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Even well-studied groups of alien species might be poorly inventoried: Australian *Acacia* species in South Africa as a case study

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Abstract

Understanding the status and extent of spread of alien plants is crucial for effective management. We explore this issue using Australian *Acacia* species (wattles) in South Africa (a global hotspot for wattle introductions and tree invasions). The last detailed inventory of wattles in South Africa was based on data collated forty years ago. This paper aimed to determine: 1) how many Australian *Acacia* species have been introduced to South Africa; 2) which species are still present; and 3) the status of naturalised taxa that might be viable targets for eradication. All herbaria in South Africa with specimens of introduced Australian *Acacia* species were visited and locality records were compared with records from literature sources, various databases, and expert knowledge. For taxa not already known to be widespread invaders, field surveys were conducted to determine whether plants are still present, and detailed surveys were undertaken of all naturalised populations. To confirm the putative identities of the naturalised taxa, we also sequenced one nuclear and one chloroplast gene. We found evidence that 141 Australian *Acacia* species have been introduced to South Africa (approximately double the estimate from previous work), but we could only confirm the current presence of 33 species. Fifteen wattle species are invasive (13 are in category E and two in category D2 in the Unified Framework for Biological Invasions); five have naturalised (C3); and 13 are present but there was no evidence that they had produced reproductive offspring (B2 or C1). DNA barcoding provided strong support for only 23 taxa (including two species not previously recorded from

South Africa), the current name ascribed was not supported for three species and, for a further three species, there was no voucher specimen on GenBank against which their identity could be checked. Given the omissions and errors found during this systematic re-evaluation of historical records, it is clear that analyses of the type conducted here are crucial if the status of even well-studied groups of alien taxa is to be accurately determined.

Keywords

Biological invasions, herbaria, inventory, invasive species, management plan, tree invasions, alien species lists

Introduction

Every country needs up-to-date lists of introduced species to ensure that management actions are directed appropriately to deal with taxa at all stages of the introduction-naturalisation-invasion continuum (Latombe et al. 2017, McGeoch et al. 2012, Regan et al. 2002). Several types of errors and biases typically exist in such species lists. These include: insufficient survey information, inappropriate data resolution, undocumented data, inaccessible data, lack of sufficient information on native range distribution, incomplete information, misidentifications, unresolved ambiguities in the nomenclature, and un-described taxa (Latombe et al. 2017, McGeoch et al. 2012, Regan et al. 2002). For plants, sources of these errors and biases in the published literature, in museums, and in herbaria need to be assessed to create more comprehensive, accurate and reliable databases to inform management.

Australian *Acacia* species (wattles) are a good group to address the dimensions of these problems because: 1) introductions and plantings of species in this group have been fairly well documented; 2) wattles are amongst the most widely transferred tree species and well-studied invasive plant species in the world; and 3) wattles are often a priority for management (Marais et al. 2004), given the substantial negative impacts they can cause and the difficulties of controlling established invasions (Wilson et al. 2011).

Wattles have been introduced to many parts of the world for many purposes (Le Maitre et al. 2002, Kull and Tassin 2012) and they have played a major role in improving the livelihoods of communities (Kull et al. 2011, van Wilgen et al. 2011) and in economic growth (Griffin et al. 2011, Richardson et al. 2011). Despite these benefits, some wattle species have also become widespread invaders, threatening biodiversity by transforming ecosystems (Le Maitre et al. 2000, 2011).

Throughout this paper, we use the terms “Australian *Acacia* species” or “wattles” to refer to species formerly grouped in *Acacia* subgenus *Phyllodineae*, although several of these species (e.g. *A. koa* and *A. simplex*) do not actually have an Australian native range. We do not, however, consider species formerly grouped in other subgenera (e.g. even though *A. bidwilli* was formerly grouped in *Acacia* subgenus *Acacia*, is native to Australia and has been recorded as being introduced to South Africa, it is not part of this analysis). Richardson et al. (2011) estimated that of the 1022 wattle species formally described as of October 2010, at least 38% of these are known to have been moved by humans to areas outside their native ranges, at least 71 have become naturalised, and at least 23 have become invasive (i.e. have spread over substantial distances from planting sites) (see also Rejmánek and Richardson 2013).

Knowledge of the introduction history of these species is crucial for understanding and predicting their performance (Wilson et al. 2011) and to guide management strategies (van Wilgen et al. 2011). The long history of introductions and widespread dissemination of Australian *Acacia* species around the world has created opportunities to investigate factors that drive the success and failure of introductions, and to determine how native species respond to such events (Castro-Díez et al. 2011, Richardson et al. 2011).

South Africa has a long history of wattle introductions. Several species (notably *A. cyclops*, *A. longifolia* and *A. saligna*) were introduced in the early 18th century by the Cape Colonial Secretary to stabilise dunes near Cape Town (Ross 1975, Poynton 2009); and, a few decades later, several species, e.g. *A. decurrens*, *A. mearnsii*, and *A. melanoxylon*, were introduced for timber production (Poynton 2009). Where these species were planted for forestry, native vegetation was removed to allow the acacias to establish without competition (Richardson and Rejmánek 2011). In the early 19th century, several other species were introduced for ornamental purposes, e.g. *A. baileyana*, *A. elata*, and *A. podalyriifolia* (Donaldson et al. 2014a, b). As a result of this long and varied history, South Africa has the greatest recorded diversity of Australian *Acacia* species introductions and the most widespread wattle invasions of anywhere in the world (Richardson et al. 2011, Richardson and Rejmánek 2011, Rejmánek and Richardson 2013).

The history of wattle species introduced and planted for forestry purposes in South Africa was reviewed by Poynton (2009). However, the information on which this assessment was based was collated in the 1970s and needs updating. For example, recent surveys have shown that some species are much more abundant and widespread than previously thought (e.g. *A. paradoxa*; Zenni et al. 2009), and several species that were not listed by Poynton (2009) are now invasive (e.g. *A. stricta*; Kaplan et al. 2014).

Despite several decades of intensive management of invasive wattles in South Africa (van Wilgen et al. 2011, 2016), we know little about species other than those with substantial commercial value and those that are well-established invaders. What is known, however, is that invasions of Australian *Acacia* species are still increasing in geographical extent, abundance, and magnitude of impact (Henderson and Wilson 2017). Even the most widespread invasive species have not reached all potentially invasible sites (Rouget et al. 2004) and many naturalised species only began spreading recently (e.g. Zenni et al. 2009, Kaplan et al. 2012, 2014). Rouget et al. (2016) quantified different aspects of this "invasion debt" for wattles and found that southern Africa has a large invasion debt. If the invasion debt were realised, there will be a substantial escalation in the overall ecological and economic impacts of wattles (Richardson et al. 2015).

Richardson et al. (2011) reported that about 70 species of Australian *Acacia* species are known to have been introduced to South Africa, some as early as the 1830s (Adamson 1938, Poynton 2009). Fourteen species are currently considered invasive in the country (Rejmánek and Richardson 2013). There are also records of naturalised populations of *A. adunca*, *A. cultriformis*, *A. fimbriata*, *A. pendula*, *A. viscidula*, (Wilson et al. 2011, van Wilgen et al. 2011) and there are localised populations of what has been termed "*A. retinodes*" (which is likely *A. provincialis* – see Table 1) and *A. ulicifolia* (Wilson et al. 2011, van Wilgen et al. 2011). The identification of these naturalised species remains to be verified, and the status of other species reported in the country is unknown. This study therefore set out to determine: 1) how many Australian *Acacia* species have been introduced to South Africa; 2) which species are still present; and 3) what is the extent of naturalised populations.

Methods

Creating a list of species that have been introduced into South Africa

We reviewed formal literature sources (e.g. Poynton et al. 2009; Street 1962), student theses, and unpublished records documenting Australian acacias in South Africa. All relevant herbaria, museums, and botanical gardens in South Africa with specimens or collections of Australian *Acacia* species were also visited or consulted. Literature and online databases were searched using the genus and species name as a search term to collate information on specimens from other herbaria around the world that were previously recorded in South Africa (e.g. www.worldwidewattle.com; http://newposa.sanbi.org; www.gbif.org; and www.ildis.org/). The dataset was expanded with data from other sources that list introduced species distributions in southern Africa, including: 1) the Southern African Plant Invaders Atlas (SAPIA, Henderson and Wilson 2017); 2) I-Spot (http://www.ispot.org.za/); and 3) the National Herbarium Computerized Information System (PRECIS online database http://newposa.sanbi.org/; Morris and Glen 1978). Locality records from herbaria data were compared with records in literature sources, databases and experts to obtain updated locality records. Data collected from different sources were filtered and duplicates were removed.

During herbaria visits, we followed a standard protocol for dealing with records of Australian acacias (Fig. 1). Records with precise coordinates were noted and added to the locality list. Google Earth was used to find the likely locality of the *Acacia* plants. Landowners and managers were contacted, and field surveys were conducted to search for plants. For records with imprecise locality description and no coordinates, the source of the record was consulted.

Determining which species are still present

After compiling the list of introduction sites for wattles in South Africa, we conducted field surveys to confirm whether species were still present. We also specifically looked for locations where many species had been cultivated (e.g. arboreta and forestry trial plantations) to determine whether other taxa that have not been formally recorded were present. In cases where a location was provided but precise co-ordinates were not given, we consulted relevant officials (e.g. local conservation officers).

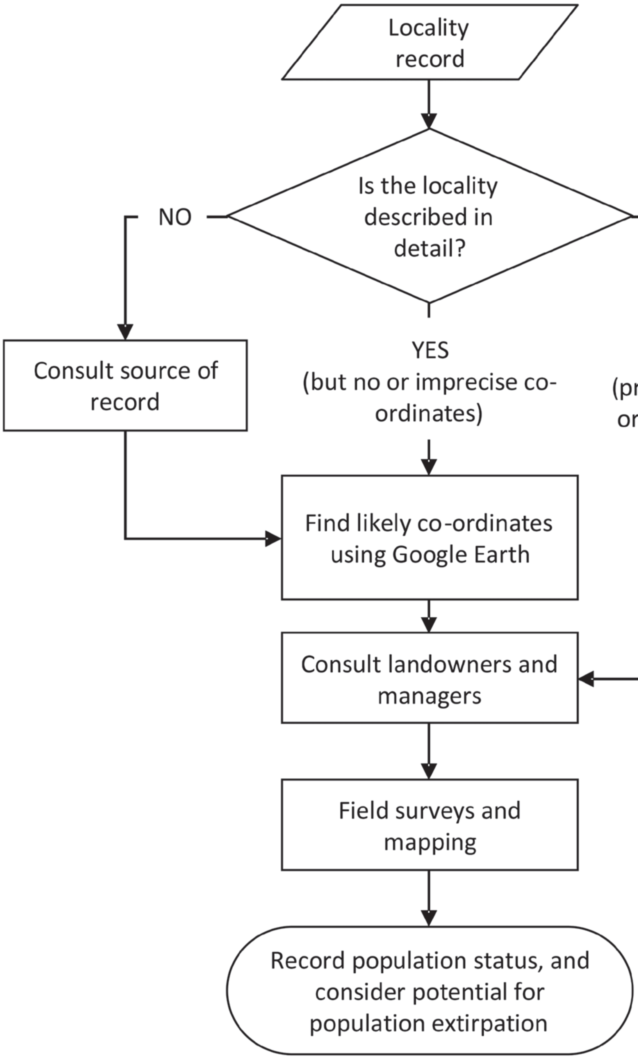

Figure 1. The protocol used in this paper for dealing with records of Australian *Acacia* species in South Africa. The protocol resulted both in an inventory of species in South Africa and recommendations for incursion response.

When comparing different lists, it was also possible to determine the types of errors (e.g. human error and species identification) in the lists (e.g. Jacobs et al. 2017). To this end, we examined 214 herbarium specimens and specifically checked the identities for 59 of these.

Many *Acacia* species are morphologically very similar and it is difficult to identify some taxa based on herbarium specimens and morphology alone. If the identity of a taxon collected in the field was not known or, if the identity of a taxon had not previously been confirmed via molecular approaches, we used DNA sequencing to verify identities. We sequenced two gene regions, the plastid *psb*A-*trn*H intergenic spacer and the nuclear external transcribed spacer region (ETS), for comparison against existing molecular data (Miller et al. 2016). DNA was extracted from silica-dried leaf material from selected taxa (Suppl. material 1) using the cetyltrimethylammonium bromide (CTAB) method as described by Doyle and Doyle (1990). *psb*A-*trn*H was amplified using the primers psbA (5'-GTT ATG CAT GAA CGT AAT GCT C-3') and trnH$^{(GUG)}$ (5'-CGC GCA TGG ATT CAC AAT CC-3') and the following polymerase chain reaction (PCR) conditions: Initial denaturation at 80 °C for 5 min; followed by 35 cycles of denaturation at 94 °C for 30 sec, annealing at 60 °C for 30 sec, and extension at 72 °C for 1 min. A final elongation step was done at 72 °C for 10 min. Each 30 µl reaction contained ca. 300 ng of genomic DNA, 200 µM of each dNTP (Thermo Scientific, supplied by Inqaba Biotec, Pretoria, South Africa), 10 pmoles of each primer, 0.3 U Taq DNA polymerase (Kapa Biosystems, supplied by Lasec, Cape Town, South Africa), PCR reaction buffer and 2 mM $MgCl_2$. ETS genes were amplified using the primers ETS-AcR2 (5'-GGG CGT GTG AGT GGT GTT TGG-3') and ETS-18S-IGS (5'-CAC ATG CAT GGC TTA ATC TTT G-3') and the following PCR conditions: Initial denaturation at 94 °C for 3 min; followed by 30 cycles of denaturation at 94 °C for 60 sec, annealing at 60 °C for 60 sec, and extension at 72 °C for 2 min. A final elongation step was done at 72 °C for 10 min. Each 30 µl reaction contained ca. 300 ng of genomic DNA, 200 µM of each dNTP (Thermo Scientific, supplied by Inqaba Biotec, Pretoria, South Africa), 10 pmoles of each primer, 0.3 U Taq DNA polymerase (Kapa Biosystems, supplied by Lasec, Cape Town, South Africa), PCR reaction buffer and 1.25 mM $MgCl_2$. PCR products for both gene regions were purified using the QIAquick® PCR Purification Kit (Qiagen, supplied by WhiteHead Scientific, Cape Town, South Africa) and sequenced using the ABIPRISM BigDye Terminator Cycle Sequencing Ready Reaction kit and an automated ABI PRISM 377XL DNA sequencer (PE Applied Biosystems, Foster City, CA, USA). DNA sequence data were aligned and edited using the bio edit version 7.0.5.3 (Hall 1999) followed by manual editing. We used BLAST searches to assign a taxonomic rank based on the similarity of individual gene sequences to exisiting data, using the NCBI's GenBank database (http://blast.ncbi.nlm.nih.gov/Blast). Taxa where putative field identifications matched those of Genbank voucher specimens and that blasted with high DNA sequence similarities (≥ 99%) for at least one gene region, were considered correctly identified. Discrepancies between putative field identifications and BLAST results were condisered as representing unresolved taxonomies, unless both genes retrieved the same taxon with high DNA sequence similarity and high statistical support (E=0). Identity was also considered to be correct when Blast results retrieved a species with high DNA sequence similarity (≥ 99%) and statistical support (E=0) for both gene regions (even if there was no putative field identification or link to planting records).

The introduction status of *Acacia* species present in South Africa

The observed populations of *Acacia* species were assigned an introduction status following the Unified Framework for Biological Invasions (Appendix 1; Blackburn et al. 2011), as interpreted and elucidated for trees by Wilson et al. (2014). We conducted field surveys to search for species at previously known or recorded sites obtained from herbarium records and literature sources. Google Earth and Google Street View were used to initially search for trees using the geographic coordinates on herbarium records [see Visser et al. (2014) for discussion on the use of Google Earth in the study of tree invasions]. This was useful for preparing for surveys and for initial work. A summary of the status of each naturalised population was prepared following the recommendations of Wilson et al. (2014).

Results

We found evidence that 141 Australian *Acacia* species have been introduced to South Africa (Table 1). For 112 species there is a literature record (this is the only evidence available for 56 species), for 81 species there is a herbarium records (this is the only evidence for 27 species), and 23 species have been confirmed using a molecular approach (this is the only evidence for 2 species).

Of these 141 species, we could confirm the presence of only 33 species (Table 1, see Fig. 2 for images of some of these). In terms of Blackburn et al.'s (2011) Unified Framework for Biological Invasions (see Appendix 1 for a full description of the categories), 13 of these species are in category E, two are in category D2 (i.e. there are 15 invasive species). Five species are naturalised but not yet invasive (category C3). We found no evidence that the remaining 13 species have produced reproductively active offspring in South Africa; these taxa thus fall in category B2 or C1. Status reports on the five naturalised and one invasive species that had not previously been studied in detail are presented in Appendix 2.

The estimate of 141 species is approximately double that of the previous estimate of 70 species (Richardson et al. 2011). These additional species include taxa not previously known from outside Australia (*A. acuaria*, *A. latipes*, *A. leptospermoides*, *A. saliciformis*, *A. ulicina*, and *A. uncifera*; Richardson et al. 2011).

We found one error and five misspellings on herbarium labels, these errors being perpetuated in subsequent literature sources. There were an additional three misspellings in literature sources (Table 2).

Only 23 species identities were confirmed either in this study or previously using a molecular approach (Table 1; Suppl. material 1). Of these two species (*A. hakeoides* and *A. ramulosa*) had not previously been recorded as having been introduced. For three species with a putative field identification, the molecular results did not correspond to the voucher specimens for the same species on GenBank (*A. adunca*, *A. fimbriata*, and *A. floribunda*). For a further three species, there was no voucher specimen on GenBank

Table 1. The presence of Australian *Acacia* species in South Africa based on herbarium specimens, molecular identification, records from historical literature sources, and the current status of populations from field sampling. Species names are as per the Plant List (The Plant List 2013, accessed 1 March 2018), with synonyms on herbarium records and literature records updated as appropriate (see notes). Herbarium records in South Africa not available on-line at http://newposa.sanbi.org/ (as of 1 March 2018) are marked with asterisks *, and details provided in Suppl. material 2. Molecular confirmation of taxonomic identities of acacias in South Africa was either based on existing records in Genbank or obtained from this study (see Suppl. material 1 for details of the results from this study). If the molecular work provided some support for the identification but not unequivocal support, the confirmation is noted as "probable". Where the putative identity did not match records of that species on Genbank (where available), then it is noted as "tested but likely to be a different species". The literature records of presence are based on the sources listed in the notes. Current status for species found during the field surveys is as per the Unified Framework for Biological Invasions (Blackburn et al. 2011; See Appendix 1 for details, and Suppl. material 3 for the range sizes of all naturalised and invasive species). The current status of species whose presence could not be unequivocally established during field visits are indicated as "not known". Several additional species have been recorded from neighbouring countries but not in South Africa as far as we know [*Acacia adsurgens*, *A. cowleana*, and *A. crassicarpa* (Poynton 2009)].

***Acacia* species**	**Herbarium record**	**Molecular confirmation**	**Literature record of presence**	**Current status**	**Locations recorded**
A. acinacea Lindl.	yes*	no	yes[b]	Not known	Cape Peninsula
A. acuaria W.Fitzg	yes*	no	no	Not known	University of Pretoria
A. acuminata Benth.	yes*	yes	yes[a,b]	B2	Paarl, Uitenhage, Knysna, Stutterheim, Robertson, Lichtenburg, Malmesbury
A. adunca G.Don	yes	tested, but likely to be a different species	yes[b,c]	C3	Paarl, Pretoria, Johannesburg
A. alata R.Br.	yes*	no	yes[b]	Not known	Johannesburg
A. ampliceps Maslin	no	no	yes[a]	Not known	Malmesbury
A. ancistrocarpa Maiden & Blakeley	no	no	yes[a]	Not known	Malmesbury
A. aneura Benth.	yes*	probable	yes[a,b]	B2	Zoutpansberg, Lichtenburg, Paarl, Malmesbury
A. argyrophylla Hook.	yes*	no	yes[b]	Not known	Johannesburg
A. aspera Lindl.	yes*	no	yes[b]	Not known	Pretoria
A. aulacocarpa Benth.	no	no	yes[b]	Not known	Johannesburg
A. auriculiformis Benth.	no	no	yes[a,b]	Not known	Malmesbury
A. baileyana F.Muell.	yes	yes	yes[b,c]	E	Multiple
A. binervata DC.	yes*	no	yes[b]	Not known	Cape Peninsula, Pretoria, Johannesburg
A. binervia (Wendl.) J.F.Macbr.	yes*	no	yes[b]	Not known	Pretoria
A. bivenosa DC.	no	no	yes[a]	Not known	Malmesbury
A. brachybotrya Benth.	yes*	no	yes[b]	Not known	Johannesburg

***Acacia* species**	**Herbarium record**	**Molecular confirmation**	**Literature record of presence**	**Current status**	**Locations recorded**
A. brachystachya Benth.	yes*	no	yes[a,b]	Not known	Pretoria, Malmesbury
[1]*A. browniana* Wendl.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. burrowii Maiden	no	no	yes[a]	Not known	Malmesbury
A. calamifolia Lindl.	yes*	no	yes[b]	Not known	Pretoria
A. calcicola Forde & Ising	no	probable	yes[a]	B2	Malmesbury
A. cambagei R.T.Baker	no	no	yes[a,b]	Not known	Malmesbury
A. cardiophylla Benth.	yes*	no	yes[b]	Not known	Johannesburg, Pretoria
A. celastrifolia Benth.	yes*	no	no	Not known	University of Pretoria
A. cognata Domin	yes*	no	no	Not known	Pretoria
A. colei Maslin & L.A.J.Thomson	no	no	yes[a]	Not known	Malmesbury
A. concurrens Pedley	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. coriacea DC.	no	no	yes[a]	Not known	Malmesbury
A. crassiuscula Wendl.	yes	no	no	B2	Newlands forest
A. cultriformis G.Don	yes	yes	yes[b,c]	C3	Pretoria, Johannesburg, Middelburg, Grahamstown
A. cyclops G.Don	yes	yes	yes[b,c]	E	Multiple
A. dealbata Link	yes	yes	yes[b,c]	E	Multiple
A. deanei (R.T.Baker) M.B.Welch & al.	yes*	no	yes[b]	Not known	Pretoria
A. decora Rchb.f.	yes*	no	yes[b]	Not known	Albany
A. decurrens Willd.	yes	yes	yes[b,c]	E	Multiple
A. difficilis Maiden	no	no	yes[a]	Not known	Malmesbury
[2]*A. difformis* R.T.Baker	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. dodonaeifolia (Pers.) Balb.	yes*	no	no	Not known	Port Elizabeth
A. doratoxylon A.Cunn.	yes*	no	no	Not known	Cape Peninsula
A. drummondii Lindl.	yes*	no	no	Not known	University of Pretoria
A. elachantha M.W.McDonald & Maslin	no	no	yes[a]	Not known	Malmesbury
[3]*A. elata* Benth.	yes	yes	yes[b,c,f]	E	Multiple
A. elongata DC.	yes*	no	no	Not known	Pretoria
A. ericifolia Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. extensa Lindl.	yes*	no	yes[b]	Not known	Johannesburg

Acacia species	Herbarium record	Molecular confirmation	Literature record of presence	Current status	Locations recorded
A. falciformis DC.	no	no	yes[b]	Not known	Cape Town
A. fasciculifera Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. fimbriata G.Don	yes	tested, but likely to be a different species	yes[b,c]	D2	Grahamstown
A. flexifolia Benth.	yes*	no	no	Not known	Johannesburg
A. flocktoniae Maiden	yes*	no	no	Not known	Pretoria, Johannesburg
A. floribunda (Vent.) Willd.	yes*	tested, but likely to be a different species	yes[b]	C1	Johannesburg; Pretoria; Bloemfontein
A. gladiiformis Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. hakeoides Benth.	no	yes	no	B2	Malmesbury, Johannesburg Botanic Gardens
A. harpophylla Benth.	yes*	no	yes[a]	Not known	Malmesbury
A. hemsleyi Maiden	no	no	yes[a]	Not known	Malmesbury
A. holosericea G.Don	no	no	yes[a,b]	Not known	Malmesbury
A. homalophylla A.Cunn. ex Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. howittii F.Muell.	yes*	no	no	Not known	Albany
A. implexa Benth.	yes	yes	yes[d,f]	E	Stellenbosch, Tokai, Wolseley
A. iteaphylla Benth.	yes*	no	yes[b]	Not known	Pretoria
A. ixiophylla Benth.	yes*	no	no	Not known	Johannesburg
A. jonesii F.Muell. & Maiden	yes*	no	yes[b]	Not known	Pretoria
A. julifera Benth.	no	no	yes[a]	Not known	Malmesbury
A. kempeana F.Muell.	yes*	no	yes[a,b]	Not known	Malmesbury, Johannesburg
A. koa A.Gray	yes*	probable	yes[b]	B2	multiple
A. lanigera A.Cunn.	yes*	no	no	Not known	Lydenburg dist.
A. latifolia Benth.	no	no	yes[b]	Not known	The Cape
A. latipes Benth.	yes*	no	no	Not known	Addo Elephant National Park
A. leprosa DC.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. leptocarpa Benth.	no	no	yes[a]	Not known	Malmesbury
A. leptoneura Benth.	yes*	no	yes[b]	Not known	Pretoria
A. leptospermoides Benth.	yes*	no	no	Not known	Pretoria
A. ligulata Benth.	no	no	yes[a]	Not known	Malmesbury
A. lineata G.Don	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. lineolata Benth.	yes*	no	no	Not known	Johannesburg

