RESEARCH ARTICLE



Assessing the association between pathways of alien plant invaders and their impacts in protected areas

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Academic editor: B. Murray | Received 10 September 2018 | Accepted 18 January 2019 | Published 5 March 2019

Citation: Foxcroft LC, Spear D, van Wilgen NJ, McGeoch MA (2019) Assessing the association between pathways of alien plant invaders and their impacts in protected areas. NeoBiota 43: 1–25. https://doi.org/10.3897/neobiota.43.29644

Abstract

Protected areas face mounting pressures, including invasion by alien plant species. Scientifically sound information is required to advise invasive species management strategies, where early detection and rapid response is particularly important. One approach to this is to determine: (i) the relative importance of pathways of invasion by which a species is introduced, (ii) the range of likely impacts associated with each species, and (iii) the relationship between pathways and impacts, to assess the relative threats posed by different pathways of alien species introductions. This assessment was performed on 139 alien plants that are invasive across the South African National Parks (19 national parks, covering ~39,000 km²), and based on available literature and expert opinion, known to have negative ecological impacts. For each species the likelihood of being introduced by each of eight pathways, and of having negative impacts in each of 13 identified impact categories, was assessed. The similarity of impact and pathway types between species was assessed using the Jaccard index and cladograms. Differences in the prevalence of impacts and pathways and relationships between these were assessed using a Chi-squared contingency and Generalised Linear Model. Nearly 80% of the species are ornamental plants and about 60% are also dispersed by rivers, highlighting the importance of managing ornamental species and surveillance along rivers in preventing future invasions. As to the impacts, ~95% of the species compete directly with native species and 70% change the

physical structure of the environment. The majority of species exert multiple impacts, with 70% of species assessed having five or more impacts. There was a significant positive relationship between the number of pathways via which a species can be introduced into an area and the number of potential impacts they can have. This suggests that species using multiple pathways reach a wider range of suitable habitats, increasing the potential for different kinds of impacts over a wider area.

Keywords

Global change, Invasive alien plants, Management, Non-native species, Ornamental plants, State of knowledge assessment

Introduction

Protected areas represent some of the last opportunities to retain intact or at least relatively naturally functioning ecosystems with a near full complement of biological diversity (e.g. Geldmann et al. 2013). However, they are increasingly becoming disconnected remnants of natural habitats embedded within a larger mosaic of varying land use types (DeFries et al. 2005, Koh and Gardner 2010, Meiners and Pickett 2013). As such, these areas are threatened by a wide range of anthropogenic actions (Carey et al. 2000). One outcome of this is the mounting pressure of invasions by alien species from a multitude of different sources (Foxcroft et al. 2013, 2017, Hulme et al. 2013), each delivering different species and intensities of pressure (Pergl et al. 2016). Therefore an improved understanding of dispersal mechanisms is needed, to minimise not only possible future impacts (Pyšek et al. 2012), but also the costs associated with maintaining densities of alien plant populations below acceptable thresholds. Unfortunately, protected areas often have inadequate budgets for basic operational costs (Dixon and Sherman 1991, Bruner et al. 2004) let alone dealing with biological invasions (van Wilgen et al. 2016, Foxcroft et al. 2017). This necessitates careful prioritisation and allocation of funds to maximise long-term benefits (Leung et al. 2002, Evans et al. 2011, van Wilgen et al. 2016).

As with all conservation practices, the control of alien plant invasions requires scientifically sound information to advise policy strategies and management approaches (Cook et al. 2010). Although there is a rapidly expanding body of literature, this knowledge is often difficult to access and remains outside the realms of policy makers and managers (Cook et al. 2010, Sutherland et al. 2013). State of knowledge assessments are useful tools to examine scientific advancements and provide policy makers with information in a concise and usable form (e.g. prioritising species, pathways and sites, McGeoch et al. 2009).

Early detection, rapid response and eradication are regarded as the first line of defence in proactively managing alien plant invasions, and are considered wholly feasible in the protected area context (Simberloff 2013). However, the size and rapid escalation of the problem and the lack of adequate resources necessitates careful planning to ensure that management approaches are able to match the scale and rate of invasions and pre-empt future problems. Preventative strategies that have been developed either aim at assessing pathways or vectors of invasion, species-based prioritisation or prioritising sites (McGeoch et al. 2016). An assessment of possible introductory pathways can direct surveillance to enhance early detection strategies (Hulme 2006, Pergl et al. 2016). Additionally, the ability to predict or at least be aware of potential impacts is required to focus attention on the species already in the system most likely to be damaging to native species and basic ecosystem services (Kumschick et al. 2012). While various risk assessment approaches have been developed for pathway analysis (Dawson et al. 2009, Hulme 2009, Essl et al. 2015), many of these are aimed at preventing introductions at points of entry at a national scale, such as harbours and airports (see reviews by Hulme 2012 and Leung et al. 2012). However, at the scale of an individual protected area, local vectors need to be assessed.

Although conceptual frameworks for prioritisation based on potential impacts are evolving (e.g. Kumschick et al. 2012, Blackburn et al. 2014, Nentwig et al. 2016, 2018, Bacher et al. 2018) there is no single method that can be used in all contexts. A method developed to jointly inform prioritisation for management needs to include species, pathways, and susceptible or sensitive sites (McGeoch et al. 2016). Such a model provides a three-way prioritisation system which combines assessments of pathways associated with high-priority species, pathways of introduction to sensitive sites, and sites most susceptible to impacts of invasion by those same species (McGeoch et al. 2016). Protected areas with high biodiversity value are often delineated as susceptible or sensitive sites. However, between a set of parks, or the biomes in which they fall, there may be areas that are considered of higher importance (e.g. fynbos in Table Mountain National Park, Rebelo et al. 2011).

We used a combined assessment of the impacts that an invasive species can have and the potential pathways of invasion, to develop an approach to determine species of highest concern and inform management strategies. To do this we assessed 139 alien plants across the South African National Parks estate that are considered to be transformer or potential transformer species (i.e. the most invasive species) and determined: (i) the relative importance of pathways of invasion by which a species is introduced, (ii) the range of likely impacts associated with each species, and (iii) the relationship between pathways and impacts, to assess the relative threats posed by different pathways of alien species introductions in different parks and biomes.

Methods

Data compilation

We used South African National Parks (SANParks) as a model system as it has 752 alien plant species recorded across 19 national parks (Spear et al. 2011, Foxcroft et al. 2017). The SANParks estate covers an area of about 39,000 km² and spans eight of the nine biomes in South Africa. Using the full list of alien species recorded in SANParks by Spear et al. (2011), we extracted a subset of those alien plants we considered to be transformer species.

Transformer species were defined as the "subset of invasive plant species that change the character, condition, form, or nature of ecosystems over a substantial area relative to the extent of that ecosystem" (Richardson et al. 2000, McGeoch et al. 2006). From the overall SANParks species list we extracted those species that we considered transformers using information from four key publications, (i) Henderson (2001), declared alien weeds and invasive plants, (ii) Nel et al. (2004), a classification of invasive alien plant species in South Africa, (iii) van Wilgen et al. (2008a), a biome scale assessment of the impact of invasive alien plants, and (iv) van Wilgen et al. (2008b) prioritising species and catchments for guiding invasive alien plant management in South Africa). We also considered national legislation that regulates the management of alien and invasive plants in South Africa (CARA; Conservation of Agricultural Resources; Act 43 of 1983, as amended 2001). The criteria for designating alien plant species as transformers in our assessment were, (i) species recorded as 'transformers' or 'potential transformers' in Henderson (2001), (ii) species classified in Henderson (2001) as 'special effect weeds' AND also listed in two or more of the other publications (but in CARA only if listed as a Category 1 prohibited species) and (iii) four species in the SANParks list were considered transformer species based on the authors' personal observations in parks and supported by expert opinion. The latter resulted in the inclusion of the following species: Austrocylindropuntia cylindrica, Aristolochia littoralis, Bryophyllum delagoense and Pontederia cordata. Pontederia cordata was also recorded in Henderson (2001) as a 'special effects weed' and in the CARA regulations as a Category 3 invader.

This selection process resulted in a list of 139 alien plants regarded as transformer species (see Suppl. material 1: Table S1 for species list and data). By using a post hoc approach we aimed to elucidate those pathways that should be considered future management priorities for these species, and also the range and frequency of types of impacts likely to be experienced.

The potential pathways of introduction and impacts that alien plant species may have in national parks in South Africa were determined by the authors as a group, using literature (for example Mack et al. 2000, Morse et al. 2004, Randall et al. 2008, Vilà et al. 2010, Wells et al. 1986). As the classification was based on information not only from South Africa but also from other parts of the world, where data on impacts and pathways associated with species on our list are available, and it has not been proven that they actually occur in the parks under study, we term the pathways and impact categories 'potential' (see Rumlerová et al. 2016). The rationalisation of categories resulted in a list of eight locally-relevant pathways (nationally and within parks) of introduction and dispersal: rivers; ornamental plants; roads, paths, trails, tracks; contaminated construction material, equipment, soils; agriculture; clothing; food or produce; and dispersal by animals (Table 1) and 13 impacts: fire properties; geomorphology; hydrological regimes; nutrient/mineral dynamics; light; pH, salinity, alkalinity; physical structure; facilitation; alteration of successional process; competition; hybridisation; poison, allelopathy; and disruption of ecological interactions (Table 2). This was done to prevent the inclusion of pathways and impacts not

Pathway	Interpretation			
Rivers	Unintentional: The species is introduced by rivers (e.g. seeds that float downstream			
	into the park).			
Roads, paths, trails, tracks	Roads, paths, trails, tracks facilitate movement of the species.			
Contaminated construction	Unintentional: The species (seeds or small plants) is spread in construction material			
material, equipment, and soils	ils (e.g. building sand, crushed stone, gravel, bricks, timber, thatch), equipment			
	(pumps) and soil (excluding material on transport vehicles like bulldozers or trucks).			
Ornamental plants	The species is deliberately introduced as an ornamental plant by staff living in a park,			
	or in landscaping in tourist facilities. Former farmsteads or abandoned structures			
	incorporated into new parks may have ornamental plants associated with them.			
Agriculture The species is deliberately introduced for agriculture (small scale for staff				
	use), or was the previous landuse in areas which now, or in the future, may be			
	incorporated into new parks.			
Clothing	Unintentional: The species is introduced on human clothing (normally seeds).			
Food or produce	Unintentional: The species is introduced along with food substances brought into			
	the park for staff, tourists, pets and animals. Note for intentional food imports the			
	category "Agriculture" should be used.			
Animal dispersed	Unintentional: The species is spread by animals (e.g. seed burs that get transported in			
	animals' coats, birds and baboons eating fruit).			

Table 1. Definition and interpretation of pathways of introduction.

relevant to the local context. While there are many recognised pathways by which alien species are introduced, for example 32 categories listed in Hulme et al. (2008), the eight included here were deemed practical for our purposes and for management application in a protected area on a local scale. While some pathways seem counterintuitive for protected areas, all eight were deemed relevant. For example, ornamental plants are often cultivated in tourist camps and staff accommodation, or can be found at former farm houses/abandoned structures now part of a protected area. Similarly, agriculture is largely relevant for former agricultural land now incorporated into protected areas, but is also relevant where species are introduced directly adjacent to protected areas.

For each species the likelihood of being introduced by each of the eight pathways, and of having negative impacts in each of the 13 impact categories, was assessed using three primary local resources (Wells et al. 1986, Henderson 2001, Bromilow 2010), supplemented by international literature, (ISSG 2015 – Global Invasive Species Database) where the findings were deemed locally applicable by our expert judgement. We acknowledge that a species that has a diverse range of potential impacts does not necessarily equate to having the most severe impact (see Blackburn et al. 2014, Rumlerová et al. 2016). We were instead interested in quantifying the range of impacts that a species may exert on a system. This would indicate the different protected areas' objectives that may be compromised and thus the threats requiring prioritisation.

Three options were used to describe whether a species has the potential to result in an impact described by each of the 13 categories: (i) Yes – the species has been docu-

Higher category	Heading/ Impact	Interpretation
Impact on	Fire properties	The species alters fire frequency, intensity or timing (of the fire regime).
ecosystem processes and		If species only occurs in forest, it is unlikely to impact on fire, because fire is not part of the system (No).
system-wide		If the species is only ruderal, it is not likely to impact on fire (No).
parameters	Geomorphology	The species affects erosion, sedimentation processes or geo-engineers soil structure or geomorphological processes.
	Hydrological regimes	The species affects run-off and other hydrological process like flow rate, the frequency of flood events or timing and seasonality of water flow – or could change the "pattern" – physical water course.
	Nutrient/Mineral dynamics	The species alters the nutrient or mineral content of its environment (soil or water). This includes eutrophication. This can be marked yes in addition to the column "pH, salinity, alkalinity".
	Light	The species affects the amount of light filtering to layers below it (in water or sub-canopy). Yes – based on the habitat the species invades, and the structure of the plant, it is likely to affect the amount of light that reaches the layer directly below it. Unknown – it is unclear from the species structure and habitat whether light is affected.
		No – light not affected (e.g. species low growing terrestrial species)
	pH, salinity, alkalinity	The species affects the pH, salinity or alkalinity of the medium in/on which it occurs. This can be marked yes in addition to the column "Nutrient/Mineral dynamics".
		Yes – species where this has been recorded. Unknown - alleopathic species have the potential to alter pH. No – no evidence of altering pH and unlikely to do so because of life-form (e.g. vine) or other traits.
Impact on community structure	Physical structure	The species adds (or removes) a new layer to the community (e.g. tree in shrub-land, aquatic plants where no plants previously covered the water).
Impact on	Facilitation	The species facilitates the invasion of other aliens.
community composition		Yes – must directly facilitate the invasion or dispersal of another alien species (e.g. by providing food for the species).
	Alteration of successional process	This species alters successional processes in areas where low level disturbance is common (e.g. flood plains). Also includes species that change the disturbance regime (e.g. creation of gaps or disturbed areas).
Impact on	Competition	The species competes with native species.
individual	Hybridization	The species can hybridise with related native species.
indigenous species	Poison / allelopathy / stinging	The species may poison, sting or have allelopathic effects on other species.
Species interactions	Disruption of ecological interactions	The species disrupts native ecological interactions (including any mutualisms (e.g. seed dispersal), predator prey interactions, pollination, herbivory or other trophic interactions). Interactions include:
		Disruption of native seed (or fruit) dispersal due to provision of alternate food source. Effects on plant herbivore interactions by displacing food sources (e.g. unpalatable grass), breeding sites and habitat (e.g. of birds, fish and crocodiles) transformed until the species can no longer use a river.
		Alteration of food webs (e.g. trophic cascade).
		Species that only restrict movement without demonstrating disruption of an interaction were excluded.

Table 2. Definition and interpretation of impact categories.

mented to impact in this way or there is other evidence, including authors' specialist judgement, that the species will do so. (ii) No – the species does not impact in this manner or the impact is very unlikely and has never been documented for this spe-

cies. (iii) Unknown – there is too little information to make a confident decision as to whether the species may impact in this manner, but this is not implausible given the biology of its taxonomic group. To be conservative, unknown records were treated as 'No' records for some analyses (detailed below). For pathways of entry, all pathways for each species could confidently be scored as 'Yes' or 'No' (i.e. no species/pathway combination was scored as 'Unknown'). In addition to the impact and pathway data we also recorded family, life-form, park invaded (Spear et al. 2011) and biome invaded (van Wilgen et al. 2008a, b).

Species were divided among authors and scored for pathways and impacts. Thereafter, a subset of species was randomly selected by category to check for consistency within, and between, categories and authors. Categories where inconsistencies were identified were systematically verified by the group for all species individually, specifically comparing entries within and between categories. The data were also checked by grouping species based on their similarity (Jaccard index) of impacts, particularly the number of impacts shared. Species that appeared to be outliers were then further examined to ensure data consistency.

Analysis

Distribution of species across life-forms, families, parks, biomes, pathways and impact categories

Species were counted across life-forms, families, pathways and impact categories, to determine the status of transformer species in SANParks. For this analysis, the aforementioned data were transformed to binary as follows: Yes -1, No -0, Unknown -0.

To determine the importance of each variable we tested for significant differences between the numbers of species counted within each category. The data were expanded into unique combinations across each category, resulting in a total of 32,718 records. The variables for impacts were maintained as Yes–No–Unknown, from which combinations including Unknown records were then excluded from the analyses. Analyses were run in R 3.0.2 (R Development Core Team 2010), using the base stats library and the chi-squared contingency table and goodness-of-fit tests.

Relationship between impact and biome, park and pathway type

A Generalised Linear Model with quasi-poisson error distribution was used to examine the relationships between the count of numbers of impacts per species, with the number of pathways by which it can invade the biomes and parks in which it occurs. The analysis was performed on all 139 species, using the glm function in R to determine the relationship of the number of impact types with the number of biomes, parks and pathways per species.

Similarity in species clusters by pathways and impacts

We assessed the occurrence of groups of species with similar pathways of introduction or similar impacts to identify groups for which particular management strategies might be effective. A statistical test for non-independence of columns, using a Spearman's rank order correlation matrix was performed in R. The variables were weighted as follows for impacts and pathways: Yes -1, No -0, Unknown -0.

Spearman rank correlations were conducted between all variables to exclude strongly correlated variables ($r_s > 0.60$). None of the pathway variables were highly correlated (See Suppl. material 2: Table S2: Spearman rank order correlation matrix of variables for pathways) nor were any of the impact variables (See Suppl. material 2: Table S3: Spearman rank order correlation matrix of variables for impacts).

