ability to fix nitrogen, it is considered an ecosystem engineer and may cause unwanted ecosystem effects (Hiltbrunner et al. 2014). In invaded habitats, *L. polyphyllus* is capable of overgrowing and shading the underlying vegetation and may cause a considerable decline in the richness of small species (Thiele et al. 2010; Hiltbrunner et al. 2014), while promoting the spread of tall-growing, nitrogen-demanding vegetation (Otte and Maul 2005). Meadows invaded by this species provide hay of low fodder quality, because of its high water-content and the presence of alkaloids in *L. polyphyllus* (Hensgen and Wachendorf 2016).

Despite the importance of seed ecology for the spread and establishment of species, there is often insufficient knowledge concerning germination and ripening characteristics of invasive species (Gallinat et al. 2018). The capability of seeds to after-ripe and germinate, which depends on the interaction between phenology and cutting date, may have important implications for the management of invasive species in grasslands. Therefore, we investigated the germination of the invasive legume *L. polyphyllus* in relation to the cutting date. Over the course of the vegetation period, i.e., weekly from the beginning to the end of fruiting, we sampled seeds from five locations invaded by *L. polyphyllus*. We combined two experiments to investigate the germination of *L. polyphyllus*: A common garden experiment to analyze the germination patterns under ambient weather conditions and a climate chamber experiment under standardized conditions. We aim to provide management recommendations based on seed traits such as seed color and hardseededness that may help to decide when fruiting lupine stands should be cut and when plant material has to be removed from the sites after mowing.

Specifically, our research hypotheses were:

- 1) The germination ability of *L. polyphyllus* seeds increases with later cutting date. Consequently, we expect a higher germination percentage, a shorter mean germination time, and a higher synchrony of germination with later cutting date.
- 2) Seed traits such as seed size, seed color, and the percentage of hard seeds provide reliable information about the germination ability of seeds sampled at different dates. We expect larger seeds, seeds with darker color and harder seeds to show higher germination percentage, shorter mean germination time and higher synchrony compared to small, green, and soft seeds.

Methods

Seed sampling, seed handling, and experimental design

Seeds were collected in the Rhön UNESCO Biosphere Reserve, in central Germany. The study area (from 50°26'N to 50°32'N and from 09°54'E to 10°05'E), a part of the Biosphere Reserve, is situated between 600 m and 950 m a.s.l. It is characterized by large and coherent semi-natural grasslands of high conservational value that are non-intensively used as meadows and pastures (e.g., Habitats Directive 92/43/EEC, habitat types 6520: mountain hay meadows, and 6230: species-rich *Nardus* grasslands). These grasslands have a centuries-long land-use history of mowing and pasturing with low nitrogen-inputs. In the 1990s, the traditional mowing date in early July was postponed to August and September, in order to safeguard the populations of protected ground-nesting birds and because the meadows decreased in importance for local farmers. This allowed *L. polyphyllus*, already present along roadsides in the area, to produce seeds before mowing and to spread extensively into the meadows. During the past 20 years, parts of the region were heavily invaded, with the area covered by *L. polyphyllus* dou-

bling in some localities (Klinger et al. 2019). This invasion is considered a major threat to the biodiversity of the mountain grasslands in the study region. Depending on site conditions, *L. polyphyllus* can reach a height of 60 to 150 cm. In June and July inflorescences are formed, each consisting of 50 to 80 single flowers (Fremstad 2010; Bundesamt für Naturschutz 2017). *L. polyphyllus* develops seed pods with four to twelve seeds, which burst at seed maturity and spread the seeds ballistically up to several meters (Otte et al. 2002; Volz 2003). Per plant, up to 2500 seeds can be produced (Aniszewski 2001).

Seeds of *L. polyphyllus* were manually collected from five meadows (*sampling locations*) over six weeks (July–August 2015; *cutting dates*). The distance between sampling locations ranged between 1500 and 5000 meters. For each cutting date and location, we sampled one inflorescence each from ten plants for the germination experiments. From each inflorescence, we randomly took one pod and determined seed size, seed color, and the proportion of hard seeds. For seed color, we distinguished between four colors: green, dark green, brown and black. Seeds with different pigmentations and puncturing (see Aniszewski 2001) were integrated to the different classes according to the predominant color, seeds were assigned the color “black” when they were considerably darker than brown seeds. Usually, seeds of several colors were found on the same location or even within the same seed pod. To determine the average color for each replicate, we gave ranks from one (green) to four (black) to each color and calculated the median. For seed hardness, we classified the seeds into five classes, from undeveloped and very soft to very hard. Based on these data, we calculated mean seed size, average seed color and the proportion of hard seeds for each replicate. For the germination experiments, we pooled the seeds within each *sampling location*. Seeds were manually cleaned, air-dried and stored in darkness at room temperature (app. 20 °C) until the start of the germination experiments on September 28th, 2015.

Laboratory experiments are a standardized tool to investigate germination in a controlled environment and can provide information on germination cues, dormancy, and other factors (Baskin and Baskin 2014). Nonetheless, germination in the laboratory often differs from germination under (semi-)natural conditions (Grime et al. 1981; Hölzel and Otte 2004) and thus gives only a limited representation of germination patterns that can be observed in the field. We combined a climate chamber experiment and a common garden experiment to study the germination of *L. polyphyllus* both under standardized and ambient weather conditions. A factorial experimental design was used to analyze the effects of *cutting date* (6 dates), *sampling location* (5 locations), and *temperature* (day/night: 20/10 °C and 15/5 °C; only in the climate chamber experiment) on seedling emergence. Germination was defined as protrusion of the radicle.

In the climate chamber experiment (from September 28th, 2015 to July 28th, 2016), seeds were placed into petri dishes with distilled water (25 seeds per replicate) in climate chambers (Rumed type 3401, Rubarth Apparate GmbH). Each treatment combination (*cutting date* × *sampling location* × *temperature*) was replicated five times, resulting in 300 petri dishes. For incubation in climate chambers, we exposed the seeds to 12 h light and 12 h darkness and two diurnally fluctuating temperatures (15/5 °C and 20/10 °C) that represent spring and early summer temperature conditions. Similar fluctuating temperature conditions have been applied by Elliott et al. (2011). Moisture

content of the Petri dish was controlled during the experiment. For seeds in the climate chambers, germination was checked once a week and seedlings were removed.

In the common garden experiment, germination was observed under ambient weather conditions from September 17th, 2015 to July 14th, 2016. The seeds were placed on a 1:1 mixture of sand and commercial potting soil (Fruhstorfer Erde, Type P, Industrie-Erdenwerke Archut GmbH, Lauterbach/Germany) in trays (18 × 28 cm) in a common garden at the research station Linden-Leihgestern of the Justus-Liebig University (50°32'N, 8°41'E). Per tray, 25 seeds were used ($n = 5$ for each *cutting date* × *sampling location* combination, resulting in 150 trays). Seeds were protected from predation using wire cages. For seeds in the common garden, germination was checked once every seven to fourteen days. After three months of incubation, germination decreased in both experiments and thus was checked every other week. After ten months of incubation, the experiments ended since no further germination was observed. By the end of the experiments, the remaining seeds were covered by mold and collapsed when pinched by hand. Thus, the remaining seeds were considered dead (following Baskin and Baskin 2014).

Germination variables and statistical analyses

As response variables, we calculated the germination percentage (%), mean germination time (days) and synchrony of germination (unitless) per replicate (according to Ranal and Santana 2006; Ranal et al. 2009). The germination percentage is the proportion of germinated seeds of the total number of seeds. Mean germination time and synchrony of germination were calculated based on seedling counts over time (Ranal et al. 2009). Mean germination time is a measurement of the weighted average time required for germination (Ranal and Santana 2006). The synchrony index is a measure for the overlapping of germination that ranges from 0 (when no two seeds germinated at the same time) to 1 (when all germinating seeds germinated at the same time; for details see Ranal et al. 2009).

Seeds from the climate chamber experiment and from the common garden experiment were analyzed separately. The effects of the experimental variables *cutting date*, *sampling location* and *temperature* on the response variables germination percentage and germination time were analyzed using linear mixed-effect models (LMM) and synchrony of germination using generalized linear mixed-effect models (GLMM) for binomial distributions. The factors *cutting date* and *temperature* were included as fixed factors in the first models. As there was no effect of the *temperature*, the final models only included cutting date or seed color fixed factors. We added an error term for repeated measures to the models to account for variation within each *sampling location*. Furthermore, we added a general linear hypothesis and multiple comparisons (glht) to determine significant differences between groups.

To identify seed traits associated with germination success, we checked for correlation of seed traits with the factor *cutting date* using Pearson's R^2 . This was the case for *seed size*, *seed color*, and *proportion of hard seeds*. We then fitted models with these traits as fixed factors (both in combinations and as single-factor models) and *sampling*

location as random factor. To choose the best seed traits or trait combination to explain germination success of *L. polyphyllus*, we compared these models via AIC and pairwise model ANOVA. To assess model quality, we calculated Nagakawa and Schielzeth's R^2 for linear mixed-effect models (Nagakawa and Schielzeth 2013). We visually checked for normality of residuals and homogeneity of variances using diagnostic plots (Zuur et al. 2010). Mixed-effect models were carried out using the 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) packages, post-hoc-tests were calculated using the 'multcomp' package (Hothorn et al. 2008), graphs were created using the 'ggplot2' package (Wickham 2016) in R (R Core Team 2016).

Results

During the sampling period, seed color became darker (changing from green via dark green and brown, to black) and the proportion of hard seeds increased gradually. Mean seed size ranged from 3.9 mm (date six, August 11th) to 6.4 mm (date three, July 21st). It increased during the first three weeks of cutting and then decreased thereafter as seeds became drier. Seed color and the proportion of hard seeds were correlated, as hard seeds usually were darker than soft seeds. There were no differences in the total germination percentages between different *sampling locations*, although the germination peaks shifted by up to two weeks between different locations.

In climate chambers, 16.3% of all collected lupine seeds germinated (Fig. 1a, b). Germination percentage was lowest after the first cutting date (July 7th, 8.6%) and increased until the third date (July 21st) where it peaked at 26% (Fig. 1a). Afterwards, we observed a significant decrease from week three (July 21st) to four (July 28th; to 13.4%; Table 1). Mean germination time was 114 days and varied from 3 days to 303 days in climate chambers (Fig. 1c, d), with seeds collected on the first date having the longest mean germination time (141 d; Fig. 2d). Mean germination time decreased until week three (98 d), then increased again and had its overall minimum in week six (74 d). Synchrony of germination was quite low with an average of 0.08 over all cutting dates (Fig. 1e, f).

In the common garden, 51.7% of seeds germinated and mean germination time was 153.6 days (Fig. 2). Thus, seeds in the common garden germinated to a higher degree compared to seeds in climate chambers, but slower. Germination percentages in the common garden were lowest in seeds sampled during the first two weeks (17.0% on July 7th and 30.6% on 14th), reached the highest level in week three (63.2% on July 21st) and stayed high afterwards (Fig. 2a, Table 1). In the common garden, mean germination time was similar for all cutting dates and averaged 153.6 days. Synchrony of germination in the common garden was quite low with an average of 0.12 over all treatments and on all cutting dates (Fig. 2e, f).

There were significant differences in germination percentages between seeds of different color (Figs 1b, 2b, Table 2). In climate chambers, dark green seeds showed the highest germination while in the common garden, germination percentages increased steadily as seeds darkened (Figs 1b, 2b). In climate chambers, germination percentage peaked when 60% of collected seeds were hard and decreased when the amount of hard seeds was lower

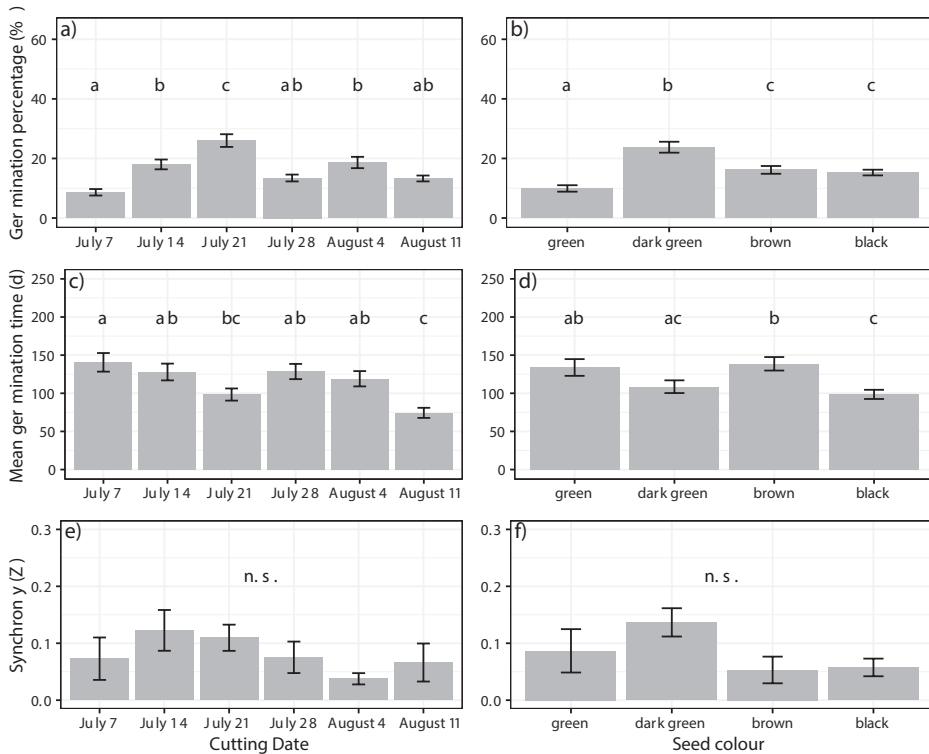


Figure 1. The effect of the factors cutting date (weekly from July 7th to August 11th) and seed color on germination percentage (**a, b**), mean germination time (**c, d**), and synchrony of germination (**e, f**) in seeds stored in climate chambers averaged over the two temperature regimes. Bars show mean values \pm standard errors.