***Acacia* species**	**Herbarium record**	**Molecular confirmation**	**Literature record of presence**	**Current status**	**Locations recorded**
A. linifolia (Vent.) Willd.	yes*	no	yes[b]	Not known	Pretoria
A. longifolia (Andrews) Willd.	yes	yes	yes[b,c]	E	multiple
A. longissima Wendl.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. lunata G.Lodd.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. maconochieana Pedley	no	no	yes[a]	Not known	Malmesbury
A. macradenia Benth.	no	no	yes[b]	Not known	Cape Peninsula
A. maidenii F.Muell.	no	no	yes[c]	Not known	None noted
A. mangium Willd.	no	no	yes[b]	Not known	Malmesbury
A. mearnsii De Wild.	yes	yes	yes[b,c]	E	multiple
A. melanoxylon R.Br.	yes	yes	yes[b,c]	E	multiple
A. microbotrya Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. monticola J.M.Black	no	no	yes[a]	Not known	Malmesbury
A. multispicata Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. murrayana Benth.	no	yes	yes[a]	B2	Malmesbury
A. myrtifolia (Sm.) Willd.	yes*	no	yes[b]	Not known	Johannesburg, Pretoria
A. neriifolia Benth.	yes*	yes	yes[a,b]	B2	Malmesbury
A. notabilis F.Muell.	no	no	yes[b]	Not known	Not recorded (seed import record only)
[4]*A. obliqua* A.Cunn. ex Benth.	no	no	yes[b]	Not known	Cape Town
A. oswaldii F.Muell.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. oxycedrus Sieber ex DC.	yes*	no	no	Not known	Pretoria
A. paradoxa DC.	yes	yes	yes[b,c]	D2	Devils Peak, Table Mountain, Cape Town
A. pendula G.Don.	yes*	no	yes[b,c]	C1	Middelburg, Excelsior district Delareyville, Lichtenburg, Bloemhof, Kroonstad dist.,Beaufort West
A. penninervis DC.	yes*	no	yes[b]	Not known	Cape Peninsula
A. piligera A.Cunn.	yes*	no	no	C3	Tokai
A. plectocarpa Benth.	no	no	yes[a]	Not known	Malmesbury

***Acacia* species**	**Herbarium record**	**Molecular confirmation**	**Literature record of presence**	**Current status**	**Locations recorded**
A. podalyriifolia G.Don	yes	yes	yes[b,c]	E	multiple
A. polybotrya Benth.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. pravissima F.Muell.	yes*	no	yes[b]	Not known	Pretoria
A. prominens G.Don	yes*	no	yes[b]	Not known	Pietermaritzburg, Zoutpansberg, Centurion
[5]*A. provincialis* A.Camus	yes*	[5]no	yes[b,c]	C3	Pretoria, Stellenbosch, Johannesburg, Tokai
A. pruinocarpa Tindale	no	no	yes[a]	Not known	Malmesbury
A. pruinosa Benth.	yes*	no	no	Not known	Cape Peninsula
A. pubescens (Vent.) R.Br.	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. pycnantha Benth.	yes	no	yes[b,c]	E	multiple
A. quornensis J.M.Black	yes*	no	yes[b]	Not known	Johannesburg
A. ramulosa W.Fitzg.	no	yes	no	B2	Malmesbury
A. richii A.Gray	yes*	no	no	Not known	Pretoria
A. rubida A.Cunn.	no	no	yes[b]	Not known	Middelburg
A. saliciformis Tindale	yes*	no	no	Not known	Pretoria
A. salicina Lindl.	yes*	probable	yes[a,b]	B2	Malmesbury, Johannesburg, Gwelo
A. saligna (Labill.) Wendl.	yes	yes	yes[b,c]	E	Multiple
A. schinoides Benth.	yes*	no	yes[b]	Not known	Stellenbosch
A. scirpifolia Meissner	yes*	no	no	Not known	Paarl
A. sclerosperma F.Muell.	no	no	yes[a]	Not known	Malmesbury
A. simplex (Sparrm.) Pedley	no	no	yes[b]	Not known	Not recorded (seed import record only)
A. spectabilis Benth.	no	no	yes[b]	Not known	Johannesburg
A. squamata Lindl.	yes*	no	no	Not known	Suurberg Nature Reserve
A. stenophylla Benth.	no	no	yes[a,b]	Not known	Malmesbury
A. stricta (Andrews) Willd.	yes	no	yes[e]	E	Knysna
A. suaveolens (Sm.) Willd.	no	no	yes[b]	Not known	Cape Town
A. subporosa F.Muell.	yes*	no	no	Not known	Cape Peninsula
A. trinervata DC.	no	no	yes[b]	Not known	Not recorded (seed import record only)

Acacia **species**	**Herbarium record**	**Molecular confirmation**	**Literature record of presence**	**Current status**	**Locations recorded**
A. truncata Hoffmanns.	no	no	yes[b]	Not known	Cape Town
A. tumida F. Muell. ex Benth.	no	no	yes[a]	Not known	Malmesbury
A. ulicifolia (Salisb.) Court	no	no	yes[b]	C1	Pretoria Cape Peninsula, Transkei
A. ulicina Meissner	yes*	no	no	Not known	Pretoria
A. uncifera Benth.	yes*	no	yes[b]	Not known	Pretoria
A. undulifolia G.Lodd.	yes*	no	no	Not known	Cape Peninsula
A. verniciflua A.Cunn.	yes*	no	yes[b]	Not known	Cape Town, Pretoria
A. verticillata (L'Her.) Willd.	yes*	no	yes[b]	Not known	Pretoria
A. vestita Ker. Gawl.	no	no	yes[b]	Not known	Cape Town
A. victoriae Benth.	no	no	yes[a,b]	Not known	Malmesbury, and as seed
A. viscidula Benth.	yes	yes	yes[b,c]	C3	Pretoria, Grahamstown, Newlands Forest, Cape Town
A. willdenowiana Wendl.	yes*	no	no	Not known	Addo Elephant National Park
A. xiphophylla E.Pritz.	no	no	yes[a]	Not known	Malmesbury

Notes on *Acacia* species

[1] Ponyton (2009) listed *A. ciliata* R.Br., but according to the Plant List, this is a synonym of either *Acacia browniana* or *A. luteola*. Only *A. browniana* is listed here to keep the number of taxa recorded consistent.

[2] Listed as "*A. difformis* (sic)" in Poynton (2009).

[3] Ponyton (2009) also lists *A. discolor* Willd., but this is a synonym of *A. terminalis*, which was misapplied for *A. elata* in South Africa, and so only *A. elata* is included in the list above.

[4] Ponyton (2009) lists *A. obliqua* and this is a valid name on the Plant List, but is not on the World Wide Wattle web-site.

[5] Communication with M. O'Leary (State Herbarium of South Australia) in April 2018 suggests that the name *A. retinodes* Schltdl. has been misapplied and that the taxon that is present in Europe and South Africa is *A. provincialis* A.Camus. As there are currently no sequences of a voucher specimen of *A. provincialis* on Genbank, it was not possible to provide molecular confirmation, but notably the gene regions sequenced showed a close, but not perfect, match to *A. retinodes*, as would be expected if it were *A. provincialis* (Suppl. material 1).

Notes on Literature records

[a] Gibbs (1998) (i.e. the trial on Damara Farm);

[b] Poynton (2009);

[c] Ross et al. (1975);

[d] Kaplan et al. (2012);

[e] Kaplan et al. (2014);

[f] Meek et al. (2010).

Table 2. Methodology followed in determining errors in lists of *Acacia* species in herbaria and in literature sources.

Errors	Explanatory questions	Method	Results
Human error	How many herbarium specimens had been misidentified?	All herbarium specimens of *Acacia* species were examined for correct identification. If a specimen was suspected to have been misidentified, the identification was verified using identification guides (e.g. online database, reference books), experts, or molecular DNA barcoding. The total number of herbarium vouchers examined and misidentifications were counted. Furthermore, any known case of species being misidentified in the literature was noted.	Only one species was found to have been clearly misidentified: *A. koa* was misidentified as *A. floribunda*
	How many entries had incorrect spellings?	A search was conducted of literature sources and online databases to determine the total number of *Acacia* species which had their names changed. When examining herbarium specimens, the number of times the records had been renamed (i.e. old names crossed out and new names recorded) was counted. To determine the number of times *Acacia* species have had their names changed, literature sources and databases (www.theplantlist.org) were used. The Plant List was used as the source for recognised names. The number of records using old names (not the currently accepted name) was counted.	Five species names on herbarium specimens were misspelled: *A. aulacocarpa as A. aulocarpa*; *A. drummondii* as *A. drummardii*; *A. ulicifolia as A. ulicifolium*; *A. iteaphylla as A. itheaphylla;* *A. verticillata as A. verticulata.* Three additional errors were found in literature sources: *A. ulicifolia* as *A. aculeatissima;* *A. aulacocarpa* as *A. aulacorpa*; *A. drummondii* as *A. drummardii*.
Which errors have been perpetuated?		The identified errors were assessed for presence in multiple data sources to determine whether an error has been repeated. The primary source of the identified errors was also assessed by conducting a literature search using the specific error as the search term.	Both the misidentification of *A. koa* and three cases of the misspelling in herbarium specimens (of *A. ulicifolia*, *A. iteaphylla*, and *A. verticillata*) were found to have been perpetuated in literature sources.

Errors	Explanatory questions	Method	Results
Resolution of data and scaling of “alien range”	For how many records was the resolution of data too coarse to be useful?	Field surveys were conducted on reported population localities from SAPIA, herbaria and literature. The number of records for which the resolution of data (e.g. quarter-degree grid cell, town or region) was too coarse to allow individuals to be located was recorded. The data from SAPIA, herbaria and literature was compared with the survey results to provide a fine resolution locality.	Using historical data was not accurate as the resolution was too coarse (recorded at the scale of quarter-degree cells). Using such data was unreliable for locating and assessing the extent of species spread. We mapped the species at finer scales to avoid such issues.
Data and knowledge not documented	How many records were not documented?	New locality records were followed up in field surveys to establish the current status of species localities. The number of records that are only the result of undocumented expert knowledge and surveys were counted. Furthermore, some species identification fliers were distributed in surveyed areas to solicit new species sightings. Any new sightings resulting from the public sightings were counted.	Two localities found. 18 putative *Acacia* species were recorded at Damara Farm and one species at the University of the Free State.

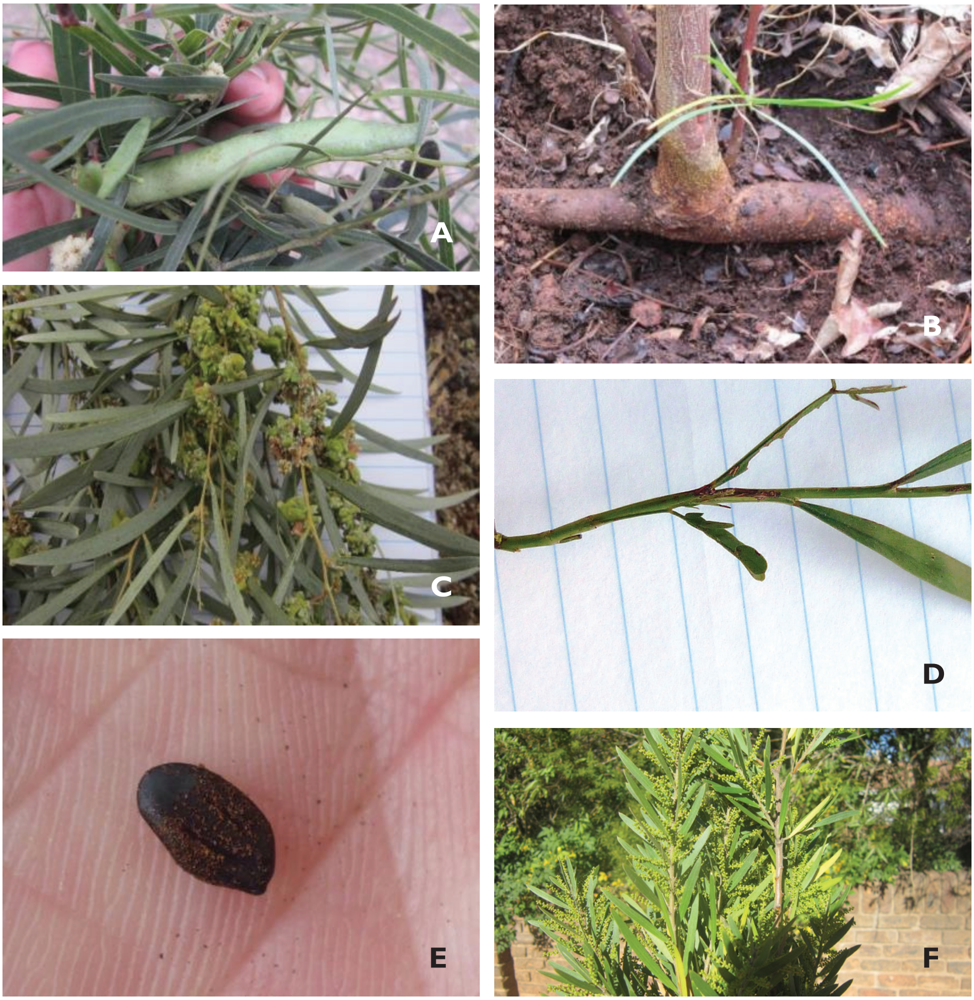

Figure 2. Examples of Australian *Acacia* species found in this study. **A** *Acacia salicina* with green pods in the Johannesburg Botanical Gardens **B** *A. viscidula* root sucker in a naturalised population in Newlands, Cape Town **C** *A. pendula*. Galls from a biological agent (*Dasineura dielsi*) released to control *A. cyclops* are visible in Bloemfontein **D** *A. provincialis* seedling showing juvenile bipinnate leaves attached to the stem and to the ends of the first few phyllodes, there are no bipinnate leaves on older phyllodes **E** A seed of *A. piligera* collected at Tokai, Cape Town **F** A planted individual of *A. floribunda* showing phyllodes and flower spikes in Johannesburg. Photos A–C, E, F: Nkoliso Magona; D: John Wilson

and so it was not possible to obtain molecular support for their putative identification (*A. piligera*, *A. provincialis*, and *A. ulicifolia*).

Notably, when this manuscript was under review, it was pointed out to us by Martin O'Leary, State Herbarium of South Australia, that *A. retinodes* had frequently been misapplied to *A. provincialis* in other countries, and, on further investigation, this appears to have been the case in South Africa as well.

Discussion

Before this study, 70 Australian *Acacia* species were known to have been introduced to South Africa (Richardson et al. 2011). We found evidence that another 71 species had been introduced to the country. Of the revised list of 141 species for which records exist for introduction to, or presence in, South Africa (Table 1), we could confirm that at least 33 species are still present in the country.

There were four major reasons for the discrepancy between the list of species recorded as having been introduced to South Africa and the list of species confirmed to be still present in the country. First, during the survey, we came across an old experimental forestry trial set up to identify species suitable for dry-land agroforestry (Damara Farm in the Western Cape; see Suppl. material 4). Thirty-three Australian *Acacia* species were reportedly planted at Damara Farm (Gibbs 1998), of which we found 18 putative taxa (based on morphology and molecular analysis). None of these taxa has naturalised.

Second, specimens of several species are present in the National Herbarium in Pretoria but had not been included in previous lists because the herbarium records had not yet been digitised.

Third, species might no longer be present at their original sites of introduction. Many of the records (particular herbarium records that have not yet been digitised) were from historical forestry plantings. When we followed up, we found that many of these planting were no longer present — they had been transformed for infrastructure development, agriculture, or other forms of land use. Most cases, where listed species are no longer present, were within the municipal areas of the cities of Johannesburg and Pretoria that have been converted to stock farms. For example, all available records of *A. cultriformis* that were assessed in Gauteng Province are now under various forms of agriculture, while several records of other species in Poynton (2009) referred to arboreta that no longer exist.

Fourth, species might not have survived at sites of initial introduction due to unfavourable climatic conditions or biotic pressures; Poynton (2009) noted that most introduced *Acacia* species were grown in trial plantations, many of which did not survive.

Finally, it is possible that, despite our best efforts, our searches were inadequate to (re)locate some species. We suspect this is unlikely to be a major cause, as Australian *Acacia* species have been extensively studied and managed in South Africa, and as the taxa are often quite distinct from the native flora. Some “missing” species might feasibly be surviving in soil-stored seed banks (seeds of many wattle species can retain viability in the soil for several decades; Richardson and Kluge 2008). However, due to the fact that many herbaria specimens and literature reports lacked detailed locality data (longitude and latitude coordinates), it is possible that we simply were not looking in the right place.

Notably, however, there may be other localities like Damara Farm where multiple species have been cultivated and potentially still exist. Poynton (2009) noted that many old trial plantations were left unmanaged due to the closure of forest stations; records of these sites might not be reflected in the information sources that we consulted.

Whatever the reasons for discrepancies in past estimates of wattle introductions in South Africa, it is clear that there is a high invasion debt for Australian *Acacia* species in the country (Rouget et al. 2016). If this debt were paid, it would lead to a substantial escalation in the extent of invasions and overall ecological and economic impacts of the group (Richardson et al. 2015). There appears to be no clear set of life-history features, or syndromes of traits, that separate invasive from non-invasive *Acacia* species (Gibson et al. 2011), nor is there a clear phylogenetic signal for invasiveness in the genus (Miller et al. 2017). This suggests that factors associated with propagule pressure and residence time have been the dominant drivers of invasiveness in this genus in South Africa. This highlights the importance of dealing with nascent invaders before population sizes and spatial extent are sufficiently large to drive self-sustaining invasions.

One way of reducing this invasion debt is through proactive management approaches, e.g. the detection, identification, assessment, and control of naturalised populations before they are widespread invaders. Some of the naturalised populations of Australian acacias in South Africa occur only at a few sites and so eradication is possible, but for some species, *A. cultriformis* specifically, it is likely that they are present at other locations that were not detected in this study. During the field visits in the cities of Bloemfontein and Johannesburg, people that had *A. cultriformis* in their gardens reported that this species was present in many gardens in neighbouring areas. As this species has been widely planted, it is likely that the extensive seed bank and high climatic suitability (Motloung et al. 2014) could make it a high invasion risk (Wilson et al. 2011). Of the naturalised species that were detected in this study, *A. cultriformis* is the only one for which nation-wide eradication is likely to be not feasible (given the problems with locating all horticultural plantings).

Some of the taxa might also have been prevented from spreading due to the impact of biological control agents released to target the widespread Australian *Acacia* species. In this study, the biological control agents *Dasineura dielsi* (target species: *A. cyclops*) and *Trichilogaster acaciaelongifoliae* (target species: *A. longifolia*) were observed on both *A. floribunda* and *A. pendula*. *Dasineura dielsi* has previously been recorded on *A. implexa*, *A. melanoxylon*, *A. longifolia* and *A. saligna* (Impson et al. 2009, Kaplan et al. 2012). It is likely that the agents reduced seed production in a variety of introduced wattles, and potentially reduced the rate of spread of populations, though it is very unlikely they have resulted in the extirpation of any populations if there were no other management or land-use change.

Unlike other taxonomic groups of alien plants, where there are many misidentified herbarium records (e.g. *Melaleuca* spp.; Jacobs et al. 2017), we did not find many such misidentifications (though there is often little congruency between the molecular and morphological identifications). Our molecular approach could not resolve all taxonomic ambiguities, especially in cases where there was insufficient reference data for vouchers specimens (Parmentier et al. 2013) or short DNA sequence reads available (Stoeckle et al. 2011). This makes differentiation between closely related species difficult. Many of the species in our list (particularly those from Damara

Farm) remained unidentified. This could be because DNA sequencing data for the gene regions that we used are not available for many wattle species and/or because many showed 100% similarity to more than one taxon for the gene regions that were sequenced. We assumed that these results indicated a very closely-related species. There is a need for detailed morphological characterisation to identify these taxa with certainty [colleagues are busy collecting comprehensive herbarium specimens (i.e. with reproductive structures) that will hopefully provide clarity on the species present]. Despite these limitations, our molecular data did yield some interesting results — including identifying new species not previously recorded in South Africa (*A. hakeoides* and *A. ramulosa*); and casting doubt on the identities of three species that have long been included in lists of alien *Acacia* species in the country (*A. adunca*, *A. fimbriata*, *A. floribunda*).

Finally, the misapplication of the name *A. retinodes* for *A. provincialis* that was only uncovered by a reviewer of this manuscript indicates the continuing need for international collaboration with identifications. Such mistakes can lead to confusions with management as *A. retinodes* suckers but *A. provincialis* does not [cf. the misapplication of the name *Melaleuca ericifolia* (a resprouter) to *M. parvistaminea* (a reseeder) — the lack of resprouting in the field was one of the main triggers for a re-evaluation of the identification (Jacobs et al. 2014)].

While the work presented here has not definitely resolved all of the issues around the identity of Australian *Acacia* species in South Africa, it is clear that available inventories of even supposedly well-known taxa can be misleading. Better quantification of current introduction status is crucial for producing effective management strategies and for estimating the resources needed control targeted populations of alien plants (Wilson et al. 2013). They are also essential if we are to have confidence in comparative analyses of invasions.

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Appendix 1

A categorisation scheme for populations according to the Unified Framework for Biological Invasions (adapted from Blackburn et al. 2011).

Category	Definition
A	Not transported beyond limits of native range
B1	Individuals transported beyond limits of the native range, and held in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place)
B2	Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them, but explicit measures to prevent dispersal are limited at best)
B3	Individuals transported beyond limits of the native range, and directly released into novel environment
C0	Individuals released outside of captivity or cultivation in location where introduced, but incapable of surviving for a significant period
C1	Individuals surviving outside of captivity or cultivation in location where introduced, no reproduction
C2	Individuals surviving outside of captivity or cultivation at location where introduced. Reproduction occurring, but population is not self-sustaining
C3	Individuals surviving outside of captivity or cultivation in location where introduced. Reproduction occurring. Population is self-sustaining
D1	Self-sustaining population outside of captivity or cultivation, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population outside of captivity or cultivation, with individuals surviving and reproducing a significant distance from the original point of introduction
E	Fully invasive species, with individual dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence

Appendix 2

Species status reports for naturalised Australian *Acacia* species (using standardised metrics proposed by Wilson et al. 2014)

Species: *Acacia adunca* G.Don [note molecular work suggests this might be another taxon]

Location: Groot Drakenstein (Bien Donne Farm). South Africa

Status: Naturalised; C3 under Blackburn: Individuals surviving outside of cultivation in location where introduced, reproduction occurring, and population self-sustaining.

Potential: Large proportion of the country is suitable.

Abundance: ~1000 plants (2014); lots of seeds stored in the seedbank

Population Growth Rate: Not known.

Extent: 1 population covering area of 0.27 ha as a closed canopy (i.e. condensed canopy area is also 0.27 ha).

Spread: From its native range, the seeds are spread by animal (ants and birds).

Impact: Has a potential to out-compete indigenous plants. *Acacia adunca* would fail a pre-border assessment as it scores higher than the threshold value of 6 that indicates species as being potentially invasive.

Threat: Not specifically studied, but likely similar to other Australian acacias (see Le Maitre et al. 2011).

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners. Herbarium specimens and the spotter website, South African Invasive Species, ISpot were examined.

Notes: Eradication plan in place

Contact: invasivespecies@sanbi.org.za

Information compiled by: Nkoliso Magona, nkoliso@sun.ac.za

Species: *Acacia cultriformis* G.Don

Location: Grahamstown (Makana Botanical Garden and Grey Dam).

Status: Naturalised; C3: Individuals surviving outside of cultivation in location where introduced, reproduction occurring, and population self-sustaining.

Potential: Large proportion of the country is suitable.

Abundance: 35 plants (2015).

Population Growth Rate: No seedlings were found during the survey, so nothing is known of population growth rates.

Extent: Two populations covering area of 1.28 ha. (Condensed area of 0.0519 ha).

Spread: In South Africa the species might be spread via seeds by people who are jogging or cycling.

Impact: Has a potential to out-compete indigenous plants. *Acacia cultriformis* would fail a pre-border assessment as it scores higher than the threshold value of 6 that indicates species as being potentially invasive.

Threat: Not specifically studied, but likely similar to other Australian acacias (see Le Maitre et al. 2011).