A binary species by impact matrix, and species by pathway matrix, was constructed and the Jaccard's index calculated in Estimate S 7.51 (Colwell 2013), and used to represent the similarity of impact and pathway types between species. Cladograms were then constructed in Primer (Clarke and Gorley 2006) using group averaging. The groupings of species were examined, noting their shared impacts and pathways, mean number of impacts and pathways, and taxonomic representation in the groups.

Results

Distribution of species across life-forms, families, parks, biomes, pathways and impact categories

The transformer plant species present in parks represent 43 families, with the three most represented families being Fabaceae (20% of all the taxa assessed), Myrtaceae (9%) and Cactaceae (8%), and all other families contributing 5% or less. There were significant differences among life forms of transformer species ($\chi^2 = 118.7626$, df = 8, P < 0.001; Table 3), with trees (37.4%) or tree/shrubs (17.2%) over-represented and the six other life-forms less represented (See Suppl. material 2: Table S4).

There were significant differences in the number of transformer species per biome ($\chi^2 = 155.7173$, df = 7, *P* < 0.001; Table 3), with the fynbos (78% of the taxa assessed), then forest (48%) and savanna (45%), having the highest number of taxa (See Suppl. material 2: Table S5). The succulent karoo (6%) and arid savanna (9%) have the fewest transformer species recorded. In agreement with this, there were significant differences between the number of species recorded per park ($\chi^2 = 372.3872$, df = 18, *P* < 0.001), the pattern thereof largely similar to the biomes. Table Mountain National Park (hereafter Table Mountain), which is fynbos dominated, including 60% of the transformers, followed by Garden Route National Park (Garden Route), which is forest and fynbos dominated including 45%, and Kruger National Park (Kruger), a savanna protected area, including 45% of the species (See Suppl. material 2: Table S6: Total count and percentage of species per biome). Golden Gate

Number of:	Chi-square	df	Significance
Species per impact category	346.92	12	P < 0.001
Number of species per pathway type	193.61	7	P < 0.001
Number of species per biome	155.71	7	P < 0.001
Number of species per park	372.38	18	P < 0.001
Number of life forms per species	118.7626	8	P < 0.001

Table 3. Differences in numbers of transformer plant species per impact category, pathway, biome, park and life-form. (Chi-square test results for individual models), (See Figures 3, 4).

Highlands National Park (Golden Gate), Agulhas National Park (Agulhas), Addo Elephant National Park (Addo) and Camdeboo National Park (Camdeboo) have moderate levels of transformers, whereas the remaining 12 parks have significantly lower transformer species richness.

We found a significant difference in the numbers of species within each pathway category ($\chi^2 = 193.6135$, df = 7, P < 0.001; Table 3). Ornamental species (78%), rivers (63%) and animal dispersion (48%) may be considered the most important pathways of introduction and spread, with numbers of species, and thus likelihood of invasion through these pathways being higher (Figure 1). Roads, paths, trails and tracks introduce less than a half (40%) of the species assessed, while the highest of the next four pathways, agriculture, contaminated materials, clothing and food is responsible for introducing less than 29% (Figure 1) (See Suppl. material 2: Table S6: Total count and percentage of species per pathway and life form).

For impacts, there is a significant difference in the numbers of species within each impact category ($\chi^2 = 346.9231$, df = 12, P < 0.0001; Table 3). Nearly all 139 species are capable of direct competition with native species (Figure 2; See Suppl. material 2: Table S7: Total count and percentage of species per impact type and life form). The next most frequent types of impacts are changes to physical structure, light and then hydrological regimes. Trees and shrubs are represented in all impact categories (Figure 2).

Relationship between impact and biome, park and pathway type

There was no relationship between the number of impact types per species and the number of biomes (P = 0.331) or parks in which the species occurred (P = 0.131) (Table 4). The only significant relationship showed that species with more impacts are likely to be introduced by more pathways (P < 0.0001; Table 4).

Similarity in species clusters by pathways and impacts

The pathway cluster analysis separated the species into three main groups and four sub-groups (Figure 3; See Suppl. material 2: Figure S1 for detailed species names). The



Figure 1. Percentage life forms and total percent species per pathway. Columns show the percent of each life form per pathway type, with the total number of species per pathway above each column. For example, 35% of the species that can be introduced as ornamental plants are trees, and trees make up 45% of the species that can be spread by rivers. Black dots show the total percent of species per pathway type. For example, 78% of the total species can be introduced as ornamental plants, 63% as rivers and 48% by animals.

Table 4. The relationship between number of impact types per species and number of biomes invaded, parks invaded and pathways per species. (General linear model with quassi-Poisson link function).

Term	Coefficient Estimate	Std. Error	t- value	Significance
(Intercept)	1.113	0.120	9.237	P < 0.001
Number of biomes per species	-0.049	0.050	-0.975	0.331
Number of parks per species	0.040	0.026	1.520	0.131
Number of pathway types per species	0.154	0.029	5.239	P < 0.001

first group (group a; Figure 3) consists of 45 species that are introduced by a mean of 3.8 pathways per species, predominantly roads, paths, trails and tracks (91% of the species that have this as a pathway fall in this group only), ornamentals (82%) and rivers (78%). The second group (group b; Figure 3) is a large group of 77 species that are introduced by a mean number of 2.3 pathways, which for most species includes introduction as ornamentals (94%) and via rivers (79%). For the most part, examination of clusters at the finest scale did not reveal readily interpretable patterns. Only five out



Figure 2. Percentage life forms and total percent species per impact category. Columns show the percent of life forms per each impact category, with the total number of species per impact category above each column. For example 37% of the species in the competition category are trees and 39% of the species that can impact through changes to physical structure are trees. The black dots show the percent of species in each impact category of the total species list. For example, 96% of the species could impact through direct competition, while 73% could impact through changing the physical structure.

of the 13 *Acacia* species comprised a single cluster (group h; Figure 3), which, falling in sub-group (d) indicates their ability to disperse via four pathways.

In the cluster analysis of impact categories, three main groups were observed (Figure 4; See Suppl. material 2: Figure S2 for detailed species names). The first group of 12 species (group a; Figure 4) had fewer impacts (mean of 1.63) with the majority of species impacting via competition (67%). The second group contains 97 species with a mean number of 5.63 impacts, representing all 13 impacts. Competition (98%) and physical structure (93%) were the most important. The third group (group c; Figure 4) includes 30 species, which are characterised by a mean number of 3.67 impacts per species. All these species include competition (100%) and 93.3 % of the species impact through poison or allelopathy.

In contrast to the cladogram for pathways, there were four instances where related species clustered together based on the similarities of their impacts. All four *Opuntia* and two *Cylindropuntia* species (group h; Figure 4) were clustered, as were all six *Eucalyptus* species (group I; Figure 4), all seven *Pinus* species (group j; Figure 4) and all 13 *Acacia* species (group k; Figure 4). The cacti include competition and physical structure as the most important impacts. The *Eucalyptus*, *Pinus* and *Acacia* species include both competition and physical structure as key impacts, but also fell into the only subgroup in which fire was important.



Figure 3. Cladogram of plant introduction pathways, based on similarities of pathways. Mean number and type of pathways have been calculated per clade (Groups **a–c**). Sub-groups **d** include 25 species (Mean: 4.5 pathways/species; 100% contaminants; 92% rivers; 84% roads; 80% ornamentals) **e** include 20 species (Mean: 2.9 pathways/species; 100% roads; 85% ornamentals) **f** include 29 species (Mean: 2.5 pathways/species; 96% ornamentals; 90% animals) **g** include 48 species (Mean: 2.1 pathways/species; 91% ornamentals). The vertical black bars indicate clustering of species, whereas all other species are scattered across the groups **h** *Acacia podalyriifolia*, *A. baileyana*, *A. elata*, *A. implexa*, *A. longifolia* **i** *Pinus pinaster*, *P. radiata*, *P. roxburghii*, *P. taeda*, *P. halepensis*, *P. patula*.



Figure 4. Cladogram of plant impacts, based on similarities of impact types. Mean number and type of impacts have been calculated per clade (Groups **a–c**). Sub-groups include **d** 24 species (Mean: 3 impacts/ species; 100% competition; physical structure 100%) **e** 11 species (Mean: 4.6 impacts/species; 100% competition; physical structure 100%; **8**2% hydrological) **f** 32 species (Mean: 7.9 impacts/species; competition, physical structure, light, hydrology, fire >90%) **g** 22 species (Mean: 6.4 impacts/species; competition, physical structure, light, hydrology >90%). The vertical black bars indicate clustering of species, whereas all other species are scattered across the groups **h** *Cereus jamacaru, Echinopsis spachiana, Opuntia aurantiaca, O. ficus-indica, O. humifusa, Cylindropuntia imbricata, C. fulgida, Opuntia stricta* **i** *Eucalyptus cladocalyx, E. lehmannii, E. sideroxylon, E. camaldulensis, E. diversicolor* **j** *Pinus radiata, P. roxburghii, P. taeda, P. halepensis, P. patula, P. canariensis, P. pinaster* **k** *Acacia dealbata, A. mearnsii, A. melanoxylon, A. paradoxa, A. podalyriifolia, A. pycnantha, A. saligna, A. baileyana, A. cyclops, A. decurrens, A. elata, A. implexa, A. longifolia.*

Discussion

The role of pathways of invasion for prioritising management actions

The two most important pathways of invasion identified for transformer species into national parks included use as ornamental species and rivers. An additional two pathways appear to play a role as vectors, although to a lesser extent, including dispersal by animals and along roads, paths, tracks and trails. The results from the analyses all point to the high likelihood that many of the species currently in SANParks (~80%) were introduced for ornamentation. This can be illustrated in two parks, Kruger and Table Mountain. Kruger has a long history of plant introductions and the control of ornamental plants was first recommended in 1935 (Joubert 1986). However, by 2003 more than 250 ornamental plant species were recorded in Kruger (Foxcroft et al. 2008), including 35% of the species in our list. Work by Spear et al. (2013) showed human population density surrounding a park to be a significant driver of invasion into a park. Similarly, areas with high levels of natural vegetation along the boundary of Kruger proved to be a filter to plant invasions into the park (Foxcroft et al. 2011). The use of ornamental plants at the urban-protected area interface has been shown to increase the threat to urban protected areas such as Table Mountain (Alston and Richardson 2006). Many ornamentals appear to have few other introduction pathways, suggesting that if these species were removed from ornamental use at least some species would potentially be prevented from invading in future. Ornamental species potentially remain one of the easier pathways to manage within protected areas using, for example, policy guidelines (e.g. in Kruger, Foxcroft et al. 2015) and incentive schemes to replace alien species with native species occurring within parks and potentially those in close proximity. However, propagule pressure from outside the park is harder to control. For many of the ornamental species, rivers also form important invasion pathways, necessitating working with the nursery and landscaping industry and promoting initiatives to plant indigenous alternatives outside parks and increasing surveillance in riparian areas.

Rivers have been widely acknowledged as key dispersal vectors for invasion (Richardson et al. 2007, Esler et al. 2008, Naiman and Décamps 1997, van Wilgen et al. 2007, Jarošík et al. 2011) and more than 60% of the species in our list can disperse along rivers. Propagules transported by water flow can be widely dispersed during floods, and riparian zones and rivers banks provide highly suitable habitat (Alpert et al. 2000). Surveillance activities along rivers should be flagged as a priority area to detect new species and changes in distribution (van Wilgen et al. 2007, Forsyth et al. 2012). Trees and tree-shrubs, which are likely to be more conspicuous and easier to detect, comprise only just over half of the list, suggesting that increased effort needs to be made to detect less visible species.

Although animals are widely considered to be major dispersers of invasive plants (e.g. Vavra et al. 2007, Guerrero and Tye 2011, Kueffer et al. 2009; Oatley 1984, Gosper et al. 2005), we found only half of the species in SANParks may disperse in this manner. This is surprising as most parks have native vertebrates that could utilise alien

plants. There are notable examples, however, where animals form an important dispersal mechanism for species introduced via other pathways into a park. For example, in Kruger *Opuntia stricta* was introduced as an ornamental plant but due to baboons and elephants utilising the fruit it became widely invasive (Foxcroft and Rejmánek 2007).

In contrast with work done in a number of studies (e.g. Pauchard and Alaback 2004, Stohlgren et al. 2013, Lonsdale and Lane 1994, Lonsdale 1999, Tyser and Worley 1992, Gelbard and Belnap 2003), we found roads and tracks to be surprisingly less frequently listed (40% of the species). As most parks have large road networks, tracks and pathways, whether for tourism or management purposes, the comparatively lower importance of this pathway is fortunate. However, there are important examples of this pathway such as alien species found along hiking and cycling trails in Table Mountain (Bouchard et al. 2015), as well as the fact that Table Mountain is an urban park within the city of Cape Town, the rapid spread of *Parthenium hysterophorus* along roadsides leading there and in Kruger (Foxcroft et al. 2009) and *Pennisetum setaceum* in Camdeboo (Masubelele et al. 2009), which is also partly an urban park. For management purposes, sections of path can be delineated for increased surveillance and fortuitously, populations confined to roadsides, should be comparatively easier to control than other pathways.

Assessing the transformer species richness per park and biome provides some insights into the potential invasibility of an area. For example, Kruger includes about 350 alien plant species, which is about 100 alien plant species more than in Table Mountain (~240) (Spear et al. 2013). However, less than 20% of the species in Kruger are transformer plants and more than a third of the species in Table Mountain and Garden Route are transformers. Moreover, the high endemism in the Fynbos biome (Rebelo et al. 2011) and high levels of habitat loss highlights that Table Mountain should be a priority for alien species management. Garden Route, containing both fynbos and forest, should likewise be considered a high management priority. Conversely, in the arid regions, parks such as Kalahari Gemsbok, Richtersveld and Augrabies Falls National Parks are less likely to become invaded by a large suite of alien plant species, of which most are likely to be restricted to rivers and drainage lines. This does not, however, indicate immunity from other invasions. Ornamental species, for example from the Cactaceae, which are introduced and nurtured in gardens could escape once established (Novoa et al. 2015). Implementing policy to prohibit the use of ornamental species in the parks therefore provides an opportunity for ongoing prevention and thereby further minimising the already low diversity of invasions in these arid parks. Species such as Prosopis spp., which are river dispersed, are highly likely to remain problematic in arid areas and the importance of the impact on hydrology, especially ground water (Dzikiti et al. 2017) highlights that this species should remain a priority.

Additional support for prioritising pathways may be gained from associations or shared traits of species that clustered together, while for some groups it is clear that prioritising one or even a few pathways will not be enough to curb spread and integrated approaches will be required. For example, all *Acacia* species share four of the eight pathways, with five of the 13 species sharing exactly the same pathways. These clus-

ters together with the large body of work on *Acacia* (Richardson et al. 2011, Wilson et al. 2011) allow broader generalisations to be inferred for this group. Similarly, six of the seven *Pinus* spp. were clustered and based on current knowledge (e.g. Richardson 2006), potential pathways for other *Pinus* spp. may be similar.

Assessing the potential impacts by alien species

That nearly all transformer species compete directly with native species is not an entirely unexpected result. More importantly, however, a large proportion (~70%) of the species showed the potential to impact in at least four additional ways. This most frequently included impacts such as altering hydrological regimes, changing light properties of invaded habitats, changing the physical structure of invaded areas, fire properties and succession. At a higher level in our categorisation these impacts were included as community structure, community composition and ecosystem level processes. These combined impacts can lead to cascading effects which are less easy, if at all possible, to reengineer (Meiners and Pickett 2013). Legacy effects can persist even after clearing has taken place (Larious and Sudding 2013) and can influence the ability of a system to recover following control efforts and whether additional interventions are required.

Four of the most represented naturalised genera globally were recorded in our list (Pyšek et al. 2017), and include some of the most frequently listed impacts. The *Opuntia* and *Cylindropuntia* spp., *Eucalyptus* spp., *Pinus* spp. and *Acacia* spp. each formed clusters of similar impacts. Excluding direct competition, physical structure was listed as the most important impact for the Cactaceae. Due to the dominance of trees and tree-shrubs in the transformer group, these species made up about half of the direct competition category and 40% of the species that can potentially change physical structure. These include the *Eucalyptus, Pinus* and *Acacia* species, but for these species specifically, impacts also included light, hydrology and fire. For example, species in the Fabaceae can significantly increase biomass and intensity of fires (van Wilgen and Richardson 1985), compounding long-term soil erosion (Scott et al. 1998) and other ecosystem level impacts on biogeochemistry (Yelenik et al. 2004). Therefore these species, in particular, are important and should be prioritised. In addition, groups of similar species may be advantageous in that similar management actions may be possible across the species.

Relationships between pathways and impacts

By assessing each species against the eight pathway and 13 impact categories, we aimed to determine a relative risk profile for each species that could assist in determining the threat that the species posed to a protected area. The significant relationship between pathways and impacts indicates that the more pathways a species can use to disperse, the higher the likelihood that the species will become problematic.

For protected areas in our study, a species introduced by multiple pathways can be expected to be distributed over a larger area and should be given a higher priority. For example, when spreading along rivers, riparian vegetation may be displaced, causing substantial changes to the geomorphology, vegetation and community structure and composition (Hejda et al. 2009), species communities and river bank collapse, while simultaneous spread across the landscape more broadly (e.g. grass or shrublands to alien tree dominated systems) can alter ecosystem processes (Raizada et al. 2008, Martin et al. 2009), fire regimes (e.g. Table Mountain, Forsyth and van Wilgen 2008, and *Andropogon gayanus* in Kakadu National Park in northern Australia, Rossiter et al. 2003), hydrology and nutrient cycling/biogeochemistry (e.g. Carbon-Nitrogen-waterleaf litter interactions, Ehrenfeld 2003).