Table 1. Differences in germination percentages of *L. polyphyllus* seeds between six cutting dates assessed in two germination experiments (climate chamber and common garden). Differences were assessed using mixed effect models for each experiment separately with sampling location as random factor (formula: Germination percentage ~ Cutting Date + (1|Sampling location)).

| Climate chamber | | n = 300 | R ² _{marginal} = 0.20 | R ² _{conditional} = 0.25 | | |
|----------------------------|----------|------------|---|--|---------|--|
| | Estimate | Std. Error | Df | t Value | p Value | |
| Date 1 (July 7; Intercept) | 8.64 | 1.86 | 22.56 | 4.65 | < 0.001 | |
| Date 2 (July 14) | 9.36 | 2.11 | 295 | 4.45 | < 0.001 | |
| Date 3 (July 21) | 17.36 | 2.11 | 295 | 8.25 | < 0.001 | |
| Date 4 (July 28) | 4.8 | 2.11 | 295 | 2.28 | 0.023 | |
| Date 5 (August 4) | 10 | 2.11 | 295 | 4.75 | < 0.001 | |
| Date 6 (August 11) | 4.64 | 2.11 | 295 | 2.20 | 0.028 | |
| Common garden | | n = 150 | R ² _{marginal} = 0.63 | R ² _{conditional} = 0.71 | | |
| | Estimate | Std. Error | Df | t Value | p Value | |
| Date 1 (July 7; Intercept) | 16.96 | 3.88 | 14.21 | 4.37 | < 0.001 | |
| Date 2 (July 14) | 13.6 | 3.86 | 145 | 3.52 | < 0.001 | |
| Date 3 (July 21) | 46.24 | 3.86 | 145 | 11.99 | < 0.001 | |
| Date 4 (July 28) | 47.68 | 3.86 | 145 | 12.37 | < 0.001 | |
| Date 5 (August 4) | 52 | 3.86 | 145 | 13.49 | < 0.001 | |
| Date 6 (August 11) | 48.8 | 3.86 | 145 | 12.66 | < 0.001 | |

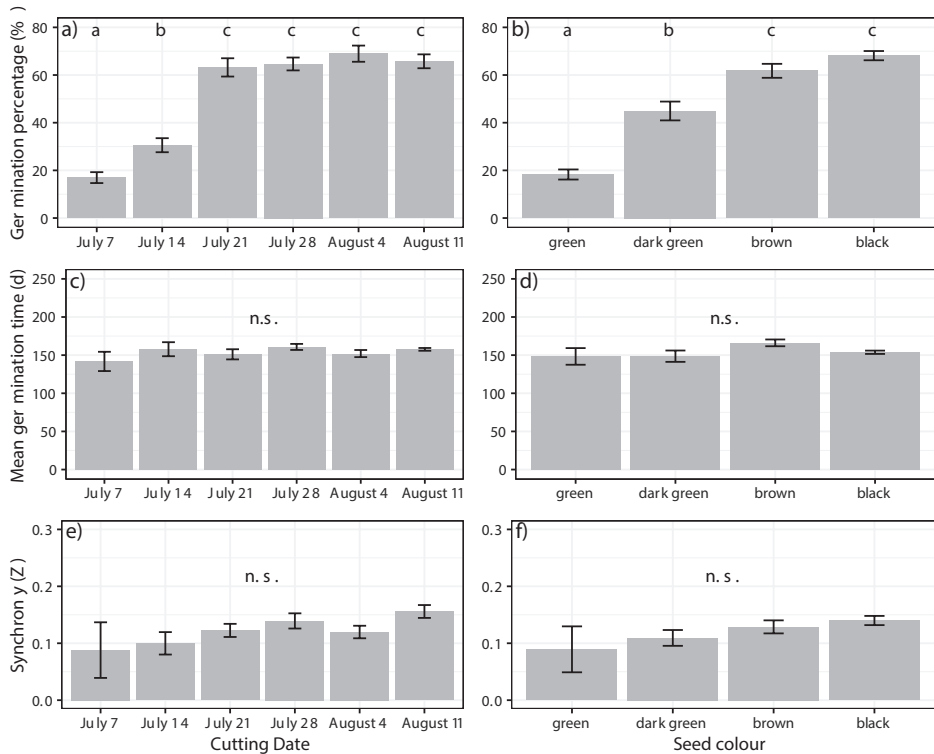


Figure 2. The effect of the factors cutting date (weekly from July 7th to August 11th) and seed color on germination percentage (**a**, **b**), mean germination time (**c**, **d**), and synchrony of germination (**e**, **f**) in seeds stored under ambient weather conditions. Bars show mean values \pm standard errors.

Table 2. Differences in germination percentages of *L. polyphyllus* seeds between four seed colors (median seed color per sample with four levels: green, dark green, brown, and black) assessed in two germination experiments (climate chamber and common garden). Differences were assessed using mixed effect models for each experiment separately with sampling location as random factor (formula: Germination percentage ~ Seed color + (1|Sampling location)).

| Climate chamber | n = 300 | R ² _{marginal} = 0.15 | | R ² _{conditional} = 0.22 | |
|-------------------|----------|---|--------|--|---------|
| | Estimate | Std. Error | Df | t Value | p Value |
| Green (Intercept) | 9.45 | 1.88 | 16.2 | 5.03 | < 0.001 |
| Dark green | 14.34 | 1.94 | 298.48 | 7.4 | < 0.001 |
| Brown | 7.71 | 2.12 | 299.21 | 3.64 | < 0.001 |
| Black | 5.64 | 1.74 | 297.85 | 3.25 | < 0.01 |
| Common garden | n = 150 | R ² _{marginal} = 0.58 | | R ² _{conditional} = 0.65 | |
| | Estimate | Std. Error | Df | t Value | p Value |
| Green (Intercept) | 17.29 | 4.11 | 12.24 | 4.21 | < 0.01 |
| Dark green | 27.78 | 3.82 | 146.4 | 7.27 | < 0.001 |
| Brown | 47.13 | 4.18 | 146.84 | 11.27 | < 0.001 |
| Black | 50.14 | 3.42 | 146.09 | 14.65 | < 0.001 |

or higher while in the common garden, germination percentage increased continuously with the amount of hard seeds. In both experiments, seeds of different color had relatively similar germination times with black (99 d) and dark green (109 d) seeds germinating most rapidly in climate chambers (Fig. 1d). In the common garden, there were no significant differences in mean germination time between seeds of different colors (Fig. 2d).

While in climate chambers, germination peaked early and decreased afterwards (Fig. 3), two peaks (in autumn and spring) characterized germination in the common garden (Fig. 4). There were no significant differences between colors in climate chamber, while synchrony in the common garden increased slightly with the increase in the percentage of hard seeds.

Germination percentage (in both experiments) and mean germination time (only in climate chambers) responded significantly to *cutting date*, while there was no effect of the different *temperature* regimes. For germination percentage and mean germination time, the best explanatory models (see Suppl. material 1: Model Tables) each contained solely one fixed factor, mainly due to high correlations between explaining factors. Germination percentage in climate chambers was best explained by seed color and showed highly significant differences between colors ($R^2 = 0.15$). Germination percentage in the common garden was well explained by both seed color ($R^2 = 0.58$) and proportion of hard seeds. For mean germination time, the best explaining factors were either color or proportion of hard seeds, while both models performed poorly overall. Synchrony was not affected significantly by any factor and there was no model of significant explanatory value.

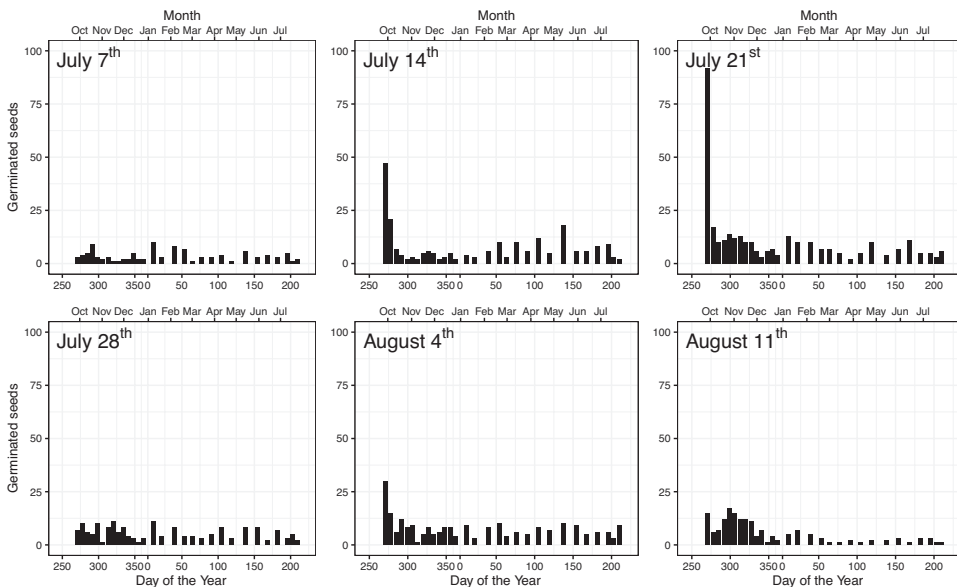


Figure 3. Germination patterns of *L. polyphyllus* in climate chambers conditions (15/5 °C and 20/10 °C diurnally fluctuating temperatures) sampled weekly on six cutting dates (July 7th to August 11th) after seed set.

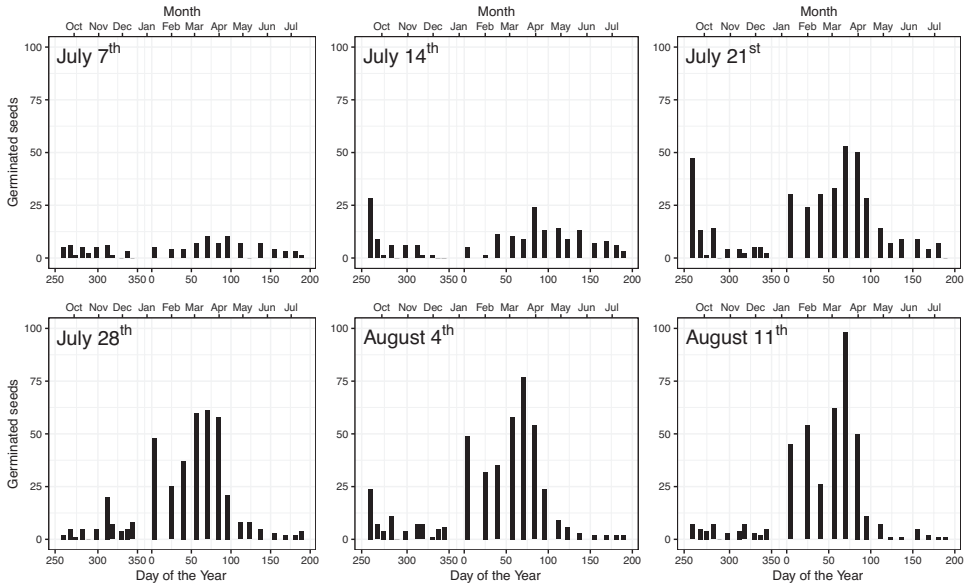


Figure 4. Germination patterns of *L. polyphyllus* under ambient weather conditions sampled weekly on six cutting dates (July 7th to August 11th) after seed set.

Discussion

The germination patterns of the invasive legume *L. polyphyllus* differed between different cutting dates, partially confirming our first hypothesis. Seeds collected early, while being green and soft, germinated to a lower degree and more slowly compared to seeds collected later. While seeds of early-cut *L. polyphyllus* plants germinated in autumn, seeds of late-cut plants were more prone to germinate in spring. This relationship may be associated with their progression through different phases of seed development. During morphogenesis the embryo develops, then during maturation, storage compounds are synthesized in the growing endosperm and thereafter, seeds may go through a phase of desiccation, in which they dry and eventually enter dormancy (Angelovici et al. 2010). Consequently, the different cutting dates of our experiment covered the phases of maturation and desiccation. Until late July, *L. polyphyllus* seeds were in the phase of maturation. Afterwards (end-July to mid-August), seeds were in the desiccation phase. Although dormancy per se was not tested in our study, the observed germination patterns and differences between climate chambers and the common garden strongly indicate that seeds from late cut *L. polyphyllus* plants expressed dormancy, which is also supported by our observation that seeds decreased in size and became harder. Physical dormancy is common in legumes (Russi et al. 1992a), but whether an individual plant produces dormant seeds at a given point in time depends on a variety of factors, such as temperature and moisture conditions during seed ripening (Masaka and Yamada 2009; Bolingue et al. 2010; D'hondt et al. 2010). Thus, the expression of dormancy can vary strongly in legume seeds, even within plants of the

same population (D'hondt et al. 2010), which may consequently lead to asynchronous germination patterns.