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners. Herbarium specimens and the spotter website, South African Invasive Species, ISpot were examined.

Notes: Eradication plan in place.

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Information compiled by: Nkoliso Magona, nkoliso@sun.ac.za

Species: *Acacia fimbriata* G.Don [note molecular work suggests this might be another taxon]

Location: South Africa

Status: Invasive; D2: Self-sustaining population outside of cultivation that is a significant distance from the putative point of introduction.

Potential: Large proportion of the country is suitable.

Abundance: ~5 000 plants (2014); lots of seeds stored in the seedbank.

Population Growth Rate: Not known,

Extent: 3 populations covering area of 53 ha. (Condensed area 0.73 ha)

Spread: In its native range, seeds are spread by animal (ants and birds). It was introduced to botanical garden and now it is found naturalised at the botanic gardens and a waste dumping site (presumably taken there as garden refuse).

Impact: Has the potential to out-compete indigenous plants. *Acacia fimbriata* would fail a pre-border assessment as it scores higher than the threshold value of 6 that indicates species as being potentially invasive.

Threat: Not quantified.

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners. Herbarium specimens and the spotter website, South African Invasive Species, ISpot were.

Notes: Eradication plan in place

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Species: *Acacia piligera* A.Cunn (Fabaceae)

Location: Tokai

Status: Naturalised; C3: Individuals surviving outside of cultivation in location where introduced, reproduction occurring, and population self-sustaining.

Potential: Not quantified.

Abundance: ~174 plants (2015); lot of seeds stored in the seedbank.

Population Growth Rate: Not known, but based on the observed seedling recruitment events occurred after rain and fire, it is believed that water and heat may be the cause of population growth rate.

Extent: One population covering area of 0.0947 ha. (condensed area of 0.0947 ha).

Spread: In its native range, the seeds are dispersed by animals (ants). In South Africa, it has not spread from its original cultivation area.

Impact: Not quantified

Threat: Not specifically studied, but likely similar to other Australian acacias (see Le Maitre et al. 2011).

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners; herbarium specimens and the spotter website, South African Invasive Species, ISpot were.

Notes: Eradication plan in place.

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Information compiled by: Nkoliso Magona, nkoliso@sun.ac.za

Species: *Acacia provincialis* A.Camus (*A. retinodes* Schltdl. mis-applied in South Africa) (Fabaceae)

Location: Tokai Arboretum

Status: Naturalised; C3: Individuals surviving outside of cultivation in location where introduced, reproduction occurring, and population self-sustaining.

Potential: A large proportion of the country is suitable for this species.

Abundance: <50 plants (2014); Relatively small seedbanks.

Population Growth Rate: Not known.

Extent: One population covering area of 0.25 ha. (as it is a closed canopy, condensed area is essentially the same, i.e. 0.25 ha)

Spread: In its native range, seeds are dispersed by animals (ants and birds).

Impact: Has the potential to out-compete indigenous plants. *Acacia provincialis* would fail a pre-border assessment as it scores higher than the threshold value of 6 that indicates species as being potentially invasive.

Threat: Not specifically studied, but likely similar to other Australian acacias (see Le Maitre et al. 2011).

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners. Herbarium specimens and the spotter website, South African Invasive Species, ISpot were examined.

Notes: Eradication plan in place

Contact: invasivespecies@sanbi.org.za

Information compiled by: Nkoliso Magona, nkoliso@sun.ac.za

Species: *Acacia viscidula* Benth. (Fabaceae)

Location: Newlands forest.

Status: Naturalised; C3: Individuals surviving outside of cultivation in location where introduced, reproduction occurring, and population self-sustaining.

Potential: Large proportion of the country is suitable

Abundance: ~1200 plants (2014).

Population Growth Rate: Not known.

Extent: Two populations covering area of 3.5 ha. (Condensed area of 0.077 ha).

Spread: In its native range, seeds are spread by animals (ants and birds).

Impact: Has the potential to out-compete indigenous plants. *Acacia viscidula* would fail a pre-border assessment as it scores higher than the threshold value of 6 that indicates species as being potentially invasive.

Threat: Not specifically studied, but likely similar to other Australian acacias (see Le Maitre et al., 2011).

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners. Herbarium specimens and the spotter website, South African Invasive Species, ISpot were examined.

Notes: Eradication plan in place. Plants are vigorous resprouters

Contact: invasivespecies@sanbi.org.za

Information compiled by: Nkoliso Magona, nkoliso@sun.ac.za

Supplementary material 1

Molecular and morphological assessments for the identity of Australian Acacia species collected in South Africa: a) from naturalised populations not previously assessed; and b) from Damara Farm near Malmesbury in South Africa

Authors: Nkoliso Magona, David M. Richardson, Johannes J. Le Roux, Suzaan Kritzinger-Klopper, John R. U. Wilson

Data type: Table linking linking samples to Genbank accession numbers.

Link: https://doi.org/10.3897/neobiota.39.23135.suppl1

Supplementary material 2

South African herbarium accession numbers for specimens that were not available online at http://newposa.sanbi.org as of 1 March 2018

Authors: Nkoliso Magona, David M. Richardson, Johannes J. Le Roux, Suzaan Kritzinger-Klopper, John R. U. Wilson

Data type: Table of species and corresponding herbarium numbers.

Link: https://doi.org/10.3897/neobiota.39.23135.suppl2

Supplementary material 3

Records of naturalised populations of wattles as per the Southern African Plant Invaders Atlas (date accessed: January 2017)

Authors: Nkoliso Magona, David M. Richardson, Johannes J. Le Roux, Suzaan Kritzinger-Klopper, John R. U. Wilson

Data type: Table of species occurrences.

Link: https://doi.org/10.3897/neobiota.39.23135.suppl3

Supplementary material 4

Details of the forestry trial at Damara Farm, South Africa, that included many species of wattles not previously recorded from South Africa

Authors: Nkoliso Magona, David M. Richardson, Johannes J. Le Roux, Suzaan Kritzinger-Klopper, John R. U. Wilson

Data type: Site description.

Link: https://doi.org/10.3897/neobiota.39.23135.suppl4

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Impact of alien plants in Turkey assessed by the Generic Impact Scoring System

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Abstract

In this paper, we present the impact categorizations of 51 alien plant species in Turkey, which were determined using the Generic Impact Scoring System (GISS). The evidence on environmental and socioeconomic impacts of these alien species was searched in literature. Impacts were classified into 12 categories (six for environmental and six for socioeconomic) and, within each category, the impact was assessed on a six degree scale. Environmental impacts were recorded for 80% of the species and mostly concern ecosystem processes (changes in nutrient or water availability and disturbance regimes), while socioeconomic impacts, identified for 78% of the species assessed, are typically associated with agricultural production or human health. Summed scores of individual species across categories of environmental and socioeconomic impacts were not significantly correlated. By taking into account the actual distribution of the assessed species, we evaluated the regional distribution of (potential) impacts in Turkey. The Black Sea region harbours the highest number of species with impacts (34 species, i.e. 67% of the total assessed for the whole country), 28 species were recorded in the Marmara, 21 in the Mediterranean, 17 in the Aegean and 12 in each of the South East Anatolia, Central Anatolia and East Anatolia regions. The species that have negative impact on forestry are only found in three regions. Altogether 21 species are agricultural weeds, but we only found evidence of a minor socioeconomic impact for some of them. Determining the impacts based on specific criteria (i) provides basis for objective risk assessment of plant invasions in Turkey, (ii) can be taken as early warning to combat these plants and (iii) contributes to the growing body of evidence of the impacts of alien plant species.

Keywords
alien species, environmental impact, GISS socioeconomic impact, regional distribution, management, sector analysis

Introduction

In the last decade, evidence has accumulated about serious negative impacts of alien species on the environment, economy and human well-being in all parts of the world (Vilà et al. 2010, 2011, Ricciardi et al. 2013, Kumschick et al. 2015b, Rumlerová et al. 2016, Nentwig et al. 2018). These impacts range from effects on individuals (e.g. competition, transfer of diseases, genetic and evolutionary changes) through populations, species and communities to those affecting whole ecosystems and their functioning (Parker et al. 1999, Ehrenfeld 2010, Pyšek et al. 2012, Simberloff et al. 2013). Many invasive species have been shown to have negative socioeconomic impacts (Perrings et al. 2010, Bacher et al. 2018). Overall, there is robust scientific evidence that biological invasions can not only decrease the diversity of native species, but can also negatively affect animal and human health in the invaded areas (Weber 2003, Richardson and Pyšek 2006, Lambdon et al. 2008, Pyšek and Richardson 2010, Hulme 2013, Schindler et al. 2015).

A strong commitment of the European Commission to provide solid and sustainable solutions regarding the management of invasive alien species in Europe is on record (Roy et al. 2013, EU 2014, Genovesi et al. 2015). According to recent European Union legislation, there will be a mandatory response by all member states to the threats that invasive species pose to biodiversity and ecosystem services. The new regulation includes, after the first update in 2017, a list of 49 invasive alien species, which may be a threat or of concern in EU member states. To be included on this list, a full risk assessment, including evaluation of impact of a candidate species, has to be completed by experts, reviewed by members of the Scientific Forum and accepted by the European Commission and member states (EU 2014).

The evaluation of the impacts of individual species varies amongst regions and stakeholders in different sectors, such as nature protection, forestry or hunting (Sladonja et al. 2015, Vítková et al. 2017). For management, identifying the most deleterious species is a priority (Pergl et al. 2016). Hence, a robust and objective approach to rank alien species impacts through standard procedures is required (Nentwig et al. 2010, Vaes-Petignat and Nentwig 2014, Kumschick et al. 2015a, 2017, Rumlerová et al. 2016). To achieve this goal, two comprehensive methods to assess socioeconomic and/or environmental impacts were proposed recently (Nentwig et al. 2010, Blackburn et al. 2014). The Environmental Impact Classification for Alien Taxa (EICAT; Blackburn et al. 2014, Hawkins et al. 2015), now adopted as an official instrument of IUCN (https://www.iucn.org/theme/species/our-work/invasive-species/eicat), enables the environmental impacts of all alien taxa to be classified. Socioeconomic impacts are covered by the recent framework SEICAT (Bacher et al. 2018), where the evaluation is based on the change in human well-being, rather than on eradication costs and monetary loss from, for example, reduced yield – approaches that were used previously. However, for risk assessments to be considered by EU as a basis for prioritization, it is required that all possible impacts of alien species be evaluated, including those on human health and economy (Roy et al. 2013). These aspects are covered by the second scheme, the Generic Impact Scoring System (GISS; Nentwig et al. 2010, 2016) which was introduced in a study on mammals alien to Europe (Nentwig et al. 2010) and then applied to other taxonomic groups (e.g. Kumschick and Nentwig 2010, Vaes-Petignat and Nentwig 2014, van der Veer and Nentwig 2014, Laverty et al. 2015, Novoa et al. 2016, Rumlerová et al. 2016). While assessment of each additional group required some specific modifications and additional features were being included in GISS, the system remained generic (see Nentwig et al. 2016 for summary and update). Out of the 12 impact categories in GISS, there are six categories for environmental impacts and six for socioeconomic impacts. The information generated through the development of such a system can provide decision-makers and other stakeholders with guidelines for prioritization of threats imposed by alien species and identify species to be targeted by management (Nentwig et al. 2010, Pergl et al. 2016, Rumlerová et al. 2016).

Our study focuses on Turkey, a country spanning three floristic (Mediterranean, Irano-Turanian and Euro-Siberian) and seven climatic zones, which results in a remarkably rich flora. Turkey harbours 9,342 species of seed plants, of which 31% are endemic (Güner et al. 2012). This diversity is threatened by many factors related to human activities, amongst which alien species represent an important issue. Unfortunately, the information on alien flora in Turkey remained rather scattered until recently. Many alien plant species were reported especially from North-East of Anatolia, the East Black Sea region in particular and mostly recorded in forest or tea plantations (e.g. Terzioğlu and Ansin 1999, Coşkunçelebi et al. 2007, Karaer and Kutbay 2007, Brundu et al. 2011, Eminağaoğlu et al. 2012, Karaer and Terzioğlu 2013). Çınar et al. (2011) presented a detailed study of naturalized alien species from the coast of Turkey and Uludağ et al. (2017), in the recently published first study on the alien flora of the whole country, reported a total number of 340 alien taxa. Of these, 228 (68%) are naturalized and 112 (32%) are casual species. About two thirds were introduced deliberately, mostly as ornamentals, forestry species or crops, while 110 species were introduced unintentionally. Of the total pool of alien species in the country, 23% occur in agricultural areas, amongst them 16% as naturalized and 7% as casual (Uludağ et al. 2017).

With this new source on the alien plant species diversity in Turkey (Uludağ et al. 2017), assessing their impacts appears the logical next step. The aims of the present study were thus to determine, by applying GISS, (i) which alien plant species have the greatest potential environmental and socioeconomic impacts, (ii) which impact types represent the greatest threat and (iii) which sectors (forestry and agriculture) and regions in Turkey are most affected.

Methods

Selection of species

To select the species for our study, we considered plants alien to Turkey (following the definition of Pyšek et al. 2004, Blackburn et al. 2011), as reported in Uludağ et al. (2017). The selection process aimed at identifying plant species with potential environmental and socioeconomic impacts in Turkey, i.e. those that were suggested as problematic in the local literature (see e.g. Eminağaoğlu et al. 2012, Karaer and Terzioğlu 2013, Uruşak et al. 2013, Uremiş et al. 2014), including master and doctoral theses (Yazlık 2001, Yıldırım 2001, Kitiş 2002). Some of these alien species are already widely distributed in the country but some were introduced to Turkey as late as the last two decades, which allows determination of their potential impacts before they start to spread across large areas, possibly further increasing their abundance. The screening yielded 51 species meeting the above criteria that were included in the evaluation of impacts. All evaluated species are neophytes, 31 are considered naturalized and 20 are still in the casual stage (according to the criteria described in Richardson et al. 2000, Blackburn et al. 2011) (Table 1).

Scoring of impacts

We used the Generic Impact Scoring System (GISS; Nentwig et al. 2016) to quantify the negative impacts (environmental, socioeconomic) of the selected alien plant species. The GISS includes 12 categories, with their impact within each category scored in the range of zero to five, giving six possible scores. A score of "zero" means that an alien species has no impact (or an unknown impact) and "five" represents the maximum impact. The impact levels were assigned based on published literature, grey literature, including master and doctoral theses and local reports (Suppl. material 3).

The data on particular impacts were searched using (i) ISI Web of Knowledge, by including a species' scientific name combined with keywords indicating its alien/naturalized/invasive status and impact; (ii) databases of invasive species with their impacts recorded, namely DAISIE, NOBANIS (The European Network on Invasive Alien Species, www.nobanis.org) and GISD (The Global Invasive Species Database, www.issg.org), also searching the references on which these impacts were based; and (iii) other bibliographic sources of information including regional and national case studies (mainly theses and reports from Turkey) and books mentioned in the primary literature. We considered evidence for the impact of individual species across their whole invaded range, not only in Turkey (see e.g. Rumlerová et al. 2016).

The environmental impacts consist of: impact on plants or vegetation (category 1.1), impact on animals (e.g. through altered food availability) (1.2), impact on other species through competition (1.3), impact through transmission of diseases or para-

Table 1. Environmental (Env.), socioeconomic (Soc.) and total (logarithmic sum; see text for explanation) impacts of alien species in Turkey. Each taxon is listed with its family, life form, life history, invasion status in Turkey (Cas = casual, Nat = naturalized; Pyšek et al. 2004, Blackburn et al. 2011), native range and distribution extent in Turkey. Status as an agricultural weed, based on literature, is indicated (see text for details).

No	Species	Family	Env.	Soc.	Total score	Agr. weed	Life form	Life history	Status	Native range	Number of grid cells (See Suppl. material 1)
1	*Acalypha australis*	Euphorbiaceae	0	2.00	2.00	Yes	Herb	Annual	Nat	Asia	1
2	*Acer negundo*	Sapindaceae	3.00	2.05	3.05	No	Tree	Perennial	Nat	N America	2
3	*Aethionema carneum*	Brassicaceae	0	1.04	1.04	Yes	Herb	Annual	Nat	SW Asia	3
4	*Agave americana*	Asparagaceae	3.04	2.00	3.08	No	Herb/ Shrub	Perennial succulent	Cas	N America	4
5	*Ailanthus altissima*	Simaroubaceae	3.48	3.00	3.60	No	Tree	Perennial	Nat	Asia	2
6	*Alhagi pseudalhagi*	Fabaceae	2.00	2.00	2.30	Yes	Shrub	Perennial	Nat	West Asia, Europe	11
7	*Alyssum dasycarpum*	Brassicaceae	0	2.00	2.00	Yes	Herb	Annual	Nat	Asia, Europe	13
8	*Alyssum sibiricum*	Brassicaceae	0	2.00	2.00	Yes	Herb	Perennial	Nat	Asia, Europe	14
9	*Alyssum strictum*	Brassicaceae	0	2.00	2.00	Yes	Herb	Annual	Nat	Asia, Europe	9
10	*Alyssum strigosum subsp. strigosum*	Brassicaceae	0	2.00	2.00	Yes	Herb	Annual	Nat	Asia, Europe	14
11	*Amaranthus caudatus*	Amaranthaceae	2.3	1.04	2.32	No	Herb	Annual	Nat	S America	1
12	*Amaranthus hybridus*	Amaranthaceae	3.04	2.05	3.08	Yes	Herb	Annual	Nat	C America, N America	3
13	*Amaranthus retroflexus*	Amaranthaceae	3.32	3.00	3.49	Yes	Herb	Annual	Nat	C America, N America	5
14	*Amaranthus spinosus*	Amaranthaceae	2.00	2.48	2.60	Yes	Herb	Annual	Nat	Trop. America	1
15	*Ambrosia artemisiifolia*	Asteraceae	4.00	3.08	4.05	Yes	Herb	Annual	Nat	N America	2
16	*Amorpha fruticosa*	Fabaceae	4.00	0	4.00	No	Shrub	Perennial	Cas	N America	1
17	*Artemisia annua*	Asteraceae	3.00	4.00	4.50	No	Herb	Annual	Nat	W Asia	7
18	*Artemisia verlotiorum*	Asteraceae	3.04	3.00	3.08	No	Herb	Perennial	Nat	Asia	1
19	*Bidens bipinnata*	Asteraceae	2.00	2.00	2.30	Yes	Herb	Annual	Nat	Asia, N America	1
20	*Bidens frondosa*	Asteraceae	3.08	2.48	3.18	No	Herb	Annual	Nat	N America	2
21	*Bromus danthoniae*	Poaceae	2.00	2.00	2.30	Yes	Herb	Annual	Nat	Asia, Europe	2
22	*Buddleja davidii*	Scrophulariaceae	0	1.04	1.04	No	Shrub	Perennial	Nat	Asia	2
23	*Camelina microcarpa*	Brassicaceae	0	1.04	1.04	Yes	Herb	Annual or biennial	Nat	Africa, Asia, Europe	6

No	**Species**	**Family**	**Env.**	**Soc.**	**Total score**	**Agr. weed**	**Life form**	**Life history**	**Status**	**Native range**	**Number of grid cells** (See Suppl. material 1)
24	*Canna indica*	Cannaceae	3.04	0	3.04	No	Herb	Perennial	Cas	S America	5
25	*Carpobrotus edulis*	Aizoaceae	4.03	0	4.03	Yes	Herb	Perennial	Nat	S Africa	4
26	*Conyza bonariensis*	Asteraceae	2.30	2.30	2.69	Yes	Herb	Annual	Nat	S America	7
27	*Conyza canadensis*	Asteraceae	3.08	3.32	3.52	Yes	Herb	Annual	Nat	N America	13
28	*Chenopodium ambrosioides*	Chenopodiaceae	1.32	0	1.32	No	Herb	Annual or perennial	Nat	N America	6
29	*Eichhornia crassipes*	Pontederiaceae	5.05	4.32	5.12	No	Aquatic	Perennial	Nat	S America	1
30	*Elatine ambigua*	Elatinaceae	2.00	0	2.00	No	Aquatic	Annual	Nat	S Asia	3
31	*Elatine triandra*	Elatinaceae	2.00	0	2.00	No	Aquatic	Perennial	Nat	N America	1
32	*Eleusine indica*	Poaceae	2.00	3.04	3.08	Yes	Herb	Annual	Nat	Africa	2
33	*Elodea canadensis*	Hydrocharitaceae	4.34	3.30	4.38	No	Aquatic	Perennial	Nat	N America	1
34	*Eucalyptus camaldulensis*	Myrtaceae	4.34	2.00	4.34	No	Tree	Perennial	Cas	Australia	5
35	*Ipomoea purpurea*	Convolvulaceae	2.00	3.00	3.04	Yes	Herb	Perennial	Nat	C America, N America	3
36	*Lantana camara*	Verbenaceae	5.05	4.11	5.10	No	Shrub	Perennial	Cas	C America, S America	4
37	*Melia azedarach*	Meliaceae	0	2.32	2.32	No	Tree	Perennial	Cas	Asia	5
38	*Mirabilis jalapa*	Nyctaginaceae	2.05	0	2.05	No	Herb/ Shrub	Perennial	Cas	C America, S America	1
39	*Nicotiana glauca*	Solanaceae	2.30	2.32	2.61	No	Shrub	Perennial	Nat	S America	5
40	*Panicum capillare*	Poaceae	0	2.30	2.30	No	Herb	Annual	Nat	N America	1
41	*Phytolacca americana*	Phytolaccaceae	1.04	1.04	1.32	No	Herb/ Shrub	Perennial	Nat	N America	7
42	*Pseudotsuga menziesii*	Pinaceae	4.01	0	4.01	No	Tree	Perennial	Cas	N America	1
43	*Robinia pseudoacacia*	Fabaceae	3.48	3.11	3.63	No	Tree	Perennial	Nat	N America	4
44	*Sicyos angulatus*	Cucurbitaceae	3.00	2.30	3.08	Yes	Herbaceous Vine	Annual	Nat	N America	2
45	*Sigesbeckia pubescens*	Asteraceae	3.00	0	3.00	No	Herb	Annual	Cas	Asia	2
46	*Solanum elaeagnifolium*	Solanaceae	3.00	2.00	3.04	No	Herb	Perennial	Nat	S America	1
47	*Solanum pseudocapsicum*	Solanaceae	2.00	2.00	4.00	No	Shrub	Perennial	Cas	S America	2
48	*Solanum sisymbriifolium*	Solanaceae	2.00	0	2.00	No	Shrub	Perennial	Nat	C America, S America	1
49	*Solidago canadensis*	Asteraceae	4.00	2.00	4.01	No	Herb	Perennial	Nat	N America	1
50	*Tagetes minuta*	Asteraceae	3.00	0	3.00	No	Herb	Annual	Cas	S America	7
51	*Tradescantia fluminensis*	Commelinaceae	4.34	2.00	4.34	No	Herb	Annual	Nat	S America	1

sites to native species (1.4), impact through hybridization (1.5) and impact on ecosystems (1.6). Socioeconomic impacts are categorized as follows: impact on agricultural production (2.1), impact on animal production (2.2), impact on forestry production (2.3), impact on human infrastructure and administration (2.4), impact on human health (2.5) and impact on human social life (2.6) (see Nentwig et al. 2016). The protocols for assessing plant impacts are described in detail in Rumlerová et al. (2016).

If more than one study assessed impacts in a category and scored them differently, we assigned the species with the highest score as we were interested in potential maximum impacts (Rumlerová et al. 2016). Suppl. material 3 provides information on detailed scoring of species in each category with corresponding references. Based on the maximum scores, for each species and impact group (environmental, socioeconomic), the logarithmic sum of all values scored across the six categories was calculated (log10(Σ(10^impact values)). The logarithmic sum was used to reflect the exponential nature of the gradual increase in the levels of the GISS system, when individual levels of impact are of different orders of magnitude (see Rumlerová et al. 2016).

Species traits

For each species included in this study we recorded information on its life history (annual or perennial; Table 1) and whether the species was considered an agricultural weed in Turkey; this information was taken from literature. The region of origin was categorized as follows: Asia, America (North America, South America and Central America), Africa, Australia and Europe. The data on species traits were taken from the databases (USDA, www.plants.usda.gov; DAISIE, www.europe-aliens.org; Council of Higher Education National Centre, https://tez.yok.gov.tr/UlusalTezMerkezi/giris.jsp), theses (e.g. Yazlık 2001, Yıldırım 2001) and published papers (e.g. Yıldırım and Ekim 2003, Brundu et al. 2011). Plant names have been verified using IPNI (International Plant Name Index, http://www.ipni.org).