Conclusions

Managers need reliable evidence on which to base their decisions about the location and nature of the species to be prioritised for management. These decisions often have substantial financial commitments with long-term ramifications. The ability to forecast which species, and the number or kinds of impacts they may have, can support decision making for different contexts. The correlation between the number of pathways and impacts per species highlights species of concern due to their ability to reach different habitats more widely. Implementing measures to curtail invasions along pathways that can be managed by implementing suitable policies (e.g. ornamental plants), or structured monitoring (e.g. along roadsides, trails and tracks), and combined with intensive surveillance (e.g. along rivers), will be important for a large proportion of the species.

Acknowledgements

This research was funded by the South African National Parks Park Development Funds and The Andrew W. Mellon Foundation as part of the Global Environmental Change Programme and the DST-NRF Centre for Invasion Biology, Stellenbosch University. LCF thanks South African National Parks, the DST-NRF Centre of Excellence (CIB) for Invasion Biology and Stellenbosch University, and the National Research Foundation of South Africa (project numbers IFR2010041400019 and IFR160215158271) for support. DS acknowledges the National Research Foundation for support through an Innovation Postdoctoral Research bursary. We thank Sandra MacFadyen for statistical assistance and Petr Pyšek for comments on the manuscript. We also thank the editor and reviewers for helpful comments on the manuscript.

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Supplementary material I

Data for species and their pathways and impacts per category

Authors: Llewellyn C. Foxcroft, Dian Spear, Nicola J. van Wilgen, Melodie A. McGeoch Data type: species data

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Link: https://doi.org/10.3897/neobiota.43.29644.suppl1

Supplementary material 2

Assessing the association between pathways of alien plant invaders and their impacts in protected area

Authors: Llewellyn C. Foxcroft, Dian Spear, Nicola J. van Wilgen, Melodie A. McGeoch Data type: measurement

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Link: https://doi.org/10.3897/neobiota.43.29644.suppl2

RESEARCH ARTICLE



Low and high input agricultural fields have different effects on pest aphid abundance via different invasive alien weed species

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Academic editor: J. Sun | Received 13 November 2018 | Accepted 28 January 2019 | Published 13 March 2019

Citation: Szabó A-K, Kiss J, Bálint J, Kőszeghi S, Loxdale HD, Balog A (2019) Low and high input agricultural fields have different effects on pest aphid abundance via different invasive alien weed species. NeoBiota 43: 27–45. https://doi. org/10.3897/neobiota.43.31553

Abstract

We conducted field surveys to detect the population density of the most important invasive weed species and their associated virus vectoring aphids in crops grown under high input field (HIF) vs low-input field (LIF) conditions, with and without fertilizers and pesticides. The most frequent invasive weed species were *Stenactis annua*, *Erigeron canadensis* and *Solidago canadensis*. These species were hosts predominantly for the aphids *Brachycaudus helichrysi* and *Aulacorthum solani* in both management systems. The 13% higher coverage of *S. annua* under LIF conditions resulted in a 30% higher *B. helichrysi* abundance and ~85% higher *A. solani* abundance compared with HIF conditions. Host plant quality was assessed by measuring peroxidase enzyme activity. There was a significantly increased POD activity at 10 µmol min⁻¹ mg protein⁻¹ unit in *S. annua* under LIF conditions, suggesting a higher stress by aphids under this management regime. The high colonization intensity of *B. helichrysi* on maize, potato and alfalfa crops were detected from both *S. annua* and *E. canadensis*. We conclude that new and faster methods need to be used to prevent colonization of such virus vectoring aphids and their host plants, even under low input regimes.

Keywords

Alfalfa, cropping systems, maize, peroxidase enzyme activity, potato

Introduction

Invasive pests represent serious threats to crop production as global trade expands and climatic conditions shift (Copping 1998; Agrow 2015; USDA Forest Service 2015). Recent estimates suggest that the losses of crop yield caused by invasive pests, especially by weeds and aphids (Hemiptera, Aphididae), will increase by 25% in the EU by 2020 (USDA Forest Service 2015). Use of conventional chemical pesticides and herbicides to control weeds and arthropod pests represents a further challenge due to pollution, accumulation of toxins, pesticide residues in food, and resistance of the target pests to pesticides (Elbehri 2015). Invasive weeds are particularly important because they may serve as a food source for several local and invasive sap-feeding, virus-vectoring insects, and also because they may represent significant sources of plant pathogenic viruses (Frey et al. 2003; Anastasiu and Negrean 2005; Zimmermann et al. 2015). In the last 25 years, 435 alien weed species from 82 families have been reported from Central Europe (Anastasiu and Negrean 2005). Although weed management strategies involve different methods, including physical (mulching, tilling, burning), chemical and cultural control (high quality seeds, rotate crop, species, herbicide) (Chitsaz and Nelson 1983; Rand and Louda 2004; Uchino et al. 2012; Mabuza et al. 2013), the areas covered by invasive weed species are still increasing (Tunaitienė et al. 2015; Pacanoski 2017). Another important factor that is rarely considered is the effect of these invasive weeds on local sap-feeding pest insect populations such as aphids (Hemiptera, Aphididae) and the influence of the invasive weeds on neighbouring crop plants via aphids (through damage and virus transmission). In terms of the direct and indirect interactions between plants in close proximity, in which the influence of one plant on another can increase (associational susceptibility) or decrease (associational resistance) susceptibility, this can be viewed in the light of the potential importance of the relative abundance of focal and neighbouring plants and their herbivore abundances (Barbosa et al. 2009). Aspects however on natural habitat diversity (i.e. diverse habitat surrounded by natural landscape mosaics) and how management systems (low vs high chemical input) influence associational susceptibility or resistance have rarely been included in such analyses (Steffan-Dewenter et al. 2001). From this standpoint, the effect of the virus vectoring aphids, whose host range naturally includes both local and invasive plant species from the same family (e.g. Asteraceae), needs to be considered in testing associational relations in plantplant interactions (Bell 1983; Popkin et al. 2017).

The aim of the present study was to: a) assess the population density of the most important invasive weed species when agricultural crops are managed with high-input fertilizers and chemical pesticides (high-input fields, HIF) and without chemical management (low-input fields, LIF); b) identify and compare population densities of the most important aphid species on dominant invasive weeds; and c), detect the most suitable weed as hosts for aphids under different cropping systems by conducting the peroxidase (POD) enzyme activation test during aphid feeding. POD-inducible weed plants would be lower quality hosts, and less likely to confer associational susceptibility to nearby crops because they would not support large aphid populations. Thus POD enzyme activation is a useful indicator of associational susceptibility or resistance to aphid colonization (Argandoña et al. 2001; Chaman et al. 2001; War et al. 2012; Mai et al. 2016; Scully et al. 2016).

Study area, focal weed and aphid species

Experiments were conducted during the crop growing (vegetative) seasons of 2015 and the 2016 in Central and Eastern Transylvania, Romania in order to assess the population density of the most important invasive weed species and infesting virus-vectoring aphids, both from low- and high-input agricultural crops.

Low-input, traditionally managed fields (LIF). This area belongs to a traditionally managed field (low-input) of the Saxon cultural region encompassing an area of 7,440 km² at altitudes between 230 and 800 mm above sea level (a.s.l.) and characterized by a landscape mosaic of different land-cover types (28% forest, 24% pasture, and 37% arable land, mostly maize, potato and alfalfa). The farming practices in the studied area were predominantly small scale, with no chemical inputs and for subsistence purposes. One consequence of this land use is the exceptional biodiversity and natural value of the farming landscape (Akeroyd and Page 2001). However, the being not economically viable, the abandonment of croplands in this region is frequent, this resulting in the establishment and high abundances of invasive weeds (Zimmermann et al. 2015).

High-input, conventionally managed fields (HIF). This study region contrasts the previously described region by large monocultures and farming landscapes with low levels of natural vegetation and heterogeneity (Eastern Transylvania). The area of about 5,500 km² was intensively treated with synthetic fertilizers and pesticides, major crops were maize, potato and alfalfa (Table 1).

The studied fields from the two regions were situated in the same altitudinal range of about 250 m a.s.l. and under comparable bioclimatic conditions. The distance between the studied areas was about 200 km.

Three weed and two native aphid species were studied, these being the most common species in the study area. The most important weed species, all of the family Asteraceae, were the annual fleabane, *Stenactis* (*=Erigeron*) *annua* (L.), Canadian horseweed, *Erigeron* (*=Conyza*) *canadensis* (L.), and the goldenrod, *Solidago canadensis* (L.). These species are known to use a diverse range of habitats and are considered economically important weeds in Europe (Anastasiu and Negrean 2005). *Stenactis annua* is often a dominant species within the invasive weed communities, and has been reported from almost all European countries, its expansion showing an increase (Edwards et al. 2006; Tunaitienė et al. 2015; Pacanoski 2017). *Erigeon canadensis* is an annual plant native throughout most of North and Central America. It is also widely naturalized in Eurasia (Nandula et al. 2006; Shah et al. 2014; Bajwa et al. 2016). *Solidago canadensis* is a perennial weed native to north-eastern and north-central America, but has established as an invasive plant throughout Europe (Abhilasha et al. 2008; Fenesi et al. 2015).

Сгор		Treatments		
Potato	Fertilizer	N, P, K (15,15,15) 0.2 t/ha		
	Herbicide	Sencore (metribuzin70%)		
		Titus 25 DF (rimsulphuron)		
	Insecticide	Calypso (tiacloprid)		
	Fungicide	Banjo (fluazinam)		
		Ridomil Gold (mefenoxam, mankoceb)		
		Infinito (62.5 g/l fluopicolide + 625 g/l propamocarb clorhidrat)		
		Consento (375 g/l propamocarb clorhidrat + 75 g/l fenamidon)		
		Acrobat Mz (difenomorf, mankoceb)		
Alfalfa	Fertilizer	N, P, K (15,15,15) 0.16 t/ha		
	Herbicide	Pallas (piroksulam)		
	Insecticide	Fastac (alfa-cipermetrin)		
		Falcon Pro (protioconazol 53 g/l + spiroxamină 224 g/l + tebuconazol 148 g/l)		
	Fungicide	Amistar Xtra (azoxistrobin)		
Maize	Fertilizer	N, P, K-15,15,15 0.15 t/ha		
	Herbicide	Adengo (isoxaflutol 225 g/l + tiencarbazon-metil 90 g/l + ciprosulfamide (safener) 150 g/l)		

Table 1. Fertilizer and pesticide input on crops under high intensity management (HIF) in the two study years.

The two native aphid species included in this study where the highly polyphagous leaf-curling plum aphid, *Brachycaudus helichrysi* (Kaltenbach) and the similarly polyphagous foxglove aphid, *Aulacorthum solani* (Kaltenbach). These are particularly important species, not only because of their wide host plant range but also for their diverse virus transmission. The host plant range of *B. helichrysi* includes members of the Asteraceae, e.g. Chrysanthemum, species of *Prunus* and also species of *Solanum*, *Fragaria*, *Trifolium*, *Medicago*, and *Citrus* and maize (Tatchell et al. 1983; Powell et al. 1992; Isac et al. 1998; Popkin et al. 2017). Viruses transmitted by these aphids include plum pox, Potato virus Y and the Beet mild yellowing virus (Isac et al. 1998). Host plants of *A. solani* includes tomato, peppers, tobacco, celery, carrots, tulip bulbs, cucurbits and legumes (Tatchell et al. 1983; Jandricic et al. 2014). Of transmitted viruses, the most important are Potato viruses A, Y and X and Potato leaf roll virus, Cucumber mosaic virus, Soybean dwarf virus, Bean yellow mosaic virus and Turnip yellows virus (Jandricic et al. 2010, 2014).

Material and methods

Invasive weeds and associated aphids assessment

First, we selected two study sites in each region, these being 10 km in a fist and 15 km distant in a second region from each other. In each site we established two transects (at least at 1 km apart) of 10 m long \times 1 m wide at an approximately equal distance of at least three major crops (maize, potato and alfalfa). In this way, each transect was surrounded by at least 8–10 ha of high-input, and at least 0.5–3 ha area of low-input, agricultural crops. Each transect was carefully measured and located using GPS. Second, inside each

transect we placed ten 1 m² quadrats. Each of these quadrats was further subdivided in 10×10 cm plots (100 for each quadrat) and all plants (native and invasive) were counted and their coverage estimated within them. (Andújar et al. 2010). Third, ten invasive weed plant individuals from each quadrat were randomly collected in plastic bags. The number of invasive plants collected for each species from each quadrat mirrored the coverage of the species within the quadrat. We subjectively decided that we will collect at least eight plants when the coverage of a given species in a quadrat was at least 80% and up to two plants if the coverage of the species was up to 20%. We decided upon these percent coverage thresholds because in each quadrat there was one highly dominant invasive plant species (its coverage having at least 80%) and one species which had a coverage between 15–20%. Therefore from each quadrat, out of the 10 plants at least eight belonged to the dominant species and 1 or 2 to the second dominant species.

Because plants contained aphid colonies, and the exact number of individual aphids was important, all bags were labelled and kept at low temperature (near 0-4 °C in a cool box), then returned to the laboratory, whereupon all samples were stored at -20 °C, and aphids counted and species identified (Blackman and Eastop 2000; Blackman 2010). In total, 100 plant samples were collected per transect and management system (400 samples per management system per collection data). Assessment started at the end of May and repeated fortnightly five times during the summer until the end of the weed vegetative season, whereupon no more aphids were found. The whole procedure was repeated the following year using the same collection methods within the same transects. All aphids were carefully counted under laboratory conditions, and the various species identified).

POD enzyme extraction and activity assays in weeds

Leaf samples used for enzyme analyses were collected each year from each abundant weed species per experimental field, sub-area and transect, starting from the first until the last assessment. Separate young leaves, all containing aphids, were collected from the weeds (n = 10 samples / 1 m² sub-transect = 100 / transect). Samples were also held at -20 °C until enzyme extraction and activity assays.

For extraction, 400 mg of frozen leaves were homogenized in 1 ml of 50 mM phosphate buffer, pH 7.0, using a FastPrep Instrument high-speed benchtop homogenizer (MP Biomedicals). The homogenate was centrifuged at 6,500 r.p.m. for 20 minutes at 4 °C, and the supernatant collected. Protein concentration of the enzyme extract was determined by the Bradford method (Bradford 1976). POD activity was determined by the method of Németh et al. (Németh et al. 2009). The reaction mixture contained 955 µl of 50 mM phosphate buffer, pH 5.5, 10 µl of 0.01 g/l 3.3'-diaminobenzidine and 30 µl of enzyme extract. The reaction was initiated by the addition of 5 µl 0.3% hydrogen peroxide. The increase in absorbance at a wavelength of 480 nm was followed in a spectrophotometer for 5 minutes and 5 and 10 µmol min⁻¹ · mg protein⁻¹ unit of POD activity was separately defined as an absorbance change of 0.01 units·min ⁻¹.

Colonization experiment of aphids from weeds to crop plants

The experiment was performed during the vegetative period of 2017 by setting-up 30 blocks of the two most abundant weed species, *E. canadensis* and *S. annua* and the most frequent crop plants cultivated (maize, potato and alfalfa; Fig. 1). Because of a relatively low density of plants and high aphid density variation on *S. canadensis*, this weed was not included in the colonization experiment. Specimens of *E. canadensis* and *S. annua* of the same age (maturity) were collected in April from the field and potted in 8 litre pots.

After acclimatization in May, similar size plants of about 30 cm were selected for experiments. Crop plants of maize, potato and alfalfa were also cultivated in 8 litre pots, and similar sized plants selected in May for experiments. All weed and crop plants were first cleared of any infesting aphids by visual checking of all leaves and shoots. In the case of any aphid colony being detected, these were removed by brushing off colonies from the plants with a soft paint brush. If other insect species were detected, these were also removed. Insect-cleared plants were then allocated for experiments. Altogether 30 experimental blocks were set-up, 15 blocks with E. canadensis and 15 with S. annua under open field conditions where no other weeds and similar crop plants were present. Weed plants were placed at a distance of 20 m from each other, and six crop plant (two maize, two potato and two alfalfa) were placed around one weed plant to a distance of 50 cm (Fig. 1). Weed plants from each blocks were then artificially colonized with aphids by collecting *B. helichrysi* and *A. solani* from naturally occurring E. canadensis and S. annua plants. Leaves or shoots of weeds with aphid colonies were carefully removed, the colony of each aphid species reared to five individuals of 4th-instar nymphs by carefully brushing down all other individuals. Thereafter, the plant leaf or shoot was placed to the top of the experimental weed plant already placed in blocks. Each weed plants received two colonies (five aphids of each) from both aphid species.

The established aphid colonies (assessed by careful visual assessment over a 10 minute period as to whether aphids were feeding consistently on plants and not moving) were checked after 24, 48 and 72 hours. If no colony establishments were detected, new colonies were placed on the weeds. The aphids were then left to reproduce for 10 days. The assessment of aphids started after 14 days after aphid colony establishment, such that enough winged individuals were present to leave weeds and colonize crop plants. Aphid numbers were assessed on both weed and crop plants of the same blocks starting from mid-May as follows: two randomly selected blocks (one with *E. canadensis* and one with *S. annua* plants) were sampled by enclosing the infested plant in a transparent polythene bag and then cutting this free with scissors or a knife.

On return to the laboratory, the entire content was stored at -20 °C and the next day all samples were carefully assessed for aphids and their respective numbers counted under a stereo microscope. By this means, all individual aphids were captured and counted. The same procedure was repeated the following day, until the total number of blocks and plants were sampled by cutting all and aphids from plants counted in lab. The entire sampling was done within a two-week period and completed by the end of May, a time when aphid migration to new host plants occurs. All aphids were counted, recorded regarding the weed and crop plants they were collected from, and identified to species level.