Despite pronounced peaks of germination in autumn and spring, germination of *L. polyphyllus* seeds was highly asynchronous. In both experiments and under all cutting dates, some seeds germinated over the whole duration of the experiments, over 300 days. The timing of germination determines which environmental conditions the seedling will experience and may influence plant characteristics, such as growth and reproduction (Donohue 2002; Casas et al. 2012). The timing of germination itself may be influenced by plant life-history traits, e.g. the phenology of flowering, seed maturation, and seed dispersal (Galloway 2001; Donohue 2002). Variations in germination depending on the time of seed collection have been observed by other authors (e.g., Greipsson and El-Mayas 2003; Samarah 2005; El-Keblawy and Al-Rawai 2006; Brobäck 2015), but there is little information on the long-term germination patterns of species and seasonal effects that are associated with this factor. In invasive species, asynchronous germination can lead to the exploitation of open germination niches throughout the year, which might contribute to their invasion success (Wolkovich and Cleland 2011; Gioria et al. 2016). In the case of *L. polyphyllus*, this effect may be amplified by its high seed production (Volz 2003), its long-lasting flowering, by its ability to resprout and produce seeds after early cutting (Brobäck 2015), and by the observation that the ballistic seed dispersal of the species takes place over many weeks if stands are left untouched (Klinger et al., unpublished data). The observed germination patterns of *L. polyphyllus* thus suggest a bet-hedging strategy (Cohen 1966), which may partly explain its invasion success and its capability to colonize many different habitats.

Our second hypothesis can be verified, as seed color and the percentage of hard seeds were good predictors of germination percentage and give information on the germination patterns that can be expected. Soft and green seeds germinated to the lowest degree and in autumn. However, germination percentages of these seed batches were relatively high, given their early developmental phase. High germination rates in immature seeds have been found in some legumes, e.g., in *Lotus* and *Scorpiurus* (Cristaudo et al. 2008), and *Vicia* (Samarah 2005), but germination failed in others, such as in green seeds of *Lupinus nootkatensis* (Greipsson and El-Mayas 2003). Black and hard seeds germinated to a high degree and in spring. In temperate climates, seedlings germinating in autumn face harsh environmental conditions during winter combined with low competition, while spring germination is associated with more favorable environmental conditions, but higher competition (Masuda and Washitani 1992). Since soft and green seeds mostly germinated in autumn, the winter survival of the emerging seedlings may be low, as *L. polyphyllus* seedlings seem to be sensitive to freezing and showed high mortality when exposed to -10°C (Arfin-Khan et al. 2018). Furthermore, unripe seeds of roadside *L. polyphyllus* stands in Sweden were prone to mold infection that led to very low germination rates (Brobäck 2015). The last cutting date represents the state in which seeds are shed by the plant. Both ballistic seed dispersal as well as the expression of physical dormancy go along with the drying of the pods and the seed coat. Black and hard seeds are more prone to germinate in spring and may thus have higher survival rates compared to green seeds. Furthermore, as *L. polyphyllus* follows a c-strategy (Grime et al. 1988), it may be able to cope with higher competition

in spring, especially in habitats with weak competitors, such as semi-natural grasslands. Additionally, water impermeable/hard seeds are more prone to being carried over into the seed bank (Russi et al. 1992b) or dispersed via endozoochory (Otte et al. 2002; D'hondt and Hoffmann 2011). Although *L. polyphyllus* may not have invaded the seed bank of meadows in our study region yet (Ludewig et al., unpublished data), a carry-over of seeds should be avoided, as it makes invasive species management lengthier and more expensive. Consequently, managers should target plants that still have green and soft seeds, which can be considered less problematic despite germination percentages being relatively high.

Germination patterns differed between climate chambers and the common garden, particularly after seeds darkened and became harder. Overall, germination percentages in the climate chamber experiment (ca. 16%) were similar to the emergence rates found by Sóber and Ramula (2013) (21.5%), but relatively low compared to other studies on *L. polyphyllus* (Elliott et al. 2011; Arfin-Khan et al. 2018; over 60%). We suggest that this is at least partly due to the fact that seeds were not scarified and that dormancy was probably not broken by imbibition in the climate chamber experiment. This is also supported by the results of the common garden experiment, in which germination percentages were considerably higher than under laboratory conditions, mainly due to a second germination peak in spring after winter-stratification *in situ*. However, germination of *L. polyphyllus* only slightly increased when seeds were pre-treated by cold in another study (Elliott et al. 2011). Our results show that, while laboratory experiments give valuable information on the environmental factors influencing germination, the germination patterns observed under artificial conditions may diverge from germination dynamics under ambient weather conditions (Hölzel and Otte 2004). A better understanding of invasive species germination under natural conditions is necessary, as it can potentially reveal windows of opportunity for invasive species management. We thus recommend to complement germination experiments in climate chambers with common garden or field experiments.

Conclusions

Seeds of *L. polyphyllus* are capable of after-ripening and germinating even if plants are cut while most seeds are still green and soft. Germination capability increased strongly during the first weeks after seed set with a maximum when most seeds were brown to black and not fully hardened. Therefore, *L. polyphyllus* stands should be cut before seed set, if possible. If this is not feasible due to different limitations, we recommend cutting while plants carry green and soft seeds. When stands with black and hard seeds are cut, the plant material should be removed immediately to reduce propagule pressure on site.

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Supplementary material I

Model Tables

Authors: Yves P. Klinger, Rolf Lutz Eckstein, David Horlemann, Annette Otte, Kristin Ludewig

Data type: table.xlsx-file

Explanation note: Model summary tables.

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A bobber's perspective on angler-driven vectors of invasive species transmission

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Abstract

Prevention of aquatic invasive species is a fundamental management challenge. With hundreds of millions of people participating in fishing trips each year, understanding angler movements that transmit invasive species can provide critical insight into the most effective locations and scales at which to apply preventative measures. Recent evidence suggests that mobile technologies provide new opportunities to understand different types of angler movement behaviour beyond what is possible with infrequently and sparsely conducted in-person boat surveys and mail questionnaires. Here we capitalise on data provided by ReelSonar's iBobber, a sonar-enabled bobber with over 5 M recorded fishing locations, globally. By quantifying geographic patterns of fishing activities and assessing how these patterns change seasonally, we explore angler behaviour across the entire continental United States in terms of fishing frequency and distance travelled between sites and characterise the attributes of fished ecosystems. We found that iBobber users (anglers) undertook 66,918 trips to 20,049 different water-bodies over a two-year period. Anglers who use iBobber were more likely to visit larger, deeper and more urbanised water-bodies and these water-bodies were over five times more likely to be a reservoir compared to a lake. Inter-water-body travel road distances averaged 93 km (SD = 277 km; range < 1–300 km) and nearly half of these movements occurred over a timespan of two days or less, a timeframe that we show falls well within the desiccation tolerance window of many prevalent plant and animal invasive species. Our study offers novel insight into spatiotemporal patterns of angler behaviour well beyond the geographical and temporal extent of conventional ground-collected approaches and carries important implications for predicting and preventing future transmission of aquatic invasive species via recreational fishing.

Keywords

big data, desiccation tolerance, invasion risk, recreational fishing, species transmission, vectors

Introduction

Technological innovations in ecology have evolved significantly in recent decades, now serving a much more common and indispensable role in scientific research and management. The application of technology in conservation biology is rapidly growing and becoming more widespread (Joppa 2015; Pimm et al. 2015; Berger-Tal and Lahoz-Monfort 2018; Toivonen et al. 2019). Mobile app-derived data, for instance, are increasingly used to provide information for management strategies related to outdoor recreational use and planning, such as hiking and nature-based tourism (e.g. Wood et al. 2013; Fisher et al. 2018). This wealth of new data allows practitioners to map human recreational activities and relate individual behaviour to real-world conditions (Levin et al. 2017; Hausmann et al. 2018). For example, digital footprints in the form of geotagged photographs proportionally reflect human visitation rates at freshwater lakes and reservoirs (Keeler et al. 2015). However, broader incorporation of these data formats into freshwater management remains limited and user-generated data continue to be under-utilised in scientific studies (Venturelli et al. 2017).

Recreational freshwater fishing generates significant net economic benefits in the United States and Canada by engaging over 30 million participants annually, whose equipment and trip expenditures total in the tens of billions USD each year (U.S. Department of the Interior 2016; Fisheries and Oceans Canada 2019). However, high rates of participation in fishing have significant social, ecological and economic consequences. Anglers have repeatedly been implicated as vectors of non-indigenous species by entraining organisms in bait buckets, on fishing lines and on boat motors, hulls and trailers (Rothlisberger et al. 2010; Drake and Mandrak 2014; Smith et al. 2020). Insufficient gear-cleaning allows hitchhiking invaders to be moved overland between water-bodies, promoting both their initial introduction into new catchments and secondary spread into adjacent lakes and reservoirs (Anderson et al. 2014). Angling activity frequently moves invasive species over short distances, but can also distribute them across regions and nations via jump dispersal (Buchan and Padilla 1999; Wilson et al. 2009). In North America, higher numbers of non-native species have been found to coincide with areas of greater recreational fishing demand (Davis and Darling 2017). Examples of ubiquitous nuisance species whose translocation has been partly attributed to angling and boat movements include zebra mussel *Dreissena polymorpha*, Eurasian milfoil *Myriophyllum spicatum*, spiny water flea *Bythotrephes longimanus* and rusty crayfish *Orconectes rusticus* (Lodge et al. 2000; Minchin et al. 2003; Rothlisberger et al. 2010; Kerfoot et al. 2011).

Mobile technologies provide new opportunities to understand angler movement behaviour in ways that have traditionally challenged researchers. Emerging methods for tracing angler movement include trip logs on online fishing forums and mobile applications, remote traffic counters, geocoding wildlife recreational licences, text and data mining of social media and personal fishing gear with enhanced technological capabilities (e.g. Martin et al. 2014; Mogollón and Villamagna 2014; Papenfuss et al. 2015; Monkman et al. 2018; van Poorten and Brydle 2018). These new mobile-based data offer prospects for more robust spatiotemporal estimation of angler activ-

ity (Venturelli et al. 2017). This contrasts with conventional approaches that rely on in-person surveys at boat launches and mail-in questionnaires to licensed anglers and thus only provide a limited snapshot in time of angling activity at a particular location (Rothlisberger et al. 2010; Anderson et al. 2014). Moreover, the shift in demographics of recreational fishing towards younger and more technologically savvy anglers (Recreational Boating and Fishing Foundation 2018) suggests that mobile-based data may shed novel insights into the movement behaviour of individuals who are less likely to engage with long-standing survey instruments.

Given the pivotal role anglers play in transporting harmful freshwater invasive species, understanding when and where fishing activity occurs is critical for providing information for more strategic preventative measures (Muirhead and MacIsaac 2005; Vander Zanden and Olden 2008). Human transportation networks determine the large-scale geographic pathways available to anglers and, hence, the routes by which invasive species may hitchhike between water-bodies. Preventative measures are placed adjacent to these pathways and at the water-body access points they connect (Drake and Mandrak 2010; Meekan et al. 2017). Joining angler movement data with existing invasive species distributions allows for the identification of invasion hubs – areas from which non-indigenous species are frequently moved into nearby locales (Muirhead and MacIsaac 2005; Stewart-Koster et al. 2015). Enhancing our knowledge of human movement behaviour will improve our ability to deploy vector management and prioritise locations for a suite of preventative approaches, including early detection monitoring at access points, roadside boat and gear inspection stations and education in the form of billboards and awareness signs (Sharp et al. 2017; Cimino and Strecker 2018; Reaser et al. 2020).

The potential for invasive species introduction into new water-bodies via angler-driven vectors is constrained not only by the spatial distributions of nuisance species and angler movement, but also by those factors that influence survival during transport, such as species' desiccation tolerance (Havel 2011; Wood et al. 2011; Leuven et al. 2014; Coughlan et al. 2018). Thus, it is important to account for the duration over which angler movement occurs across the landscape after potential entrainment of non-indigenous propagules in an angler transportation pathway (Johnson et al. 2001). In comparison to recreational boaters, anglers may enhance the likelihood for dispersing aquatic invasive species as they are more capable of accessing smaller water-bodies in remote locations (Drake and Mandrak 2010). Previous studies, however, have been unable to account for time when assessing risk of invasive species' introduction and spread via angler movement because such fine-scale data are not generated from conventional survey approaches. Consideration of the temporal dimension of angler movement provides greater resolution into this invasion vector by allowing for explicit consideration of movement events that are shorter in duration and likely to entrain viable propagules (Jerde et al. 2012; Banha and Anastácio 2014). Additionally, this approach has the advantage of integrating species-specific information (i.e. desiccation tolerance) into vector-based invasive species risk assessments.

In this study, we demonstrate how large-scale angler movement behaviour – a major contributor to the spread of invasive species – can be estimated from data col-

lected by mobile fishing technology. Specifically, we used angler location data from ReelSonar's iBobber – a sonar-enabled castable fish-finder with over 5,000,000 georeferenced global records of fishing activities uploaded since the device's launch – to analyse spatial patterns in angler movement across the continental United States. iBobber devices passively collect data upon submersion in water and, thus, have the advantage of representing all angling activity regardless of whether a user actively records a fish catch. Our objectives were to assess the geography of angler activities and movement dynamics while explicitly accounting for spatial distributions of aquatic nuisance species and limitations on propagule viability between water-bodies according to species' desiccation tolerance. The findings of this research offer novel insights into spatiotemporal patterns of angler behaviour and carry important implications for predicting and preventing future transmission of aquatic invasive species via recreational fishing.