Species distribution

The distribution of the studied species in Turkey was expressed using a grid system (Fig. 1, Suppl. material 1) following the Flora of Turkey (Davis 1965–1985, Davis et al. 1988) and East Aegean Islands (Güner et al. 2000). The distance between the two latitudinal degrees is 220 km and that between the two longitudinal degrees 175 km, with the area of a grid cell being 38,500 km^2 (Akaydın and Erik 1996). The biogeographical distribution (Fig. 1) was used to assess regional differences in the types of impacts. The geographical system divides Turkey into seven regions (Marmara; Black Sea; Aegean; Mediterranean; Central Anatolia; South East Anatolia; and East Anatolia; Tuncel 2011). Data on the distribution of the species studied was taken from the following sources: Babaç (2004), Bakış et al. (2011), Eminağaoğlu et al.

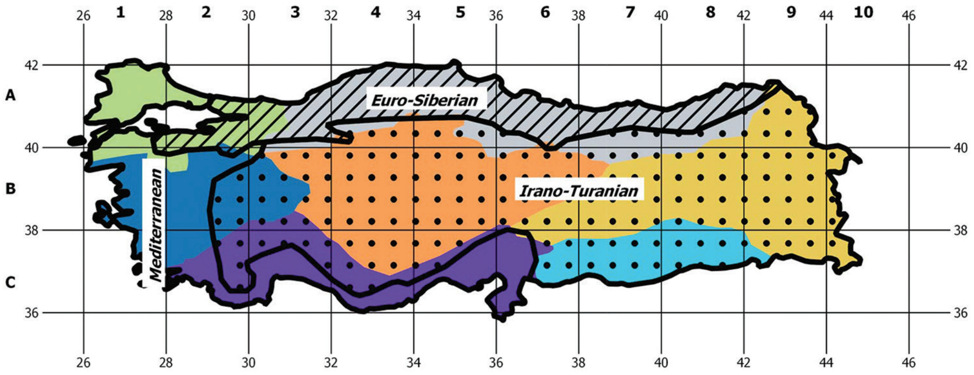

Figure 1. The sections of Turkey in different systems. (i) Biogeographical system: Euro-Siberian – hatching, Mediterranean – no hatching and Irano-Turanian – dots; (ii) geographical system: 🟩 Marmara region, ⬛ Black Sea region, 🟪 Mediterranean region, 🟧 Central Anatolia region, 🟦 South East Anatolia region, 🟨 East Anatolia region, 🟦 Aegean region and (iii) the grid system according to Davis (1965–1985, 1988) is overlaid over the map.

(2012), Karaer and Terzioğlu (2013), Uruşak et al. (2013) and Uremis et al. (2014). Data on the extent of agricultural area was taken from the Turkish Statistical Institute (http://www.tuik.gov.tr).

Statistical analyses

The relationships between the impacts, the species and their distribution were analysed by using exploratory analyses. We compared the relationships between the scores for environmental and economic impacts with the distribution of species in Turkey (explanatory variable) by linear regression, to find out whether widely distributed species have a higher or lower than average impact in some categories. We also tested the correlation between environmental and socioeconomic impacts of individual species. The relationship between the extent of agricultural area in the region and the mean impact on agriculture of species occurring in that region was also tested by correlation. The correlations were tested by standard Pearson correlation tests (Crawley 2007). In addition, the t-test was used to analyse whether the *a priori*, literature-based assignment of a species as an agricultural weed was associated with its impact on agriculture and its total socioeconomic impact, as scored in our study. The analyses were done in R (Crawley 2007, R Development Core Team 2013).

Results

A total of 125 publications and 15 databases/factsheets from ISSG, USDA, CABI and NOBANIS (Suppl. material 2) were used to assign 439 individual GISS scores to the

Table 2. The origin of the assessed species. Note that the total sum of species by regions of origin exceeds the 51 species analysed, because some of them have their origin in more than one region.

Origin	No
Asia	17
Africa	3
Americas:	32
North America	16
South America	10
Central & North America	3
Central & South America	3
Australia	1
Europe	7
Species analysed	**51**

species assessed (see Suppl. material 3). The 51 species studied belong to 41 genera and 26 families. In terms of life history, the data set included 26 perennial, 23 annuals and two species classified in both groups. There were 32 herbs, seven shrubs, three herb/shrub, six trees, four aquatic plants and one vine. Twenty-one species are considered as agricultural weeds in literature (Table 1). Considering the origin, most of the species originate from the Americas (32) and Asia (17) (Table 2).

The five most widely distributed species occur in at least 35% of grid cells (Table 1, Suppl. material 1): *Alyssum sibiricum*, *Alyssum strigosum* subsp. *strigosum* (in 14 out of 29), *Alyssum dasycarpum*, *Conyza canadensis* (13) and *Alhagi pseudalhagi* (11). In terms of geographical regions, the Black Sea region harbours 34 species, Marmara 28, Mediterranean region 21, Aegean region 17 and East Anatolia, Central Anatolia and South East Anatolia harbour 12 species each (Fig. 2). Species, for which we recorded impact on forestry, are present in Black Sea, Marmara and Mediterranean regions. There was a significant negative relationship between the environmental impact and the number of grid cells the species occupies in Turkey (env. impact = -0.14 × grid no.; $F_{1,50} = 7.1$; $p = 0.01$) and non-significant relationship for socioeconomic impact ($F_{1,50} = 0.00$; $p = 0.96$) (Figs 3A, B).

There is evidence that 41 of the 51 alien plants considered in this study have environmental impacts. The impacts on ecosystem (category 1.6) and on plants or vegetation (1.1) were the most frequent amongst environmental impacts, recorded for 24 species (59% of those with environmental impacts). Impact on other species through competition (1.3) was recorded in 18 species (43%). Socioeconomic impacts were recorded for 40 species. The most frequent socioeconomic impact, applying to 28 species (70% of those with socioeconomic impact), was recorded on agricultural production (2.1). The impact on human health (2.5) was recorded in 22 species (55%) and on human social life (2.6) in eight species (20%).

The top 22 alien species ranked according to the decreasing logarithmic sum of all impact scores across categories of environmental and socioeconomic impacts are shown in Fig. 4. *Eichhornia crassipes*, *Lantana camara*, *Elodea canadensis*, *Eucalyptus*

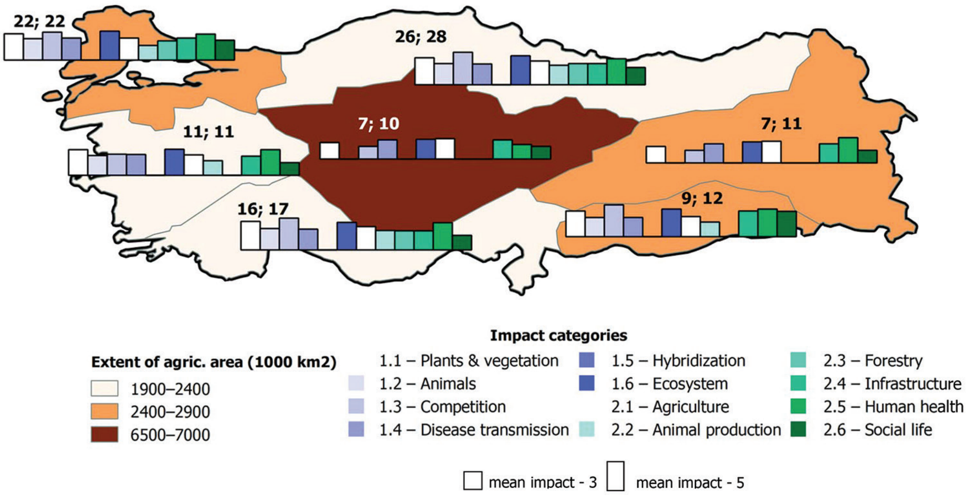

Figure 2. Map of impact types per individual geographical region. Shading of the regions reflects the extent of agricultural area (thousands of km^2 in that region; TUIK 2015). The heights of the bars in the main figure are proportional to the assessed impact of alien species in the regions; two bars with mean impacts of 3 and 5 are shown as a reference. Numbers above the bars show the number of species with environmental and socioeconomic impact in the region.

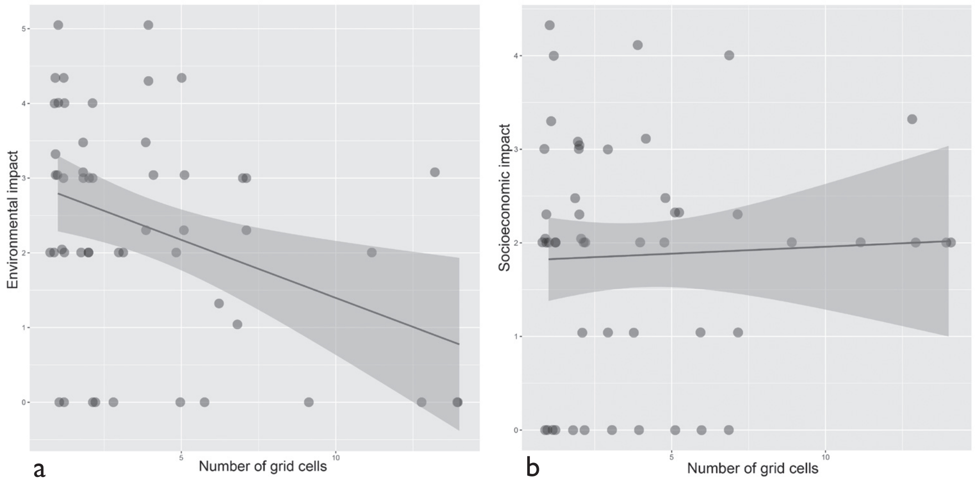

Figure 3. Correlation between the **a** environmental and **b** socioeconomic (logarithmic score) impact and distribution of alien species in Turkey (no. of occupied grid cells). Each dot represents a species.

camaldulensis, *Tradescantia fluminensis*, *Carpobrotus edulis*, *Ambrosia artemisiifolia* and *Artemisia annua* ranked the highest. The species scores of impact in socioeconomic and environmental categories were not correlated (r = 0.17; df = 50; t = 1.36; p = 0.18).

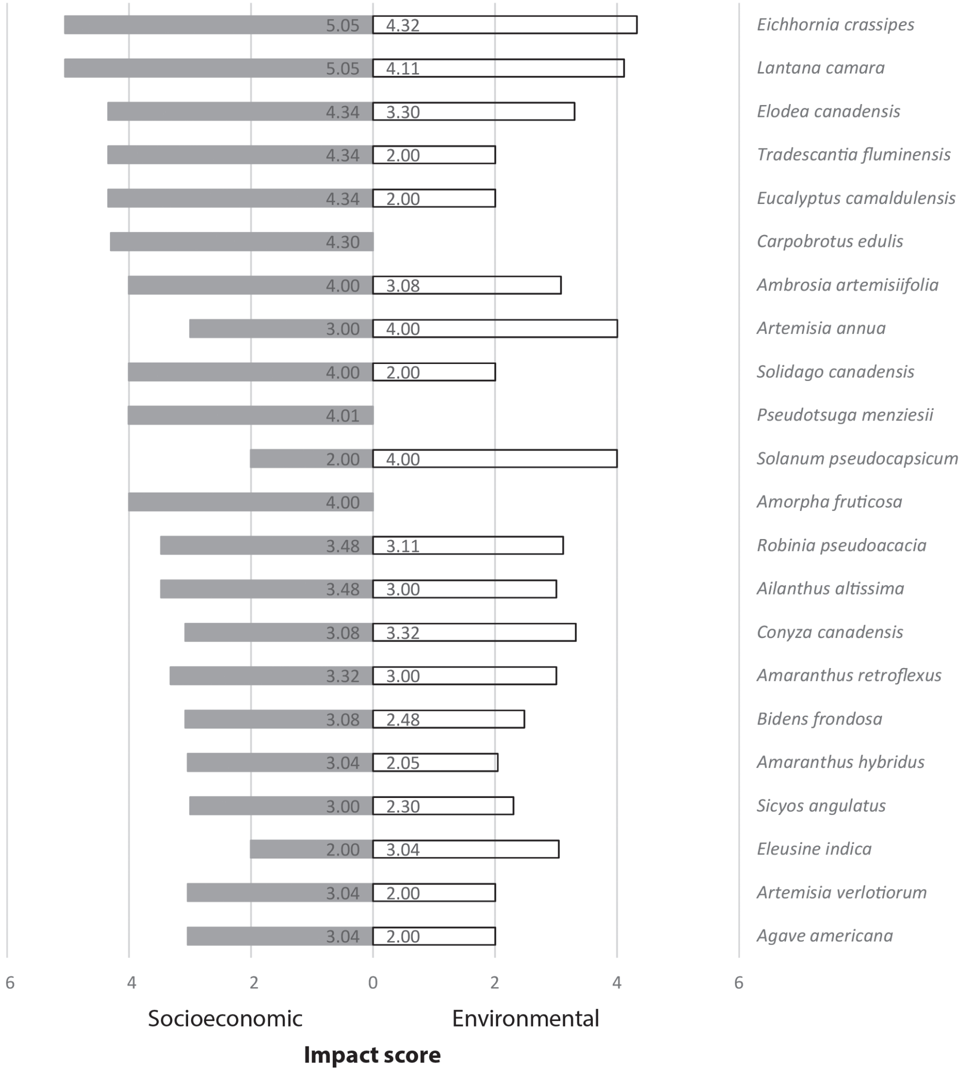

Figure 4. Top 22 alien species ranked according to decreasing logarithmic sum of all impact scores across categories of environmental (white bars) and socioeconomic (grey bars) impacts. Note that by using the logarithmic sum, the highest score recorded has the most influence on the overall score while the other scores have relatively little influence on the overall value; this approach ensures that emphasis on the maximum impact of species is maintained.

An analysis, focused on agriculture, revealed that *Conyza canadensis*, *Amaranthus retroflexus* and *Ipomoea purpurea* have high impacts on agricultural production (category 2.1). We found marginally significantly greater impacts on agriculture of species *a priori* classified as 'agricultural weeds' than of other species, not considered agricultural weeds in literature (t-test = 2.08; df = 15; p = 0.06) and no significant difference between these two

Table 3. Overview of categories scored in the two impact groups (environmental and socioeconomic), numbers of alien species for which the data were found, and % of the 51 species screened. The numbers of scored species in categories include also zero scores.

	Environmental (total 41 species)						Socioeconomic (total 40 species)					
Impact type	**1.1**	**1.2**	**1.3**	**1.4**	**1.5**	**1.6**	**2.1**	**2.2**	**2.3**	**2.4**	**2.5**	**2.6**
Total plant	24	11	18	6	0	24	29	6	4	5	22	8
%	59	27	44	15	0	59	71	15	10	12	54	20

groups in overall socioeconomic impact (t-test = 1.38; df = 55; p = 0.17). Of the 21 ‘agricultural weeds’, the evidence for impact on agriculture was found for 20, with an average score of 2.1, while, for the 30 non-weedy species, nine had a record of impact, with an average 1.8. No significant relationship between the extent of agricultural area with mean impact on agriculture (2.1) was found (r = -0.41, df = 5, t = 0.993, p = 0.37).

Discussion

The vast majority of species assessed in this study can potentially have some impact in Turkey; of the 51 species scored, we found evidence in literature of environmental and socioeconomic impacts for 41 and 40 species, corresponding to 80% and 78%, respectively. For 30 assessed species, we found evidence of both environmental and socioeconomic impacts, while 11 species have only environmental and 10 species only socioeconomic impacts. Since our evidence database was compiled from primary sources in which the impacts were tested by original authors, we minimized the potential bias that might occur due to incorrect interpretation or reporting in secondary references. Another potential bias is associated with uncertainty in recording the impacts in the primary studies. We tried to minimize this by using multiple assessments of the same impact type for the same species where such data were available and taking the maximum value as in previous studies employing GISS (Kumschick et al. 2015a, Rumlerová et al. 2016).

The impacts of alien species have been traditionally evaluated to address the economic costs of invasion (Perrings et al. 2010) or to quantify direct eradication costs (Reinhardt et al. 2003); a system for a broader evaluation of a wide range of socioeconomic aspects of invasion has been developed only recently (Bacher et al. 2018). Not so long ago, environmental assessments were rather rare and those that were available used mostly economic currencies (see Jeschke et al. 2014 for overview of definitions related to impact); this has changed recently when new methods for evaluation of environmental impacts were developed (Nentwig et al. 2010, Blackburn et al. 2014, Kumschick et al. 2015b).

In our study, we considered both environmental and socioeconomic impacts of alien species that may become problematic in the near future. The highest economic impacts are likely to occur in agriculture and human health sectors. In total, 22 species (out of the 51 we assessed) occurring in agricultural areas are considered as problematic (Yazlık 2001, Yıldırım 2001, Kitiş 2002). Some plants with strong impacts on agriculture such as *Conyza canadensis* and *Amaranthus retroflexus* occur in high abundances in different biogeographic regions and colonize a range of different habitats. This corresponds to previous reports about these species as agricultural weeds in different biogeographic regions of Turkey; in the Irano-Turanian region, *Amaranthus retroflexus* was recorded in 19% and 15% of pear and apple orchards sampled, respectively (Yazlık 2001). In the Mediterranean region, 91% tomato fields were infested by this species and *A. retroflexus* occurred with an average density of 6.5 plants/m^2 (Kitiş 2002). The large impact of *Conyza* spp. (including *C. canadensis*; N. Doğan, personal communication) determined in this study is corroborated by evidence from the Mediterranean and Aegean regions, where herbicide-resistant biotypes have been identified (Doğan et al. 2016).

Turkey consists of three different biogeographic zones, which represent natural barriers in the naturalization-invasion process for some species, because of climatic characteristics, such as extreme temperature, or precipitation in the dry season; only five aliens with impacts assessed here are widespread across the country. Our data suggest that the cumulative impacts of many alien species only occur in some regions because the species with highest impact are not yet widely distributed over the whole country. This finding can be important for management, because the eradication of localized populations is more feasible and less costly compared to populations of widespread invaders (Pluess et al. 2012). In addition, the non-significant relationship between economic impact and distribution indicates that the overall impact of alien species in a region is proportional to their distribution and can be predicted on the basis of assumed future spread of weedy species.

For environmental impact, the highest scores were found for a diverse group of species containing *Eichhornia crassipes*, *Lantana camara*, *Tradescantia fluminensis*, *Elodea canadensis*, *Eucalyptus camaldulensis*, *Carpobrotus edulis*, *Pseudotsuga menziesii* and *Ambrosia artemisiifolia* as prominent examples. They are representatives of various life forms of plants from aquatics to shrubs and trees. This corresponds to previous findings from other regions that the impact is positively associated with height and depends on the environment, with aquatic plants having the greatest impacts (Rumlerová et al. 2016). The most common mechanism for environmental impact in our study was via ecosystem changes with direct negative effects on plants and vegetation. Compared to Rumlerová et al. (2016), competition was not the most frequent mechanism for impact in our study. Nevertheless, the above-mentioned ecosystem changes can be a consequence of indirect effects on other organizational levels that result in complex changes due to invasion.

Eichornia crassipes, Lantana camara, *Artemisia annua*, *Solanum pseudocapsicum*, *Conyza canadensis*, *Elodea canadensis* and *Robinia pseudoacacia* are also species with the greatest socioeconomic impacts, reaching values comparable to those of major agricultural weeds discussed above. We found only a marginally significant relationship between the species' weed status and their impacts on agriculture as scored in our study. This indicates that, in previous assessments, these species were assigned their weed status rather subjectively and probably on the basis of their high abundance, which does not necessarily translate into high impact.

Vilà et al. (2010) found a relatively weak correlation between the economic and ecological impacts for terrestrial plants. Our analysis provided similar results, with no relationship between the two types of impacts. This can be explained by the fact that invasive terrestrial plants are preferentially studied for selected types of impacts and the priorities about what impact to target can largely differ amongst individual assessors (Vilà et al. 2011, Hulme et al. 2013). The fact that environmental and socioeconomic impacts of plants are, to some extent, independent from each other, as indicated by the lack of correlation, calls for measuring and recording both types of impact.

For some species, potential impacts recorded here are greater than reported in a study that assessed the impacts of plant invaders in Europe using the same methods (Rumlerová et al. 2016). Theoretically, impact values should be the same across the two studies because the data should reflect the maximum impact of the species in its entire alien range. Some of these differences can be attributed to the fact that the current study used literature that was published after the scoring for the paper of Rumlerová et al. (2016) was performed and the fact that we also used local reports (e.g. Yazlık 2001, Yıldırım 2001, Kitiş 2002) to make our study as relevant for Turkey as possible. Despite some differences in the scores of some species, in general, species with the highest impacts from both studies have similar scores. For instance, the top ranked species in Turkey and Europe were the same (*Lantana camara*, *Eichhornia crassipes*, *Elodea canadensis*, *Robinia pseudoacacia*, *Eucalyptus camaldulensis*, *Tradescantia fluminensis*, *Solidago canadensis* and *Carpobrotus edulis*) and exhibited the greatest impacts in the same categories. In addition, some recently recorded species in Turkey (e.g. *Tradescantia fluminensis*; Eminağaoğlu et al. 2012) were classified in our study, similar to the scoring performed by Rumlerová et al. (2016), as having high impacts. This, together with the negative relationship that we found between the environmental impact of a species and its distribution, a relationship that is hard to interpret, points to the importance of scoring the impacts before the species becomes widely distributed.

A precautionary approach to invasive plants should be adopted not only in protected areas (Foxcroft et al. 2017) but also in agricultural and urban areas where alien plants with environmental and socioeconomic impacts are concentrated (Hoffmann and Broadhurst 2016, Schiffleithner and Essl 2016). The public and policy-makers more often perceive species as having negative impacts if socioeconomic sectors are affected. However, although the environmental and socioeconomic impacts were not correlated in our study, it is obvious that many species with impacts on economic sectors such as agriculture or forestry also negatively affect biodiversity and environment, for example *Alhagi pseudalhagi*. The same applies to competitive agricultural weeds, for example *Amaranthus retroflexus* (Costea et al. 2004, Vilà and Gimeno 2006), the management of which is often constrained by their increased herbicide resistance. Such assessment is needed to underpin the pathway management (Wilson et al. 2016, Pergl et al. 2017, Saul et al. 2017).

Our study is the first systematic assessment of the impacts caused by alien plants in Turkey and represents complementary information to the recently compiled inventory of alien plants in this country (Uludağ et al. 2017). The data presented here should be included into the decision process to prioritize alien species to be targeted by management and have potential to provide local authorities with a knowledge-base for addressing the regional risks for individual socioeconomic sectors and biodiversity.

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Supplementary material 1

Distribution of alien species assessed in this study

Authors: Ayşe Yazlık, Jan Pergl, Petr Pyšek

Data type: Distribution.

Explanation note: Distribution in Turkey of the alien species studied using the grid system according to Davis (1965–1985, 1988).

Link: https://doi.org/10.3897/neobiota.39.23598.suppl1

Supplementary material 2

List of references

Authors: Ayşe Yazlık, Jan Pergl, Petr Pyšek

Data type: References.

Explanation note: List of references used for scoring the impact of the studied species.

Link: https://doi.org/10.3897/neobiota.39.23598.suppl2

Supplementary material 3

Scoring of the impact

Authors: Ayşe Yazlık, Jan Pergl, Petr Pyšek

Data type: Impact scores.

Explanation note: Scoring of environmental and socioeconomi impact. File contains values (Impact score) and categories in which these scores are assigned (Impact type), with source references.

Link: https://doi.org/10.3897/neobiota.39.23598.suppl3

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Time to cut: population models reveal how to mow invasive common ragweed cost-effectively

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Abstract

Roadsides are an important habitat for invasive common ragweed, *Ambrosia artemisiifolia* L., by facilitating seed dispersal. Reducing the size of roadside populations is therefore essential for confining this highly allergenic species. Here, we aim to determine the cost-effectiveness of mowing regimes varying in frequency and timing, by analysing population-level effects and underlying demographic processes. We constructed population models of *A. artemisiifolia* parameterised by demographic data for four unmanaged reference populations across Europe in two years. We integrated the effects of four experimental mowing regimes along Austrian road sides on plant performance traits of five years and experimental data on seed viability after cutting. All four experimental regimes reduced the projected intrinsic population growth rates (*r*) compared to the unmanaged controls by reducing plant height and seed viability, thereby counteracting increased size-dependent fecundity. The prevailing 2-cut regime in Austria (cutting during vegetative growth, here in June and just before seed ripening, here in September) performed least well and the reduction in *r* was mainly due to reduced seed viability after the second cut. The efficacy of the two best experimental regimes (alternative schemes for 2 or 3 cuts) was mainly due to cutting just before female flowering (here in August) by decreasing final adult plant height dramatically and thereby reducing seed numbers. Patterns were consistent across reference populations and years. Whether regimes reduced *r* below replacement level, however, varied per population, year and the survival rate of the seeds in the soil bank. Our model allowed projecting effects of five theoretical mowing regimes with untested combinations of cuts on *r*. By plotting *r*-cost relationships for all regimes, we identified the most cost-effective schemes for each cutting frequency (1–3 cuts). They all included the cut just before female flowering, highlighting the importance of cutting at this moment (here in August). Our work features i) the suitability of a modelling approach for the demography of an annual species with a seed bank, ii) the importance of seed viability in assessing mowing effects, iii) the use of population models in designing cost-effective mowing regimes.