Figure 1. Aphid colonization experiment design, weed plants of *E. canadensis* or *S. annua* surrounded by two maize, two potato and two alfalfa plants.

Data analyses

For weed data, the mean coverage in each 1 m² quadrats was determined by averaging the plant values from 10 × 10 cm plot. Next the inter-annual differences in coverage were tested using multivariate analysis of variance (MANOVA) and mean coverage values obtained for one 1 m² quadrat (40 data / field type / collection dates) were considered. No significant difference in weed coverage was detected between years (P =0.12). Therefore, data from the two years, collected on the same dates, were combined for the analyses. The weed frequency data were tested using Poisson-distributed errors and residuals for normality of errors (Kolmogorov-Smirnov test) and for equality of variance (Levene's test). Because residuals did not meet the assumption of normality, we used the non-parametric Kruskal-Wallis- and Mann-Whitney U test to compare variables. Weed species and management systems (HIF vs LIF) were used as fixed factors and the average weed coverage in 1 m² sub-transect as random factor.

All aphid species were correlated with particular weed species. In the case of one individual weed plant hosting two aphid species, the percentage of the species were considered. This was the case in only 7% of all the samples examined. It was then determined how cropping system differentially affected associational susceptibility to the two aphid species, *B. helichrysi* and *A. solani*. General linear modelling was used with mean aphid abundance on *S. annua, E. canadensis* and *S. canadensis* as response variable. Initial analyses indicated no difference (P < 0.23) between study years and aphid abundance averaged across study years were analysed. The model included cropping system type (HIF vs LIF), aphid species (*B. helichrysi* and *A. solani*) and their interaction as explanatory variables. Because aphid abundance is a discrete variable, Poisson-distributed errors were assessed. Aphid abundances on *S. annua* was normally distributed, so factorial ANOVA was used, followed by Tukey testing. Aphid abundance on *E. canadensis* and *S. canadensis* did not meet the assumption of normality, hence the Kruskal-Wallis test was used, followed by the Mann-Whitney U test. Significant (P < 0.05) interactive effects (cropping system type x species) suggest that the effect of cropping system depended on aphid species. All analyses were made using R version 3.0.1 (R. Core 2013). Only a small number of other aphid species (e.g. *Macrosiphum* spp.) were detected, and we did not include them in the analyses.

POD activity values obtained were compared between years (MANOVA) considering values from 1 m² sub-transects per sampling period. No significant year effect was detected (P = 0.61); therefore, data between years were averaged. Thereafter, POD values were compared between cropping system type (HIF vs LIF) for S. annua. This was done because only this weed was present during the whole vegetation period in all areas in both years, while the abundance of the other weed species sampled decreased in the HIF regime; thus the POD enzyme data were not compared statistically. POD values at 5 and 10 µmol min⁻¹ · mg protein⁻¹ unit were analysed separately and compared between fields from the first to the last day of sample collection. Because the residuals meet the assumption of normality, a complete randomized factorial ANOVA of POD specific activity values (5 and 10 µmol $\min^{-1} \cdot \max$ protein⁻¹ unit) was performed to test for effects of treatment (HIF vs LIF) and time (data collections). The analysis of Tukey test with P < 0.01 and LSMEAN (Minimal quadratic means) according to statistic package SAS were included and the average POD quantity / 10 plants / 1 m² sub-transect were used. Linear correlation between POD activity level at 5 and 10 μ mol min⁻¹ · mg protein⁻¹ unit and aphid (*B. helichrysi* and *A. solani*) abundances on S. annua plants under low and high input management were computed using the SPSS package version 3.14. Correlations were made between data (POD and aphids abundance) of the same sampling periods, and *r* and *P* values computed.

Effects of weed plants on *B. helichrysi* colonization toward each crop plant (maize, potato and alfalfa) were tested using repeated measures MANOVA. Interactions were then compared using χ^2 tests on the differences between the covariance matrices and by the root mean square error of approximation. The initial comparison was made between the two aphid species (*A. solani* and *B. helichrysi*) when these were on *E. canadensis*. Because of low density of *A. solani*, comparisons were made separately for those blocks where both aphid species were present (five blocks of *E. canadensis*), and for those where only the *B. helichrysi* persisted. The next analyses followed the comparison between aphids densities found on crop plants (maize, potato and alfalfa) when these were set in blocks with *E. canadensis* or *S. annua* were made using Student's t-tests, following the t-distribution. The statistical analyses were performed in R version 3.0.1 (R Core 2013).

Results

Dominant invasive weed species and their variations between management systems

Three invasive weed species were dominant during the two years field assessment. *Stenactis annua* was the most frequent weed, and dominated both LIF (97.5%) and HIF regimes (84.5%). Two other invasive weed species were present at lower densities. *S. canadensis* was only present in LIF, with an average coverage of 2.5%. No other invasive weeds were detected under this management system during the assessment *E. canadensis* was only present under HIF with an average coverage of 15%. Other weed species, mostly amaranth, *Amaranthus* spp. in HIF regimes with an average coverage of 0.5%, were detected during the end of the vegetation of the previous weed species. Dominance of *S. annua* was significant under both LIF and HIF (Table 2).

Table 2. The most frequent invasive weed average coverage between management systems. LIF = low-input field, HIF = high-input field. Data were compared using Kruskal-Wallis test, followed by Mann-Whitney U test.

Management	Weed species	Aver. Cov.(%)	median	25 th /75 th quart.	U	Р
LIF	Stenactis annua	97.50%	98.5	95/99	2.19	0.02
	Solidago canadensis	2.50%	1.5	1/5		
HIF	Stenactis annua	84.50%	84.5	83/86	2.16	0.03
	Erigeron canadensis	15%	14.5	13/16		

Aphids and their abundances on invasive weeds

The two important aphid species were detected in high densities on all three dominant invasive weeds. The most frequent species was *B. helichrysi*; its abundance was high and dominated the most frequent weed, *S. annua* under both HIF and LIF regimes (LIF-*B. helichrysi* and LIF-*A. solani* $F_{1-40} = 6.4$, P < 0.001; LIF-*B. helichrysi* and HIF-*A. solani* $F_{1-40} = 8.1$, P < 0.001) (Fig. 2). The next most abundant aphid was *A. solani*, also present on *S. annua* plants under both management systems; its density was significantly higher under LIF compared with HIF ($F_{1-40} = 8 P < 0.001$) (Fig. 2). Higher density of *B. helichrysi* was detected on *S. canadensis* under LIF ($U_{1-40} = 3.4$, P < 0.01) but its density varied greatly between assessment data (Fig. 3A). Furthermore, the dominance of the *B. helichrysi* on *E. canadensis* was detected under HIF conditions ($U_{1-40} = 3.1$, P < 0.01) (Fig. 3B). A very low number of other important aphid species were detected, i.e. about 12 individuals of *Macrosiphum* spp. were collected on *S. canadensis*.

POD enzyme activity on invasive weeds under aphids' feedings

No observable differences in POD enzyme activity were detected for *S. annua* at 5 µmol min⁻¹ · mg protein⁻¹ unit between HIF and LIF regimes ($F_{1-40} = 1.2, P < 0.2$) (Fig. 4A). When the POD activity was compared for the 10 µmol min⁻¹ · mg protein⁻¹ unit aliquot



Figure 2. The average *B. helichrysi* and *A. solani* aphid densities on *S. annua* in LIF and HIF. Aphids from 1 m² sub-transect (cumulated and averaged between years) were considered by factorial ANOVA, followed by Tukey testing. Arrows on bars represent standard errors; different letters indicate statistically significant differences at P < 0.01 level.



Figure 3 A, B Average *B. helichrysi* and *A. solani* aphid densities on *S. canadensis* and *E. canadensis* in LIF (**A**) and HIF (**B**) field. Aphids from 1 m² sub-transect (cumulated and averaged between years) were considered by Kruskal-Wallis test followed by Mann-Whitney *U* test. Stars above boxplots indicates statistical significant differences at P<0.01 level.

sample, there was a significantly higher enzyme activity, suggesting a significantly higher stress by aphids feeding on *S. annua* in LIF system ($F_{1-40} = 3.8$, P < 0.004) (Fig. 4B). Higher POD enzyme activity at both 5 and 10 µmol unit was detected on *E. canadensis* than on *S. canadensis*, again indicating higher stress as a result of aphid feeding; however, because of low samples numbers no statistics were performed here. There was a strong negative relationship between POD level at both 5 and 10 µmol unit and aphid density (both *B. helichrysi* and *A. solani*) abundances on *S. annua*. No such strong correlation between POD level and aphids abundance for HIF was observed (Table 3).


Figure 4 A, B POD enzyme activity at 5µmol (**A**) and 10 µmol min⁻¹ · mg protein⁻¹ unit (**B**) on *S. annua* and its variation between LIF and HIF. Analysis of Tukey test with P < 0.01 and LSMEAN (Minimal quadratic means) were used and the average POD quantity / 10 plants / 1 m² sub-transect were considered. Bars represent standard errors. Different letters indicate statistically significant differences at P < 0.01 level.

Table 3. Linear correlation between POD activity level at 5 and 10 μ mol min⁻¹ · mg protein⁻¹ unit and aphids (*B. helichrysi* and *A. solani*) abundances on *S. annua* plants under LIF and HIF. Correlation were made between data (POD and aphids abundance) of the same sampling periods.

Correlation	POD 5 µmol				POD 10 µmol			
	B. helichrysi		A solani		B. helichrysi		A solani	
	r	Р	r	Р	R	Р	r	Р
LIF	-0.67	0.21	-0.74	0.14	-0.76	0.12	-0.72	0.16
HIF	0.42	0.46	0.34	0.56	-0.48	0.4	-0.3	0.61

Colonization of aphids from weeds to crop plants

The number of *A. solani* were low and colonies persisted in five blocks on *E. canadensis* only, which shows a very similar trend with field observations of only 7% of *A. solani* detected together with *B. helichrysi*. The *B. helichrysi* colonies persisted in all blocks on both weed plants. Therefore, comparisons were made separately for those blocks where both aphid species were present, and separately for those where only the *B. helichrysi* persisted. Colo-



Figure 5. Colonization rate of *B. helichrysi* and *A. solani* from *E. canadensis* towards maize, potato and alfalfa plants. The average number of aphids / plots / plants / sampling data were considered. Interactions were then compared using χ^2 tests on the differences between the covariance matrices, and by the root mean square error of approximation. Numbers represent χ^2 -values for significant path coefficients. **P* < 0.05, ****P* < 0.001. Because of low *A. solani* numbers, no statistics were possible.

nization of *B. helichrysi* from *E. canadensis* was significant on all crop plants, with a higher number of aphids detected on maize. Low or no colonization of *A. solani* was detected from this weed to crop plants, hence no statistics were here possible (Fig. 5). By comparing the colonization of *B. helichrysi* from both weed species, again a significant effect toward all crop plants was detected (Fig. 6). The number of aphids on maize was significantly higher ($F_{1-14} = 5.8$, P < 0.01) when maize was in close vicinity with *S. annuus*. No differences in aphid abundance were detected for potato ($F_{1-14} = 2.5$, P < 0.28) and alfalfa ($F_{1-14} = 1.5$, P < 0.57) when these plants were in close vicinity with *S. annua* or *E. canadensis* (Fig. 6, bar charts).

Discussion

Here we showed that associational susceptibility can be detected between the most frequent weed and crop plants under the different crop management regimes. The



Figure 6. Comparison between colonization rate of *B. helichrysi* from *E. canadensis* and *S. annua* towards each crop plant (maize, potato and alfalfa). The average number of aphids / plots / plants / sampling data were considered. Interactions were then compared using χ^2 tests on the differences between the covariance matrices, and by the root mean square error of approximation. Numbers represent χ^2 -values for significant path coefficients. ***P* < 0.01, ****P* < 0.001. Bar chart represent comparison between aphids densities found on crop plants (maize, potato and alfalfa) when these were set in blocks with *E. canadensis* or *S. annua.* To compare variables, t-tests were used. Different letters indicate statistical significant differences at *P* < 0.01 level. Error bars = ±1 standard error.

high invasive weed density harbours a concomitantly higher aphid population density comprising local species. More precisely, a 13% higher coverage difference of *S. annua* in LIF further resulted in a significantly higher (about 30% higher) *B. helichrysi* aphid abundance under this management system. The same trend can also be detected for *A. solani*, where the 13% higher coverage of *S annua* resulted in an increase of about 85% for this aphid species under LIF compared to HIF (Table 2, Figs 2, 3). Altogether these results also show that the response to cropping system varied according to the aphid species (i.e. *A. solani* was less polyphagous than *B. helichrysi*), a scenario also supported in the case of lower *A. solani* density on weeds in the field and low colony persistence during the colonization experiment.

The colonization experiment also revealed that *S. annua* and *E. canadensis* can be considered suitable host plants for both aphid species examined, especially for *B. helichrysi*. Significant colonization from both weeds toward the most important crop plants

of this last aphid species were detected. Virus symptoms on potato crops (Potato virus Y and Potato leaf roll virus) were widely observable during the experiment (SZKA pers. obs.). Other previous studies, also reported similar findings, e.g. attack of the weevil, Rhinocyllus conicus (Coleoptera, Curculionidae) on the native Wayleaf thistle, Cirsium undulatum (Nutt.) Spreng increased three- to fivefold with increasing invasive Musk thistle, Carduus nutans (L.) density (Rand and Louda 2004). In a similar vein, frequency-dependence in terms of insect herbivore damage of Carolina horsenettle, Solanum carolinense (Asteraceae) was positively influenced by higher herbivore density on neighbouring Canada goldenrod, Solidago altissima (Kim 2017). The mechanisms that may influence associational susceptibility, the likelihood of detection of neighbouring plants, and the factors that can directly affect the survival of aphids on these plants may include the natural habitat diversity as well as the lack of chemical management under the LIF regime. The low distance between weeds and crop plants and the high habitat diversity may also clearly influence associational susceptibility of crop plants. This was clear in the present study when the abundance of both aphid species on S. annua were higher under LIF. In contrast to the present study, the densities of bean flies, Ophiomyia phaseoli (Tryon) and O. spencerella (Greathead) (Diptera, Agromyzidae) in Malawi and their rates of parasitism were not changed significantly when the field with non-host plants (bean-maize cultures) were diversified, while fertilizers had significant positive effect on fly densities (Letourneau 1995). In our case, the high habitat diversity and non-use of chemical pesticides in LIF probably had the most important effect on associational susceptibility and can explain the higher aphid abundance on *S. annua* under LIF (Fig. 2).

No clear associational susceptibility was however detected when comparing POD enzyme activity on S. annua. Higher POD activity of S. annua by B. helichrysi feeding was confirmed at 10 µmol unit only under LIF, but no such differences were detected at 5 µmol unit between LIF and HIF (Fig. 4A, B). High POD activity strongly suggests that S. annua would be a lower quality host, and less likely to confer associational susceptibility to nearby crops because these would not support large aphid populations, as also demonstrated by Dicke (1998). In our study, the relatively strong negative relationship between POD levels at both 5 and 10 µmol unit and aphids (both B. helichrysi and A. solani) abundances on S. annua under LIF were detected (Table 3). This clearly argues for a significantly higher stress by aphids feeding on S. annua, a lower quality host, thereby supporting a lower aphid density on this weed plant, a result not confirmed following aphid abundance assessment (Fig. 2). We explain this apparently contradictory result again by the fact that the habitat effect (via landscape mosaics diversity) had a stronger effect on aphid density, and recolonization of S. annua by aphids was faster than the repulsive effect of the high POD activity, a scenario that needs to be further tested.

The idea that plant-induced POD activity increases as a consequence of sap-feeding insect activity was first suggested by Felton et al. (1989; reviewed by War et al. 2012b). Furthermore, the evidence for an anti-herbivore role of POD derives from the discovery that the herbivore defence-inducing signal molecules systemin and methyl jasmonate (MeJA) induce POD activity levels in tomato leaves (Constabel et al. 1995; Constabel and Barbehenn 2008; Mai et al. 2016). Hence, the increased POD level indicating an intensive feeding process, especially from the aphid nymphs that injure plant cells, is consistent with high aphid preferences toward these particular plants (Dicke 1998; Argandoña et al. 2001b; Balog et al. 2017). Other studies have reported that other plant species, i.e. barley, *Hordeum vulgare* L. infested with greenbug aphids, *Schizaphis graminum* (Rondani) increased the total soluble POD activity in cv. Frontera, with a maximum level of hydrogen peroxide activity, H_2O_2 , observed after 20 minutes of infestation (Argandoña et al. 2001b). No influence of landscape diversity on POD activity as a consequence of aphid feeding have been detected until now, and the present study only suggests that such effect may exist. Therefore, additional empirical and laboratory studies are required to test possible landscape effects on plant molecular mechanisms influencing associational susceptibility and/or resistance.

Conclusion

The relevance of our study is threefold: environmental, crop management, as well as aphid control. In terms of environmental management, although low-input management farming systems are widely studied (Akeroyd and Page 2011; Fischer et al. 2012; Mikulcak et al. 2013) and are supposedly low-cost, effective systems (i.e. no or low management costs) with high biodiversity and cultural values (Hartel et al. 2013), the abandonment or absence of management may cause serious problems with increased virus vector aphid densities. Damage produced in this way may overcome the costs of any environmentally friendly weed controls. This effect, caused by aphids via invasive weeds, therefore needs to be considered when low-input management systems are directly compared with high-input ones in terms of costs and environmental values.