Methods

iBobber technology and data processing

iBobbers are small castable, personal fish-finders that sync through Bluetooth with a smartphone application to provide users with real-time information on fish and vegetation presence in the water column, map water-body depth and estimate water and air temperature, wind speed and direction and a suite of additional weather variables. iBobber users include shore-based anglers and those fishing from kayaks, canoes and other boats. iBobbers (distributed by ReelSonar of Seattle, WA) are widely available for purchase in stores and on the web and are primarily used in North America, Europe and east Asia.

Anonymised data were acquired from all iBobber devices that were used over a two-year period (January 2017 – December 2018). When submerged in water, each bobber records a "hotspot" of its geographic location in 30-second intervals, along with time, date, fish presence, depth and a host of other variables. Each device is identified by its unique bobber ID code and iBobber users can view these metrics in real-time using the iBobber phone app. As owners often test their devices initially in their home sinks and pools, we first filtered the data spatially by excluding hotspots that were located outside of a 50-m buffer of the > 379,000 lakes and reservoirs contained in the National Hydrography Dataset, v2 (NHD) for the continental U.S. (U.S. Geological Survey 2018). Timestamped locations were then compiled into single fishing trips by pooling hotspots with the same bobber ID, water-body and date.

Angling trip and water-body metrics

We calculated summary metrics to describe angler fishing activities according to iBobber records, including the number of trips (i.e. distinct visits to a water-body in time)

by each user, total trips per month and day of the week across all water-bodies and users and density of trips (# km²) across the continental U.S. Water-body characteristics were obtained from the EPA's LakeCat Dataset, which classifies lakes and reservoirs within the NHD by surrounding land use and lithography, size, surface area and additional variables (Hill et al. 2018). We compared the percent urban land cover in the contributing basin of water-body and the maximum depth and surface area of water-bodies fished by iBobber users to that of all water-bodies within LakeCat using a parametric comparison of means according to a two-sample Z-test. In addition, we identified which lakes were reservoirs with USGS' Reservoir Morphology Dataset (Rodgers 2017), compared the likelihood of natural lakes and reservoirs being fished by iBobber users with a two-tailed chi-squared test of independence and assessed the effect size of this likelihood using the odds ratio.

Angler movement events and duration between water-bodies

Least-cost ground transportation distances between consecutive anglers' trips to water-bodies were determined by routing angler locations through GraphHopper's route optimiser, which uses OpenStreetMap as a base map. This is termed an angler (inter-water-body) movement event. GraphHopper routes geographic coordinates through the closest road access point for each water-body, thus most often estimating the transportation distance between public boat launches. We calculated the duration of each angler movement event as the number of days between consecutive trips by iBobber users. Furthermore, we conducted a literature search to identify all nuisance freshwater invasive species with reported tolerated exposure to desiccation (the length of time) in an overland vector, resulting in values for hydrilla *Hydrilla verticillata* (16 hours: Barnes et al. 2013), Eurasian milfoil (2 days: Barnes et al. 2013), New Zealand mudsnail *Potamopyrgus antipodarum* (3 days: Havel et al. 2014), zebra mussel (5 days: Ricciardi et al. 1995), Asian clam *Corbicula fluminea* (23 days: Collas et al. 2014) and Chinese mystery snail *Cipangopaludina chinensis* (63 days: Havel et al. 2014). We then calculated the number of movement events that fell within each species desiccation tolerance range. Lastly, we visualised a subset of angler movements in a region of Wisconsin, U.S. to demonstrate high traffic road routes utilised by anglers and to assess the frequency of movements from non-invaded to invaded water-bodies. We first determined whether angling was a potential vector for a range of invasive species using the USGS Nonindigenous Aquatic Species database (2018) and then classified invaded water-bodies within the angler movement subset as those containing at least one of the identified species (Asian clam, banded mystery snail *Viviparus georgianus*, curly-leaf pondweed *Potamogeton crispus*, Chinese mystery snail, Eurasian milfoil, flowering rush *Butomus umbellatus*, purple loosestrife *Lythrum salicaria*, ornamental water lilies *Nymphaea* sp., rusty crayfish, spiny water flea, zebra mussel) according to presence/absence records from the Wisconsin Department of Natural Resources (2016).

Comparison to other angler participation data

We evaluated the correspondence of angling activity, based on iBobber data with existing creel-based data collected at the scale of individual lakes and states of the U.S. The lake-level analysis obtained data from a state-wide survey of lake users on 86 lakes in Iowa over 5 years (2002–2005 and 2009) (Evans et al. 2009), which we compared with the proportion of trips by lake according to iBobber activity. The state-level analysis compared the percent distribution of annual fishing trips by state reported in the U.S. Fish & Wildlife Service's (USFWS) 2011 National Survey (U.S. Department of the Interior et al. 2011) to the calculated percent of trips made annually to each state by iBobber users. Great Lakes trips were attributed to the state with the nearest shoreline to the trip's coordinates, but North Dakota was excluded as the state did not report data for the 2011 survey. Both lake- and state-level comparisons were measured by the Pearson correlation coefficient. All spatial analyses were completed in ESRI ArcMap version 10.0 (Redlands, CA) and all statistical analyses were completed in R 3.5.1 (R Core Team).

Results

An extensive geographic footprint of angler activities exists across the continental United States according to 66,918 trips taken by 10,768 iBobber users over a two-year period (Fig. 1A). Angler trips were concentrated in more urbanised regions, particularly in the eastern and western states. As expected, trip frequency peaked during the late spring-early summer months (June-July) and was at its lowest in late autumn-early winter (October-November) (Fig. 1B). Moreover, the frequency of trips on weekends (24%) was more than double that of midweek days (Fig. 1B inset). Over half (55%) of iBobber users made more than one trip during the study period (Fig. 1C), up to a maximum of 88 trips.

During the study period, iBobber users visited 20,049 different water-bodies, of which 46% were visited more than once (Fig. 2A). The most-visited water-body was Lewisville Lake – one of the largest lakes in north Texas – with 427 trips by 128 different anglers. Water-bodies fished by iBobber users were characterised by having statistically significant higher mean catchment urbanisation (24.3% vs. 9.4%, $z = 3.02$, $p = 0.001$), maximum depth (8.4 m vs. 2.6 m, $z = -2.01$, $p = 0.022$) and surface area (18.3 km² vs. 0.65 km², $z = -2.31$, $p = 0.011$) compared to all 379,090 water-bodies across the continental United States. iBobber users were over five times more likely to make a trip to reservoirs compared to lakes (two-tailed χ^2 , $df = 1$, $p < 0.001$, logistic regression odds ratio = 5.68).

Anglers engaged in wide-ranging travel distances and durations amongst fished water-bodies. According to 23,363 movements between two successive water-bodies by iBobber users, mean and median road distance travelled was 93 km (SD = 277 km) and 23 km, respectively, ranging from short-distance movements of < 1 km to long-distance movements of ca. 300 km (Fig. 2B). The GraphHopper routing algorithm

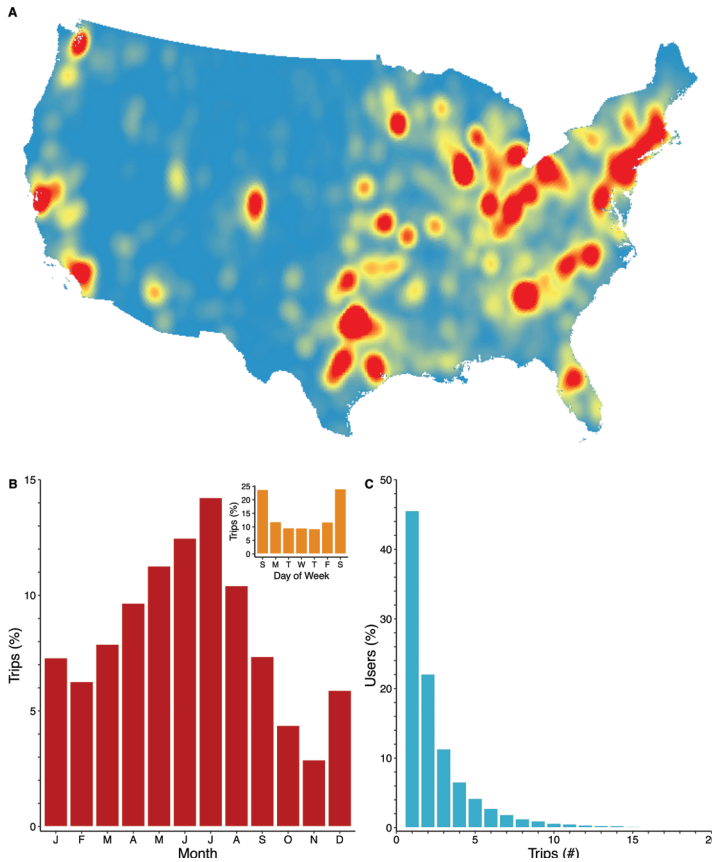


Figure 1. From January 2017 through December 2018 **A** trip density across the continental U.S. ranging from zero (blue) to 1,523 (red) trips per km² **B** percentage of trips by month and (**inset**) day of the week and **C** iBobber users (%) by total number of trips taken, truncated at 20 trips (bin size = 1).

returned a road distance of zero for 7% of inter-water-body movements ($N = 1,677$ movements), indicating users walked between water-bodies or travelled on roads not contained in the Open Street Map data layer. Nearly half of inter-water-body movements by iBobber users occurred over a timespan of two days or less, which falls well within the desiccation tolerance window of many prevalent invasive species (Fig. 3). For example, the literature search for invasive species' desiccation tolerance revealed the species with the shortest and longest quantified desiccation tolerance was Hydrilla (16 hours) and Chinese mystery snail (63 days), respectively (Barnes et al. 2013; Havel et al. 2014). This results in 32% (Hydrilla) to 89% (Chinese mystery snail) of all inter-lake movements having a duration that falls within the range of desiccation tolerance.

Estimates of angler visitation frequency, according to iBobber user records, corresponded with previous estimates according to creel surveys. Lake-level visitation by iBobber users was correlated with surveyed visitation of Iowa lake users ($R^2 = 0.425$,

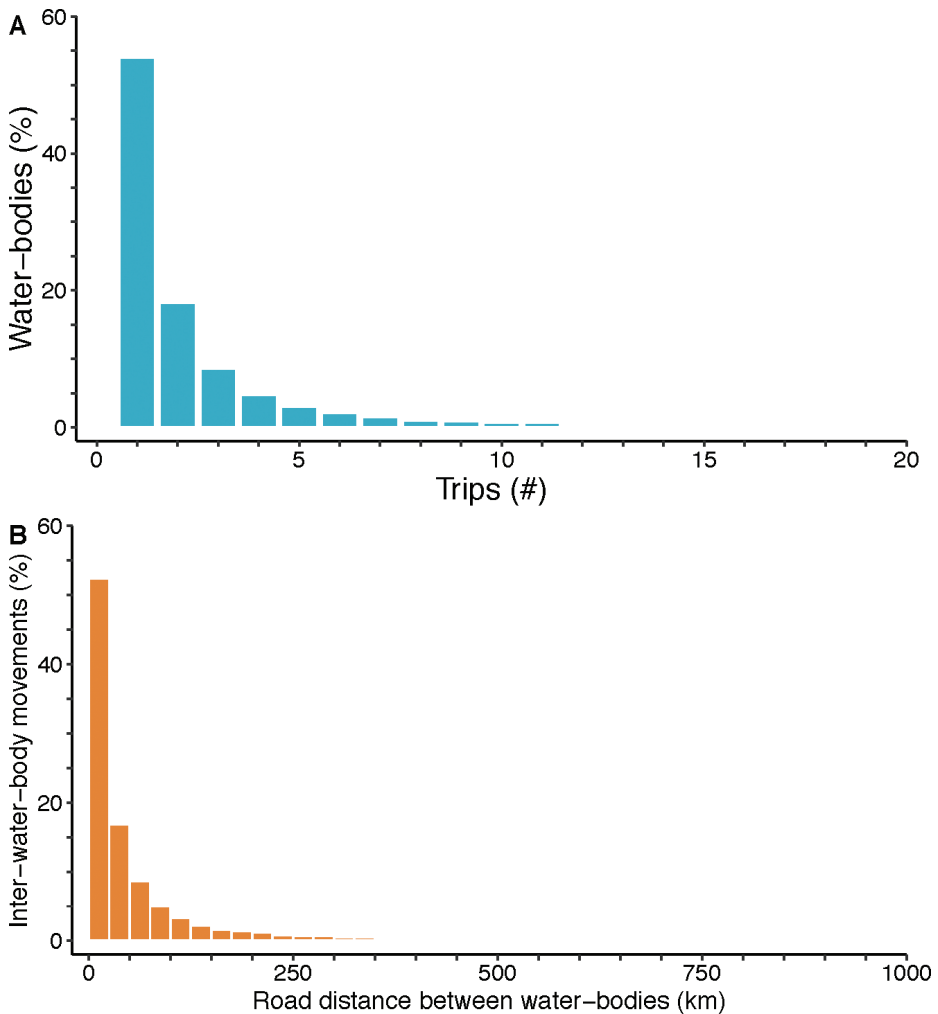


Figure 2. **A** Percentage of water-bodies according to the number of trips taken by iBobber users, truncated at 20 trips (bin size = 1) and **B** the frequency (%) of movements between two subsequently visited water-bodies by road distance (km) (bin size = 25), truncated at 1,000 km.