Keywords

Annual plant, population model, cost-effective management, population growth rate, seed viability, soil seed bank

Introduction

Successful management of invasive plant populations requires a cost-effective reduction of their population size, sufficient to mitigate their negative impact (Kerr et al. 2016; Simberloff 2003). Population models are used for predicting ecological benefits of management options (Crone et al. 2011). Realistic models require not only good demographic data covering the entire life cycle of the target species (i.e. all vital rates), but also knowledge of effects of management on each of these vital rates. The prediction of future effects and the implementation of management on a large geographic scale demands quantification of temporal and spatial variability of both vital rates and management effects (Crone et al. 2013; Salguero-Gómez and De Kroon 2010). Such extended data collection is, however, beyond the capacity or scope of most studies. Demographic data often cover not more than a few years for a limited number of populations on a small geographic scale (Crone et al. 2013), while management effects are typically estimated through experimentation at a single location (e.g. in a greenhouse or experimental field) and are often limited to assess individual-level effects. Moreover, often only a single aspect of disturbance is varied (intensity, frequency, timing, duration or extent), while the total effect of management likely results from interactions between these aspects, requiring a multi-aspect experimental approach as well (Zhang and Shea 2012). Besides, economic costs are only rarely incorporated into demographic studies (Kerr et al. 2016).

Common ragweed (*Ambrosia artemisiifolia* L.) is a worldwide invasive plant which has rapidly expanded in Europe in the past decades (Essl et al. 2015). Linear transport structures, such as roadsides, are amongst the most prevalent habitat types for the species in central and north western Europe (Essl et al. 2009; Karrer et al. 2011; Skálová et al. 2017; Tokarska-Guzik et al. 2011) and they are important pathways for introduction and dispersal (Chapman et al. 2016). For instance, seeds directly attach to machines used for road maintenance (Vitalos and Karrer 2009) and are indirectly moved by the airflow of passing vehicles (Karrer et al. 2011; von der Lippe et al. 2013). Management of populations of *A. artemisiifolia* along roadsides is hence a key priority for reducing population growth and limiting the number of seeds available for dispersal. Commonly, however, roadside vegetation management aims to reduce the vegetation height for safety on the road. The frequency of mowing is limited to keep costs low and the timing is adapted to the availability of the personnel. Therefore, the commonly applied regime is likely not suitable for reducing populations of *A. artemisiifolia* on roadsides (Milakovic et al. 2014b).

A multi-aspect experiment testing alternative mowing regimes along Austrian roadsides in multiple years showed that adapting the timing and/or frequency is required to reduce the seed production of individual *A. artemisiifolia* plants (Milakovic et al. 2014b). Although this is an annual species, data on seed production alone are insufficient to assess population-level effects because the species has a long-lasting seed bank (Bassett and Crompton 1975). Studying effects on population growth therefore also requires the inclusion of vital rates of seeds. A first assessment of the soil seed bank after 3 years supports the positive effect of some of these alternative mowing regimes in reducing the *A. artemisiifolia* population size compared to the untreated controls (Milakovic and Karrer 2016). The underlying demographic mechanisms, the effect of specific cuts and the projected population-level effects, however, have not yet been studied.

Here, we address these gaps in order to understand the efficacy of the tested mowing regimes in limiting growth of *A. artemisiifolia* populations, link these to management costs and design additional cost-effective mowing regimes. Specifically, we ask how mowing frequency and timing affect population growth of *A. artemisiifolia*? To answer this question, we analysed i) how mowing frequency and timing affect vital rates of plants in roadside populations and how these effects vary from year to year, ii) how mowing affects seed viability and iii) how much each of these mowing effects contribute to changes in population growth in different populations across Europe in different years. We construct population models for the study system and parameterise these with newly-collected demographic data from geographically distant populations across Europe and by integrating several existing and new data on the effect of mowing. Finally, we simulate new theoretical mowing regimes and compare their cost-effectiveness to the experimentally tested ones.

Methods

Study species

Ambrosia artemisiifolia originates from central USA and has invaded a wide range of habitat types on most other continents (Essl et al. 2015). It has severe adverse effects on agriculture (Bassett and Crompton 1975; Domonkos et al. 2017) and human health (Smith et al. 2013) due to its vast production of seeds and allergenic pollen, respectively. The monoecious annual typically develops pollen-producing flowers from mid-summer onwards, followed by female flowers in late summer, both aggregated in flowering heads. Each female flower can develop into a single seed, falling straight to the ground after maturation in autumn. Plants normally die before winter while shed seeds may accumulate in a long-lasting soil seed bank if not recruited in the next spring (Bassett and Crompton 1975; Toole and Brown 1946) (Fig. 1).

Data

Overview of data and approach

In order to parameterise all vital rates and integrate the effects of mowing (Fig. 1), we combined four different data sets: data from i) a roadside mowing experiment, ii) a post-harvest seed quality experiment, iii) a demographic survey and iv) seed burial experiments. The mowing experiment comprised a five-year application of four mowing regimes to roadsides in Austria, varying in the timing and frequency of cutting and an untreated control (main experimental results of the first three years can be found in Milakovic et al. 2014b). These data allowed quantifying the effect of the tested mowing regimes on individual plant height in September *y*, flowering *fl*, fecundity *fec* and seed ripening *sr* and how effect sizes of the reproductive rates depend on adult plant height *y* (one of the size variables in our population model) and vary from year to year (for stochastic population models). Since mowing can also affect seed quality (Bohren et al. 2008; Sölter et al. 2016), we obtained the effects of cutting on seed viability *sv* from a separate post-harvest seed quality experiment (Karrer 2016c). Neither of these experiments was designed for demographic modelling and, together, they provided insufficient data to parameterise all vital rates. We therefore chose to parameterise our models with demographic data from other populations of *A. artemisiifolia,* which were

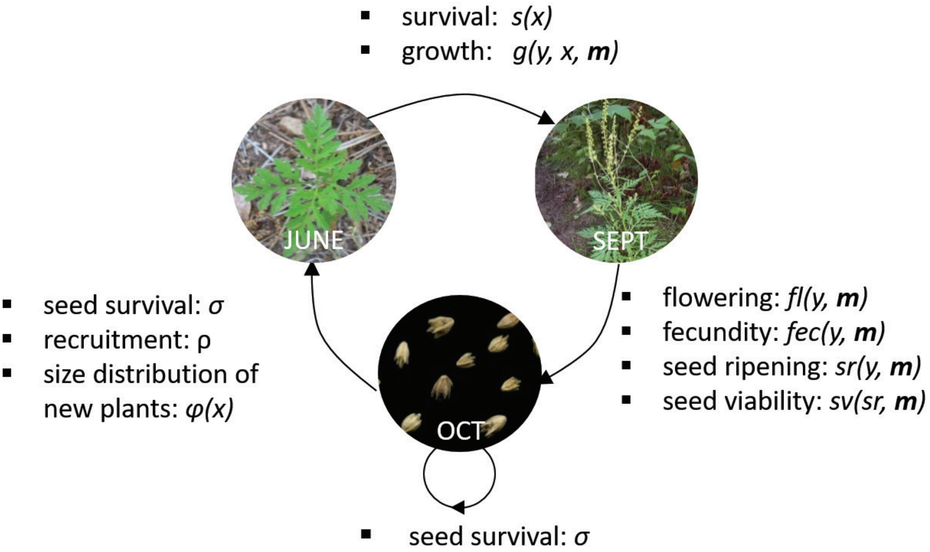

Figure 1. Life cycle of the annual plant *Ambrosia artemisiifolia*. Months indicated are representative for populations in Europe where most new plants have established in June, have developed into seed-producing plants in September and then die while the seeds shed overwinter on or in the soil. The small loop represents (dormant) seeds that do not recruit but stay in the soil until the next year. The vital rates and corresponding parameters in the demographic model are listed for each period. The *x* represents new plant size in June, *y* the plant size in September, ***m*** the effect of mowing.

not mown. We chose four unmanaged populations elsewhere in Europe with similar vegetation and bioclimatic conditions. We conducted a demographic survey in two years providing data on all vital rates except seed ripening *sr*, seed viability *sv* and seed survival σ in the soil seed bank. The species has a long-lasting seed bank (Bassett and Crompton 1975) and such age-structured seed banks may play an important role in the population dynamics of an annual, for instance determining the time to extinction (Kalisz and McPeek 1992, 1993). We therefore complemented these demographic data with survival rates in the soil seed bank σ from long-term burial experiments (Karrer 2016a; Karrer et al. 2016) and used these to parameterise reference models representing untreated controls. We then integrated the experimental mowing effects *m* into these reference models to obtain models of mowing treatments. All analyses and models were performed using R (version 3.3.3, R Core Team 2017).

Roadside mowing experiment

A 5-year mowing experiment was set up along roadsides at six locations in 2009 and in a seventh location in 2010 in Austria. All locations were already infested with *A. artemisiifolia* for an unknown period and managed by a regular mowing regime for road maintenance, comprising a cut around June (during vegetative growth of *A. artemisiifolia*) and in September (just before seed ripening of *A. artemisiifolia*). In summary, each location was divided into five blocks of 20 m length each and, at each location, each of five treatments was randomly assigned to one block. Apart from the untreated control, experimental treatments were yearly applied by road service maintenance teams and included the prevailing mowing regime in eastern Austria and three alternative mowing regimes varying in the timing and frequency of cutting (upper half of Table 1). For ease, we named the mowing regimes according to the months in which cuts were performed (see corresponding phenological stages in Table 1). Details on the experimental design, data collection and results of the first three years are given in Milakovic et al. (2014b). For our demographic model we used data of all five years collected in September before the last cut, when adult plants were bearing seeds. Data were available from a random 20 individual ragweed plants per treatment per location per year or fewer, if fewer were present (see Suppl. material 1, fig. S1 for sample sizes and missing data). Measurements included maximum plant height, female flowering (female reproductive structures absent or present), the total number of individual seeds on the plant (irrespective of their developmental stage) and the most advanced developmental stage of these seeds per plant (classified as still flower, developing seed or ripe seed). We analysed interactive effects of mowing treatment, year and plant size where possible and applicable on all of these response variables by generalised mixed effect models. Plant size was included because mowing effects may vary with plant size, which can be incorporated into a population model. Best statistical models were revealed by comparing values of corrected *Akaike* information criterion and used to obtain estimates of coefficients of vital rates for their integration into the demographic models. Suppl. material 1 provides details on the statistical analyses, including an overview of the factors in the statistical models (Suppl. material 1, Table S1).

Table 1. Overview of the experimental (upper half of table) and theoretical (lower half) mowing treatments. Their treatment code (indicating the calendar months in which cuts were conducted), the number and timing of cuts (each × indicating a cut) are shown.

			Timing of cuts					
	Treatment code	**# cuts**	**Last week June (vegetative growth)**	**Last week July (before peak male flowering)**	**3rd week Aug (before peak female flowering)**	**2nd week Sept (before seed ripening)**	**Remarks**	**Model equation used**
Experimental	0	0					Uncut control treatment (treatment 1 in mowing experiment)	1
	69	2	×			×	Prevailing regime in eastern Austria (treatment 2 in mowing experiment)	2
	89	2			×	×	Experimental new treatment (treatment 3 in mowing experiment)	2
	679	3	×	×		×	Experimental new treatment (treatment 4 in mowing experiment)	2
	689	3	×		×	×	Experimental new treatment (treatment 5 in mowing experiment)	2
Theoretical	6	1	×				Modelled as treatment 69 ***without*** September cut	2
	8	1			×		Modelled as treatment 89 ***without*** September cut	2
	67	2	×	×			Modelled as treatment 679 ***without*** September cut	2
	68	2	×		×		Modelled as treatment 689 ***without*** September cut	2
	9	1				×	Modelled as control treatment 0 ***added with*** a September cut	2

Post-harvest seed quality experiment

The effects of cutting on seed viability were obtained from a post-harvest seed quality experiment (Karrer 2016c). Plants cultivated in a common garden in Vienna, Austria, bearing female reproductive structures were harvested by cutting them at different dates, corresponding to different developmental stages of the flowers and seeds. The harvested plants were left on the ground until the end of the growing season, when the developmental stage of the seeds was scored and their viability tested. We used the resulting percentage of ripe, viable seeds for each developmental stage harvested as seed viability. If plants were cut when female structures were still in the flowering stage (stages 1 and 2 in Karrer 2016b), these produce only 0.1% of viable seeds. Of plants cut while bearing unripe seeds, 27% of the seeds in early developmental stages (stage 3 in Karrer 2016b) and 43% of those in late developmental stages (stage 4 in Karrer 2016b) developed into ripe viable seeds. As the mowing experiment did not distinguish the age of unripe seeds, we used the average of these values (35%) for all unripe seeds. Of the seeds that were ripe when the plant was harvested (stage 5 in Karrer 2016b), 87% turned out to be viable.

Demographic survey

To serve as "reference" populations for the current mowing effect study, we selected *A. artemisiifolia* populations located in the same bioclimatic region as the Austrian sites of the mowing experiment (Continental or Pannonian), with the most similar habitat type possible (grasslands, since no unmanaged roadsides were available) and with plant heights covering the range of plant heights observed in the untreated controls of the mowing experiment. This yielded four populations located in Austria (AT), Hungary (HU), Italy (IT) and Poland (PL) (details in Suppl. material 2, Table S2). For the survey, we used specific standardised protocols developed for a coordinated European-wide demographic study of unmanaged populations of *A. artemisiifolia* across Europe started in 2014 (full demographic survey protocol available on https://www.protocols.io/, https://doi.org/10.17504/protocols.io.mmyc47w, see also Suppl. material 2). In summary, over a hundred individually labelled plants per population were monitored from June, when they were young vegetative plants, to seed set in September. This provided estimates of new plant size, survival, growth and flowering. Another set of 21 mature plants was harvested at seed set for estimates of fecundity (i.e. coinciding with the time in the year that plants in the mowing experiment were assessed before the cut in September). Numbers of new plants in quadrats and estimates of the associated soil seed bank size from soil samples provided estimates of recruitment rates. We monitored all four populations in 2014 and 2015, but no plants in the populations in Austria and Hungary survived until the end of the growing season of 2015 due to harsh competition by grasses. We therefore had six suitable reference data sets (AT14, HU14, IT14, IT15, PL14 and PL15) available for the analysis.

Seed burial experiments

To obtain values of seed survival rates, we used three of the largest available data sets for burial experiments with yearly measurements on our study species to date (Karrer 2016a; Karrer et al. 2016) (see overview in Suppl. material 3). Replicated bags with 50 seeds from plants from locations in Austria and Hungary had been buried at two different locations in Austria (details in Suppl. material 3, Table S3). Yearly sampling of subsets and subsequent viability tests provided three time series over 5 years, which we used to fit an exponentially declining model assuming age-independent mortality (Suppl. material 3, fig. S5). This provided three estimates of yearly seed survival rates in the soil seed bank (scenario “H” with seeds from Hagenbrunn, Austria: 0.792; scenario “K” with seeds from Kaposvar, Hungary: 0.963; scenario “U” with seeds from Unterpurkla, Austria: 0.921).

Population models

Population models of unmanaged references

Our discrete-time population model describes a time step of a year, from October (after seeds have been shed and plants have died) to October. As, in our model, individuals only exist as seeds in October, our model could be seen as unstructured. However, most vital rates in the model describe individual performance of plants from June to October and are functions of the continuous size variables x (plant height in June) or y (plant height in September). Our model is hence similar to a periodic Integral Projection Model with size as a continuous state variable (Ellner and Rees 2006) and consists of the three periods indicated in the large loop in Fig. 1. For the unmanaged reference populations, the number of seeds in seed bank *SB* in October after seed dispersal is described by equation 1:

EQ 1.

$$SB(t+1) = SB(t)\,\sigma(1-\rho) + SB(t)\,\sigma\,\rho\,\varphi(x)\int_{min}^{max} s(x)\,g(y,x)\,nx(x)\,dx \int_{min}^{max} fl(y)\,fec(y)\,\Sigma(sr(y)\,sv(sr))\,ny(y)\,dy \quad [1]$$

The first part of the equation describes the seeds that survived the entire year in the soil seed bank (small life cycle loop in Fig. 1) with survival σ, assuming that mortality occurs in winter (M. Leitsch-Vitalos, unpublished results). The second part describes the number of newly produced seeds in October at t+1 per seed at t and follows the large life cycle loop in Fig. 1 with integrals describing the transitions from June till September and from September till October, respectively. We use log-transformed plant height as a continuous variable describing individual size, because size classes are hard to distinguish in *A. artemisiifolia* and because this variable was the only common measure of size occurring in all data sets, while log-transformation yielded best fits of vital rate models. After seeds have survived the winter with probability σ, they recruit with probability ϱ, resulting in *nx* new plants with distribution φ of size *x* in June. If they survive, *s*(*x*), they grow, *g*(*y*, *x*), into *ny* plants of size *y* in September. If they flower, *fl*(*y*), they produce *fec*(*y*) new seeds. The total number of new viable seeds incorporated into the soil seed bank in October (*t* + 1) depends on the distribution *sr*(*y*) of seeds over the ripening stages (flower, unripe seed, ripe seed) and the associated viability *sv*(*sr*) of each ripening stage. We did not include density-dependence in the model to conserve the ability to analyse intrinsic population growth rates analytically and because excluding density-dependence may be inappropriate when models are parameterised with realised levels of interspecific and intraspecific competition (Crone et al. 2013), which is the case in our demographic survey.

Using equation 1, we parameterised population models for all combinations of the six reference data sets and the three seed survival rates (i.e. a total of 18 reference scenarios, representing unmanaged controls). For details of the parameterisation, we refer to Suppl. material 4, which includes estimates of vital rates for each reference data set (Suppl. material 4, Table S4 and Figs S6–10). Integrations were applied to an extended range of plant sizes observed across all reference populations, from *min* (0.8 * the minimum height of new plants in June) to *max* (1.2 * the maximum plant height in September). We dealt with potential eviction (Williams et al. 2012) by adding all projected size values exceeding the size range to the corresponding most extreme size class.

Population models of experimental mowing treatments

To project the effects of the experimental mowing treatments, equation 1 was extended by including dependence on mowing treatment *m* into all the relevant vital rate functions, resulting in equation 2 (modifications to equation 1 are indicated in bold):

EQ 2.

$$SB(t+1) = SB(t)\,\sigma\,(1-\rho) +$$

$$SB(t)\,\sigma\,\rho\,\varphi(x) \int_{min}^{max} s(x)\,g(y,x,\boldsymbol{m})\,nx(x)\,dx \int_{min}^{max} fl(y,\boldsymbol{m})\,fec(y,\boldsymbol{m})\,\Sigma(sr(y,\boldsymbol{m})\,sv(sr,\boldsymbol{m}))\,ny(y)\,dy \;[2]$$

Details of the parameterisation are elaborated in Suppl. material 5. Mowing effects on growth *g*, flowering *fl*, fecundity *fec* and seed ripening *sr* were derived from the mowing experiment, mowing effects on seed viability *sv* from the post-harvest seed quality experiment. Other parameters remained unchanged. We hence parameterised a set of 360 population models with equation 2, integrating the effects of each of the four experimental mowing treatments into each of the five mowing years into each of the 18 unmanaged reference scenarios. In order to understand the mechanisms by which treatments affect population growth, we quantified the relative contribution of each of the affected vital rates to changes in population growth (Δr). For that, we integrated mowing effects of single vital rates one by one in equation 2 for each of the 360 population models.

Simulating new theoretical mowing treatments with population models

Our approach allowed assessing the effect of new, experimentally untested combinations of cutting dates. Since the cut in September only affects population growth by modifying seed quality (through reduced seed ripening and corresponding lower seed viability) and no other vital rates, we were able to theoretically simulate removal or addition of this cut from the experimentally tested mowing regimes (Table 1, lower half). Thus, by removing the effect of the September cut from the four experimental mowing treatments 69, 89, 679 and 689, we simulated four new theoretical mowing treatments (6, 8, 67 and 68, respectively. To assess their effects for each reference model in each year, we created a second set of 360 population models equivalent to the 360 described above, maintaining mowing effects on growth, flowering and fecundity, but removing effects on seed ripening and viability. We also simulated a new theoretical mowing treatment 9 constituting mowing only in September by integrating the effect of mowing in September into the 18 reference scenarios (untreated controls, treatment 0), resulting in a second set of 18 alternative population models. Specifically, we integrated the effect of mowing in September on seed viability for each seed developing stage.

Analyses of population models

We obtained the projected intrinsic population growth rate, *r*, for each population model parameterised and compared them to assess the effect of treatments and the contribution of single vital rates. Since the effect of seed ripening only exerts an effect on *r* through the corresponding reduction in seed viability, we calculated the contribution of seed ripening alone as the difference between the growth rate when seed viability only was integrated and the growth rate when integrating both seed ripening and viability. To acknowledge temporal variation in experimental mowing effects (Metcalf et al. 2015), we also estimated a stochastic intrinsic population growth rate (r_s) for each experimental mowing treatment in each reference scenario by iterating a population vector through a time series, sampling population model matrices of different mowing years with equal probability at every time step, using the R package IPMpack (version 2.1, Metcalf et al. 2013).

Results

Effects of mowing on vital rates of plants

For plant height in September, the full model with the interaction of treatment and year fitted the data best. The pattern of treatment effects was nevertheless fairly consistent across the years without a clear pattern over time (Fig. 2A and Suppl. material 1, fig. S2). Experimental treatments with a previous cut in August (89 and 689) reduced final plant height in September most, the treatment with a previous cut in July (679) moderately, while the treatment with a previous cut in June (69) increased or reduced height slightly, depending on the year and location (Suppl. material 1, fig. S1). All vital rates related to reproduction were strongly affected by treatment and plant height. In the best model of flowering, treatment and plant height had independent effects (Suppl. material 1, fig. S3). All mowing treatments and especially treatment 89 reduced flowering probability compared to the control, but the effect decreased with plant height and became negligible for plants taller than 40 cm (Fig. 2B). The best model of fecundity had no treatment × year interactions (Suppl. material 1, fig. S4), so the relative treatment effect was similar for all years (Fig. 2C). All mowing treatments increased size-dependent seed production, but the magnitude of this compensation changed with plant height, increasing for treatments 69 and 679 (i.e. the larger the plant, the stronger compensation of seed production), but decreasing for treatments 89 and 689, which include a cut in August (Fig. 2C).

Effects of mowing on seed quality

The best model for seed ripening contained the interaction between treatment and plant height. We found that mowing treatments generally delayed the development of seeds, especially for the transition from flowers to unripe seeds in smaller plants (Fig. 2D). Cutting in June resulted in relatively more ripe seeds if plants were not consecutively cut in July or August (Fig. 2D, treatment 69). Since the post-harvest experiment indicated that cutting reduces the viability of flowers and unripe seeds, this change in seed ripening has implications for the seed quality.