From a crop management perspective, new management systems and new assessment methods are necessary to evaluate the possible effect of weeds on vegetable and cereal crops due to aphid activity, both physical (i.e. direct feeding damage) and more importantly, via transmission of one or more plant pathogenic viruses.

Lastly, from the standpoint of aphid control and associated virus transmission, the complete lack of any management needs to be reconsidered. This is because high aphid density and possible virus infestation can make the cultivation of some crops under low-input systems difficult, if not impossible. These crops (potato) are, however, considered low-cost and low-input crops, and hence are widely cultivated under low-input management regimes. From our study, it is clear that cultivation methods, including invasive weed control, need to be synchronised and vector controls reconsidered, even if no other management is planned.

Acknowledgements

The authors are grateful to all those, especially local people, who made our assessments possible. We would especially like to thank Rajmund Simpf and Zsófia Simó for assisting in the initial stages of weed and aphid assessment. This research was supported

by the Higher Education Institutional Excellence Program (1783-3/2018/FEKUT-STRAT) awarded by the Ministry of Human Capacities within the framework of plant breeding and plant protection researches of Szent István University.

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REVIEW ARTICLE



Research on the social perception of invasive species: a systematic literature review

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Academic editor: I. Kühn | Received 14 November 2018 | Accepted 19 February 2019 | Published 14 March 2019

Citation: Kapitza K, Zimmermann H, Martín-López B, von Wehrden H (2019) Research on the social perception of invasive species: a systematic literature review. NeoBiota 43: 47–68. https://doi.org/10.3897/neobiota.43.31619

Abstract

We conducted a systematic literature review of the current state of research on the social perceptions of invasive species, aiming to provide guidance towards transdisciplinary research and participatory decision making. In order to detect patterns regarding publication trends and factors determining social perceptions of invasive species, we applied qualitative content as well as quantitative data analysis. By applying content analysis, we identified five main categories of influence on the perception of invasive species: ecological conditions, social conditions, values and beliefs, impacts, and benefits. The disciplinary focus of the research was predominantly interdisciplinary, followed by a social sciences approach. Our review revealed a disproportionate use of quantitative methods in research on social perceptions of invasive species, yet quantitative methods were less likely to identify benefits as factors determining the perception of invasive species. However, without the understanding of perceived benefits, researchers and managers lack the socio-cultural context these species are embedded in. Our review also revealed the geographical, methodological and taxonomic bias of research on perceptions of invasive species. The majority of studies focused on the local public, whereas fewer than half of the studies focused on decision-makers. Furthermore, our results showed differences in the social perceptions of invasive species among different stakeholder groups. Consensus over the definition and terminology of invasive species was lacking whereas differences in terminology were clearly value-laden. In order to foster sustainable management of invasive species, research on social perceptions should focus on a transdisciplinary and transparent discourse about the inherent values of invasion science.

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Keywords

conservation management, disciplinary bias, human perception, introduced species, stakeholders, transdisciplinary research

Introduction

Ecological research has been investigating the phenomenon of invasive alien species increasingly since the midst of the 20th century. Early research mainly focused on ecological aspects of biological invasions like principles of the invasion process (Sakai et al. 2001; Keane and Crawley 2002; Pyšek et al. 2008, Vaz et al. 2017a) and invasive species impacts on ecosystems (Parker et al. 1999; Ehrenfeld 2003; Gurevitch and Padilla 2004; Stricker et al. 2015). The economic costs incurred by biological invasions have gained more attention in recent studies (van Wilgen et al. 2001; Pimentel et al. 2005; Brunson and Tanaka 2011). However, the lack of social and cultural perspectives on invasive species has been repeatedly criticized (Gobster 2005, 2011; Gozlan et al. 2013; Abrahams et al. 2019). The exclusion of public perceptions from science and conservation management research creates a gap between the dynamics of invasions' processes and stakeholders' interests. First, since perceptions of invasive species are diverse (García-Llorente et al. 2008), opposing attitudes towards invasive species can only be understood by implementing social perspectives in research and decisionmaking. While decision-makers and scientists may hold more extreme views in relation to species' nativeness and abundance (Fischer et al. 2014), rural communities in South Africa, for example, perceived higher densities of an invasive cactus species as positive. This was on account of the usage of its fruits that provide notable socio-economic value (Shackleton et al. 2007). Second, the public may refuse to engage in, and even oppose, management measures concerning invasive species if their perspectives are ignored or misunderstood (Simberloff 2011; Woodford et al. 2016). To this end, Rotherham and Lambert (2011) show that county bird recorders in the UK simply withhold the location details of invasive ruddy duck breeding and wintering sites to save them from culling. Moreover, opposition from the public can result in conflicts with far-reaching consequences (Keulartz and van der Weele 2009), as in California, USA, where the eradication program targeting a pike species widely ignored stakeholders from the public, triggering lawsuits against the responsible authorities (Lee 2001). The examples imply that the integration and understanding of social and cultural perspectives in research on invasive species, and the consideration of biological invasions as socialecological phenomena, is crucial for their sustainable, i.e. both ecologically and socially successful, management (Kueffer 2013).

Recently, research on biological invasions has recognized the importance of social perceptions of alien invasive species for their management (Kueffer 2017, Shackleton et al. 2019a) with some rare exceptions focusing on human dimensions of biological invasions earlier (e.g. McNeely 2001; McNeely 2005). Research on social perceptions of invasive species is rather broad and has considered different aspects, such as stakeholders' knowledge concerning invasive species (Eiswerth et al. 2011), economic impacts

of invasive species (Osteen and Livingston 2011; Shackleton et al. 2011; Humair et al. 2014a), cultural values and beliefs (Coates 2011; Notzke 2013; Bhattacharyya and Larson 2014) or socio-demographic variables (Norgaard 2007; Haab et al. 2010; Beard-more 2015). Despite these advancements in understanding social perceptions of invasive species, a synthesis of published literature on the issue is lacking (but see Shackleton et al. 2019b for a different approach). To this end, we need to gain a better understanding on how values and perception translate into practices and to develop methods for assessing the complex factors that influence people's perceptions (Shackleton et al. 2019a).

This study provides a systematic review of the current state of research on social perceptions of invasive species. Our definition of social perception is rooted in the literature that we reviewed; to this end, we define perception broadly as the diverse ways in which people consciously recognize invasive species. We particularly aim to identify research patterns concerning publication trends, methodological approaches, study objects, invasive species concept and factors determining the social perceptions of invasive species. A review of the perception of invasive species, and especially on the factors influencing these perceptions, can provide an important step towards transdisciplinary research and participatory decision making and thus may contribute to invasion biology as well as to sustainable conservation management and environmental policy.

Material and methods

The systematic literature review focusing on the social perceptions of invasive alien species follows the guidelines of previous systematic reviews (e.g. Abson et al. 2014; Nieto-Romero et al. 2014; Luederitz et al. 2015, 2016). For our consideration, invasive alien species are those that reached new geographic areas by human introduction and are currently leading to major impacts on the environment or society (Richardson et al. 2011). In January 2016, a keyword-based search was conducted using the Scopus database (https://www.scopus.com/), thereby including peer-reviewed English journal articles. Peer-reviewed literature is widely dominated by English articles and keeping the review restricted to one language also ensured comparability, especially when analyzing the use of terminology. Furthermore, the aim of our systematic review was to investigate research on the perception of invasive alien species and therefore we reviewed research articles and not grey literature. We opted for Scopus as our search engine, because the scientific literature is slightly biased towards Natural Science in ISI Web of Knowledge. Being aware of the application of different terms to describe invasive species in different scientific disciplines, the keywords were selected in order to cover a broad range of scientific concepts of invasive species. This review is about the scientific literature that designates invasive or alien species as the underlying construct. We did not exclude articles based on the invasion stage within the introduction-naturalizationinvasion continuum. However, we expect articles on the perception of invasive alien species to be predominantly about invasive species based on the definition that they have self-replacing populations and produce reproductive offspring often in very large

numbers in the new environment (Richardson et al. 2011). We were especially interested in data about the perception of invasive alien species that are established and call for management action.

Thus, the four different search keyword strings were

- (1) perception* AND invasive* AND species* (n = 288);
- (2) perception* AND non-native* AND species* (n = 79);
- (3) perception* AND alien* AND species* (n = 99) and

(4) perception* AND exotic* AND species* (n = 103).

Overall, we established an initial database of 569 records which could be reduced to 436 records by removing all duplicates. During the screening process, there were two different stages of selection (Suppl. material 1). First, records that were not peerreviewed articles were excluded (n = 55). Second, we removed 251 articles that did not focus on the issue of social perception of invasive alien species by screening the abstracts (not related to invasive species (n = 139), not related to social perception (n = 81), no survey conducted (n = 31). For example, the publication by Rudrappa and Bais (2008) was returned by our search string; however it dealt with the perception strategies between plants which was not part of our research question. In another example, Finnoff et al. (2007) investigated the perception of control measures and not the perception of invasive alien species itself. These two publications were excluded together with 79 other publications that did not investigate how invasive alien species were perceived.

Then we conducted a full-text screening of the remaining 130 articles and excluded a further 53 articles that did not address our guiding questions and a further 9 articles that were not accessible. Finally, 77 articles were used for data extraction and analysis (Suppl. material 2). Our search was limited to the keyword perception, which we believe encompasses relevant concepts like attitude or opinion. However, thereby we also lost some amount of the literature that did not use the keyword perception. By counterchecking our search strings with the knowledge of important studies we verified that landmark papers were caught by our search string. Therefore, we believe that we have a consistent search string with a high specificity.

We applied quantitative data analysis of multiple variables around four criteria (Table 1): publication characteristics, methodological approach, study objects and invasive species concept. Then, to analyze the factors determining the social perception of invasive species, we applied qualitative content analysis by using MAXQDA – a software for qualitative and mixed methods data analysis (http://www.maxqda.com). Qualitative content analysis was guided by a grounded theory approach (Peterson et al. 2010) and entailed reading and re-reading the text for determining emerging patterns as categories of analysis (Fereday and Muir-Cochrane 2006). To this effect, we followed an inductive approach and developed the factors driving social perception from the material. During this iterative process, we derived five distinctive broad categories of influences (Table 2):

Criteria	Variables				
Publication characteristics					
year of publication	1995–2016				
disciplinary focus	Interdisciplinary ¹ , natural sciences, social sciences, transdisciplinary ²				
study site	name of the region				
Methodological approach					
type of survey	interview, questionnaire, mixed, others ³				
type of data	qualitative, quantitative, both				
Study objects					
species identification	name(s) of the examined species				
taxonomic groups	mammals, birds, fish, reptiles, invertebrate insects, invertebrate non-insects, plants				
species' environment	terrestrial, marine-coastal, fresh water				
type of stakeholders	local public ⁴ , decision-makers ⁵ , scientists ⁶ , others ⁷				
Invasive species concept					
definition of 'invasive species'	present, absent				
terminology	invasive, alien, invasive alien ⁸ , exotic, introduced, non-native				

¹Studies covering a social-ecological perspective including natural and social science perspective

²Studies involving academic researchers from several disciplines as well as non-academic participants in a joint problem framing process

³Includes workshops, discussions, focus-groups, case-studies, observation

⁴Includes residents, public and resource users like farmers, ranchers, foresters, fishers, anglers, hunters, retail professionals, gardeners, horticulturists

⁵Includes conservation professionals and managers, government employees and politicians

⁶Includes scientist and students

⁷Includes NGO-members, activist, tourists, journalists, web-users

⁸Includes 'alien invasive'

ecological conditions, social conditions, values and beliefs, impacts, and benefits of invasive alien species. Ecological conditions (EC) refer to the effect of invasive alien species' traits, abundance or spread on social perception. They were sub-coded into factors that referred to species' traits (EC,) and species' invasion status (EC,). Social conditions (SC) identify the societal framework's effects on social perceptions of invasive species, sub-coded as socio-demographics and interests (SC₁), power, trust and responsibility (SC₂), language use and communication (SC₂), and knowledge and awareness (SC₄). Values and beliefs (VB) label culturally and historically evolved mindsets' influences on social perceptions and were sub-coded into factors referring to beliefs about nativeness (VB,), beliefs about nature (VB_2) , socio-cultural values (VB_3) , and sense of place (VB_4) . Impacts (I) referred to the damaging potential of invasive species and were sub-coded into ecological (I1), economic (I_{2}) and *socio-cultural impacts* (I_{2}) . Finally, *benefits* (B), referring to beneficial effects of invasive species' traits and use, were sub-coded - complementary to impacts - into eco*logical* (B_1), *economic* (B_2) and *socio-cultural* (B_3) benefits. The derived categories and factors influencing the social perception of invasive species with description and relevant examples from the corpus can be found in Table 2 and in more detail in Suppl. material 3. To determine significant differences and dependencies between all the collected variables (Table 1) and factors (Table 2), we conducted Chi-Square tests with R, a free software for statistical computing and graphics (https://www.r-project.org/).

Categories	Factors	Relevant examples from the set of data
Ecological conditions (EC)	Species' traits (EC ₁) Invasion status (EC ₂)	Pastoralists' observations indicated that the presence of heavy and elongated thorns and its symbiotic relation with biting ants leads to the labeling of A. drepanolobium as the most invasive woody plant with no contribution to livestock feed (Terefe et al. 2011: 1069). (EC ₁)
Social conditions (SC)	Socio-demographics and interests (SC ₁) Power, trust and responsibility (SC ₂) Language use and communication (SC ₃) Knowledge and awareness (SC ₄)	Poorer people will rely more on acacias for subsistence needs, whereas in richer economies tree use depends on specific commercial markets. The opportunities for such uses will be affected by the structure of land tenure (state-owned, community access and private farm) and by prevalent environmental discourses, policies and development levels in a particular region (Kull et al. 2011: 825). (SC ₁ ; SC ₂)
Values and beliefs (VB)	Beliefs about nativeness (VB ₁) Beliefs about nature (VB ₂) Socio-cultural values (VB ₃) Sense of place (VB4)	Conflicts over wild and free-roaming horses in the Chilcotin are a political and economic expression of the clash over deeper cultural and environmental values (Bhattacharyya and Larson 2014: 674). (VB ₂ ; VB ₃)
Impacts (I)	Ecological impacts (I ₁) Economic impacts (I ₂) Socio-cultural impacts (I ₃)	Since its introduction Mimosa pigra has exerted a considerable impact on the environment, agricultural resources and people's livelihoods in densely populated regions in Cambodia, the weed invades and virtually 'locks up' productive floodplain areas, transforms riparian habitats, and – directly or indirectly – causes significant, economically relevant damages on the paddy fields (Rijal and Cochard 2015: 10). (I, i, I,)
Benefits (B)	Ecological benefits (B ₁) Economic benefits (B ₂) Socio-cultural benefits (B ₃)	The wattle is an important resource for village households; virtually all households used it as their primary heat source and for building materials. Other uses included medicine extraction and 20% of the interviewed households gained income from selling firewood (de Neergard et al. 2005: 217). (B ₂ ; B ₃)

Table 2. Categories influencing the social perception of invasive alien species with factors and relevant examples from the set of data.

Results

Historical trends, disciplinary and geographical distribution of studies

While in the 1990s and early 2000s, publications analyzing the social perception of invasive species were scarce, with one publication in 1995, 1999, 2003 and 2005 respectively, there has been an acceleration of publications since 2010. Seventy-three percent of the publications included in this review were published between 2010 and 2015, with peaks in 2011 (19%) and 2014 (16%) (Fig. 1). The disciplinary focus of the research was predominantly interdisciplinary (62%), followed by a social science approach (31%) whereas the remaining disciplinary approaches were comparatively low with 4% of the studies using a transdisciplinary and 3% using a natural science approach (Fig. 2a). The research is dominated by studies conducted in North America (32%) and Europe (28%), followed by Africa (17%), Asia, Oceania (9% respectively) and South America (6%) (Fig. 2b).

Methodological approach, study objects and invasive species definitions

Methodological approach of the studies was dominated by quantitative (46%) and mixed methods (40%) whereas qualitative methods (14%) were used less frequently



Figure 1. Number of publications included in this systematic review published per year.

(Fig. 2c). This is also reflected by the type of the surveys: the majority of studies used questionnaires (40%) or a mix of different methods (35%) followed by interviews (18%) and other approaches (7%), including workshops, discussions, focus-groups or observation (Fig. 2d). The majority of the studies focused on invasive plants (58%) and mammals (23%) (Fig. 3a) and were conducted on terrestrial environments (78%) (Fig. 3b). The complete list of study species is presented in Suppl. material 4. The majority of publications analyzed the local public's perception of invasive species (79%), followed by decision-makers (35%), scientists (23%) and 'others' (9%), including NGO-members, activists, tourists, journalists and web-users (Fig. 3c). A clear majority of 65% of the studies did not define their concept of invasive species' (13%), 'non-native species' (9%), 'exotic species' and 'introduced species' (8% respectively) (Fig. 2e).

Trends concerning research characteristics

Research on the perception of invasive alien species showed clear trends, mainly referring to disciplinary bias. First, studies that were published between 2010 and 2015 were less likely to have an interdisciplinary focus than former years ($\chi^2 = 4.6$; p < 0.05). Second, disciplinary focus of the studies impacted geographical distribution and methodological approach of the research as well. Studies with an interdisciplinary focus were more likely to conduct their research in Africa ($\chi^2 = 10.3$; p = 0.001) and to use a mixed-methods ap-



Figure 2. Percentage of studies covering publication characteristics (**a**, **b**), methodological approach (**c**, **d**) and invasive species concept (**e**).

proach ($\chi^2 = 4.0$; p < 0.05), whereas studies with a social science focus were more likely to conduct their research in North America ($\chi^2 = 6$; p < 0.05). Third, the disciplinary focus of the research significantly influenced the approach concerning definition and terminology of invasive species. Studies with a social science focus were more likely to define their concepts of invasive species ($\chi^2 = 6.9$; p < 0.01) and to use the term 'non-native' to describe invasive species ($\chi^2 = 5.1$; p < 0.05). In contrast, studies with an interdisciplinary focus were less likely to give a definition of their concept of invasive species ($\chi^2 = 6.9$; p < 0.01) and to use the term 'alien invasive' to describe invasive species ($\chi^2 = 6.9$; p < 0.01).