$p < 0.001$, $N = 53$) (Fig. 4A). Similarly, for the continental United States, the state-level visitation frequency by iBobber users was positively correlated with relative angling activity by state reported in the most recent USFWS National Survey ($R^2 = 0.342$, $p < 0.001$, $N = 47$) (Fig. 4B). Amongst states, Texas had the greatest disparity between percentage of angling activity in the iBobber (11.6%) and USFWS (5.5%) datasets.

The utility of data from mobile fishing apps to elucidate regional-scale angler movement behaviour was demonstrated using water-bodies around Milwaukee, WI (Fig. 5). For 29 water-bodies, we observed 50 angler trips along 41 visualised road routes – demonstrating the diffuse geographic routes by which non-native species could be

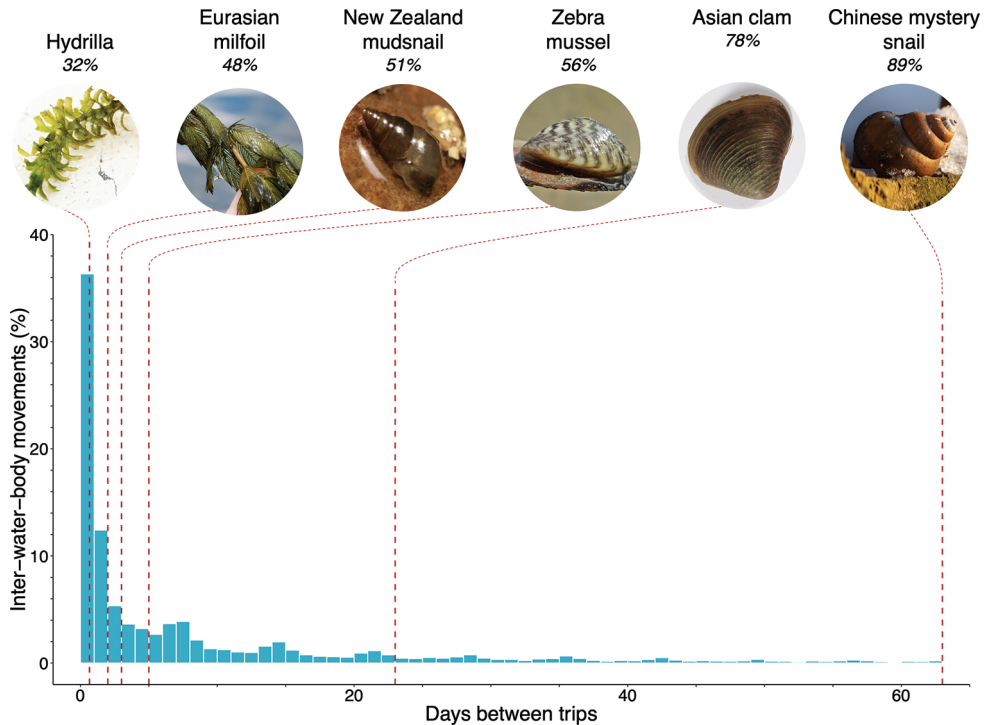


Figure 3. Percentage (%) of iBobber user movements between water-bodies according to the number of days between trips. Vertical lines represent published estimates of survival time when exposed to desiccation in an overland vector for indicated invasive species (% of total movements stated). Photo credits: “Bay grasses on the Susquehanna Flats in Harford County, Md.” by chesbayprogram is licensed under CC BY-NC 2.0, “Eurasian Watermilfoil, Susquehanna Flats” by chesbayprogram is licensed under CC BY-NC 2.0, *Potamopyrgus antipodarum*” by fturmog is licensed under CC BY-NC-SA 2.0, “File:Dreissena polymorpha (Zebra mussel), Arnhem, the Netherlands.jpg” by Bj.schoenmakers is licensed under CC0 1.0, “File:Muschel Aller 7987.jpg” by NobbiP is licensed under CC BY-SA 3.0, “Chinese Mystery Snails in winter” by brentsvew is licensed under CC BY-NC 2.0.

transported. Movements tended to originate from a small number of water-bodies (i.e. hubs), with four lakes (Beaver Dam Lake, Lake Monona, Fox Lake, Pewaukee Lake) serving as the origin lake for 64% of movements, which terminated at 20 destination lakes. According to the current distribution of aquatic nuisance species in the region, 100% of angler movements involved visiting an invaded water-body and 8% of movements were from an invaded lake to a non-invaded lake (Fig. 5).

Discussion

Mobile technologies offer new insights into risks of human-assisted transport of aquatic invasive species. Our investigation of user-generated angling data from iBobber users

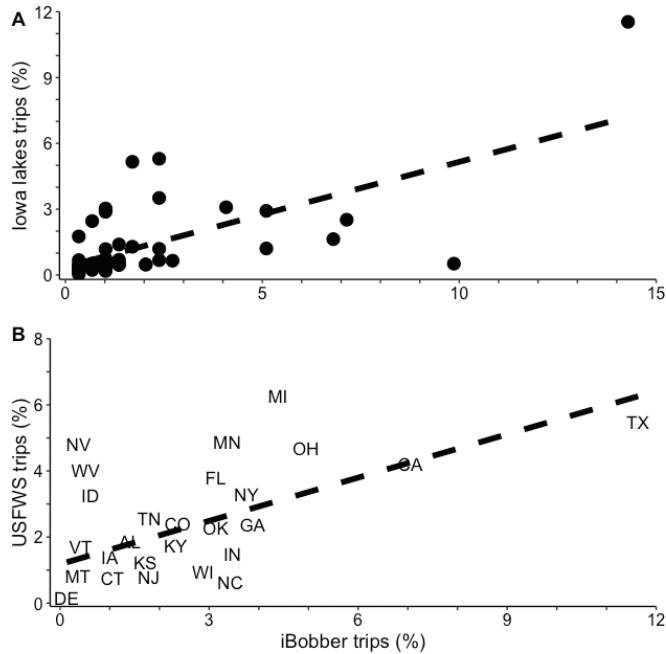


Figure 4. A Total Iowa iBobber user activity by lake (%) versus the total visits by lake (%) as quantified by an Iowa State University state-wide survey ($p = 7.5 \times 10^{-8}$, $R^2 = 0.425$) (Evans et al. 2011) **B** total iBobber user activity by state (%) versus total angling activity by state (%) as quantified by the 2011 USFWS National Survey (U.S. Department of the Interior 2014).

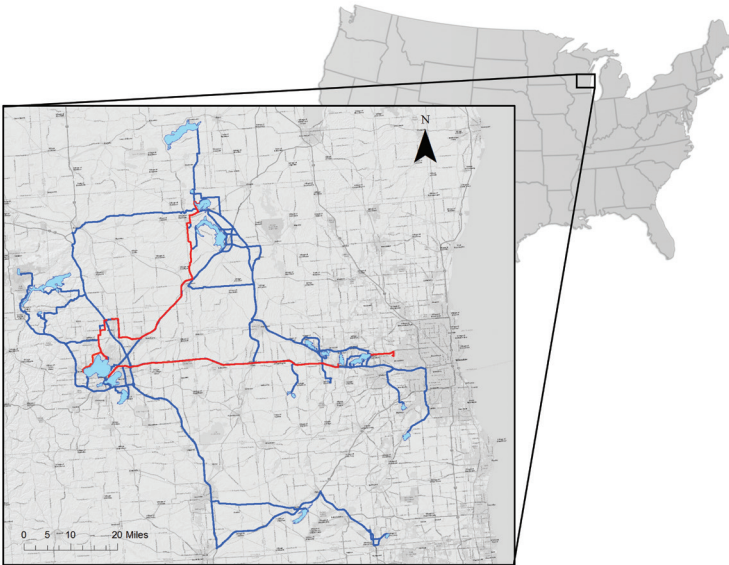


Figure 5. Road-routed movements by iBobber users between lakes in the greater Milwaukee, WI area. Movements between lakes with invasive species present are indicated by blue routes while movements from an invaded lake to a non-invaded lake are indicated by red routes.

across the United States demonstrates the potential to characterise angler site preference and movement activities well beyond the geographical and temporal extent of conventional ground-collected approaches. Furthermore, our mobile data affirms previous observations that fished water-bodies are commonly large, urban reservoirs. Here, we discuss the relevance of our findings for enhanced prevention of invasive species, evaluate the key benefits and challenges of employing new mobile data forms and suggest future steps to enhance the value of mobile data in invasion biology.

User-generated data sources represent a cost-effective means of mapping human geography of interactions with environments (Dewille et al. 2014; Toivonen et al. 2019). iBobbers, as well as similar devices and mobile applications, could provide resource managers with information regarding angler traffic at broader spatiotemporal scales than have previously been available (Venturelli et al. 2017). Given the importance of interstate pathways in facilitating transmission of invasive species and water-borne diseases between lake networks (e.g. Buchan and Padilla 1999; Muirhead and MacIsaac 2005; Stewart-Koster et al. 2015), understanding the dynamics of angler movement across traditional jurisdictional boundaries that often serve as spatial limits for conventional creel surveys is vital (Peters and Lodge 2009). Indeed, data that support coordinated management decisions across neighbouring regions are fundamental to successful management of invasive species in complex social landscapes (Epanchin-Niell et al. 2010). We found that the road distance travelled between water-bodies by iBobber users, for example, exceeded estimates for Wisconsin (mean: 93 vs. 34 km: Buchan and Padilla 1999), but was significantly less than Ontario, Canada (median: 23 vs. 292 km: Drake and Mandrak 2010) according to angler surveys.

Use of geotagged angler data from mobile technology allows for seamless cross-referencing of information about angler behaviour with characteristics of source and destination lakes, such as the pool of non-indigenous species available to be entrained into the vector and key environmental determinants of species establishment. For example, by linking to readily-available species distribution databases for a region in Wisconsin, we showed that approximately one-in-ten movements were from lakes containing aquatic invasive species to lakes currently not invaded. For the U.S., we show that the large population of iBobber users fish reservoirs at five times the rate relative to natural lakes, while concurrent research shows that reservoirs are two to 300 times more likely to support established aquatic invasive species (Johnson et al. 2008). Other predictors of angling activity included facility quality (e.g. boat launch presence) and destination size (e.g. lake area), both well-established determinants of site choice in recreational fisheries (Hunt et al. 2019). Taken together, many opportunities exist to integrate angler movement patterns derived from mobile technology with spatiotemporal data describing propagule pressure and factors related to establishment success.

Timestamped mobile-based data offer opportunities to capture the temporal dimension of angler movements across the landscape by estimating the duration of time between visits to water-bodies. As most iBobber user movement between water-bodies occurs over relatively short timeframes, our analysis suggests that a greater diversity of potential hitchhikers transported by users will be viable, according to desiccation

tolerance, upon arrival at a destination water-body. If entrained on angling or boating gear, species with a longer desiccation tolerance, such as the Chinese mystery snail, are more likely to survive and establish (89% of inter-water-body movements taken by iBobber users) than species with shorter tolerances, such as *Hydrilla* (32% of movements) (Havel et al. 2014). As an aside, our literature search returned robust estimates of temporal limitations on desiccation tolerance for relatively few species, suggesting that further studies are needed to clarify the length of time invasive species can withstand exposure out of water.

Mobile technologies also facilitate road routing of angler movement between fishing locations. Geotagged fishing locations are particularly amenable to this method, because they allow us to identify the most likely access point of a water-body, which determines the direction from which anglers may approach a lake or reservoir. Understanding the spatial configuration of human movement helps identify crucial nexuses across time and space for intercepting hitchhiking invaders. For example, junctions at which frequently-travelled routes between invaded and non-invaded lakes converge can be prioritised for interceptive approaches, such as watercraft inspection stations and recent modelling efforts to optimise the operating times and locations of such stations will benefit tremendously from the fine-scale timing and direction data that mobile sources offer (Fischer et al. 2020).

Angler mobile applications represent a cost-effective approach to understand angler-assisted vectors for aquatic invasive species and, in some instances, as in the case of iBobber, offer an opportunity for passive collection of angler activity data. This offers a number of advantages. First, as younger anglers' participation in fishing increases, mobile platforms offer management agencies an opportunity to outreach and learn more about these demographics, as these are also less likely to engage with mail-in or in-person surveys (Fisher 1996; Recreational Boating and Fishing Foundation Outdoor Foundation 2018; Gundeland et al. 2020). Second, mobile-based data provide information about the movement of a largely unknown group of anglers accessing water-bodies using non-motorised recreational boats, such as canoes and kayaks and who are similarly dispersal vectors for aquatic invasive species (Stasko et al. 2012; Anderson et al. 2014), but are not subject to conventional creel surveys conducted at boat launches. In summary, while prior work has demonstrated that actively collected mobile data (i.e. records of angler presence at a location which must be initiated by the user, such as fishing logs or catch records) generally reflect the spatiotemporal distribution of creel surveys, here we have shown that passively collected data are similarly valuable (Martin et al. 2014; Papenfuss et al. 2015). This is an important distinction, as self-initiated logs of angler presence at a water-body may not include all fished locations (we also recognise that iBobber users may not always use their device). Anglers will likely prefer to record and share trips during which they made a catch and, thus, actively collected data may be prone to success bias.