Effects of mowing on population growth

We projected stochastic intrinsic population growth, r_s, for all 360 integrations of experimental mowing treatments and reference models. Although different seed survival

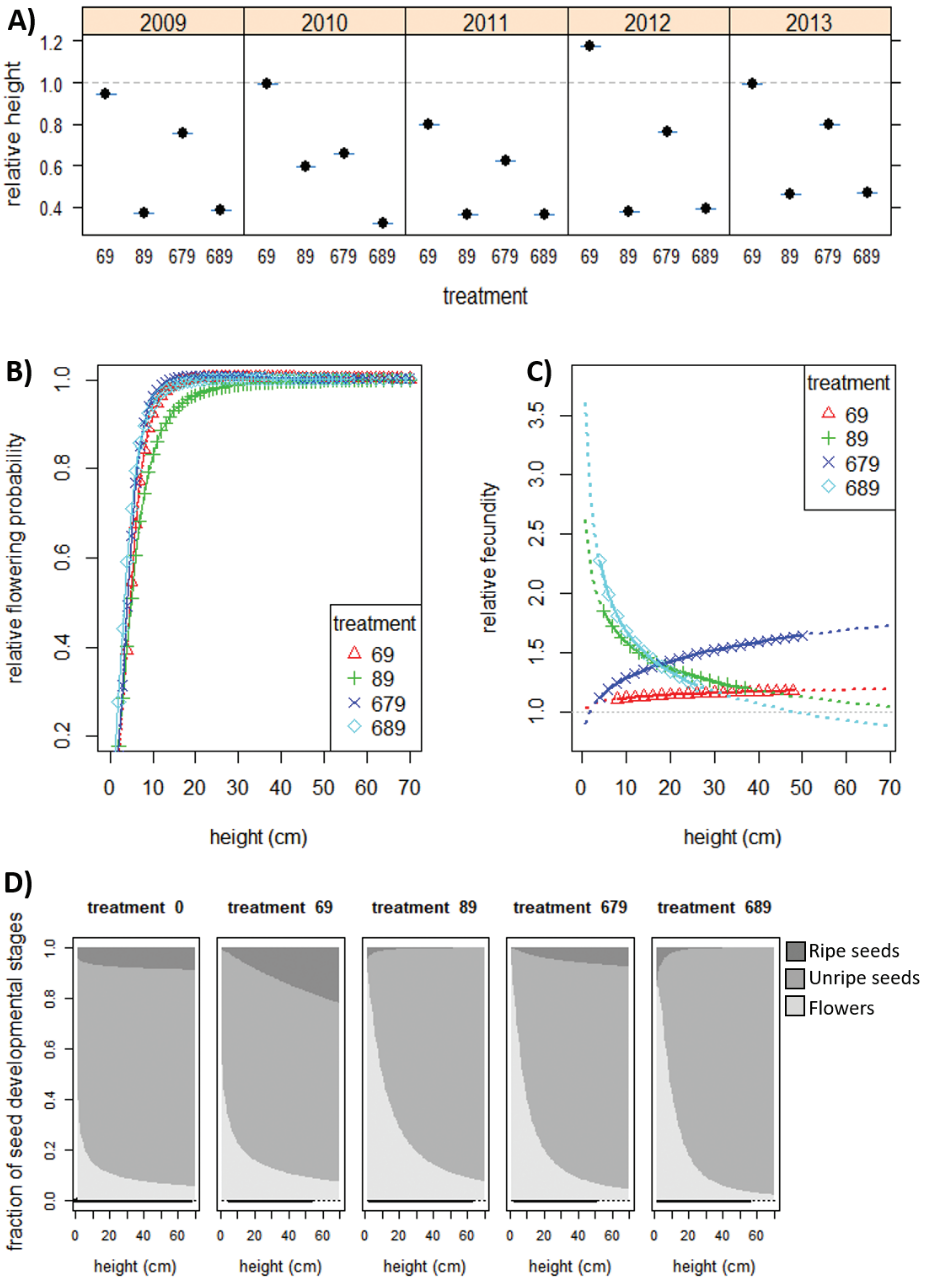

Figure 2. Fitted effects of experimental mowing treatments on vital rates. Experimental mowing treatments are indicated by their code (69, 89, 679, 689, see Table 1) and figures present fitted effects on **A**) mean plant height in September per year, **B**) flowering probability, **C**) fecundity and **D**) the development of seeds (see details of statistical models in main text and Suppl. material 1). Suppl. material 1 Effects in **A–C** are relative to that of the control treatment (0) and for **B–D** across all years as a function of the back-transformed covariable plant height in September. Dotted ends of lines in **C** and of the horizontal line at the bottom of **D** indicate where models were extrapolated beyond the range of observed plant height values.

scenarios resulted in very different values of r (Suppl. material 6, fig. S11), they did not alter patterns of experimental treatment effects. Therefore, we here report results based on seed survival scenario H, which had the lowest survival rates and best matched observed population dynamics in the reference data sets (S.T.E. Lommen, unpublished data). Projected r_s varied a lot between reference data sets, but patterns of treatment effects were consistent (Fig. 3). Experimental treatments with cuts in August (89 and 689) always resulted in the lowest r_s and, in most cases, r_s was reduced until below replacement level ($r = 0$, where population size remains constant). The commonly applied treatment 69 performed worst by only decreasing r_s somewhat, whereas treatment 679 had intermediate effects. The deterministic growth rates, r, based on mowing effects in single years (Suppl. material 7, fig. S12), are in line with the pattern of r_s, except in reference IT14 where effects of mowing treatment 69 in 2012 project increased r compared to the control treatment.

Contribution of vital rates and seed quality to population growth

We assessed the contribution of all vital rates and seed quality to changes in projected deterministic intrinsic population growth r, which were independent of seed survival. All treatments reduced r mainly through the decrease in growth (i.e. lower plant height in September) and seed viability counteracting the increased size-dependent seed production (Fig. 4). The importance of each of these vital rates, however, differed between treatments (Fig. 4) and reference models (Suppl. material 7, fig. S13). In the most successful treatments 89 and 689, changes in growth contributed most to reduction in r (medians of -77% and -82%, respectively), while seed viability was the second most important (-34% and -31% respectively). The cut in September thus contributed to reducing r, but did not have the strongest effect. In treatment 679, reduction in seed viability and growth were equally important (-71% and -67%, respectively), but only achieved an overall intermediate effect due to strong increased size-dependent fecundity (+49%). In the least effective treatment 69, the reduction in r was largely due to reduced seed viability (-136%) opposing the effect of increased fecundity (+30%), while the effect of growth was negligible (-5%). In this treatment, the cut in September is crucial to obtain reduction in r. Mowing effects on flowering probability were of negligible importance in all mowing regimes.

Cost-effectiveness of mowing regimes

We plotted r-cost relationships of all experimental and theoretical mowing treatments, assuming that each cutting intervention has the same costs. Therefore, the relative costs are represented by the number of cuts. Fig. 5 shows the r-cost relationships for the Austrian reference population in 2014 (AT14) and seed survival scenario H, but the main patterns are independent of the seed survival scenario (Suppl. material 8, fig. S14) and are similar in other reference data sets (Suppl. material 8, fig. S15). The figure reveals that the effec-

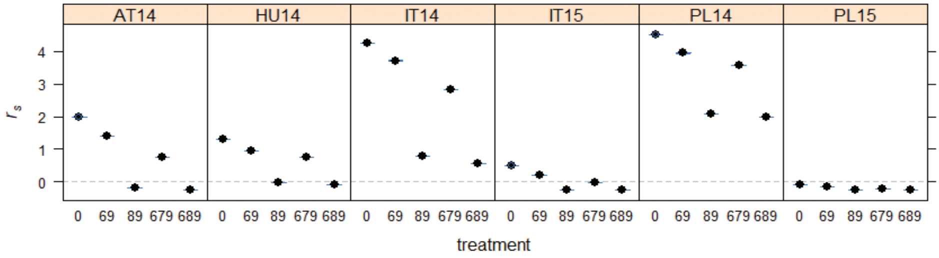

Figure 3. Effect of experimental mowing treatments on stochastic population growth rates r_s for seed scenario H. Panels represent different populations (AT, HU, IT, PL) in year 2014 or 2015 (14 and 15, respectively) as detailed in Suppl. material 2, Table S2. The dashed line indicates the population replacement level.

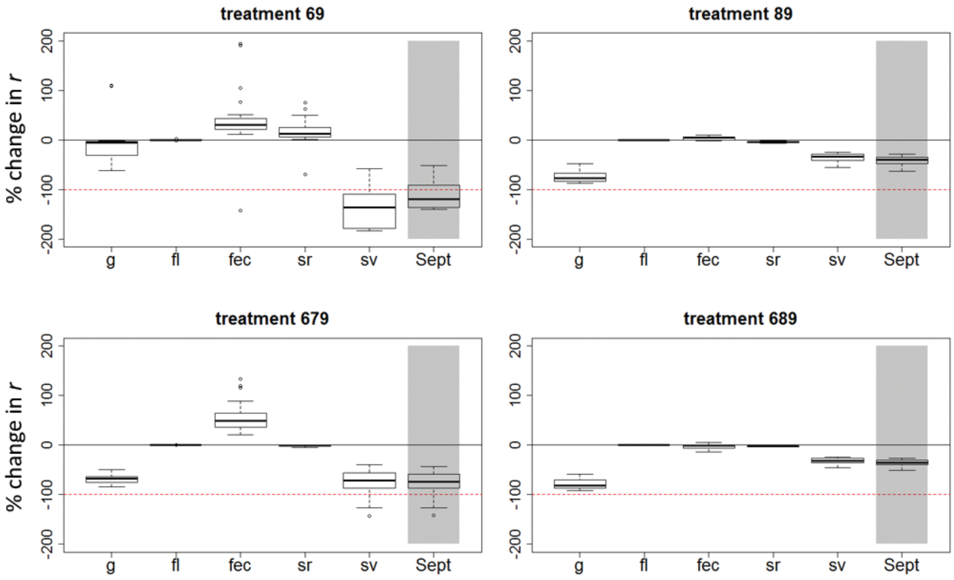

Figure 4. The influence of single vital rates and the September cut on population growth. Figures show the relative contributions of each vital rate (g = growth, fl = flowering, fec = fecundity, sr = seed ripening, sv = seed viability, see Fig. 1) and the cut in September (Sept, i.e. combined effect of sr and sv) to the total change in the population growth *r* per treatment. The y-axis represents the percentage change in *r* compared to the untreated reference, relative to the total change due to the mowing treatment (red dashed line at -100%). Boxplots indicate variation across reference data sets (N = 6) and years (N = 5, if applicable).

tiveness of a given number of cuts is highly dependent on the timing of these cuts. With a budget for a single cut, cutting just before female flowering (here in August) is by far more cost-effective than cutting during vegetative growth (here in June) or before seed set (here in September). When a budget for two cuts is available, cutting just before female flowering and before seed set (here August and September) was most cost-effective and reduced ragweed growth rate more than the best 1-cut treatment. With a budget for three cuts, cutting during vegetative growth, just before female flowering and before seed set (here June, August and September) was the most cost-effective, but was hardly better in reducing ragweed growth rate than the best 2-cut regime. These three most cost-effective

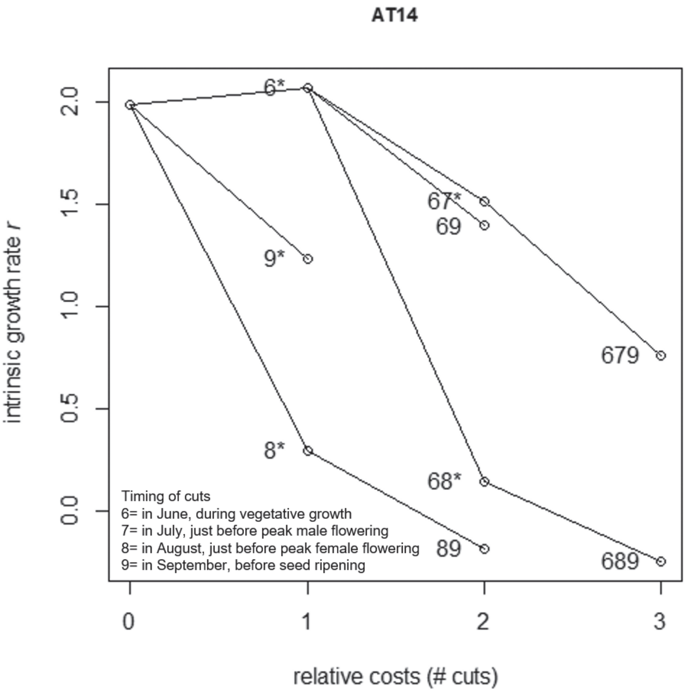

Figure 5. Effect-cost relationships of mowing regimes for the Austrian reference population in 2014 (AT14) for seed survival scenario H. For each mowing regime (dots with labels indicating the months of cutting, see Table 1) and the untreated control (the dot at x = 0), the intrinsic growth rate *r* (as mean of the 5 years of experimental data) is plotted versus the relative costs of the regime (equalling the number of cuts). Mowing regimes theoretically simulated (by removing or adding the September cut to experimental treatments in the model, see Table 1) are indicated with an asterisk. Lines connect consecutive cuts, showing how extending mowing regimes with additional cuts at specific moments alters *r*.

regimes thus all include a cut just before female flowering (here August). The graph also shows that some theoretical regimes are more effective than experimentally tested regimes with the same or a higher number of cuts (for instance, treatment 8 and 9 are more effective than 67 and 69 and treatment 68 is more effective than 679).

Discussion

We show that optimising both the frequency and timing of cuts is the key to achieving the largest reductions in population growth rates (*r*) of *A. artemisiifolia* of roadsides by mowing. An increased frequency of cuts does not necessarily improve the effect, as was also found when mowing invasive thistles in the field (Bourdôt et al. 2016; Zhang and Shea 2012). Our *r*-cost chart (Fig. 5 and Suppl. material 8) allows the most cost-effective timing of cuts to be chosen for a given relative financial budget (i.e. allowing a certain number of cuts). It shows that the prevailing 2-cut mowing regime in Austria with cuts in June (during vegetative growth of *A. artemisiifolia*) and September (just before seed ripening of *A. artemisiifolia*) performs poorly while being relatively expensive. With a similar budget, the efficacy can be tripled by shifting the timing of the two cuts. Even cheaper options (i.e. mowing only once, either in August just before peak female flowering or in September) would be more effective in limiting *r* than the prevailing regime. The most effective regimes in reducing ragweed population growth rate were the experimentally tested 2-cut regime with a cut in August and September and the experimentally tested 3-cut regime with an additional cut in June. Our results are well in line with observed reductions in soil seed bank numbers after three years of the mowing experiment by Milakovic et al. (2016). They also found the common 2-cut regime with a cut in June and September to be least effective, while the two most effective regimes were the 2-cut regime with a cut in August and September, followed by the 3-cut regime with an additional cut in June.

We have provided a mechanistic understanding of how the experimental mowing regimes change projected population growth rates (Fig. 4). Mowing regimes had differential and size-dependent effects on the vital rates (Fig. 2). Importantly, the relative contribution of these effects to changes in projected intrinsic population growth (*r)* was also different for each regime (Fig. 4), as was earlier found for mowing an invasive thistle (Bourdôt et al. 2016). In the poor-performing prevailing 2-cut regime (with a cut in June and September), reduced seed viability is the largest determinant of the change in *r*, overruling effects of reduced plant size and compensation in seed ripening and fecundity (Fig. 4). In contrast, the best experimental mowing regimes (cutting in August and September or, additionally, in June) were effective because the extreme reduction in final plant size in September (Fig. 2A) contributed most to reduction in *r* (Fig. 4), while reduced seed viability contributed somewhat and the contribution of fecundity was negligible in these regimes. In the intermediately performing treatment (cutting in June, July and September), reduction in plant size and seed viability were equally important to counteract strongly compensating fecundity.

Our population modelling approach also unveiled the value of cuts at specific times through their effect on vital rates. Cutting during vegetative growth (here in June) has a small effect on final plant height (here in September) and the direction of the effect varied with year. Indeed, the species is known for its large regrowth capacity (Barbour and Meade 1981) and compensatory growth after cutting in early summer was also found in other cutting experiments with *A. artemisiifolia* (Basky et al. 2017; Bohren et al. 2008; Milakovic et al. 2014a). A single-cut regime at this time might, therefore, even lead to an increased *r* in some years. Comparing similar regimes with and without cutting during vegetative growth reveals that cutting at this stage has little added value to changing *r* when later cuts are conducted (Fig. 5, experimental treatments 89 and 689). If not followed by a cut just before female flowering (here in August), cutting just before male flowering (here in July) reduces plant size moderately but exerts a large compensation in seed production by larger plants (up to 1.7-fold, treatment 679 in Fig. 2C) and is therefore not very effective. Cutting just before female flowering (here in August) obviously leads to the strongest reductions in plant size in September as plants have very little time left to regrow before seed set (here in September). In addition, this cut triggered overcompensating seed production only in the smallest plants which bear the fewest seeds. As the total effect on *r* for regimes including this cut is mainly determined by a reduction in plant height, cutting at this moment is very effective in reducing *r*. Indeed, our *r*-cost figure shows that, for each given budget (i.e. allowing a certain number of cuts), the most cost-effective regime includes a cut just before female flowering (in our case in August). The value of the cut just before seed ripening (here in September), which reduces seed viability, depends strongly on the cutting history. This can be seen by following the connected lines in the *r*-cost chart (Fig. 5). After a single cut during vegetative growth (here in June, hence indicated by "6"), an additional cut before seed ripening largely reduces the projected population growth (indicated by "69"). In contrast, after a cut just before female flowering (here in August, e.g. "8" or "68"), an additional cut before seed ripening adds relatively little.

The results have wider implications for designing management strategies by using population models. A common approach is the identification of key life-cycle stages having the greatest impact on population growth rates (Caswell 1978) as a target for management strategies (Buckley et al. 2003; Karrer 2016b; Ramula et al. 2008; Shea and Kelly 1998). Our results, however, suggest taking care when relying on interventions affecting these vital rates, as their importance for population growth can vary with the timing of the interventions. This has also been observed when cutting at different moments for the control of invasive milkweed (Zalai et al. 2017). In addition, the large contribution of seed viability to changes in *r* in some regimes highlights the importance of including seed quality in population models in addition to seed quantity.

Our population models are not meant to predict absolute values of intrinsic population growth. Firstly, we have shown that the reported *r* values highly depend on the persistence in the soil seed bank. Our best estimates for seed survival came from burial experiments, while in roadside populations, seeds are unlikely to be buried deeply. When they remain on the surface of the ground, they are exposed to different abiotic conditions and other factors that may cause additional mortality, such as seed predation. Our scenarios for seed survival are therefore conservative. Although the pattern of the *r*-cost curves is independent of seed survival, mowing will bring *r* to lower values when seed survival is lower. It is known in other systems, especially annuals with a seed bank, that demographic models can be strongly influenced by seed survival rates (Gross and Mackay 2014), but long-term data on spatial variation in soil seed banks are scarce for many invasive species (Gioria et al. 2012). Secondly, we do not, unfortunately, have field data on how mowing affects recruitment, sizes of new plants and plant survival of our species and hence, we did not include such effects in our models. Plant survival is unlikely to be directly affected much by mowing as our species has large capacity for re-growth, forming new lateral shoots when the main stem is cut (Bohren et al. 2008; Kazinczi et al. 2008; Milakovic et al. 2014a). Such resprouting was even observed in 75–100% of plants cut two or three times (Milakovic et al. 2014a; Patracchini et al. 2011). If mowing removes or weakens competitors, recruitment, survival and the size of new *A. artemisiifolia* plants may be promoted (Bazzaz 1979). In contrast, litter deposition resulting from mowing could potentially limit these vital rates, as has been shown for a biennial grassland forb (Lennartsson and Oostermeijer 2001). Thirdly, we have projected (stochastic) exponential population growth assuming no change in environmental variables. We acknowledge that this assumption is unrealistic in our study system. The species thrives by disturbance (Bassett and Crompton 1975), which is inherent in roadsides. The environment is also likely changing by processes such as succession, change in land use and, in the long term, climate change, all altering vegetation composition and hence plant competition (Essl et al. 2015). Altogether, our models should be used for comparing relative efficacy of mowing regimes, but not for predicting absolute sizes or extinction rates (Crone et al. 2013) of ragweed populations along roadsides.

Our *r*-cost chart shows the relative costs, corresponding to the number of yearly cuts which a mowing regime comprises. The absolute costs for mowing along roadsides per cut per kilometre are unavailable. They depend on very specific circumstances of the responsible authorities. For instance, the number of workers and machinery needed at distinct dates for spatiotemporally fitted optimal mowing varies between countries and regions (personal observation, G. Karrer). In many cases, additional personnel and machinery have to be rented, adding costs to the fixed expenses for regular personnel and machinery.

We are aware that we used our models mainly to assess mowing effects on population size, while other results of local demography and treatments may be of interest to managers as well, such as the total seed output (discussed above), pollen production or population spread. Optimal management for reducing the number of plants does not necessarily need to coincide with optimal management of other target variables (Shea et al. 2010). Considerations, other than reducing population size, may require different or additional timing of cutting. For example, road safety may demand cutting early in the growing season, while roadside management may also be targeted at reducing ragweed pollen numbers. Experimental studies indicated that cutting twice was more effective in reducing pollen production than cutting once (Basky et al. 2017; Simard and Benoit 2011). Our *r*-cost chart can be helpful in determining which mowing regime to choose to reduce population sizes best, given such constraints. Further optimisation of mowing strategies may be achieved by adjusting other aspects of the disturbance framework of Zhang and Shea (2012), such as adapting the total duration of the management of an invasive grass (Hansen 2007). Adapting the intensity of the mowing intervention (i.e. altering cutting height) is, however, technically limited by the machinery used and the micro-scale morphology of the terrain surface along roadsides (Patracchini et al. 2011).

Our study focused on cost-effective local management of roadsides and evaluated management impact by population size of the target. For a comprehensive economic assessment of the efficacy of management of *A. artemisiifolia* at the regional level, however, efficacy beyond the population level should be assessed. As *Ambrosia artemisiifolia* occurs in different climatic areas (Sun et al. 2017) and in a wide range of habitat types

(Essl et al. 2015), a recent European-wide study showed that differences in performance of populations are related to such environmental variations (Lommen et al. 2017). This variation in performance and population-level effects of management (as shown in this paper) should therefore be linked to effects on spatial distribution and spread (Normand et al. 2014; Shea et al. 2010), the latter taking into account the landscape structure (Caplat et al. 2012) and habitat suitability (Richter et al. 2013b). As the habitat types (e.g. grassland, crop land, riversides) often have various stakeholders and managers and require different management measures (Buttenschøn et al. 2009), interactions between managers and their management efforts also need to be considered (Caplat et al. 2012). Regional management efforts could then be optimised cost-effectively by spatial prioritisation of local management methods in prioritised habitat types (Richter et al. 2013a; Richter et al. 2013b). Population models can thus contribute to refining regional management efforts. A protocol, recently launched, describes a method for systematically reviewing the effectiveness of different management options on *A. artemisiifolia*, including effects of confounding factors such as habitat, climate, frequency and timing of the treatments (Schindler et al. 2016).

Conclusions

Overall, our population modelling approach has proven to be a useful tool for comparing population-level effects of different mowing regimes for an annual plant with a long-lasting seed bank. Integration of mowing effects into reference models of four geographically distant populations in Europe in two different years showed that patterns of projected population effects were consistent across time and space (Suppl. material 4, Figs. S6–10), despite the variation in dynamics amongst the reference locations and years (Suppl. material 4, Table S4). The results of our study can thus inform management in a wide geographic area and are robust to temporal variation in population dynamics. This is likely partly due to the annual life cycle of this species and the drastic effects of mowing. By disentangling effects of cutting at specific moments, our method also proved capable in designing new mowing regimes (i.e. new combinations of cuts at specific moments) that were experimentally untested. Even more regimes could be theoretically tested in this way if future management experiments were designed to single out effects of cuts at specific moments and if the measurements were adapted to provide input for demographic models (Bourdôt et al. 2016). We have shown that the effect of a mowing regime on *A. artemisiifolia* population size is not simply a function of the total number of cuts, but highly depends on the timing of the subsequent cuts it comprises. Fewer well-timed cuts can therefore be more effective in reducing population sizes of *A. artemisiifolia* along roadsides than regimes with a higher number of cuts. Our work highlights the importance of a cut before female flowering (in our case in August), as this was part of all most cost-effective management options found in our study.

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Supplementary material 1

Analysis of mowing experiment data (statistical analysis of empirical data)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

Link: https://doi.org/10.3897/neobiota.39.23398.suppl1

Supplementary material 2

Demographic survey of reference populations (location table, methods)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

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Supplementary material 3

Burial experiments (location table, methods, graphic results)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

Link: https://doi.org/10.3897/neobiota.39.23398.suppl3

Supplementary material 4

Parametrisation of population models of unmanaged references (model parameterisation)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

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Supplementary material 5

Parametrisation of population models of experimental mowing treatments (model parameterisation)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

Link: https://doi.org/10.3897/neobiota.39.23398.suppl5

Supplementary material 6

Stochastic population growth for alternative seed bank scenarios (graphic results, population dynamics)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

Link: https://doi.org/10.3897/neobiota.39.23398.suppl6

Supplementary material 7

Deterministic population models per reference data set (graphic results, population dynamics)

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

Link: https://doi.org/10.3897/neobiota.39.23398.suppl7

Supplementary material 8

***r*-cost curves for different seed survival scenarios and reference data sets (graphic results, population dynamics)**

Authors: Suzanne T. E. Lommen, Eelke Jongejans, Melinda Leitsch-Vitalos, Barbara Tokarska-Guzik, Mihály Zalai, Heinz Müller-Schärer, Gerhard Karrer

Data type: statistical data

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Patterns and traits associated with invasions by predatory marine crabs

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Abstract

Predatory crabs are considered amongst the most successful marine invasive groups. Nonetheless, most studies of these taxa have been descriptive in nature, biased towards specific species or regions and have seldom considered traits associated with invasiveness. To address this gap in knowledge, this study presents a global review of invasions by this group and applies biological trait analysis to investigate traits associated with invasion success. A total of 56 species belonging to 15 families were identified as having spread outside their native ranges. The family Portunidae supported the highest number of alien species (22). Most crabs had their origin in the North West Pacific IUCN bioregion while the Mediterranean Sea received the most species. No traits associated with successful establishment were identified, but this finding may reflect the paucity of basic biological knowledge held for many species. This lack of foundational knowledge was unexpected as crabs are large and conspicuous and likely to be well studied when compared to many other groups. Addressing this knowledge gap will be the first step towards enabling approaches like biological trait analysis that offer a means to investigate generalities in invasions.