Factors determining the social perception of invasive species

The publications analyzed in this study referred differentially to factors influencing the social perception of invasive species. *Social conditions* (SC) were mentioned most



Figure 3. Study objects distinguished by a taxonomic group b species' environment and c type of stakeholders.

frequently by 75 out of 77 publications, followed by *impacts* (64 publications), *values and beliefs* (61 publications), and *benefits* (50 publications). *Ecological conditions* (EC) were least often determined as only 42 out of 77 publications mentioned EC as having an influence on the social perception of invasive species (Fig. 4). Factors of *social conditions* (SC) had a wide spectrum from *knowledge and awareness* (SC₄) being mentioned most often by 83% of publications, to *language use and communication* (SC₃) being mentioned least often by only 36% of publications. In contrast, the distinct factors of *values and beliefs* (VB) were quite equally distributed (Fig. 4). Notably, impacts (I) and benefits displayed a reverse distribution as 77% of the studies mentioned *ecological impacts* (I₁), followed by 56% of the studies mentioning *economic impacts* (I₂) and 48% of the studies mentioning *socio-cultural impacts* (I₃) were mentioned in 57% of publications, followed by *economic* benefits (B₂) mentioned in 55% and *ecological benefits* (B₁) mentioned in 35% of publications (Fig. 4).



Figure 4. Factors determining the social perception of invasive species identified by the studies in percentage, distinguished by the five main categories: social conditions N = 75, ecological conditions N = 42, values and beliefs N = 61, benefits N = 50 and impact N = 64.

Dependencies of factors determining the perception of invasive species

When testing for dependencies between variables extracted from the papers (Table 1) and factors determining the perception of invasive species (Table 2), we mainly identified significant relations for *benefits* (B) and *values and beliefs* (VB).

In contrast to *impacts* (I), *benefits* (B) showed more diverse and significant relations to research characteristics. First, we found spatial differences influencing the identification of benefits of invasive species, with studies conducted in Africa being more likely to identify *ecological benefits* (B₁, $\chi^2 = 4.1$; p < 0.05) whereas studies in Europe were less likely to identify *ecological* (B₁, $\chi^2 = 5.3$; p < 0.05) and *socio-cultural benefits* (B₃, $\chi^2 = 4.4$; p < 0.05) as factors determining the social perception of invasive species. Second, results indicate a methodological bias in determining *benefits* (B). Studies using quantitative methods were less likely to identify *ecological* (B₁, $\chi^2 = 7.2$; p < 0.01), *economic* (B₂, $\chi^2 = 7.8$; p < 0.001) and *socio-cultural benefits* (B₃, $\chi^2 = 4.3$; p < 0.05) as factors determining the species. Third, terminology to describe invasive species also determined the identification of *benefits* (B). Notably, studies that used the term 'exotic' to describe invasive species had a focus on *benefits* (B) as they were more likely to identify *ecological* (B₁, $\chi^2 = 5.1$; p < 0.05) and *economic benefits* (B), as studies that analyzed the perception of invasive invertebrate insects were less likely to identify *socio-cultural benefits* (B), $\chi^2 = 5.8$; p < 0.05) and *economic benefits* (B), as studies that analyzed the perception of invasive invertebrate insects were less likely to identify *socio-cultural benefits* (B₃, $\chi^2 = 5.8$; p < 0.05) and *economic benefits* (B), as

ferences in species' environments also influenced the perception of invasive species. For example, studies analyzing the social perception of invasive species in marine-coastal environments were less likely to identify *ecological benefits* ($B_{1;}\chi^2 = 6.1$; p < 0.05) as determining perception.

Furthermore, results indicate that terminology is characterized by a focus on *values* and beliefs (VB). Studies that used the term 'introduced' to describe invasive species were more likely to identify *socio-cultural values* (VB₃, $\chi^2 = 5.4$; p < 0.05) as well as *sense* of place (VB₄, $\chi^2 = 5.1$; p < 0.05). In contrast, studies that used the term 'non-native' to describe invasive species were more likely to examine *beliefs about nature* (VB₂, $\chi^2 = 4.6$; p < 0.05), *socio-cultural values* (VB₃, $\chi^2 = 8.6$; p < 0.01) and *beliefs about nativeness* (VB₁, $\chi^2 = 11.7$; p = 0.001) as factors influencing the social perception of invasive species.

Finally, results also indicate that there is a distinction in the perception of invasive species by stakeholders. Whereas the local public were more likely to focus on *socio-cultural benefits* ($B_{3,}\chi^2 = 4.3$; p < 0.05), academics attached special importance to *beliefs about nativeness* ($VB_{1,}\chi^2 = 5.4$; p < 0.05). Studies that examined decision-makers' perception of invasive species were more likely to identify *socio-demographics and interests* ($SC_{1,}\chi^2 = 7.7$; p < 0.01), *ecological impacts* ($I_{1,}\chi^2 = 6.8$; p < 0.01) and *sense of place* ($VB_{4,}\chi^2 = 7.0$; p < 0.01) as determining their view.

Discussion

Despite the entanglement of humans and invasive species and the essential role of perception in the management of invasive species, our study shows that research on social perceptions of invasive species is still in its infancy. For example, whereas Lowry et al. (2012) identified almost 300 publications per year investigating biological invasions in general in 2009 and 2010 respectively, our review focusing on social perceptions of invasive species identified only 2 publications from 2009 and 8 publications from 2010. However, more recently, researchers increasingly called for studies on the entanglement of humans with invasive alien species in order to move managing invasions forward (Shackleton et al. 2019a). Our findings complement a framework published in a special issue on the human and social dimension of invasion science which is based on six key factors that influence people's perception of invasive alien species developed during an interdisciplinary expert workshop (Shackleton et al. 2019b). Overall, our five main categories drawn from 20 years of publications correspond to the key factors developed during the expert workshop. Their key factor "attributes of individuals perceiving the invasive alien species" is reflected in our main categories values and beliefs (VB) and social conditions (SC). These factors describe the demography, values and knowledge system of the individual person. Shackleton et al. (2019b), on the other hand, summarize all attributes within the key factor "Individual(s)", based on the literature we differentiated between values and belief (VB) that describe beliefs about nativeness, nature, aesthetic values and sense of place and social conditions (SC) that describe demographics, interests, language use and communication, knowledge and awareness as well as trust or distrust in governmental and decision-making structures. Overall, our review focused on research about the individual's perception of invasive alien species, which is reflected in the individual perspective of our categories, while Shackleton et al. (2019b) nested their key factors within a landscape, socio-cultural and institutional context. The personal perspective of trust or distrust in governmental and decisionmaking structures is incorporated in the framework's "Institutional, governance and policy context" which represents more formalised and larger scale structural socio-cultural factors. However, as a starting point, both approaches confront the individuals' with the species' attributes. Species' attributes are defined by species traits and invasion status and are labelled here ecological conditions (EC). Our results indicate that social conditions have been dominating social perceptions of invasive species whereas ecological conditions were less relevant (Fig. 4). Following the attributes of people and invasive alien species, the effects of invasive alien species are the third cornerstone in both studies. Matching the classification made by Shackleton et al. (2019b), our review confirmed the differentiation of ecological, social and economic effects of invasive alien species; however, we further distinguished between impacts (I) and benefits (B). The main difference between our categories and the Shackleton et al. (2019b) framework is that while we extracted some information on ecosystem type during the review process (Table 1) the landscape context is not part of our main categories driving the perception of invasive alien species. We did not include land tenure or land use as review categories, since these factors were not sufficiently abundant during the coding process.

One of the challenges to conduct research on social perceptions of invasive species is the need for inter- and transdisciplinary approaches. Our study shows that the interdisciplinary perspective is dominating, yet it shows decreasing trends with a concurrent increase of social sciences whereas transdisciplinary perspectives are still underrepresented. These findings are in line with Vaz et al. (2017a) who have shown that interdisciplinarity in invasion science is mostly remaining within the natural sciences. Thus, they plea for reframing biological invasions as a social-ecological research field, so fostering collaboration between science, governance and society.

Moreover, our findings reveal that research on social perceptions of invasive species comprises geographical, methodological, and taxonomic biases. First, most research has been conducted in North America and Europe (Fig. 2b). Similar results have been found previously regarding research on invasive species. For example, Pyšek et al. (2008) indicated that more than half of the studies on invasive species were conducted in North America. Similarly, Kenis et al. (2009) revealed that two thirds of studies on invasive insects are conducted in North America. This geographical bias can be explained by historical, societal, political and economic differences between Global South and Global North (Nuñez and Pauchard 2010). Second, our results indicate that there is a methodological bias in research on the social perception of invasive species (Fig. 2a). Publications are dominated by the use of quantitative and mixed methods. However, our results show that studies using quantitative methods were significantly less likely to identify benefits of invasive species. The disproportionate use of quantitative methods in research on social perceptions of invasive species may lead to

positive bias towards impacts rather than benefits. However, without the understanding of perceived ecological, economic and/or socio-cultural benefits, researchers and managers lack the socio-cultural context in which these species are embedded. The inclusion of local stakeholders' perceptions into invasive species research and management may lead to a more balanced and thus more representative view on invasive species impacts and benefits. Our findings are in line with previous systematic reviews that showed that research in different fields of invasion biology is biased, e.g. towards methods and study regions (Dana et al. 2014; Stricker et al. 2015). Third, our findings confirmed the general taxonomic bias that more studies are conducted on invasive plants than on any other taxonomic group (Pyšek et al. 2008). However, in contrast to Pyšek et al. (2008) who found that invertebrates were also abundantly studied, we found that mammals are the second largest group in the research focus (Fig. 3a). This is in accordance with Fleming and Bateman (2016) who showed that species that are particularly charismatic, large, attractive or economically valuable are more likely to be studied by invasion biologists. Our finding that invasive invertebrate studies were less likely to identify socio-cultural benefits of invasive species results from the focus of the reviewed literature that was either on invasive insects as vector of diseases (e.g. Abramides et al. 2013), pest species (e.g. Mackenzie et al. 2010), or species that were introduced as plaque control but became invasive (e.g. Otieno et al. 2013).

In addition, our results indicate that social conditions have dominated social perceptions of invasive species whereas ecological conditions were less relevant (Fig. 4). Furthermore, our results show differences in the social perceptions of invasive species concerning different stakeholder groups. Whereas scientists focused on invasive species' origin, decision-makers were more attached to ecological impacts and sense of place. This follows the results from Boonman-Berson et al. (2014) revealing that invasiveness is constructed differently in science and policy. Notably, decision-makers seem to form an exposed view on invasive species. Since early prevention of biological invasions is most effective compared to cost-intensive control or eradication programs, decision-makers are encouraged to implement management measures at a premature stage of invasion. They are under pressure to provide an urgent response to emerging biological invasions with only limited funding and high uncertainties (Larson et al. 2011; Liu et al. 2011; Sims et al. 2016). As scientists and conservation managers hold different priorities, motivations and approaches to engage with invasive species, communication barriers and conflicts can occur (Shaw et al. 2010). Therefore, research on invasive species is urged to integrate decision-makers' perspectives into transdisciplinary research processes, in which knowledge is co-produced by different stakeholders. Vaz et al. (2017b), for example, propose a framework for integrating ecosystem services and disservices into human valuation of plant invasions, fostering a social-ecological management of invasive species. In fact, the inclusion of different stakeholders' perspectives in the research of social perceptions of invasive species is one of the major gaps that can jeopardize the implementation of management programs aiming at resolving social conflicts associated with invasive species. Recent accounts emphasized that the problem of invasive species can also be a mutual learning process (Bryce et al.

2011; Gaertner et al. 2016), underlining the importance of including diverse stakeholders when considering management options (Novoa et al. 2018).

In particular, there is scarce research focusing on perspectives of marginalized groups. For example, Bhattacharyya and Larson (2014) criticize the lack of indigenous perspectives on invasive species in science as well as in decision-making processes. Robbins (2004), for example, addresses classed and gendered aspects of the phenomenon of invasive species. Carruthers et al. (2011) emphasize that since power transforms dominant interests of stakeholders into management decisions, power relations are strongly influencing the perception of invasive species. Thus, further research should focus on the transdisciplinary integration of balanced perspectives into invasive species management and research and conservation management should engage with power relations among stakeholders.

Our research identified an apparent lack of consensus in definition and terminology of invasive species, which is in line with an ongoing debate in invasion biology and beyond (Soulé 1990; Colautti and MacIsaac 2004; Murphy et al. 2006, Humair et al. 2014b). Existing definitions of 'biological invasions' and 'invasive species' have been critically scrutinized. Origin, behavior and impacts are identified as the main criteria defining invasive species but are criticized for being ambiguous and remaining subjective to a certain degree (Boonman-Berson et al. 2014). Whereas the terminology to describe invasive species is inconsistent and value-laden, terms like 'invasive', 'nonnative', 'exotic' or 'introduced' are often used synonymously and without clear definition (Richardson et al. 2000; Bowker 2014; Parejo et al. 2015). Our results indicate that the use of different terms reflects a particular focus on different aspects of invasive species research and perception. Here, we cannot be certain how the use of different terminology by researchers already determines the outcome of species perception. For example, when the term 'exotic' was used in the research, studies focused on the benefits of invasive alien species. This is in accordance with Hall (2003) emphasizing that 'exotics' historically have been associated with providing human benefits. Ideologically motivated terminology in invasion biology is criticized massively (Warren 2007). With our present study we therefore support efforts that are undertaken to redefine the concepts of invasive species and to develop a clear common and neutral terminology (Falk-Petersen et al. 2006; Young and Larson 2011).

Furthermore, we could show that values and beliefs are an integral part of the research on perceptions of invasive species. The decisive influence of values and beliefs has also been confirmed for invasion biology and conservation management (Carruthers et al. 2011; Bocking 2015). Different conceptualizations of nature, culture and their relationships profoundly determine the perception of invasive species of both scientists and the public. There is a diverse typology of human values and heuristic rules available from Estévez et al. (2015), who present the different ethical underpinnings that people have regarding invasive species.

As biological invasions are associated with the loss of biodiversity and sense of place as well, it may demarcate a promising initial point for transdisciplinary research to include both social and ecological perspectives on invasive species (Bardsley and Edwards-Jones 2006; Keulartz and van der Weele 2009, Kueffer 2013, Essl et al. 2017). Instead of blaming certain values as false and counterproductive, further research on invasive species should focus on a transdisciplinary and transparent discourse about the inherent values of invasion biology in order to foster negotiation of social-ecological concepts of invasive alien species and to develop sustainable valuation and management on biological invasions. In addition, based on our results, future research would clearly benefit from a consistent terminology and a plurality of method approaches (von Wehrden et al. 2017) in order to hold true on the promise that invasion science should not only highlight and enumerate problems but move management of invasive species on the ground forward.

Acknowledgements

H. Zimmermann received funding from the State of Lower Saxony (Niedersächsisches Ministerium für Wissenschaft und Kultur) and the Volkswagen Foundation in line with the research projects "Bridging the Great Divide" (Grant Number VWZN3188).

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Supplementary material I

Flow diagram of the selection process used in this systematic review

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Data type: background information

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Link: https://doi.org/10.3897/neobiota.43.31619.suppl1

Supplementary material 2

Articles included in the analysis

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Data type: background information

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Link: https://doi.org/10.3897/neobiota.43.31619.suppl2

Supplementary material 3

Factors influencing the social perception of invasive species

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Data type: background information

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Link: https://doi.org/10.3897/neobiota.43.31619.suppl3

Supplementary material 4

Species examined in the publications analyzed in this review

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Data type: background information

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Link: https://doi.org/10.3897/neobiota.43.31619.suppl4

REVIEW ARTICLE



Assessing the environmental impacts of invasive alien plants: a review of assessment approaches

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Academic editor: J. Kollmann | Received 27 September 2018 | Accepted 26 February 2019 | Published 15 March 2019

Citation: Bartz R, Kowarik I (2019) Assessing the environmental impacts of invasive alien plants: a review of assessment approaches. NeoBiota 43: 69–99. https://doi.org/10.3897/neobiota.43.30122

Abstract

Assessing the impacts of alien plant species is a major task in invasion science and vitally important for supporting invasion-related policies. Since 1993, a range of assessment approaches have been developed to support decisions on the introduction or management of alien species. Here we review the extent to which assessments (27 approaches) appraised the following: (i) different types of environmental impacts, (ii) context dependence of environmental impacts, (iii) prospects for successful management, and (iv) transparency of assessment methods and criteria, underlying values and terminology. While nearly all approaches covered environmental effects, changes in genetic diversity and the incorporation of relevant impact parameters were less likely to be included. Many approaches considered context dependence by incorporating information about the actual or potential range of alien species. However, only a few went further and identified which resources of conservation concern might be affected by specific alien plant species. Only some approaches acknowledged underlying values by distinguishing negative from positive impacts or by considering the conservation value of affected resources. Several approaches directly addressed the feasibility of management, whereas relevant factors such as availability of suitable management methods were rarely considered. Finally, underlying values were rarely disclosed, and definitions of value-laden or controversial terms were often lacking. We conclude that despite important progress in assessing the manifold facets of invasion impacts, opportunities remain for further developing impact assessment approaches. These changes can improve assessment results and their acceptance in invasion-related environmental policies.