Though user-generated datasets of angling activity derived from mobile technology successfully address a number of limitations of traditional creel surveys in terms of their spatiotemporal resolution, they may also introduce new biases. In our analysis, slightly more than half of users only used their iBobber on more than one trip during

the two-year period. However, the substantial number of total iBobber users does allow us to infer movement patterns of a large sample population. Angler activity, according to iBobber users, was found to be comparable to estimates according to creel-based data collected at the scale of individual lakes and entire states of the United States. Much like creel surveys, the demographics of users of a particular mobile application or device are also unlikely to be fully representative of the entire population of interest (Hargittai 2015). For example, the cost of a single iBobber starts at 100 USD, thus imposing a socioeconomic filter on which anglers are likely to purchase and use the device. In fact, the number of iBobber users is estimated to represent less than 1% of anglers across the U.S.; this is similar to the proportion of angler populations represented in traditional survey-based approaches. Additionally, iBobber owners must possess a smartphone, because real-time data from an iBobber is communicated to users via the device's associated phone application. Previous work analysing spatial and demographic biases in other social media applications (Twitter) across the US identified a significant positive influence of higher median income, urbanisation, higher proportion of younger residents and higher proportion of minority residents on the frequency of geotagged posts (Malik et al. 2015). Despite these considerations, it is well recognised that conventional approaches are limited by the tendency to: (1) favour surveying anglers of higher economic status who own boats, (2) demonstrate biases in gender, age and location of respondents to mail questionnaires (Dempson et al. 2012), in part because of non-response and recall bias (Tarrant et al. 1993) and (3) potentially measure intended rather than actual angler behaviour (Venturelli et al. 2017). Moving forward, the extent to which demographic biases may influence the conclusions drawn from user-generated datasets about water-bodies remains unclear and should be a priority for future study.

Creel surveys and other traditional data forms continue to be highly valuable sources of information regarding angler movement of invasive species, particularly when implemented by a dedicated team of resource managers and volunteers aiming to intercept identified target species (Cooke et al. 2015). For example, boat inspection station volunteers at a single location can ask boaters which water-body they visited last and cross-reference their responses in databases of invaded water-bodies. However, for the vast majority of water-bodies with limited local funds and resources dedicated to support such intensive outreach efforts, managers working to prevent invasive introductions into an entire state or region may benefit significantly from insights gained from readily-available, even possibly real-time, mobile data. Despite this, such data are often not publicly available and will require data agreements with technology companies. Moreover, even when data are public (e.g. citizen science initiatives), lack of data sharing with larger initiatives and databases continues to pose a barrier to implementation of emerging data sources in research and management (Johnson et al. 2020). The most effective management strategies will couple an appropriate synthesis of traditional and emerging data sources based on the scope and connectivity of target water-bodies, but this will require a significant investment in web infrastructure to collate, update and disseminate disparate data sources and formats.

The ongoing creation of fishing-orientated technology and mobile applications presents an exciting opportunity for collaboration amongst researchers, technology devel-

opers and resource managers. Integration of mobile data into angler network models, for example, could lead to new developments in graph-theory methods to identify the most influential nodes (water-bodies) and edges (pathways between water-bodies) in terms of propagule pressure (Martin et al. 2017), beyond what is currently supported by more limited in-person or mail survey data (e.g. Muirhead and MacIsaac 2005; Stewart-Koster et al. 2015). Ultimately, such network approaches will benefit substantially from incorporation of water-body-level invasive species records to enable identification of movements from invaded to non-invaded water-bodies. Collaborative efforts could also identify long-standing data gaps in understanding angler behaviour (e.g. bait and gear use tendencies) and intentionally request this information in trip logs and user profiles (Venturelli et al. 2017). iBobber users have the option to self-report this information in their application profile, but our analysis of this data revealed that the vast majority leave these fields blank. Application developers often increase platform use through promotional incentives, such as gear giveaways and similar incentives could also be developed to encourage profile completion. Bait and gear use are particularly informative for invasive species prevention, as the pool of potential species moved by anglers is dependent on their gear (e.g. bait buckets) and method (shore versus boat) of fishing (Drake and Mandrak 2014). Incorporating more specific data on the type of fishing engaged in by recreational anglers into our understanding of propagule pressure will allow resource managers to further narrow preventative approaches to target the specific species most likely to be relocated between water-bodies, based on common fishing practices in a given region.

Conclusion

Mobile fishing applications and devices such as iBobber represent a valuable new passively-collected mobile data source which, along with other types of actively-collected mobile data (e.g. Papenfuss et al. 2015), offer new opportunities to provide information about invasive species management, particularly as it relates to propagule pressure from angler behaviour. User-generated, mobile data expand spatiotemporal estimates of angling activity beyond what is possible with traditional creel surveys and potentially minimise survey costs. The future holds many exciting possibilities to incorporate both digital user-generated and ground-collected data into modelled social-ecological systems to guide more efficient and effective invasive species prevention campaigns.

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Estimating the benefit of quarantine: eradicating invasive cane toads from islands

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Abstract

Islands are increasingly used to protect endangered populations from the negative impacts of invasive species. Quarantine efforts on islands are likely to be undervalued in circumstances in which a failure incurs non-economic costs. One approach to ascribe monetary value to such efforts is by modeling the expense of restoring a system to its former state. Using field-based removal experiments on two different islands off northern Australia separated by > 400 km, we estimate cane toad densities, detection probabilities, and the resulting effort needed to eradicate toads from an island. We use these estimates to conservatively evaluate the financial benefit of cane toad quarantine across offshore islands prioritized for conservation management by the Australian federal government. We calculate density as animals per km of freshwater shoreline, and find striking concordance of density estimates across our two island study sites: a mean density of 352 [289, 466] adult toads per kilometre on one island, and a density of 341 [298, 390] on the second. Detection probability differed between our two study islands (Horan Island: 0.1 [0.07, 0.13]; Indian Island: 0.27 [0.22, 0.33]). Using a removal model and the financial costs incurred during toad removal, we estimate that eradicating cane toads would, on average, cost between \$22 487 [\$14 691, \$34 480] (based on Horan Island) and \$39 724 [\$22 069, \$64 001] AUD (Indian Island) per km of available freshwater shoreline. We estimate the remaining value of toad quarantine across islands that have been prioritized for conservation benefit within the toads' predicted range, and find the net value of quarantine efforts to be \$43.4 [28.4–66.6] – \$76.7 [42.6–123.6] M depending on which island dataset is used to calibrate the model. We conservatively estimate the potential value of a mainland cane toad containment strategy – to prevent the spread of toads into the Pilbara Bioregion – to be \$80 [52.6–123.4] – \$142 [79.0–229.0] M. We present a modeling framework that can be used to estimate the value of preventative management, via estimating the length and cost of an eradication program. Our analyses suggest that there is substantial economic value in cane toad quarantine efforts across Australian offshore islands and in a proposed mainland containment strategy.

Keywords

Cane Toad, density, detection probability, eradication, islands, quarantine

Introduction

It is a truth universally acknowledged that an ounce of prevention is worth a pound of cure. In alien invasive species management, prevention of impact is achieved by conducting routine surveillance programs aimed at early detection (Holden et al. 2015), and by minimizing human-mediated dispersal of non-indigenous species (Chen et al. 2018). Despite the regular use of such quarantine approaches, conservation managers rarely explicitly value this preventative management. Preventative measures are increasingly being adopted to save imperiled taxa (Burns et al. 2012; Commonwealth of Australia 2015), but without explicitly valuing these efforts, we risk falling prey to cognitive biases (e.g., immediacy bias) and so will tend to commit substantially more money and effort to tactical, “cure” type approaches, than to strategic “prevention”. Indeed, vastly more resources are spent controlling the spread and impact of invaders than are spent on preventing their arrival and establishment (Hoffman and Broadhurst 2016).

Quarantine is particularly likely to be undervalued in circumstances in which a failure incurs non-economic costs (e.g., biodiversity loss) (Leung et al. 2002) or when costs or damages persist over long-time scales (Epanchin-Niell et al. 2015). In cases where restoration is feasible, one way to place monetary value on such quarantine efforts is to calculate the cost of restoring the system to its former state (Kimball et al. 2014; Rohr et al. 2016). In the case of an invasive species with primarily non-economic impacts, where invasion is certain or extremely likely, we can calculate the ongoing benefit of quarantine as this expense, i.e., a subsequent eradication program. Such a valuation is a lower bound on the benefit of quarantine for a number of reasons. First, the same quarantine effort typically protects against many potential invasive species, while eradication costs would apply separately to each species. In addition, any impact that an invasive species has before it is eradicated (e.g., local extinction of a native species) must be added to the cost of restoration (Hoffmann and Broadhurst 2016; Jardine and Sanchirico 2018). Lastly, as more area is invaded the value ascribed to remaining quarantined areas will be of greater value. Thus, the cost of eradicating a single invader is a very conservative estimate of the true value of quarantine efforts. Given the above it is important to note that it is unlikely that all potential islands will be invaded, and as such, the estimated costs of eradication have the potential to be significantly lower than ‘worse case’ cost modeling. Even in the face of reduced costs it is prudent to recognize the likelihood that governments and land managers will respond to the large eradication cost of inaction, or the withstanding preference to attempt eradication when incursions inevitably happen.

Islands are important resources for conservation quarantine because they offer a natural barrier to the spread of invasive species. Conservation biologists routinely exploit this property of islands, not only to protect species that naturally occur on

islands, but also to provide refuge for species under threat on the mainland (Thomas 2011; Tershy et al. 2015; Legge et al. 2018). In Australia alone, a minimum of 47 conservation translocations to islands have been carried out to date (Department of the Environment, Water, Heritage and the Arts 2009). In these circumstances – where the conservation value of an island has been artificially bolstered – the subsequent arrival of invasive species can have a larger impact than they otherwise would. Typically, island quarantine is used by conservation managers to protect native species from wildlife disease (e.g., Tasmanian devil facial tumor disease; McCallum et al. 2009) or invasive predators (e.g., foxes, cats, weasels, rats). In Australia, however, islands are also used to mitigate the impact of cane toads (*Rhinella marina*) on native predators (Moro et al. 2018; Ringma et al. 2018). Cane toads were introduced to northeastern Australia in the 1930s and, in northern Australia, continue to spread westerly at a rate of ~50 km per year (Phillips et al. 2010). This invasion has had major impacts on populations of native predators, many of which have no resistance to the toad's toxin (Greenlees et al. 2010; Nelson et al. 2010; Llewelyn et al. 2014). In response to declines of multiple predator species (e.g., dasyurids, monitors, snakes) the Australian government implemented the Cane Toad Threat Abatement Plan (2011), which aimed to identify, and where possible reduce, the impact of cane toads on native species (Shanmuganathan et al. 2010). A lack of viable methods for broad-scale control, however, has since led the Australian government to place an increased emphasis on containment (on the mainland) and on quarantine (on offshore islands) to mitigate the biodiversity impacts of cane toads (Tingley et al. 2017).

While quarantine is currently the best available strategy, it is not a panacea: cane toads have already established themselves on at least 48 islands across northern Australia (McKinney et al. 2018 unpub data), with potential for further self and anthropogenic introductions. In addition, whilst many methods are being proposed to combat the spread of toads, the most likely control method is quarantine (Tingley et al. 2017), possibly aided by targeted gene flow. Thus, execution of the strategy outlined in the Cane Toad Threat Abatement Plan requires ongoing quarantine, eradication, and containment efforts. Here we estimate the lower bound of the monetary value of these ongoing efforts by estimating the effort required to eradicate cane toads from two islands in northern Australia and generalizing this cost to islands and areas that are currently free of toads. We approach this problem by estimating the density and detection probability of toads on each island and use these estimates to calculate the amount of time and money it would take to remove toads across a subset of islands prioritized for conservation in Australia.

Materials and methods

Study Area

This study was carried out on two islands in northern Australia: Horan Island on Lake Argyle, Western Australia and Kabal (Indian Island) in the Northern Territory. Lake

Argyle, located within the East Kimberly region, is Western Australia's largest constructed reservoir covering $> 880 \text{ km}^2$. The study site is composed of exposed spinifex-covered hilltops and sparse savanna woodland. Freshwater is available year-round, with the lake contracting from May–November. Toads are thought to have colonized islands on the lake in the wet seasons of 2009/2010 (Somaweera and Shine 2012). Indian Island is an offshore island, 40 km west of Darwin in the Northern Territory. It supports predominantly savanna woodland and monsoonal vine thicket, with a large ephemeral freshwater swamp located on the northern tip of the island. Depending on the magnitude of the wet season, standing water can be present in this swamp year-round or dry up by late September. Toads are thought to have colonized Indian Island via rafting events around 2008. Access to Indian Island was granted by Kenbi Traditional Custodians (Northern Land Council permit 82368).

Field sampling

Cane toad surveys occurred over six nights, on each island, denoted, $t = \{0, 1, \dots, 5\}$, during November 2017 (Horan Island) and October 2018 (Indian Island). Surveys commenced at sundown each evening and lasted four hours, with ambient temperatures ranging from $24\text{--}35^\circ\text{C}$. As Horan Island sits within a freshwater lake, the entire island was walked around each night (7.6 km) by two people using head torches; one individual focused on the higher part of the shoreline, the other on the lower shoreline. Indian Island is an oceanic island, with the northern half (an area of 6.28 km^2) separated from the southern half by a tidal saltmarsh. The island contains a single freshwater swamp present in the dry season (circumference of 1.1 km). This swamp was navigated each night by two people using head torches over a period of four hours, with shoreline areas being surveyed more than once each night due to the reduced shoreline. On both islands, every toad encountered was collected and humanely killed on site in accordance with The University of Melbourne animal ethics protocol (1714277.1) and State laws regarding handling of non-native species. Each night, we recorded the number of individual toads collected, c_t . Surveys were conducted immediately prior to the breeding season so that only post-metamorphic age classes were encountered.