Keywords

Biological invasions, establishment success, shipping, trait analysis

Introduction

Studies reviewing the distribution and vectors of marine alien species are numerous and include those that focus at the global (e.g. Bax et al. 2003, Ruiz et al. 2011) and regional scale (e.g. Europe (Galil et al. 2014); South Africa (Mead et al. 2011)). However, these studies are often descriptive in nature, providing first insights into the marine invasions of a region. Recently, there has been a move to advance this approach by identifying invasion patterns and applying biological trait analysis to identify taxa that are likely to invade. The use of these approaches adds statistical power to the conclusions drawn about the factors that may play a role in the spread and establishment of alien species (Cardeccia et al. 2018). An additional approach to understanding patterns of invasions comes in the form of taxon-specific reviews (e.g. Novoa et al. 2015, Marchini and Cardeccia 2017). Such reviews can be insightful as they focus on highly invasive taxa from well-studied groups, enabling detailed analyses of factors driving their invasion success (Kolar and Lodge 2002, Hänfling et al. 2011).

Brachyuran crabs that spend all or part of their life-cycle in the marine environment (hereafter collectively referred to as marine crabs) are a globally successful invasive group (Brockerhoff and McLay 2011), associated with significant ecological (Kraemer et al. 2007, Garbary et al. 2014) and socio-economic impacts (White et al. 2000, Chakraborty et al. 2002). This success likely reflects the diverse nature of this group, which is known for broad salinity and temperature tolerances (Dittel and Epifanio 2009), good dispersal abilities (Gust and Inglis 2006) and high reproductive potential (Brousseau and McSweeney 2016). In light of the large invasive ranges and notable impacts associated with some crab species (e.g. *Hemigrapsus sanguineus* (Kraemer et al. 2007); *Charybdis hellerii* (Felder et al. 2009) and *Carcinus maenas* (de Rivera et al. 2011)), crab invasions have received considerable attention in the literature. However, studies considering these invasions have been mostly region specific (e.g. Mediterranean (García Muñoz et al. 2008)) or species specific (e.g. *Eriocheir sinensis* (Veilleux and de Lafontaine 2007)). While some species-specific studies have considered traits, they have generally applied one of two approaches: comparing the traits of alien species in their native and invaded ranges (Grosholz and Ruiz 2003) or comparing traits between an established alien species and native species in a particular region (Brousseau and McSweeney 2016). These studies were, however, biased towards well known species and have considered only a few select traits and, thus, do not reveal general patterns about the invasiveness of marine crabs as a group. While there has been one review of crab invasions (Brockerhoff and McLay 2011), this study was broad in its taxonomic focus (i.e. it considered brachyuran crabs as well as two families from the crab-like anomurans). The application of a multi-species, multi-trait approach to identify trait profiles associated with the successful invasion of crabs is thus lacking.

In an effort to address this gap, we used predatory brachyuran crabs (i.e. those that kill prey for food) as a case study. This study reviewed invasions within this functional group. This study aimed to 1) compile a list of marine predatory crabs with an invasion history; 2) document their donor and receiving bioregions and

3) consider traits that may be associated with their successful establishment. Based on literature (Weis 2010, Hänfling et al. 2011), it was hypothesised that traits that predispose species to being able to survive under a variety of conditions (e.g. broad habitat requirements) would typify crab species that have established alien populations. In contrast, traits that facilitate transfer by humans (e.g. long larval development) would be shared by both established species and those that are represented by only single records outside of their native ranges. Identifying traits that are important in the invasion process will help to further our understanding of which species are predisposed to becoming successful invaders.

Methods

Species and variables reviewed

To compile a list of predatory crabs with an invasion history, we reviewed the literature reporting on marine crab invasions across the globe. Information regarding each species in both their native and alien ranges was recorded (Table 1). Brachyuran crabs were included if they met the following inclusion criteria: (1) they could be classified as alien following Robinson et al. (2016); (2) they were fully marine or catadromous; (3) they were predatory in nature (i.e. they kill live prey) and (4) their native ranges could be defined. A total of 39 species were excluded based on these criteria (see Suppl. material 1 for a full species list and the exclusion criteria applied to each). Species were classified to family level following the World Registry of Marine Species (WoRMS).

The list of alien species was established using scientific literature and a variety of online databases including WRIMS: World Register of Introduced Marine Species (http://www.marinespecies.org/introduced/), CABI: Centre for Agriculture and Biosciences International (http://www.cabi.org/isc/), GISD: Global Invasive Species Database (http://www.iucngisd.org/gisd/) and CIESM: The Mediterranean Science Commission Atlas of exotic crustaceans in the Mediterranean (http://www.ciesm.org/atlas/index.html). Smaller regional databases were used when appropriate. Additional sources of information used included published books, technical reports and online theses, all sourced using Google Scholar (see Suppl. material 2 for a complete list of sources). Compilation of the species list was undertaken between September and November 2015, while the extraction of relevant information was carried out between November 2015 and February 2016.

It has been suggested that the most appropriate method for characterising traits of invasive species is to compare invaders with those of the same taxonomic group that have not spread outside their native ranges (Nawrot et al. 2015, Novoa et al. 2015). While the strengths of this approach are clear, it was not viable to do so for crabs. This was because this group is large (containing 1271 genera and an estimated 6793 described species (Ng et al. 2008)) and widely distributed, occurring on all continents. In addition, trait information is simply not available for most species. While this

Table 1. Information that was recorded for each predatory crab in their native and alien ranges.

Variables	Data recorded
Invasion status	Species reported only from a single record or established populations.
Distribution range	Using reports in the literature, species ranges were defined in terms of provinces (as defined by Spalding et al. (2007)). If a species had been reported from a location within a province, its distribution was taken to include that whole province.
Donating and receiving regions	These regions were defined following the IUCN bioregions defined by Kelleher et al. (1995a, b, c, d).
Biological traits	Size, adult longevity, adult mobility, fecundity, migratory behaviour, larval development time, generation time (See Table 2 for details).
Ecological traits	Range size, substratum type (See Table 2 for details).

approach was pursued using species from a well-studied region (i.e. China using the Chinese Registry of Marine Species; ChaRMS), trait information was available for less than 3% of crab species, resulting in the abandonment of this methodology. As a result, to get a better understanding of the patterns of crab invasions and the traits that may play a role in invasion success, we compared those alien species that have been documented as supporting established populations with those species for which no evidence exists for their successful establishment. Single record species were defined as those with single or sporadic recordings, in contrast to established species that were defined as those with self-sustaining populations. To assess if the number of established species is related to the number of alien species known from a family, a Spearman's rank correlation was undertaken. All univariate analyses were done in Statistica (version 13) unless otherwise stated.

Distribution ranges

Native and invaded range sizes were determined for each species. Range size was defined as the number of marine provinces (as defined by Spalding et al. 2007) in which a species occurred. The relationship between native and invaded range was investigated using a Spearman's rank correlation.

Donating and recipient regions

Determining the origin of introductions can be challenging. While the origin of species can be confirmed through the use of genetic techniques, in the absence of such studies, two pragmatic approaches can be applied. The first, considering the whole native range as a potential source, is the most conservative approach. The second, deducing origins using the most likely shipping routes (Seebens et al. 2013), is founded on the assumption that most marine alien species are introduced via shipping, an assumption that can introduce error. This process has seldom been undertaken with respect

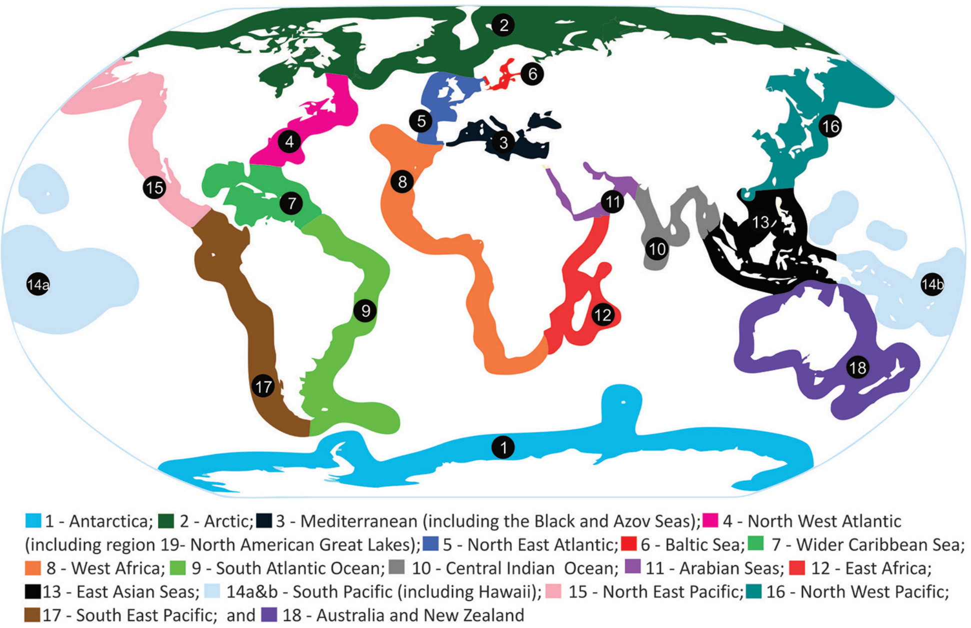


Figure 1. Map illustrating the 18 IUCN bioregions. The 18 IUCN bioregions used for identifying the donating and receiving regions of crab invasions. Bioregions defined by Kelleher et al. (1995a, b, c, d). Figure modified from Hewitt et al. (2011).

to crab introductions. As such, in this study, both approaches were applied if a species origin was not explicitly given in the literature. This enabled the two approaches to be contrasted. Potential donating and receiving regions were defined in terms of the 18 IUCN bioregions (Kelleher et al. 1995a, b, c, d; Figure 1). The package circlize in R (version 3.3.2) was used to visualise the relationships between the various regions through the use of a chord diagram.

Analysis of traits

Detailed information on the biological and ecological traits (hereafter referred to as traits) of each species were recorded and categorised. Each trait had a minimum of two and maximum of four categories (Table 2). Nine of the traits suggested to be important in contributing to invasion success were included (Crawley 1989, Ehrlich 1989, Weis 2010, Hänfling et al. 2011) (Table 2). While it would have been preferable to include salinity and temperature tolerance and growth rate, these had to be excluded due to a lack of information in the literature. Definition of traits and categories were adapted from Bremner et al. (2006), MarLIN (2006) and Cardeccia et al. (2018).

The affinity of each species to the trait categories was captured by allocating a score from 0–4 to each category of every trait, where 0 reflects no affinity and 4 a high affinity. As the “fuzzy coding” approach (Chevenet et al. 1994) was applied, a

Table 2. Trait information that was recorded for each alien species.

Traits	Information recorded	Categories
Size	Maximum carapace width (cm)	Small (≤ 5), Medium (5.1–10), Large (10.1–15), X-large (≥ 15.1)
Longevity	Maximum age (years)	Short (≤ 2), Medium (3–5), Long (6–8), Very long (≥ 9)
Adult mobility	Mode of movement and behaviour	Walking, Swimming, Burrowing, Drifting
Migratory behaviour	Migratory or not	Seasonal migration, Non-migratory
Larval development time	Development time (days)	Short (≤ 20), Long (21–40), Protracted (≥ 41)
Fecundity	Number of eggs/year	Low (≤ 0.25 mil), Medium (0.25–0.5 mil), High (0.5–2 mil), Very High (≥ 2 mil)
Generation time	Average time between two consecutive generations (months)	Short (≤12), Medium (13–23), Long (≥24)
Range size	Number of provinces (Spalding et al. 2007)	Small (1), Medium (2–5), Large (6–10), Very Large (≥ 11)
Substratum type	Types of substratum in which species are present	Sandy (sandy/ muddy/ saltmarsh/ seagrass/ eelgrass/ clay), Rocky (rocky/ oyster beds/ algae/ seaweed), Artificial, Biogenic reefs (syllid tubes/ coral)

species could receive several scores for any trait, thus incorporating variation in the affinity of a species to trait categories. For each trait, the sum of the scores for the various categories added up to 4. This allowed the transformation of trait data into quantitative affinity values that could be used in multivariate analysis. To attribute affinities consistently across traits, set criteria were applied. When a species showed an affinity for multiple categories, the category most frequently displayed received the highest score while, if two categories were equally represented, an affinity of 2 was allocated for both. For example, the habitat generalist *Carcinus maenas* was assigned an affinity of 1 for all substratum types, *Charybdis japonica* was assigned an affinity of 2 for both sandy and rocky substrata but zero for biogenic reefs and artificial habitats as it has not been reported from these substrata, while the sandy shore specialist *Scylla serrata* was allocated an affinity of 4 for sandy habitats. When literature detailing traits was contradictory, scores were assigned based on expert judgement. Information was obtained at the species level, but in the event that information was not available at this level, a search was conducted at the genus level. Following Fleddum et al. (2013), if information was still unavailable, a zero was allocated to all categories within that trait. When information was not available for three or more traits for any species, it was excluded from the analysis. Traits were thus analysed for 28 species (Table 3). Please see Suppl. material 3 for full details of the trait affinities of each species. To identify if certain suites of traits predispose species to successfully establishing alien populations, the traits of single record species were compared to those of established species.

Table 3. List of 56 alien crab species from 15 families. Labels apply to Figure 5. (*) denotes single record species. (#) indicates the 28 species that were included in the trait analysis.

Taxa	Labels	Taxa	Labels
Calappidae		**Portunidae**	
Calappa hepatica	_CalH_	_Callinectes bocourti_	_CalB_
		Callinectes danae *#	_CalD_
Cancridae		_Callinectes exasperatus *#_	_CalE_
Cancer irroratus #	_CanI_	_Callinectes sapidus #_	_CalS_
Glebocarcinus amphioetus #	_GleA_	_Carcinus aestuarii #_	_CarA_
Metacarcinus magister *#	_MetM_	_Carcinus maenas #_	_CarM_
Metacarcinus novaezelandiae #	_MetN_	_Carupa tenuipes_	_CarT_
Romaleon gibbosulum	_RomG_	_Charybdis feriata *#_	_ChaF_
		Charybdis hellerii #	_ChaH_
Carpiliidae		_Charybdis japonica #_	_ChaJ_
Dyspanopeus sayi #	_DysS_	_Charybdis longicollis_	_ChaLo_
		Charybdis lucifera*	_ChaL_
Dairidae		_Charybdis variegata*_	_ChaV_
Daira perlata*	_DaiP_	_Gonioinfradens paucidentatus_	_GonP_
		Liocarcinus navigator *#	_LioN_
Grapsidae		_Necora puber #_	_NecP_
Metopograpsus oceanicus	_MetO_	_Portunus pelagicus #_	_PorP_
Pachygrapsus marmoratus #	_PacM_	_Portunus segnis #_	_PorS_
Pachygrapsus transversus #	_PacT_	_Scylla serrata #_	_ScyS_
Percnon gibbesi #	_PerG_	_Thalamita gloriensis_	_ThaG_
		Thalamita indistincta	_ThaI_
Hymenosomatidae		_Thalamita poissonii_	_ThaP_
Elamena mathoei*	_ElaM_		
Halicarcinus innominatus	_HalI_	**Raninidae**	
Halicarcinus planatus *#	_HalP_	_Notopus dorsipes*_	_NotD_
Matutidae		**Varunidae**	
Ashtoret lunaris*	_AshL_	_Brachynotus sexdentatus*_	_BraS_
Matuta victor*	_MatV_	_Eriocheir hepuensis #_	_EriH_
		Eriocheir japonica *#	_EriJ_
Menippidae		_Eriocheir sinensis #_	_EriS_
Sphaerozius nitidus*	_SphN_	_Hemigrapsus sanguineus #_	_HemS_
		Hemigrapsus takanoi #	_HemT_
Oregoniidae			
Chionoecetes opilio #	_ChiO_	**Xanthidae**	
		Atergatis roseus	_AteR_
Panopeidae		_Xanthias lamarckii*_	_XanL_
Panopeus lacustris	_PanL_		
Pilumnidae			
Actumnus globulus*	_ActG_		
Eurycarcinus integrifrons	_EurI_		
Pilumnopeus vauquelini	_PilV_		
Pilumnus minutus*	_PilM_		
Pilumnus spinifer*	_PilS_		

A combination of multivariate methods was used to analyse traits. This allowed the identification of patterns in the trait profiles of a cluster of species (Bremner et al. 2006). A hierarchical cluster analysis was performed on the matrix of species by trait categories and used to identify clusters of species sharing similar suites of traits (i.e. groups displaying corresponding trait affinities), ecological equivalents (i.e. species sharing exactly the same traits) and outliers (i.e. species displaying a unique combination of traits). This analysis enabled the measurement of the level of similarity of the trait profiles amongst the alien crab species and the consideration of differences between established and single record species (Cardeccia et al. in press). Analyses were performed in PRIMER (version 6) and applied to fourth-root transformed non-standardised data, based on Bray-Curtis similarities.

As cluster analysis is unable to identify the traits responsible for the variation observed, Fuzzy Correspondence Analysis (FCA) was performed on the data matrix to explore this feature. This multivariate analysis is adapted to analyse fuzzy coded data and applies Euclidean distances that are calculated from the frequencies of each trait category to ordinate the species (Chevenet et al. 1994; Bremner et al. 2006). The plot, generated by the FCA, was used to identify patterns in the trait profiles of species and identify the traits responsible for the variation in the data. The traits of a species determines its distribution across the plot, with species sharing similar traits located close to each other. To enable consideration of status (i.e. single record or established species) and family in relation to species that share similar traits, species were labelled according to these variables on the FCA plots. These analyses were conducted in R (R Core Team 2018) using the library ade4. Traits were also considered separately to identify those traits that varied most amongst species. The correlation ratio between each trait and the FCA axes was calculated. The higher the correlation ratio, the more that trait accounts for variation within the data.

Results

A total of 56 alien predatory brachyuran crab species from 15 families were identified as having spread outside of their native ranges (Table 3). The highest number of alien species (22) was supported by the family Portunidae (i.e. the swimming and shore crabs). Of the 56 alien species, 36 (64%) had been reported as supporting established populations (Figure 2). In contrast, 20 were classified as single record species (supporting information is presented in Suppl. material 4). The largest number of established species was from the family Portunidae and included species such as the European shore crab, *Carcinus maenas*. Other families supporting notable numbers of established alien species were the Varunidae (i.e. mitten crabs), Cancridae (i.e. rock crabs), Pilumnidae (i.e. hairy crabs) and Grapsidae (i.e. marsh crabs), highlighting a positive correlation between the number of alien species known from a family and the number of established species in that family (Spearman's rank correlation; $r = 0.79$, $p < 0.001$). Notably no such relationship was found between the number of established species within a family and the total number of species known from the family (Spearman's rank correlation; $r = 0.50$; $p = 0.057$).

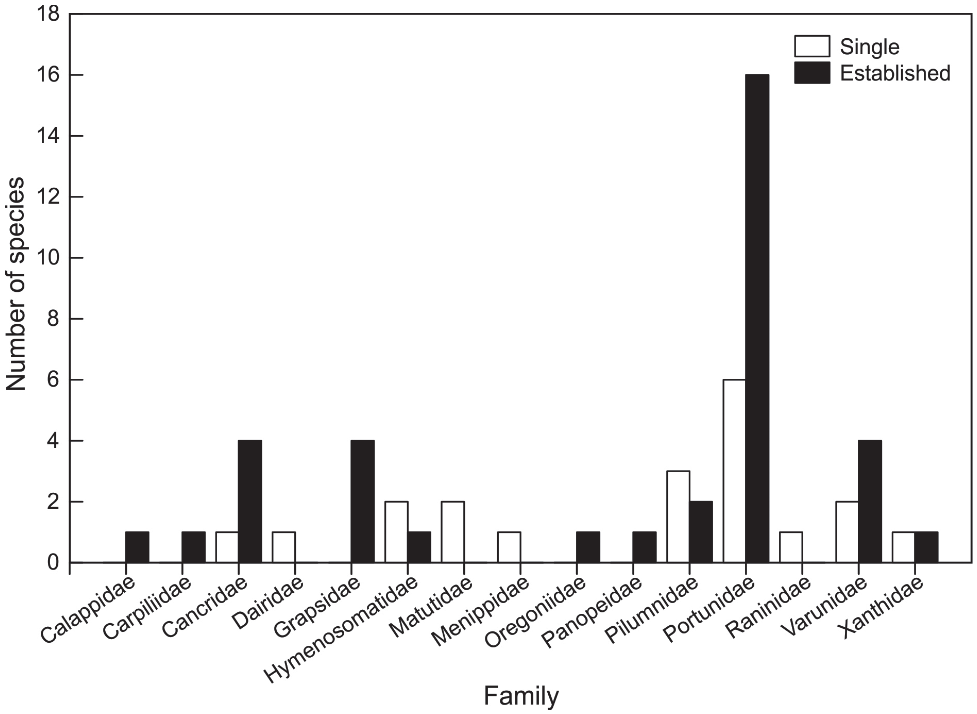


Figure 2. Number of established and single record predatory alien crab species recorded in each family.

Distribution ranges

Only 15 species had very large native ranges (≥ 11 provinces) and it was notable that the invaded ranges of these crabs were amongst the smallest (≤ three provinces) with the exception of one species, the Indo-Pacific swimming crab, *Charybdis hellerii*, that had an invaded range size of eight provinces (Figure 3). Notably, no correlation was found between native and invaded range sizes of alien crabs (Spearman's rank correlation; $r = -0.08$, $p = 0.57$).

Potential donating and recipient regions

When considering native bioregions as the potential source for each alien crab introduction, it was found that all 18 IUCN bioregions have potentially acted as source regions (Figure 4a). This is in contrast to 15 bioregions that were identified when shipping routes were used to deduce source regions (Figure 4b). The Mediterranean Sea was the most invaded bioregion, receiving 33 species. Notably, the Arabian Seas were the source of most of these introductions when using shipping connectivity to identify donor regions. However, because of the large native range of many of these species, they could in fact have been introduced from any of 11 bioregions including the South Pacific, East Asian

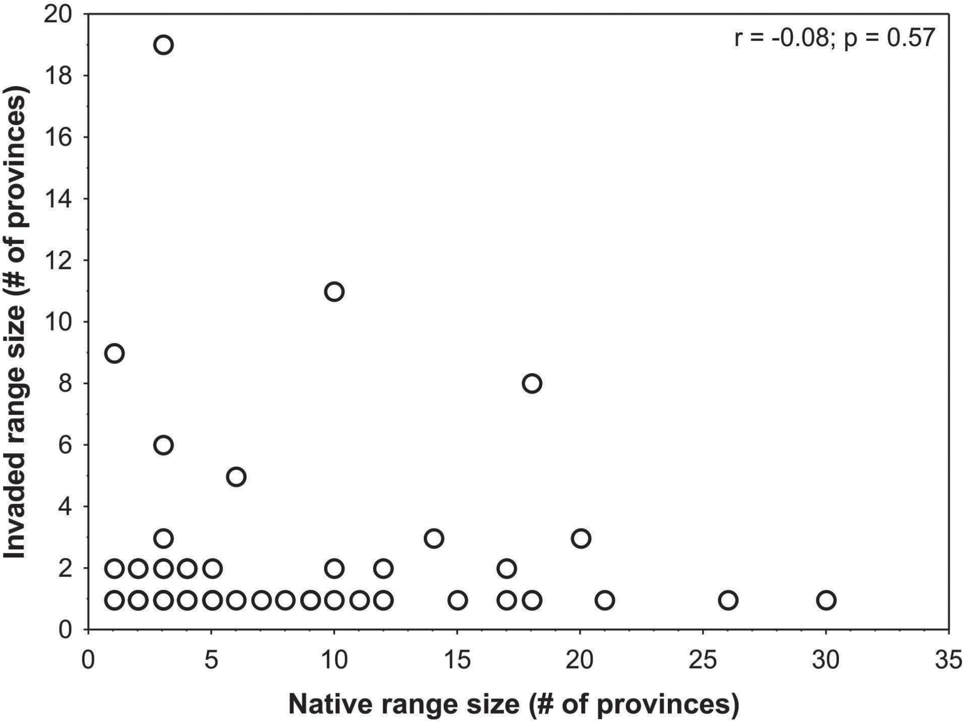


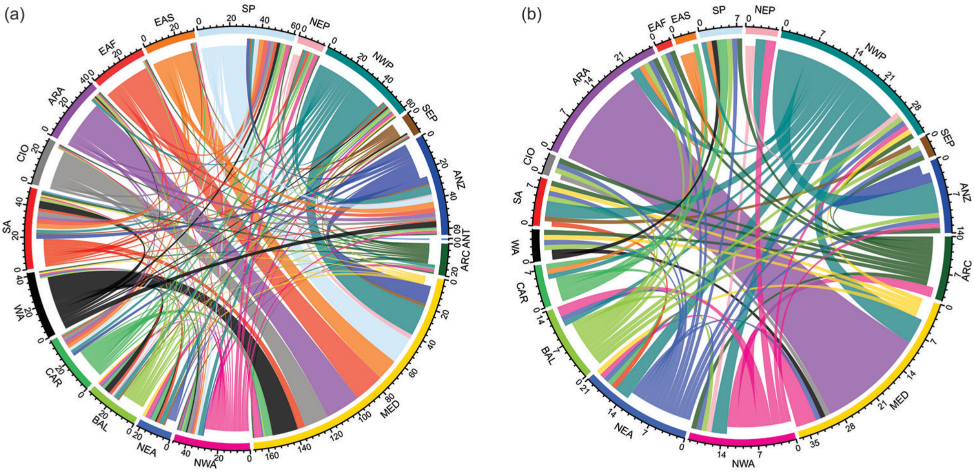
Figure 3. Invaded range size of alien crab species in relation to their native range size. Range size reflects the number of provinces in which a species has been recorded. Provinces as defined by Spalding et al. (2007).