Keywords

Alien species, biological invasions, environmental damage, environmental impacts, impact assessment, invasive species, risk assessment

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Introduction

Invasive alien species (IAS) can significantly threaten biodiversity by inducing multiple environmental effects that change community composition, biotic interactions and other ecosystem processes (Vilà et al. 2011, Pyšek et al. 2012, Ricciardi et al. 2013, Gallardo et al. 2016, Schirmel et al. 2016, David et al. 2017, Vilà and Hulme 2017). IAS can also cause socio-economic damages (Bacher et al. 2018), for example, by decreasing ecosystem services (Pejchar and Mooney 2009, Vilà and Hulme 2017) or affecting infrastructure (Booy et al. 2017). Furthermore, necessary management usually requires considerable financial and personnel resources (Hoffmann and Broadhurst 2016).

Biological invasions are high on both scientific and political agendas (Hulme et al. 2009, Fleishman et al. 2011, Sutherland et al. 2013, Genovesi et al. 2015). Yet as only a rather small portion of alien species causes negative impacts, most ecologists do not oppose alien species per se (Simberloff et al. 2011, Russell 2012). Even widespread alien species may have negligible effects (Hulme 2012). Moreover, some alien species may also benefit native species (Schlaepfer et al. 2011) or underpin ecosystem services (Riley et al. 2018). Accordingly, relevant legislation such as EU Regulation 1143/2014 focusses on IAS, i.e. alien species that threaten or adversely impact biodiversity and related ecosystem services (Tollington et al. 2015).

The key challenges in invasion biology are therefore to figure out which alien species will naturalise and spread ('invasive' sensu Richardson et al. 2000) or which alien species will adversely impact biodiversity or other resources ('invasive' sensu Mack et al. 2000, Tollington et al. 2015). To respond to the latter challenge, an array of assessment approaches has been developed over the past 25 years, starting with Panetta (1993) and Tucker and Richardson (1995). All approaches share the same major aim, i.e. to support decisions regarding the introduction or management of IAS, but differ in the underlying purposes, criteria, methods, legal status and target area. There are already some reviews on invasion-related assessment approaches (e.g. Fox and Gordon 2009, Verbrugge et al. 2010, Essl et al. 2011, Leung et al. 2012, Kumschick and Richardson 2013, Dana et al. 2014, Buerger et al. 2016, Roy et al. 2018). These studies partly differ from our analysis in terms of considered approaches, analysed issues or geographical range. For example, the review by Fox and Gordon (2009) mainly analysed U.S. approaches. Essl et al. (2011) focussed on issues such as legal status, purpose or target area of considered approaches, and the range of incorporated assessment criteria. Our study aimed at providing an update in a rapidly developing field and covering issues such as context dependence and management prospects that are highly relevant but less prominent in previous reviews, e.g. Roy et al. (2018).

Challenges in assessing invasive alien species impacts

Adequate assessment approaches must meet several challenges such as defining (Sagoff 2005, Bartz et al. 2010, Jeschke et al. 2014) and quantifying impacts (Kumschick et al.

2015) and considering the context dependence of impacts (Thiele et al. 2010, Pyšek et al. 2012, Kumschick et al. 2015). The feasibility of management is another important issue to be considered, e.g. in the context of EU legislation 1143/2014 on IAS (Tanner et al. 2017), and often requires site-specific approaches (Sádlo et al. 2017). Moreover, ensuring transparency within risk assessments will facilitate decision making (Vanderhoeven et al. 2017).

Against this background we reviewed assessment approaches applicable to alien plant species. We analysed how the impacts of alien plants were addressed and which dimensions of the context dependence of these impacts were considered, how prospects of a successful management were incorporated and to what extent the assessment approaches were transparent in their methods towards defining major terms and disclosing underlying values. In the following we describe the key issues and the related research questions.

Environmental impacts of IAS

Environmental impacts resulting from biological invasions have been conceptualised as measurable (Ricciardi et al. 2013) or significant (Simberloff et al. 2013) changes to an ecosystem property such as species composition or ecosystem functioning. Such impacts can be multidirectional (Jeschke et al. 2014) as alien species can increase or decrease an ecological feature. Furthermore, not every negative impact constitutes serious damage because societies usually accept minor negative impacts caused by alien species (Bartz et al. 2010). A certain threshold must thus be exceeded before a negative impact, such as a decrease in a native species population size, becomes significant and can thus be addressed as damage (Bartz et al. 2010; Figure 1). The German Nature Conservation Act, for example, calls for action only against alien species that endanger ecosystems, habitats or other species. Likewise, the list of IAS of Union concern according to EU Regulation 1143/2014 focusses on alien species with significant negative impacts on biodiversity. Assessing impacts of alien species that justify any type of action is thus a key issue in risk assessment (Powell 2004, Hulme 2011, Genovesi et al. 2015, Tanner et al. 2017).

Despite remarkable progress in classifying and understanding the environmental impacts of alien species (Pyšek et al. 2012, Ricciardi et al. 2013, Simberloff et al. 2013, Foxcroft et al. 2017), the great complexity of the issue is still challenging (Hulme 2011, Jeschke et al. 2014, Courchamp et al. 2017), raising the question of how assessment approaches address invasion-mediated impacts. In detail, we analysed how existing approaches considered the following issues: (i) Covered biodiversity levels: are impacts at all levels of biodiversity considered, as targeted by the Convention on Biological Diversity (CBD), i.e. genes, species and ecosystems, and how are these impacts incorporated into the assessment? (ii) Impact magnitude: are parameters such as magnitude of overall impact, effect size or irreversibility of impacts – thereby distinguishing impacts from significant impacts – incorporated as indicated by relevant legislation (e.g. EU Regulation 1143/2014)?



Figure 1. From environmental changes to environmental damages by invasive alien plants. In an assessment approach, invasion-mediated changes become environmental damages or benefits when human values are incorporated. Human values matter in selecting relevant assessment endpoints and categories of impact, in distinguishing mere changes in ecological properties from negative or positive impacts, and in setting thresholds that separate impacts from significant impacts. Only significant negative impacts represent damage or harm (after Bartz et al. 2010).

Context dependence of environmental impacts

We differentiated three dimensions of context dependence (Figure 2). The first is the context of the alien species itself: what potential due to its characteristics (e.g. seed production, competitiveness) does a specific species have in order to induce environmental changes? That different species differ in characteristics and performance and thus need to be assessed individually is widely accepted (Simberloff et al. 2011). Furthermore, intraspecific differentiation should also be considered in assessment approaches because it can lead to different environmental impacts. Infertile varieties of an invasive alien species might be 'safe'-but not necessarily. Dispersal of vegetative propagules, for example, is a powerful pathway to invasions in *Fallopia* taxa (Pyšek et al. 2003). Moreover, introduced subspecies of a native species may produce significant negative environmental impacts as reported for European subspecies of *Phragmites australis* in North America (Pyšek et al. 2018).

Some IAS 'blacklists' cover national scales, translating impact assessments from at least one well-documented case of impact at the local scale to the country scale (e.g. Essl et al. 2011, Nehring et al. 2013). In this way, evidence of negative impacts at the local or regional scale is generalised to larger spatial scales. This generalisation may be justified by the precautionary approach (Essl et al. 2011), but ignores the fact that invasive species may perform quite differently in other parts of their range (Hulme et al. 2013). Accord-


Figure 2. Context dependence of environmental impacts of invasive alien plants. Invasion impacts differ with different context dimensions: **a** the context of the alien species itself **b** the environmental context within the actual or potential range of the alien species, and **c** the context of the values that are incorporated in impact assessments and that may be different among and within societies. All contexts may change with time.

ingly, invasion impacts may be over- or underestimated when ignoring environmental variation of invaded habitats (Thiele et al. 2011). We thus considered as a second dimension of context dependence the environmental context. Prominent examples include two tree species: *Cinchona pubescens* shows differences across vegetation zones: it is threatening endemics in Galàpagos (Jäger et al. 2009), while facilitating endemics in managed Hawaiian forests (Fischer et al. 2009). *Robinia pseudoacacia* performs differently under diverse climatic conditions in Europe, with both positive and negative effects (Cierjacks et al. 2013, Vitková et al. 2017). Sádlo et al. (2017) correspondingly argued for considering the local context when deciding whether to manage *R. pseudoacacia*.

Third, we considered the context of societal values, which is of fundamental importance within any impact assessment as values differ among societies and over time (Estévez et al. 2015). Assessment approaches link environmental impacts with values of affected ecosystem properties ('resources'). Beyond this, linking impacts with values requires decisions that are themselves value-laden. Examples include (i) the selection of assessment endpoints and impact categories; (ii) the differentiation between changes to ecological properties and negative or positive impacts; and (iii) the setting of thresholds of significant impacts (Figure 2; Opdam et al. 2009; Bartz et al. 2010). In the latter case, it is not only the magnitude or severity of impacts that is important, but also the value of the affected resources (Robu et al. 2007, Lawler 2009, Bartz et al. 2010). For example, the risk of Red-listed species being displaced by invasive species might justify greater management efforts than would be appropriate if only ubiquitous species were affected.

Considering context dependence within impact assessments is challenging as many interfering factors vary, e.g. the local biotic and abiotic parameters or the time since introduction or appearance of an alien species at a site (Hulme et al. 2013, Kumschick et al. 2015, Pyšek 2016). The assessment of impacts is also complicated by the fact that ecological and social contexts may change with time. For example, alien species that do not

currently cause negative impacts may become problematic with ongoing climate change and vice versa (Bellard et al. 2013). The changing valuation of the Chinese tree *Ailanthus altissima* in the USA in the wake of the Opium Wars in the 19th century (Shah 1997) demonstrates how changing societal values may modulate assessments of alien species. To date, knowledge about the context dependence of invasion impacts is rather fragmentary, and a better prediction of impacts requires considerable further research (Kumschick et al. 2015). Moreover, uncertainty about the alien status of a species may exist and may result in unknown invasion impacts of cryptic alien species (Essl et al. 2018, Jarić et al. 2019).

To better understand context dependencies in the assessment approaches, we asked the following questions: (i) Species context: does the approach consider a species' potential to cause environmental impacts, and how is this potential addressed in the assessment approach? (ii) Environmental context: does the approach account for the potential or actual distribution of the alien species and the identity of habitats, species or other resources that may be affected? (iii) Context of societal values: does the approach differentiate between positive and negative effects and account for the value of (potentially) affected resources?

Management of biological invasions

Managing IAS can involve high costs (Woldendorp and Bomford 2004, Panetta 2009) that may account for a considerable part of the overall costs associated with IAS (Hoffmann and Broadhurst 2016). Yet, management actions are not necessarily successful (van Wilgen et al. 2012, McConnachie et al. 2012, Kerr et al. 2016, Kraaij et al. 2017). Thus it is reasonable to consider the prospects for successful management within the scope of risk assessments. This is particularly true for assessment approaches whose main objective is to guide management decisions. Taking account of management prospects is relevant for pre-introduction assessments as well, as the absence of suitable management methods might justify a denial of introduction (Heikkilä 2011). Accordingly, Tanner et al. (2017) recommended considering issues of risk management (e.g. the availability and cost-effectiveness of preventative measures) when prioritising species in the context of IAS EU legislation 1143/2014.

Many factors may impede successful management of IAS, including the availability of effective methods and sufficient funding to conduct all necessary measures within the required time frame (Panetta and Timmins 2004, Cacho et al. 2006, Gardener et al. 2010). We thus analysed (i) whether management prospects are considered in assessment approaches and (ii) which factors relevant to successful management are addressed.

Transparency of assessment approaches

The transparency of assessment approaches is essential for application by different users. Powell (2004, p. 1306) highlights the problem of subjectivity by emphasising that

'different assessors may mean very different things by "low" environmental impact, for example'. In particular, qualitative approaches risk a high subjectivity that reduces the comparability of assessment scores. Transparency further supports the communicability and acceptance of assessment results. For transparency, a clear terminology is required, especially for value-laden terms such as 'impact' (Jeschke et al. 2014), 'damage' (Sagoff 2005, Bartz et al. 2010) and 'invasive'. Using such ambiguous terms without exact definition may lead to confusion in policy debates or even undermine management efforts (Ricciardi and Cohen 2007, Hulme 2011). More generally, normative assumptions that underlie impact or risk assessments should be disclosed (EPA 2000, Jardine et al. 2003) as relevant values differ among and within societies (Schüttler et al. 2011, Kumschick et al. 2012, Estévez et al. 2015).

We thus analysed if (i) the assessment methods of reviewed assessment approaches and the incorporation of applied criteria are transparent, (ii) relevant terms are clearly defined, and (iii) underlying values are disclosed.

Methods

Identification of relevant papers

We conducted a query in the Web of Science (WoS, accessed 11 July 2018, search in all databases) for literature containing the search terms *woody OR weed* OR non-native OR invasive OR exotic OR alien OR nonindigenous AND assess* OR evaluat* OR analy* OR predict* OR prioritiz* OR scor* OR classif* OR rank* OR screen* AND risk* OR impact* OR effect* OR hazard* OR consequence* OR invasion* OR invad* OR introduction* OR entry OR threat OR potential* OR tool* in its title (the asterisk ensures that all relevant endings of a root term are considered). Though we concentrated on impact assessment we included the term 'risk' in our search. Because risk is a function of both consequences, i.e. effects or impacts, should also be addressed in risk assessment approaches.

This search yielded about 3,450 papers. From this result we excluded articles from research areas such as "acoustics", "system cardiology" or "transplantation". By reading the title and abstract of the remaining 680 papers, we narrowed our focus to 158 articles dealing with the assessment of impacts or risks resulting from the introduction or spread of alien species. For our analysis we chose from this subset all approaches that were developed to assess impacts or risks of alien plants or alien species in general. We did not consider approaches explicitly developed for other taxa such as mammals, birds or fishes. We further ruled out papers that focussed on testing the validity of already existing approaches. All in all, our search led to 19 papers (Tucker and Richardson 1995, Reichard and Hamilton 1997, Pheloung et al. 1999, Kil et al. 2004, Olenin et al. 2007, Parker et al. 2007, Molnar et al. 2008, Ou et al. 2008, Randall et al. 2008, Stone et al. 2008, Feng and Zhu 2010, Magee et al. 2013, Blackburn et al. 2014, Nentwig et al.

2016, Davidson et al. 2017). We included eight further papers that we found through cross-references and that met the selection criteria (Panetta 1993, Kowarik et al. 2003, Weber and Gut 2004, Virtue et al. 2008, Kumschick et al. 2012, EPPO 2012, Nehring et al. 2013, Branquart et al. 2016). Ultimately, we reviewed 27 papers that provide approaches to assess risks and impacts of alien plants or alien species in general.

Analysis of papers

We analysed our set of 27 assessment approaches according to the key issues, criteria and parameters shown in Table 1. In the supplemental material, we document detailed results of our analysis (see Suppl. material 1: assessment results) and offer examples of how we applied the criteria (see Suppl. material 2: assessment criteria).

Caveats

As our study is mainly based on a literature search in the WoS, relevant scientific work might not be captured when published in reports, working papers or other publications that are not listed in the WoS or that are written in other languages than English. Beyond this, papers addressing the topic but not using the defined search terms in their title might have been missed. We did include relevant papers in our analysis that were found through cross-referencing but not listed in WoS. Thus, we believe that the chosen subset of articles reflects a broad scope of existing approaches.

Results and discussion

In the following, we first present an overview of the major objectives and assessment methods of the 27 approaches. We then provide some quantitative analyses on the major issues covered by this review and use examples to illustrate important points. All results are shown in Suppl. material 1.

Major objectives and assessment methods

The assessment approaches can be grouped into three main categories according to their main objectives. The first group comprises predictive systems that aim to support decisions about the introduction of an alien species to an area. Such decisions are relevant for the initial introduction of a species at the national scale (Pheloung et al. 1999) and for subsequent secondary releases, e.g. in different regions of a country (Kowarik et al. 2003). The second group provides prioritisation tools to support decisions about the management of alien species that are already present in a given region (Skurka

Table 1. Key issues, criteria and parameters used to analyse assessment approaches. For detailed information on how criteria and parameters were applied, see Suppl. material 2 on assessment criteria. (CBD = Convention on Biological Diversity).