Statistical analysis

We do not encounter every individual on a given night, and so incorporate imperfect detection. For each island, we aim to estimate two parameters: N_0 , the true number of toads on the island at the commencement of surveys and p the mean per-individual detection probability. Due to our experimental design we hold p constant across time but recognize that adding variance in p will likely increase costs. We can then use these to estimate α , the length of time (in days) required to eradicate toads from our treat-

ment areas. The number of individuals collected each night, c_t , can be considered a draw from a binomial distribution:

$$c_t \sim \text{Binom}(N_t, p).$$

Where N_0 , the pre-sampling population size, is a latent variable with a mean and variance equal to λ , such that:

$$N_0 \sim \text{Pois}(\lambda).$$

For $t > 0$:

$$N_t = N_0 - \sum_{i=0}^{t-1} c_i.$$

We used a Jefferys prior (Jefferys 1961) to model our prior distributions for p (beta (0.5,0.5)). We specify λ as uniform between 200–10 000 (Indian Island) or 1500–10 000 (Horan Island) respectively. The lower bound of priors for λ are informed by densities of cane toads in their native range (Lampo and Bayliss 1996) and represent a conservative lower bound.

The length of time required to remove a population, α from a treatment area is described via the relationship:

$$\alpha = \frac{\ln(r_{crit})}{\ln(1-p)},$$

where, r_{crit} , the critical removal threshold (i.e. the proportion of the population remaining if there are less than two individuals left), is equal to $1/N_0$ (see Suppl. material 1: File S1 for workings).

Models were fitted with Markov chain Monte Carlo (MCMC) in JAGS v.4.6.0, run through R v3.4.1 via the package rjags v4.6.0 (Plummer 2013). Three model chains were run for 30,000 iterations, with the first 10,000 iterations discarded as a burn-in, which was sufficient for the MCMC chains to converge. Convergence was checked using the Gelman-Rubin diagnostic (Gelman and Rubin 1992); all chains produced potential scale reduction factors < 1.1 , indicating convergence of chains. The remaining samples were thinned by a factor of 2, resulting in 10,000 samples per chain for post-processing.

We denote a successful eradication to have occurred when only a single toad remains (i.e., no further breeding pairs remain). In order to successfully eradicate a population, the number of immigrants (i.e., propagule pressure) must be controlled prior to eradication efforts. We assume that our system is closed for the six consecutive nights of sampling. We then apply the outputs of our model to estimate the removal cost of toads across a range of Australian islands, under the assumption that immigration is zero for the duration of any subsequent eradication program.

Cost analysis

We estimate the cost of eradicating toads on prioritized islands (see below) from incurred personnel, consumable, and travel costs during toad collection (Table 1). Relative to most islands across northern Australia, both Horan and Indian Islands are readily accessible, thus our travel costs are modest. We assume that eradication is conducted by a fully equipped organization; thus, we do not include vehicle/boat purchase or hire (i.e., set-up costs), nor do we consider organizational in-kind associated with utilizing existing capital. Removal efforts are carried out in subsequent five-day blocks until eradication is reached; and we assume that travel to and from our site is incurred weekly in order to resupply staff. Travel costs include a \$85/hour consultant rate (for travel time) plus the additional costs of fuel, insurance, and vehicle maintenance (an extra \$36/hour). Thus, total travel costs are \$111/hour of travel. For Horan Island we assume a travel duration of four hours each way (to and from Katherine). For Indian Island the travel time is also four hours each way (to Darwin).

Cost Scenarios

We use our estimates of the length of time required to eradicate toads from our treatment areas on Horan and Indian Islands (with their attendant detection probabilities) to explore the potential of quarantine efforts on a subset of high priority islands (Table 2). Our chosen islands are drawn from a list of 100 oceanic islands that the Australian Commonwealth has prioritized for conservation, due to their biodiversity

Table 1. Example areal metric costing and assumptions associated with a cane toad eradication program on Horan Island. Derived from incurred field costs and estimated mean removal estimates (75 days). All figures are in Australian Dollars (\$AU).

| Item Description | Item Category | Unit type | Number of units | Cost per unit | Total Cost | Assumption |
|---|---------------|--------------|-----------------|---------------|------------|---|
| Conducting toad surveys/removal | Personnel | Per hour | 1500 | \$85 | \$127 500 | Hourly rate of \$85. Removal efforts are based on two people each getting paid for ten hours a day at survey rates. |
| Motorized travel to and from study site | Travel | Per hour | 120 | \$111 | \$13 320 | Hourly rate of \$111 per hour of vehicle use (survey rate, insurance, maintenance and fuel). Return travel nearest town is 4 hours. Field member returning to town to resupply once per week (75 days/5 = 15 trips of 8 hours). |
| Motorized travel within site | Travel | Per hour | 75 | \$36 | \$2 700 | Additional hourly rate of \$36 per hour of in-site vehicle use. This captures insurance, maintenance and fuel costs. One hour of in-site travel each day. |
| Food and sustenance | Consumable | Per day | 75 | \$60 | \$4 500 | Food at \$30 per head, per day. |
| AA Batteries for night surveys | Consumable | Per four | 75 | \$14 | \$1 050 | Single set of batteries required for each sampling night. |
| Refill of CO ₂ canister (8kg) | Consumable | Per canister | 1 | \$150 | \$150 | Single canister required for euthanizing cane toads. |
| Calico Bags for holding individuals | Consumable | Per bag | 63 | \$1 | \$63 | A Calico bag required for every 20 individuals removed (n = 1251). |
| Theoretical cost to eradicate cane toads from Horan Island (0.78km ²) | | | | | \$149 283 | |

Table 2. Islands included in analyses from the top 100 islands prioritized by the Australian Commonwealth for conservation actions (Department of the Environment, Water, Heritage and the Arts (2009)). Estimates for the benefit of quarantine are in '000s (AUD). Mean benefit reports the cost of removal, averaging over costs calculated with the detection probabilities of each of our island systems.

| Jurisdiction | Island Name | Toads Present | Distance to mainland (km) | Area (km ²) | Length of freshwater shoreline (km) | Mean benefit of quarantine (000s) | Lower Est. | Upper Est. |
|--------------------|-------------------------|---------------|---------------------------|-------------------------|-------------------------------------|-----------------------------------|------------|------------|
| New South Wales | Lord Howe Island | No | 570 | 11 | 1 | 18 | 10 | 28 |
| Western Australia | Barrow Island | No | 56 | 139 | 21 | 373 | 200 | 580 |
| | Bernier Island | No | 38 | 171 | 2 | 36 | 19 | 55 |
| | East Intercourse Island | No | 5.5 | 51 | 2 | 36 | 19 | 55 |
| | Faure Island | No | 6.1 | 8 | 2 | 36 | 19 | 55 |
| Queensland | Badu Island | Yes | 90 | 53 | 10 | 178 | 95 | 276 |
| | Bentineck Island | Yes | 25 | 269 | 5 | 89 | 48 | 138 |
| | Boigu Island | Yes | 7.8 | 6 | 55 | 977 | 524 | 1519 |
| | Darnley Island | Yes | 70 | 195 | 0 | 18 | 10 | 28 |
| | Dunk Island | Yes | 4 | 170 | 1 | 18 | 10 | 28 |
| | Goold Island | Yes | 15 | 101 | 1 | 18 | 10 | 28 |
| | Hammond Island | Yes | 18 | 104 | 3 | 53 | 29 | 83 |
| | Horn Island | Yes | 16.7 | 396 | 8 | 142 | 76 | 221 |
| | Macleay Island | Yes | 3 | 16 | 0.7 | 12 | 7 | 19 |
| | Magnetic Island | Yes | 6.3 | 6 | 2 | 36 | 19 | 55 |
| | Moa Island | Yes | 52 | 72 | 21 | 373 | 200 | 580 |
| | Moreton Island | Yes | 20 | 7 | 54 | 959 | 514 | 1491 |
| | Mornington Island | Yes | 29 | 1662 | 102 | 1812 | 971 | 2817 |
| | North Stradbroke Island | Yes | 3.8 | 1001 | 105 | 1865 | 1000 | 2900 |
| | Prince of Wales Island | Yes | 16 | 148 | 27 | 480 | 257 | 746 |
| | Sweers Island | No | 30 | 7 | 4 | 71 | 38 | 110 |
| Northern Territory | Bathurst Island | No | 61 | 235 | 137 | 2434 | 1305 | 3783 |
| | Centre Island | Yes | 7.8 | 64 | 20 | 355 | 190 | 552 |
| | Croker Island | No | 3 | 11 | 152 | 2700 | 1447 | 4197 |
| | Groote Eylandt | No | 45 | 42 | 203 | 3606 | 1933 | 5606 |
| | Marchinbar Island | No | 21 | 5 | 59 | 1048 | 562 | 1629 |
| | Melville Island | No | 24 | 2 | 1054 | 18724 | 10036 | 29106 |
| | North Island | Yes | 28 | 13 | 3 | 53 | 29 | 83 |
| | Peron Island | No | 3.4 | 3 | 3 | 53 | 29 | 83 |
| | Raragala Island | No | 36 | 52 | 11 | 195 | 105 | 304 |
| | Vanderlin Island | Yes | 7 | 6 | 68 | 1208 | 647 | 1878 |
| | West Island | Yes | 4 | 576 | 30 | 533 | 286 | 828 |
| | Yabooma Island | No | 2.7 | 2 | 3 | 53 | 29 | 83 |

value and the presence of species listed under the Environment Protection and Biodiversity Conservation Act (Department of the Environment and Energy [DEE] 1999). To ascertain feasible islands for quarantine, we refine this list to include only islands that are ≥ 2 km from the Australian mainland and occur within the potential distribution of cane toads in Australia (Kearney et al. 2008). For each island in our dataset, we map the length of permanent freshwater shoreline available, using either satellite maps, government/landholder records, or a combination of both – resulting in a net kilometer length of shoreline for each island in our dataset (Table 2). We apply our survey effort per unit length that our estimates are based upon across the resultant length of shoreline. For islands in our dataset which possess a large length of shoreline we assume organizations have adequate staff to maintain the survey effort on which our estimates are based (see field sampling). All islands were cross-checked for the presence of cane

toads via the ‘Feral Animals on Offshore Islands’ database (DEE, 2016) in addition to the presence of human settlement. In cases where islands had no permanent freshwater but did have human settlement (or known livestock presence), a one-kilometer circumference was assumed around dwellings and visible watering points.

In addition to the islands derived from this report, we explore the value of a potential cane toad containment strategy outlined in a revised version of the Cane Toad Threat Abatement Plan (Tingley et al. 2013). This strategy aims to develop a ‘waterless barrier’ on the Australian mainland by excluding cane toads from artificial water bodies on cattle stations between Broome and Port Hedland in Western Australia. If implemented successfully, this strategy could keep toads out of the Pilbara (and subsequent regions) – an effective quarantine of 268 000 km² of the Australian mainland (see Florance et al. 2011; Tingley et al. 2013; Southwell et al. 2017 for further information). Using a dataset on the presence of bore holes, cattle watering points, dams, and permanent freshwater bodies in the Pilbara Bioregion (see Southwell et al. 2017) we estimate the economic benefit of the proposed barrier. A one-kilometer circumference was applied to all waterpoints, dams and pools, in addition to a per-kilometer of shoreline rate along permanent watercourses within the region.

Results

The number of cane toads removed from both Horan and Indian Island, c_p , declined over time (Figure 1). Across the duration of our surveys, we captured and removed a total of 1550 cane toads (1251 on Horan Island, 299 on Indian Island). The estimated posterior probability of detecting an individual toad on a given night differed between our two study sites (Horan Island: mean p [95% credible interval] = 0.10 [0.07, 0.13]; Indian Island: 0.27 [0.22, 0.33]) (Suppl. material 4: Figure S3). Given site-specific detection probabilities, the estimated number of toads present at the initiation of our surveys (N_0) was much higher on Horan Island (2696 [2183, 3549]) than on Indian Island (353 [308, 407]) (Suppl. material 5: Figure S4).

Horan Island – situated in a freshwater lake – has a circumference of 7.63 km, which translates to a cane toad density of 352 [287, 466] individuals per kilometer of freshwater shoreline. The freshwater source on Indian Island has a circumference of 1.04 km, translating to a density of 341 [298, 391] individuals per kilometer of freshwater shoreline. We could also express toad density as animals per km² of island, in which case we calculate an average density of individuals of 56/km² on Indian Island and 2899/km² on Horan Island.

Cost Sensitivity

Applying our parameter estimates derived from our Horan Island site, we estimate a removal cost of \$22 487 [\$14 691, \$34 480] per kilometer of freshwater shoreline, or

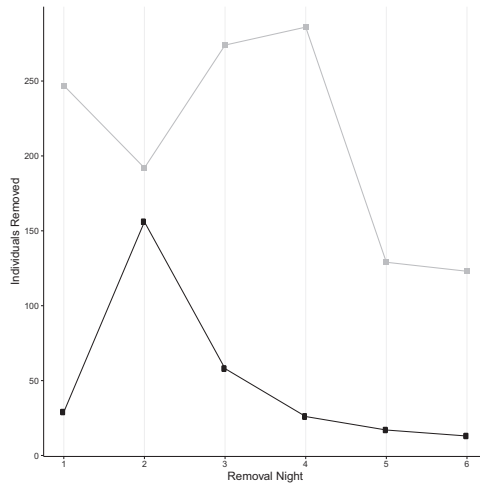


Figure 1. Numbers of individual cane toads captured per night on Horan (gray) and Indian (black) Islands.