Seas, East Africa, North West Pacific or the Arabian Seas. (See Suppl. material 5 for details of each species alien and native ranges). Regardless of the method used to identify potential donor regions, the majority of alien crabs were donated from the North West Pacific. Similarly, the South Pacific received species from the most bioregions (i.e. 15 and 7 bioregions when identified by native range and shipping, respectively).

Analysis of traits

When exploring traits using cluster analysis, no species were found to be ecological equivalents and no outliers were identified (Figure 5). All species grouped until 38% similarity, at which point two groups were identified. At the 50% similarity threshold, 6 groups of species (G1–G6) were identified. Single record and established species did not group together, but were distributed amongst the groupings, suggesting that they do not have separate suites of traits. Although one group contained only species from the family Portunidae, no pattern related to family was evident.

Fuzzy Correspondence Analysis enabled the identification of those traits responsible for the most variation seen within the data. In the FCA plot, the traits associated with each species determine where it is located on the plot. The FCA axes explain the



Code	Bioregion	Code	Bioregion	Code	Bioregion
ANT	Antacrtic	EAF	East Africa	NWP	North West Pacific
ARA	Arabian Seas	EAS	East Asian Seas	SA	South Atlantic
ARC	Arctic	MED	Mediterranean	SEP	South East Pacific
ANZ	Australia and New Zealand	NEA	North East Atlantic	SP	South Pacific
BAL	Baltic	NEP	North East Pacific	WA	West Africa
CIO	Central Indian Ocean	NWA	North West Atlantic	CAR	Wider Caribbean Sea

Figure 4. Bioregions that receive and potentially donate alien crab species. Where donating regions were not confirmed in the literature, they were determined using (a) the native range of the alien crabs and (b) using the most likely shipping routes (Seebens et al. 2013). Bioregions are represented by the different coloured segments. Lines that are the same colour as the segments represent species donated from that bioregion. Lines radiate to the bioregions to which species were donated. The numbers around the diagram represent the numbers of species (both native and alien) in each bioregion.

variability within the dataset, with the first axis explaining the most variability. For this dataset, very little of the total variability was explained by trait similarity (Axis 1 + Axis 2 = 31%; Figure 6). To investigate if any patterns in the traits displayed by the crabs were related to their invasion status or family, these variables were overlaid on Figure 6. Unexpectedly, species did not form separate groups based on either of these variables, rather they were interspersed across the plot indicating that separate suites of traits are not associated with the different status levels or families. To fully interpret the FCA results, Figure 6 should be considered along with Figure 7. Each block in Figure 7 represents one of the nine traits considered and the stars represent the distribution of the different categories within that single trait. The centre of each star corresponds to the centre of gravity of all the species that display that trait category and the rays link the species to their categories. While some traits, such as migratory behaviour and carapace size, explained variability in the data (i.e. they separate out along the two axes), most traits showed little separation amongst categories (e.g. substratum type).

Together with the correlation ratios (Table 4), Figure 7 was used to identify the most important traits driving the variation observed in Figure 6. High correlation

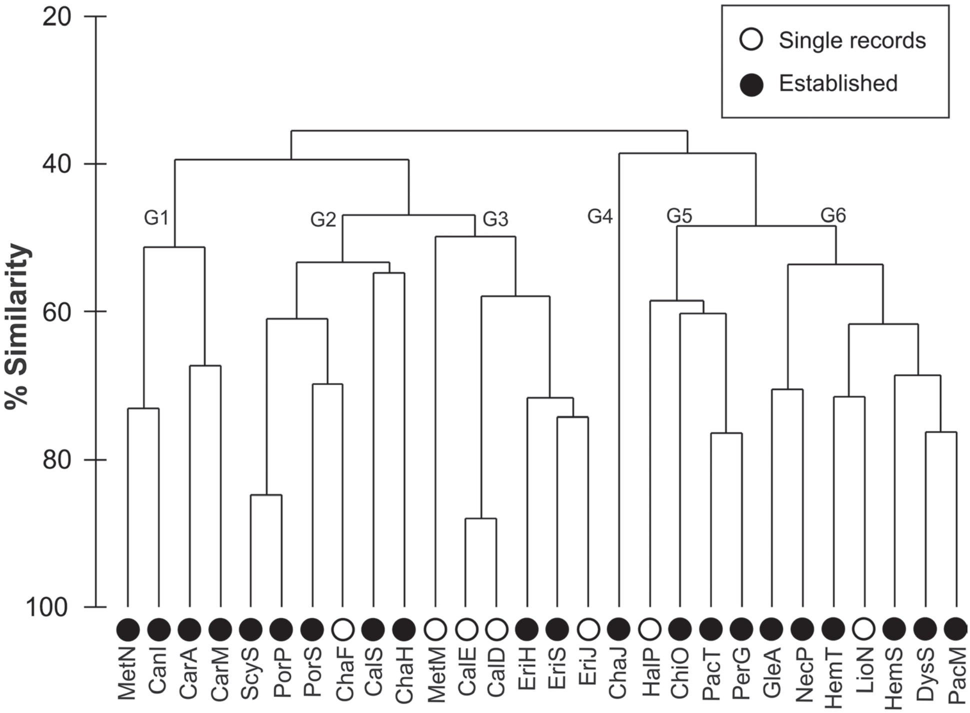


Figure 5. Dendrogram based on Bray-Curtis measures of similarity for single record and established species. The 6 groups of species identified at the 50% similarity threshold are indicated by G1–G6. See Table 3 for species labels.

values identify traits that explain high levels of variability in the data and are reflected in Figure 7 as traits that have stars that separate out along the two axes. Carapace size was identified as being responsible for the most variation along the axes as it has the largest correlation ratios for both axes (Table 4). This is demonstrated by the categories separating out on both axes (Figure 7). Other important traits accounting for variation along the axes included fecundity (for both axes), migration for Axis 1 and longevity, generation time and range size for Axis 2. In contrast, some categories (e.g. substratum type) did not separate out across the axes, but rather clustered at the origin, indicating that these traits did not vary amongst species.

Discussion

Due to the prevalence of, and threats posed by, alien species (Simberloff et al. 2013), there is great value in understanding generalities governing invasions. Predatory crabs are amongst the most successful marine invasive taxa (Brockerhoff and McLay 2011, Brousseau and McSweeney 2016). To better understand the complex drivers and traits behind this success, we reviewed all invasions within this functional group and compiled a list of 56 alien marine predatory crab species from 15 families. Most alien

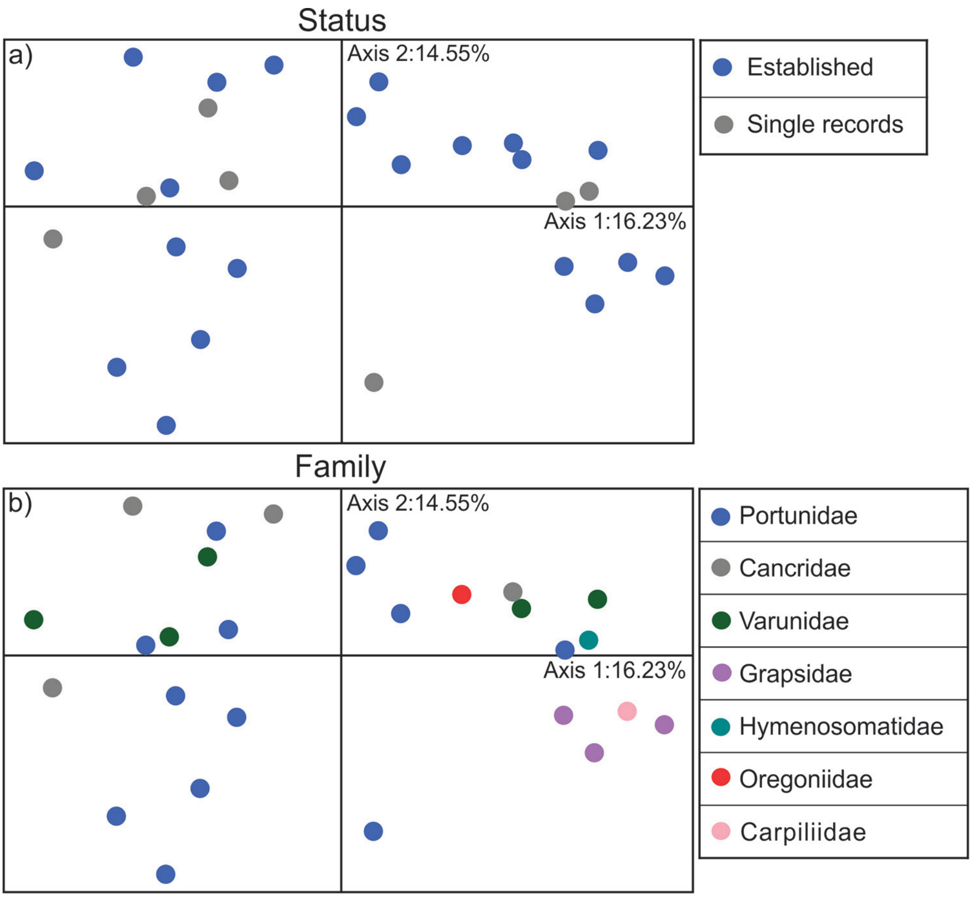


Figure 6. Fuzzy Correspondence Analysis (FCA) bidimensional plot where every dot represents one of the 28 alien crab species. Species are labelled according to status [in **a)**] and family [in **b)**].

crabs originated in the North West Pacific, while the Mediterranean Sea was the most invaded bioregion. Unexpectedly, it was found that neither ecological nor biological traits were good predictors of establishment success.

Patterns observed in crab invasions

Similarly to the findings of Brockerhoff and McLay (2011), the family from which the greatest number of alien brachyuran crab species was noted, was the Portunidae. It is notable that, despite supporting the highest number of alien and established species, the Portunidae are not the largest family of brachyuran crabs. The most speciose family is the Xanthidae, which supports more than double the number of species than the Portunidae, but has only two species known to be alien. While this may suggest that the Portunidae possess traits that predispose them to being successful invaders, this was

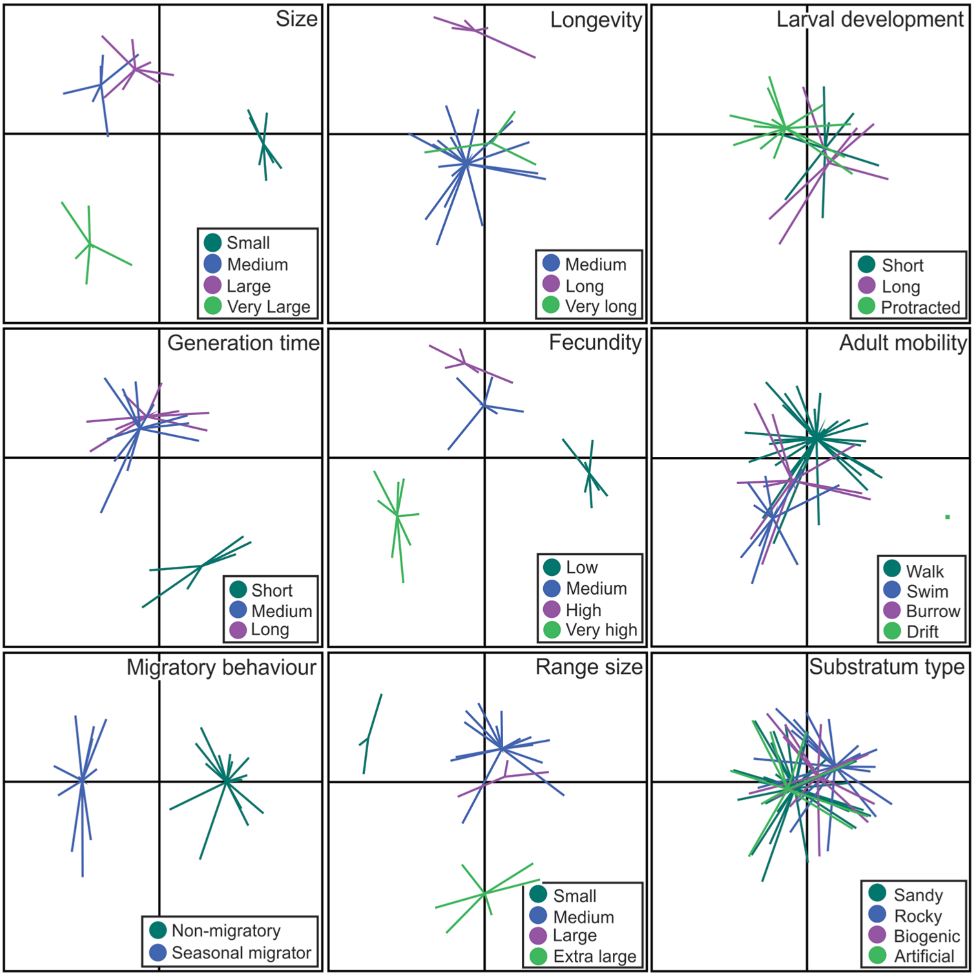


Figure 7. Fuzzy Correspondence Analysis bidimensional plot depicting the nine traits analysed. Each graph represents a single trait and the stars represent the categories within that trait.

not evident during the detailed trait analysis undertaken in this study and the mechanism behind the high number of Portunid invasions remains unclear. Despite 56 alien crabs being identified in this study, this number may be an under-representation of the true number of crab invasions, as records are not always genetically verified. This was the case in South Africa where *Carcinus maenas* was first reported (Le Roux et al. 1990), but a later genetic study highlighted the presence of the morphometrically similar sister taxa *Carcinus aestuarii* (Geller et al. 1997). The presence of such cryptic species may obscure the true prevalence of invasions (Marchini and Cardeccia 2017).

It has been suggested that species with large native ranges are likely to be successful invaders (Bates et al. 2013, Novoa et al. 2016). This is due to their tendency to have broad physiological tolerances ranges and generalist food and habitat requirements (Vazquez 2006, Troost 2010). This study, however, found no correlation between na-

Table 4. Correlation ratios per trait for the first two axes of the Fuzzy Correspondence Analysis (FCA). Traits highlighted in bold have highest correlation values for the respective axes.

Trait	Axis 1	Axis 2	Σ
Size	**0.775**	**0.600**	
Longevity	0.008	**0.302**	
Adult mobility	0.067	0.144	
Migratory behaviour	**0.745**	0.000	
Laval development	0.046	0.024	
Fecundity	**0.716**	**0.414**	
Generation time	0.073	**0.428**	
Range size	0.241	**0.507**	
Substratum type	0.050	0.017	
Variability explained (%)	16.23	14.55	30.78

tive and invaded range size. This outcome may be reflective of the coarse scale applied when defining range size. Due to the limited information available on the distribution of crabs, range size was unavoidably defined by the number of marine provinces from which a species had been reported. This is in contrast with the use of georeferenced records used in other studies that have detected a relationship between native and invaded range size (Hui et al. 2011, Bates et al. 2013). Nonetheless, such a relationship has been detected for some groups, even when the broad measure of latitudinal bands was used to quantify range size (Novoa et al. 2016). This may suggest that crab invasions are not truly characterised by a relationship between native and invaded range size or that, in the absence of genetic confirmation of taxonomic identity (both in their native and alien ranges) and baseline ecological surveys, it is not possible to detect such a pattern for crabs. Thus, while present data suggest no relationship between native and invaded range size for crabs, it is unclear if this is an artefact of the data used or a real reflection of the nature of these invasions.

The relationship between regions donating and receiving alien species can be complex, especially as receiving regions can themselves become donors (Grosholz and Ruiz 1995, Ruiz et al. 2000). As such, without genetic confirmation, the donor regions of most crab invasions remain unresolved. Nonetheless, by applying two different approaches, this study was able to identify some general relationships between donor and recipient regions of crab introductions. The first method, i.e. using native range as a proxy for donating region, is likely to be the more accurate for species with restricted native ranges. However, as native range size increases, so will the uncertainty associated with identification of donor regions. This problem was most evident in this study with respect to identifying the source of Mediterranean crab introductions. Many of these crabs have large native ranges spanning multiple bioregions, including the Arabian Seas, East Africa, North West Pacific, East Asian Seas and the South Pacific. Thus, despite the most parsimonious explanation being that these crabs invaded from the Arabian Seas via the Suez Canal (Galil et al. 2014), this method identified many bioregions as potential sources. In contrast, using shipping vector strength to identify donor regions assumes that all introductions are related to the dominant vector of shipping. While this assumption may in fact be valid in many cases, when used on a species by species basis, this is likely to introduce significant error. Nevertheless, these methods identified two convergent patterns in predatory crab introductions. Firstly, the majority of alien crabs were found to be donated from the North West Pacific and secondly, the South Pacific received species from the most bioregions. The greater Western Central Pacific, which includes the North West Pacific bioregion, is one of the regions that supports the largest number of native crabs (Ng et al. 2008), suggesting that the large number of species originating from this region simply reflects high native diversity. This region is central in the shipping network (Seebens et al. 2013), suggesting high potential vector strength. As Brockerhoff and McLay (2011) highlighted shipping as the dominant vector of alien crabs and crab-like anomurans, it seems likely that high vector strength from this species-rich region accounts for the high number of alien crabs originating in the North West Pacific. The reason for the diverse sources of alien crabs recorded in the South Pacific remains unclear, but may reflect the diverse shipping network in the region.

Reflecting the highly invaded nature of the Mediterranean Sea (Galil 2009, Zenetos et al. 2012), this region was found to support the most crab invasions. While the well-studied nature of this region may contribute to the high number of recognised invasions, these elevated numbers are also likely explained by its central position in the shipping network (Seebens et al. 2013), its close proximity to many neighbouring regions and maybe most importantly, as a result of the Suez Canal (Katsanevakis et al. 2013, Galil et al. 2015). This canal offers a pathway from the Indo-West Pacific to the Mediterranean through which most crab species were introduced from the Arabian Seas. No Mediterranean species are found in the Arabian Seas as the sea water flow in the Suez canal is from the Red Sea to the Mediterranean Sea and not vice versa (Rilov and Galil 2009). The Australia and New Zealand bioregion is the second most invaded region, with more species known from New Zealand than Australia. However, as with the Mediterranean region, high search effort in both these countries may be reflected in this pattern. The absence of introductions to the Antarctic and the single introduction of Atlantic Rock Crab, *Cancer irroratus*, to the Arctic bioregion (Gíslason et al. 2014) mirrors the general pattern observed in marine alien species (Tavares and De Melo 2004) and is likely driven by the inhospitable nature of polar environments.

The role of traits in crab invasions

Traits suggested to be associated with successful invaders include longevity, large body size, high fecundity, long larval development, planktonic dispersal and broad environmental tolerance (Crawley 1989, Ehrlich 1989, Weis 2010, Hänfling et al. 2011). Despite specific traits having been identified as important for the invasion success of taxa such as cacti (Novoa et al. 2015), bivalves (Nawrot et al. 2015) and amphipods (Grabowski et al. 2007), this study found no patterns in the traits of alien crabs that were associated with their invasion status or taxonomic identity (i.e. at the family level). This finding was unexpected and offered no support to the *a priori* hypotheses that (1) crabs with established populations would be characterised by traits allowing them to survive under a variety of conditions and (2) established and single record species would possess traits facilitating transfer by humans. Nonetheless, these results could be explained by several factors. Firstly, trait analysis requires the inclusion of as many species and traits as possible to provide the greatest resolution of important suites of traits (Bremner et al. 2006). While this study strove to address these requirements, limitations in the available literature resulted in nine traits being considered for 28 alien species. While this represents the first time that the traits of crabs have been assessed in such detail, the inclusion of more species and more traits in future analyses may result in the identification of important traits that were not detected in this study. Traits that have been suggested as important for invasion success, but which could not be included in this study due to the lack of information, included growth rate (Weis 2010), salinity tolerance (Hänfling et al. 2011), feeding activity (Spilmont et al. 2015) and larval dispersal potential (Brousseau and McSweeney 2016). Secondly, high levels of plasticity within traits enable species to adapt to a range of environmental conditions between and within the native and invaded habitats, thereby increasing their establishment success (Smith 2009). As such, the variability within traits and the plasticity with which they manifest might be key to invasion success. For example, *Eriocheir sinensis* and *C. maenas* show a significant increase in body size in their introduced region (Grosholz and Ruiz 2003). Similarly, alien populations of *Hemigrapsus sanguineus* show earlier sexual maturation (Brousseau and McSweeney 2016), while *E. sinensis* shows variability in sexual maturation rates when compared to native populations (Rudnick et al. 2005). Unfortunately, not all traits have been assessed in this detail and so this study was unable to consider variability in traits. An additional consideration relating to the assessment of traits relates to the theoretical approach applied. Ideally, studies should compare the traits of alien species with those that have never been recorded outside of their native ranges (Novoa et al. 2016). While the strength of such an approach lies in the fact that it contrasts information about species that have and have not spread outside their native range, this is also its greatest weakness as it is data demanding. Due to a paucity of knowledge on traits, even in native ranges, this approach is currently not viable for crabs. This lack of knowledge is notable, especially as crabs tend to be large, conspicuous and thus likely to be a well-studied group. Nonetheless, this approach may hold the key to identifying traits that are important for the invasion success of crabs in the future.

While some studies have highlighted traits that may be important in crab invasions, contrasting the findings of this study, it is important to consider the scale at which these were undertaken. These studies undertook single species comparisons, i.e. contrasted alien species between their native and invaded ranges (Grosholz and Ruiz 2003) or compared alien species with native species in a specific region (Brousseau and McSweeney 2016). While these studies are informative, it is important to acknowledge that their findings may be context dependent (Crawley 1989). The greatest strength of multi-species analyses, such as the one undertaken in this study, is that they are able to elucidate general patterns present at a high taxonomic level. Nonetheless, they are limited by the availability of basic biological information and, while the limitations of the present study are acknowledged, this line of enquiry should be pursued when the underlying information becomes available.

Conclusion

The factors interacting to ultimately govern invasion success in crabs, as with marine alien species in general, are complex and it was not possible to identify traits predisposing species to being successful invaders with the data presently available. The application of trait-based analysis to answer this question does, however, hold promise. Presently, the greatest impediment to its extensive use in an invasion context is the lack of foundational biology knowledge for many taxa and an understanding of how basic biology varies geographically, i.e. across alien and native ranges. This could, however, be addressed by primary research aimed at developing a sound knowledge-base of species distribution and trait data. This would be most efficiently done through geographically broad collaborative projects, targeting groups that are already well studied. While many such groups are terrestrial, e.g. plants (Pysek et al. 2011) and birds (Blackburn et al. 2009), the collation of biological trait information for marine taxa has been receiving increasing attention (Costello et al. 2015). Most notable is the free access to trait data provided through the World Registry of Marine Species (http://www.marinespecies.org). It is thus suggested that coordinated research on well-studied taxa, such as intertidal mussels and barnacles, may offer a promising avenue for pursuing trait analysis as a methodology for advancing our understanding of invasion success in the marine context.

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Supplementary material 1

List of 42 marine alien brachyuran crab species

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: List of 42 marine alien brachyuran crab species that were not considered in this study. Species are listed per family and the reason for the exclusion is indicated for each: P (Not a predator); D (Diet not defined); N (Native range not defined).

Link: https://doi.org/10.3897/neobiota.39.22002.suppl1

Supplementary material 2

Sources used for reviewing crabs

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: Databases and publications used in the compilation of the list of predatory marine crabs and information on their distribution, vectors and traits.

Link: https://doi.org/10.3897/neobiota.39.22002.suppl2

Supplementary material 3

Fuzzy coded trait data utilised in the FCA analysis

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: Fuzzy coded trait data utilised in the FCA analysis. Details are provided for established and single record species.

Link: https://doi.org/10.3897/neobiota.39.22002.suppl3

Supplementary material 4

List of species assigned 'Single record' status

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: List of species assigen 'Single record' status and the reason for doing so. The references from which the information was sourced are also provided.

Link: https://doi.org/10.3897/neobiota.39.22002.suppl4

Supplementary material 5

The native and recipient regions of the 56 alien crab species

Authors: Cheruscha Swart, Vernon Visser, Tamara B. Robinson

Explanation note: The native and recipient regions of the 56 alien crab species considered in this study. Regions were defined in terms of the 18 IUCN bioregions (Kelleher et al. 1995a, b, c, d).

Link: https://doi.org/10.3897/neobiota.39.22002.suppl5