\$184 564 [\$120 582, \$282 998] per km² of land. Using the values derived from our Indian Island site, we estimate it would cost \$39 724 [\$22 069, \$64 001] per kilometer of freshwater shoreline, or \$6 559 [\$3 644, \$10 568] per km² of land.

Benefit of quarantine on Prioritized Australian Islands

Using our estimates of eradication costs per-kilometer of freshwater shoreline, we examine the economic benefit of cane toad quarantine on all toad-free islands (by jurisdiction), as well as the cost to restore all toad-inhabited islands to a toad-free state (Figure 2). The current economic benefit of quarantine on all prioritized toad-free islands is estimated to be between \$43.4 [28.4–66.6] million (based on Horan Island) and \$76.7 [42.6–123.6] million (Indian Island). We estimate it would cost, on average, between \$6.0 [3.9–9.2] million (Horan Island) and \$10.6 [5.9–17.0] million (Indian Island) to remove toads from all prioritized islands currently occupied by toads. Finally, we estimate the economic benefit of the ‘waterless barrier’ protecting the Pilbara to be between \$80.5 [52.6–123.4] million (Horan Island) and \$142.1 [79.0–229.0] million (Indian Island).

Discussion

As the number of alien invasive species requiring management increases, practitioners must identify efficient strategies for allocating resources to various management activities. Although conventional wisdom places emphasis on prevention measures, the practice of valuing such actions in the face of non-economic costs can be challenging.

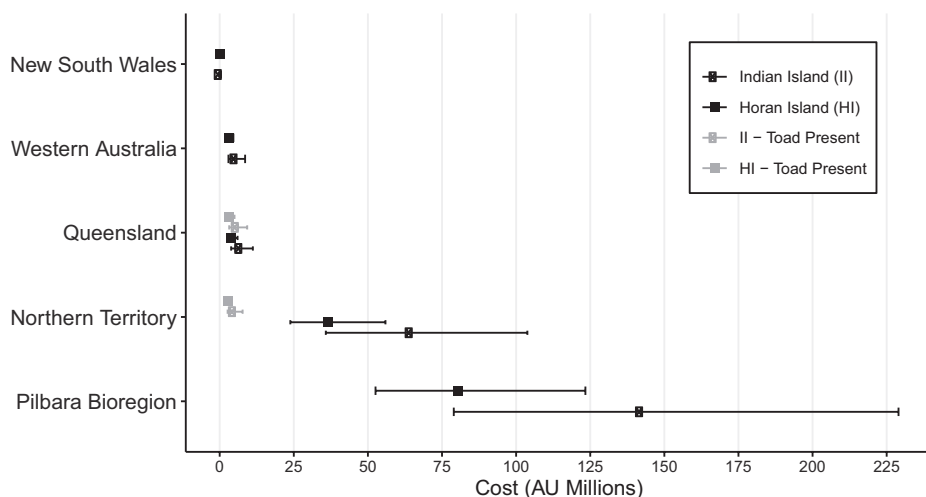


Figure 2. Distribution of the benefit of cane toad quarantine across different jurisdictions within Australia. Toad present distributions denote areas where toads are known to occur and represent the cost to remove toads. No islands in either New South Wales, Western Australia or the Pilbara Bioregion have confirmed toad presence.

Placing monetary value on a conservation benefit will most often require some value judgement as to the monetary worth of biodiversity. Using estimates of a species' detectability, population density, and subsequent eradication costs, we aim to sidestep such value judgement when investigating the benefit of quarantine measures in combatting the impact of the invasive cane toad across Australia's prioritized offshore islands.

Despite substantial community and research effort into cane toad removal via trapping and hand capture, there are only a handful of published detection estimates for the species (Griffiths and McKay 2007). Our detection estimate is, of course, specific to the details of our survey. Nonetheless, it is surprisingly low for our large-shoreline site (Horan Island). Here, the length of shoreline meant we only passed each location once per night, and individual toads in this closed system had, on average, a 0.10 [0.07–0.13] probability of being seen on any given night. This contrasts with our small-shoreline site (Indian Island), where we were able to make multiple passes of the same point each night. Here, individual toads had a 0.27 [0.22–0.33] probability of being detected on a given survey night. Whilst individual toads are relatively easy to see when they are active, our results suggest that this might give a misleading impression of their detectability, especially if the size of area surveilled prevents more than a single pass during each survey. Additionally, physiological correlates are likely to affect individual detection probability, with both sex and body condition linked to activity levels (and hence detectability) of adult cane toads (Yeager et al. 2014). Further work is required to examine how both physiological and environmental correlates influence cane toad detectability as they invade into, and interact with novel environments in Australia.

We compared two density metrics: linear density (per km) and areal density (per km²). Our areal density estimate for Horan Island (2 893 individuals/km²) is similar to estimates derived from previous studies of invasive cane toads in the Solomon Islands archipelago (1 035/km²; Pikacha et al. 2015), the islands of Papua New Guinea (3 000/km²; Zugg et al. 1975; Freeland et al. 1986), and density estimates of an analogous invasive toad on Madagascar (3 240/km²; Reardon et al. 2018). A single study conducted on the Australian mainland reported densities as high as 256 300 individuals per km² (Cohen and Alford 1993), but this estimate was predominantly of the metamorph life stage, which occurs at very high densities prior to dispersal. Metamorphs are strongly constrained to the edges of water bodies (Child et al. 2008), and typically suffer high mortality from predation and desiccation before reaching maturity (Ward-Fear et al. 2010). While an areal density would make sense in a habitat where animals are constrained by some factor that scales with area (e.g., primary productivity), it is clear that toads in northern Australia are often constrained by access to water in the dry season, and thus length of shoreline is more appropriate. Length of shoreline not only defines access to water, but also the density of infectious parasites (such as *Rhabdias pseudosphaerocephala*) that use moist conditions and high toad densities along shorelines as opportunities for transmission (Kelehear et al. 2011, 2013). It is also likely that the survival rate of emergent metamorphs is dependent on length of shoreline, because this will set the density of conspecifics and so moderate the rate at which these conspecifics cannibalize each other (Pizzatto and Shine 2008). In comparing the areal and linear densities between our sites, we find a large difference between sites in the areal metric, but a strikingly similar density value across sites in the linear metric. Our results suggest that across these two different systems, adult toads achieve a density of around ~350 adults per kilometer of shoreline.

Because toads in dry conditions require regular re-hydration (Seebacher and Alford 2002; Tingley and Shine 2011) it is a logical step to conduct removal efforts when toads are restricted to a subset of semi-permanent hydration points during drier sections of the year (Letnic et al. 2015). Given the ecological reasons discussed above, and the fact that the linear density metric is so concordant across sites, we suggest that the linear metric should be used to calculate eradication costs. Certainly, if we use the areal metric, we find a wide gulf in the possible eradication values relative to our shoreline metric (Suppl. material 3: Figure S2). Encouragingly, our cost estimates using the shoreline metric are similar to estimates derived from a successful eradication program associated with removing the American bullfrog from two locations in Canada (\$8 200–\$23 000 CAN per kilometer of freshwater shoreline).

To our knowledge, there is only one instance in which the cost to eradicate cane toads from an island has been documented (Wingate 2011). Carried out on Nonsuch Island in Bermuda, this removal occurred over six years and included countless volunteer hours, hand collection and fencing methods, and an investment of \$10 000 USD (~\$14 330 AUD) to remove toads from an area of 0.6 km². In addition, two successful eradications from extralimital mainland sites have been documented, occurring beyond

the southern border of the cane toads' current range in Australia (White 2010; Greenlees et al. 2018). The low incidence of successful removals of the invasive cane toad mirrors a broad trend in the eradication of invasive amphibian populations globally (Adams and Pearl 2007; Kraus 2009; Beachy et al. 2011; Orchard 2011). As such, there is scant information available to guide policy makers and management agencies when evaluating the feasibility of implementing amphibian quarantine and eradication measures.

Hand removal of individuals is required if eradication is to be successful. In landscapes where hydration points are localized or scarce, the use of fencing to exclude individuals from waterbodies can be a cost-effective solution (e.g., Wingate 2011). In these cases, the effectiveness of fencing relies predominantly on the proportion of the population excluded outside the fence (those not excluded still need to be removed by hand), as well as the cost of materials and the person hours associated with installing and maintaining the fence (see Brooke et al. 2004 for a full costing). For small waterbodies where fencing is feasible, the cost will be directly reduced by the proportion of the population retained outside the fence. Our goal was to provide a general cost metric comparable across prioritized islands and jurisdictions, and to place a lower bound on the value of cane toad quarantine more generally. As such, we refrain from exploring a multi-method approach, although acknowledge this may reduce the overall cost of an eradication program in some instances.

If we are to shift away from tactical, post-invasion approaches, to a preventative strategic approach, management practitioners require an estimate of the economic value that quarantine holds. Our analysis of the feasibility and benefit of cane toad quarantine is timely, given renewed emphasis on Australia's offshore islands as safe havens to buffer biodiversity against cane toad impacts. Sixty-two Australian offshore islands designated as 'high conservation status' fall within the cane toad's predicted distribution; more than a third of these (21) have already been colonized by toads. Given our criteria (see Methods), we estimate the remaining value of toad quarantine across toad-free islands in northern Australia to be up to \$77 [43–124] million. This value is conservative for a number of reasons. It is a reasonable expectation that as islands become home to increasing numbers of insurance populations or endangered species, the benefit of maintaining those islands as pest-free (measured as the cost of restoration) will increase. In addition, as toads establish themselves in an increasing number of these islands, those remaining toad-free will, by their scarcity alone, attain a greater environmental value.

At the same time, our estimate of the remaining value of toad quarantine across toad-free islands may overestimate the total quarantine benefit because it is unlikely that all islands without quarantine will be invaded. For example, islands that only contain hydration opportunities in the form of cultivated lawns or watering gardens (e.g., Darnly Island, Table 2) may be suitable for toads to invade, but reproduction and long-term persistence are unlikely. The benefit of quarantine within our dataset is held primarily by a few large islands (e.g., Melville Island, Table 2). These larger islands often have human settlements, competing management objectives (e.g., economic growth activities, multi-species quarantine), or more convoluted invasion pathways associated

with anthropogenic activity. For those that contain large human settlements, the use of organized community groups to conduct local removals or population suppression may reduce costs, although eradication is unlikely without a defined management goal and coordinated effort. In short, quarantine needs to be prioritized and carefully managed on these large islands.

Eradication efforts for taxa other than toads have been successful on large islands, such as a goat eradication program on Santiago Island (5 465 km² at a cost of \$7.08 million) (Cruz et al. 2009) or rat eradication carried out on Macquarie island (128 km² at a cost of \$21.25 million) (Raymond et al. 2011). These efforts on larger islands require careful planning, intersectional management, and investment in post-eradication surveillance and monitoring (Moore et al. 2010; Rout et al. 2011; Carwardine et al. 2012) and the monetary cost associated with a successful eradication will vary depending on the biology of the target species in question.

The vanguard of the cane toad invasion is currently sweeping across Western Australia at ~50 km per annum, but recent research suggests that a waterless barrier between the Kimberley and the Pilbara could halt the toad invasion (Florance et al. 2011; Tingley et al. 2013; Southwell et al. 2017; Gregg et al. 2019). This barrier represents the only option remaining to exclude cane toads from realizing their entire potential distribution across the Australian mainland. Applying our results to this management strategy revealed that the benefit of quarantine over such an area (\$80–142 M) is roughly double the value of quarantine across all offshore islands combined (\$49–77 M). The cost of quarantine in this case has been rigorously estimated at around \$5 million dollars over 50 years (Southwell et al. 2017), only a fraction of what we estimate it would cost to eradicate toads from this area.

Here we demonstrate the immense benefit of toad quarantine across northern Australia. We avoid value judgement and simply calculate the cost of eradication in the case of quarantine failure. Our valuation is certainly a lower bound on the true benefit, but valuing preventative management is important and will become more so as conservation actions increasingly rely on offshore islands and fenced areas as cost-effective avenues to protect biodiversity from the impacts of alien invasive species. Quarantine measures often protect against multiple potential invaders but our results suggest that even when considering a single species, the monetary value of quarantine can be substantial. Prevention, it seems, is worth more than we might naively guess, even with aphorisms to remind us.

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Supplementary material 1

File S1

Authors: Adam S. Smart, Reid Tingley, Ben L. Phillips

Data type: statistical data

Explanation note: Working to support the formulation of the critical removal threshold (r_{crit}) – the number of days required to reduce a population to less than two individuals.

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Link: <https://doi.org/10.3897/neobiota.60.34941.suppl1>

Supplementary material 2

Figure S1. Estimated density of cane toads on each island using density calculated per km of shoreline, and per km² of landmass

Authors: Adam S. Smart, Reid Tingley, Ben L. Phillips

Data type: statistical data

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Link: <https://doi.org/10.3897/neobiota.60.34941.suppl2>

Supplementary material 3

Figure S2. Costs of eradication calculated per km of shoreline and per square kilometre of landmass

Authors: Adam S. Smart, Reid Tingley, Ben L. Phillips

Data type: statistical data

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Supplementary material 4

Figure S3. Posterior distributions of the detection probabilities of cane toads on Horan and Indian Islands

Authors: Adam S. Smart, Reid Tingley, Ben L. Phillips

Data type: statistical data

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Supplementary material 5

Figure S4. Posterior distributions of cane toad population size (N_0) before removal effort

Authors: Adam S. Smart, Reid Tingley, Ben L. Phillips

Data type: statistical data

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