Key issue	Criteria	Parameters to be incorporated in assessment approaches
Environmental impacts	Biodiversity levels according to CBD	Genetic diversity (Huxel 1999, Parker et al. 1999)
		Species diversity (Parker et al. 1999, Vilà et al. 2011, Pyšek et al. 2012, Schirmel et al. 2016)
		Ecosystem diversity (Parker et al. 1999, Vilà et al. 2011, Pyšek et al. 2012, Schirmel et al. 2016)
	Impact magnitude	Magnitude of overall impact (Robu et al. 2007, Bartz et al. 2010)
		Effect size (Parker et al. 1999, Hulme 2011)
		Spatial extent (Parker et al. 1999, Hulme 2011)
		Abundance (Parker et al. 1999)
		Cumulativeness (Landis 2003, Hulme 2011)
		Irreversibility (Hulme 2011)
Context dependence	Species context	A species' ability to cause impacts based on specific traits and characteristics (Simberloff et al. 2011)
	Environmental context	Potential or actual distribution of the alien species (Hulme et al. 2013, Pyšek 2016)
		Identification and localisation of (potentially) affected resources (Hulme et al. 2013, Pyšek 2016)
	Context of values	Differentiation between positive and negative impacts (Bartz et al. 2010)
		Value of (potentially) affected resources (Lawler 2009, Estévez et al. 2015)
Management of biological invasions	Management prospects	Availability of effective and practicable methods (Cacho et al. 2006, Panetta and Timmins 2004)
		Availability of personnel and financial resources within the required time frame (Child et al. 2001, Panetta 2009)
		Size of (potentially) infested area (Rejmánek and Pitcairn 2002, Woldendorp and Bomford 2004)
		Number, detectability, accessibility of infestations (Cunningham et al. 2004, Harris and Timmins 2009)
		Species traits or characteristics that might impede management (Simberloff 2003, Panetta 2009)
		Unwanted management effects (Carroll et al. 2001, Pearson et al. 2016)
		Restorability of affected resources (Jäger and Kowarik 2010, Panetta et al. 2019)
		Cooperativeness of landowners (Gardener et al. 2010)
Transparency of assessment approaches	Transparency of criteria and assessment methods	Criteria (Powell 2004)
		Assessment methods (Powell 2004)
	Definition of terms	Invasive (Richardson et al. 2000, Ricciardi and Cohen 2007, Hulme 2011)
		Damage, harm, impact, negative effect (Bartz et al. 2010, Jeschke et al. 2014)
	Disclosure of values	Substantiation of criteria, thresholds and assessment methods by explicit reference to normative requirements (lardine et al. 2003)

Darin et al. 2011). Some authors described their approach as meeting both prediction and prioritisation objectives (Ou et al. 2008, Feng and Zhu 2010). As a third category, we grouped approaches that function as information tools that present the impacts, invasiveness etc. of alien species without explicitly guiding decisions on introduction or management (Parker et al. 2007). The approaches fundamentally differed in their methods for merging criteria and deriving final assessment results. They can be assigned to three major categories (Figure 3): decision trees, scoring systems and matrix tools. Decision trees are hierarchical systems based on yes/no questions (e.g. Tucker and Richardson 1995). Scoring systems derive assessment results by adding or multiplying scores for different parameters (e.g. Feng and Zhu 2010). Finally, some approaches use a two-dimensional matrix in which the main criteria are combined to generate assessment results (e.g. Sandvik et al. 2013). More than half (n = 15) of all analysed approaches were scoring systems. While only three approaches were designed as a matrix tool, others did combine several methods. For example, Virtue et al. (2008) used a scoring system to assess 'weed risk' but used a matrix to combine 'weed risk' and 'stage of introduction' to derive recommendations on management actions. Four approaches included a small decision tree as a pre-evaluation step, e.g. to determine which species should be further assessed, while the core assessment relied on a scoring system (e.g. Weber and Gut 2004, Randall et al. 2008).

As each assessment method has strengths and weaknesses (Fox and Gordon 2009, Hulme 2011, Kumschick and Richardson 2013, Buerger et al. 2016), there is no preferable method per se. The performance of a method may be influenced by the availability of relevant information or other factors. In scoring systems, for example, the final score assigned to an alien species usually depends on the number of questions answered. Thus, in the case of poorly studied species, risks may be underestimated (Dawson et al. 2009).

Environmental impacts of IAS

In this section, we describe how the 27 assessment approaches incorporate environmental impacts in relation to biodiversity levels and magnitude of impacts.

Biodiversity levels

According to the CBD, biodiversity comprises genetic diversity, species diversity and ecosystem diversity, and the interdependencies within and between these levels of biodiversity. Alien plants may, for example, interact with other species at different trophic levels or change ecosystem processes (Vilà et al. 2011, Pyšek et al. 2012, Schirmel et al. 2016). Of the approaches, only 12 considered the impacts of alien species at all levels of biodiversity (e.g. Randall et al. 2008, Blackburn et al. 2014). More than threequarters of all approaches considered the species or ecosystem level (Figure 4a), while the genetic level was covered by only half of the papers. This is a clear shortcoming as hybridisation is broadly acknowledged to be a relevant impact mechanism (Huxel 1999, Meyerson et al. 2012). Our analysis suggests that some invasion risks may be underestimated as many approaches did not cover the main biodiversity levels equally.



Figure 3. Methods used by assessment approaches of invasive alien plants. To determine final assessment results, all assessment approaches were based on one or a combination of the following methods: (a) decision tree, (b) scoring system and (c) matrix tool..



(a) Biodiversity levels

Fully / directly considered Partly / indirectly considered Not considered

Figure 4. Assessment of environmental impacts of invasive alien plants. Incorporation of impacts in analysed assessment approaches (n = 27), related to \mathbf{a} covered biodiversity levels and \mathbf{b} parameters relevant to magnitude of impact.

although this has changed over time. The more recent approaches (since Kumschick et al. 2012, see Suppl. material 1) regularly considered all biodiversity levels.

The way in which approaches incorporated environmental impacts clearly differed. Many approaches accounted for the displacement of other species through a discrete criterion (e.g. 'interaction with native species'; Sandvik et al. 2013) and thus referring to concrete effects. Others relied on species characteristics that may indicate (potential) impacts. One example is the 'ability [of a species] to form large, dense, persistent populations' (EPPO 2012). Deriving potential impacts from species characteristics may be appropriate when data about effects in the reference area are missing, but such indications can mislead decision makers. Whether a given biological feature, e.g. the potential of an alien species to form dense populations, translates to a relevant effect starkly differs among species (Hejda et al. 2009).

Relating impact assessments to observed effects instead of potential effects is thus preferable but depends on the objective of the assessment and the availability of data. Some approaches that are intended to support decisions on whether an alien species can be introduced refer to anticipated impacts of this species (e.g. Stone et al. 2008, Koop et al. 2012). Such pre-introduction assessments usually rely on transferring experiences from other regions (Kulhanek et al. 2011, Kumschick and Richardson 2013) and are burdened with uncertainties due to the context dependence of invasion impacts. At the very least, it is important that the regions be comparable in terms of climate, soil, habitats etc. Accordingly, Sandvik et al. (2013) prioritised data as follows: a) the area of interest, b) regions with comparable eco-climatic conditions, c) other regions with different eco-climatic conditions, and d) other (preferably closely related) species with comparable ecological and demographic characteristics. The decrease in data reliability along this spectrum is a strong argument for filling the gaps in databases.

The number of criteria considered under environmental impacts also differed among the assessment approaches. While Blackburn et al. (2014) covered many mechanisms that may lead to impacts at the species level (e.g. competition, predation, hybridisation, transmission of diseases, interaction with other alien species), other approaches emphasised 'competition' as the main impact mechanism at the species level (e.g. Virtue et al. 2008, Magee et al. 2010). Some approaches were much less detailed, when covering environmental impacts, for example, by 'ecological disturbance on ecosystems' (e.g. Kil et al. 2004). There was thus a gap between the inclusion of a relevant issue, e.g. different biodiversity levels, and the scope and detail of criteria that were used to detect or quantify the impact. Only a few studies (e.g. Randall et al. 2008, Kumschick et al. 2012, Blackburn et al. 2014) combined a full coverage of biodiversity levels with a broad range of criteria for quantifying invasion impacts.

Impact magnitude

Quite often legislation on biological invasions (e.g. EU regulation 1143/2014) requires the significance of impacts to be considered as a prerequisite for any de-

cision or action against specific IAS. In addition to the value of the affected resources, the overall magnitude or severity of the impacts is important for assessing the significance of an impact (Robu et al. 2007, Lawler 2009, Bartz et al. 2010). Some approaches summed scores for different impact types (e.g. competition, hybridisation) to calculate final overall impact classes. Blackburn et al. (2014), for example, differentiated minimal, minor, moderate, major and massive impacts. Such classes help distinguish between negative and significant negative impacts. This also holds for systems which assign impact scores (e.g. Randall et al. 2008, Kumschick et al. 2012).

Most approaches, however, did not provide explicit information on the magnitude of impacts (Figure 4b). Alternatively, information on certain parameters may enable conclusions on the magnitude of impacts. Among these are effect size, irreversibility, and cumulativeness of impacts, the latter caused by different alien species in the area of interest; and the abundance and distribution of the alien species as drivers of impact (Parker et al. 1999, Hulme 2011). While more than half of all approaches incorporated effect size and spatial extent, other impact parameters were underrepresented. Only three approaches (e.g. Magee et al. 2010) considered the cumulative effect of several alien species in the reference area; no approach considered the interplay of alien species with other pressures such as land use or pollution. Again three approaches explicitly stipulated the abundance of an alien species in the region as an issue, usually in the form of a request for data on distribution (e.g. Olenin et al. 2007). Blackburn et al. (2014) included the irreversibility of impacts most extensively by using it as a characteristic feature to discriminate between massive and major impacts for each criterion.

Environmental impacts: synthesis

Environmental impacts were considered in different ways within the assessment approaches. Quite often impacts were addressed in terms of species characteristics related to potential effects rather than a direct assessment of impacts. The former is reasonable when data about concrete effects in the reference area are missing, for instance in pre-introduction assessments, but it also might be error-prone as species impacts are context dependent. Given that IAS can considerably threaten all levels of biodiversity it is striking that impacts on genetic diversity were neglected by many approaches. Although it may be more difficult to account for impact mechanisms such as hybridisation than, for example, a decline in native species populations, covering all relevant impact mechanisms and assessment endpoints (i.e. affected resources of concern) is of vital importance to generate resilient assessment outcomes. Although there are different options for assessing the significance of impacts, the overall magnitude of impacts should be considered. However, our analysis shows that this measure was not regularly included. Likewise, important impact parameters such as cumulativeness or irreversibility were underrepresented.

Context dependence of environmental impacts

It is common knowledge in invasion science that invasion impacts are context-dependent as they depend on (i) the characteristics of the invading species (Simberloff et al. 2011), (ii) the environments in which the invasion occurs (Pyšek and Richardson 2010, Thiele et al. 2010, Hulme et al. 2013, Kumschick et al. 2015), and (iii) the societal values that may be affected by the invasion (Estévez et al. 2015). We analyse here whether existing assessment approaches considered these three dimensions of context dependence (Figure 2).

Context of species

All assessment approaches (except Reichard and Hamilton 1997) considered the species-related context dependence of invasion impacts (Figure 5). Some approaches took into account effect-related species characteristics, e.g. a species' ability to form large and dense monocultures (e.g. Weber and Gut 2004); other approaches assessed concrete effects, e.g. decrease in abundance of affected species (e.g. Kowarik et al. 2003, Blackburn et al. 2014). Most assessment approaches accounted for effect-related species characteristics as well as concrete effects and additionally included information about the establishment or distribution of a species in the reference area.

Context of environments

To incorporate the environment-related context of invasion impacts, assessments should consider information on the (potential) distribution (1) of alien species and (2) of (potentially) affected environmental resources. Only half of all approaches (Figure 5) considered the former, mainly by accounting for the potential (e.g. Panetta 1993) or actual distribution of an alien species (Parker et al. 2007), or both (Weber and Gut 2004). The spatial scale for considering the distribution of species, however, varies from the local to the global context, depending on the purpose of the assessment approach. According to the German Nature Conservation Act, alien species that have not been classified as invasive (i.e. that do not threaten biodiversity) may be planted in the wild if risks can be excluded. To assess risks in such cases, the assessment approach by Kowarik et al. (2003) focused on a local context: the place of release and the area of subsequent potential distribution. In contrast, for marine ecosystems, where dispersal limitation is less relevant for invasion processes, Molnar et al. (2008) considered the actual distribution is narine ecosystems in a global context.

Only one-quarter of the assessment approaches further addressed the environmental context of impacts by referring to (potentially) affected resources, such as species or habitats of conservation concern. Approaches by Ou et al. (2008) and Randall et al. (2008) included questions about the proportion of the species' current range where



Figure 5. Assessment of context dependence of invasive alien plants. Incorporation of context dependence

Figure 5. Assessment of context dependence of invasive alien plants. Incorporation of context dependence of environmental impacts in the analysed assessment approaches (n = 27) in relation to different dimensions of context dependence: **a** species **b** environments and **c** societal values. (IAS = invasive alien species).

negative impacts have been measured. A few other approaches (e.g. Kowarik et al. 2003, Miller et al. 2010, Skurka Darin et al. 2011) went further by overlaying the occurrence of alien species with the occurrence of (potentially) affected resources. Yet, even this does not allow for a proper context-related assessment, as many factors influence context dependence (e.g. time since introduction, propagule pressure; Pyšek 2016). Moreover, the co-occurrence of alien species and resources of conservation concern at a site does not necessarily lead to negative effects on resources (Ramírez-Cruz et al. 2019). In the end, linking both, i.e. impacts and potentially affected environments, would allow for a better consideration of environmental contexts than would assessments that are merely based on (effect-related) species characteristics or impacts observed in other regions.

Distinguishing impacts across environmental conditions would also allow for multiple responses to IAS. This can be appropriate when the effects of a given species may be positive, negative or neutral depending on the environmental context. Incorporating the environmental context in assessments would allow positive impacts to occur and help allocate management efforts to counteract negative impacts. This is most feasible at the local scale. Assessment approaches designed to support management decisions consider species that are already present, which should enable a more concrete differentiation of the environmental context – either for a specific regional context or at the typological level by considering different biotope types [as proposed by Sádlo et al. (2017) for managing invasions by *Robinia pseudoacacia*]. In contrast, approaches aimed at a pre-introduction assessment usually refer to the national scale, thus largely requiring that different environmental settings be considered at a rather rough level.

Our analysis shows that only a few post-introduction assessment approaches allowed for such a concrete differentiation of the environmental context. Kil et al. (2004) for instance simply asked whether a species is 'widely distributed' within the country. On the one hand, this approach stands out for its simplicity as it is applicable with little information. On the other hand, it does not enable a differentiated assessment that accounts for different environmental conditions.

Context of societal values

Environmental impacts on species assemblages or ecosystem properties can be positive or negative (Ricciardi et al. 2013, Simberloff et al. 2013). Several studies focussed on these issues with a main emphasis on economic aspects; only six explicitly differentiated between negative and positive impacts (Figure 5; e.g. Kil et al. 2004, Davidson et al. 2017). Kumschick et al. (2012) went furthest by scaling every criterion with regard to positive and negative effects and applying a weighting factor according to stakeholder preferences.

Nearly half of all approaches considered the value of (potentially) affected resources (Figure 5). Six of these provided a rather basic approach: for example, Molnar et al. (2008) and Davidson et al. (2017) considered the conservation value of affected resources to distinguish the highest from the second highest impact level. Another six approaches stipulated a more systematic assessment of values. Skurka Darin et al. (2011) determined the distance between populations of alien species and valuable resources such as 'concentrations of threatened and endangered species and rare plant communities' and used this measure for setting management priorities. Stone et al. (2008) posed the question 'Could the species reduce the biodiversity value of a natural ecosystem, either by reducing the amount of biodiversity present (diversity and abundance of native species), or degrading the visual appearance?' Randall et al. (2008) included a separate criterion 'conservation significance of the communities and native species threatened' and ascribed to this criterion the second highest weighting within the subcategory 'impacts'. Sandvik et al. (2013) went a step further, basing their final impact categories on the value of the affected resources, i.e. 'the ecological effect is classified as milder if none of the species affected by the alien species is threatened or a keystone species'. Finally, Kowarik et al. (2003) derived the significance of impacts from a matrix combining the magnitude of impacts with the conservational value of the affected resources. This approach used several criteria for assessing the conservation value of affected resources, whereas other approaches relied only on the status of a species or habitat as threatened or rare.

Context dependence: synthesis

The performance of invasive species may vary depending on environmental conditions. Moreover, societal values, which vary from society to society – and within societies – affect the perception of invasive species. Thus, the operationalisation of context dependence remains an important challenge for assessment approaches. Our analysis shows that nearly all approaches incorporated species-related context dependence by considering species identity, species traits, or the ability of a species to cause environmental impacts. A step forward would be to incorporate the actual (or potential) exposure of relevant resources to alien species in assessment approaches. Although many approaches requested at least basic information about the (potential) distribution of the given alien species only three approaches explicitly included the exposure of (potentially) affected resources. At the management level, exact information about the occurrence of alien species as well as (potentially) affected resources should be available.

Given that about half of all approaches mentioned the support of management decisions as an important objective, it is surprising that environment-related context dependence was not more strongly represented. Finally, all approaches inherently incorporated values, ranging from the choice of relevant assessment endpoints to the classification of impacts based on thresholds. The latter mainly depends on the magnitude of impacts but also the value of the resources affected. Yet, only a few approaches comprehensively incorporated the value of such resources. Species or habitats can be valuable without being threatened or rare, e.g. due to a global responsibility for their conservation or because they are protected for cultural reasons. Thus, the exclusive focus of the analysed approaches on criteria such as endangement or rareness may be seen as a further deficit, in particular with respect to prioritisation of management actions.

Management of biological invasions

Successful management of biological invasions is a basic supposition for preventing, mitigating or removing negative impacts of IAS. Moreover, feasibility of management may be a prerequisite for listing an invasive species, e.g. according to EU Regulation 1143/2014. As management success depends on many factors (Table 1), the availability of effective and practicable eradication or control methods, and of sufficient personnel and financial resources are essential requirements for successful management (Panetta and Timmins 2004). Against this background we analysed whether and how management prospects were incorporated in the studied set of assessment approaches (Figure 6).

About half of all approaches directly considered prospects for successful management. Among these, most focussed on several relevant parameters, but there were substantial differences in how clearly the parameters were operationalised. For example, the approaches provided by Ou et al. (2008) or Skurka Darin et al. (2011) included different criteria, i.e. availability of effective methods, costs of control or eradication. In



Fully / directly considered Partly / indirectly considered Not considered

Figure 6. Assessment of prospects for successful management of invasive alien plants. Incorporation of factors relevant to successful management of invasive alien species within analysed assessment approaches (n = 27).

contrast, Parker et al. (2007) simply asked whether an alien species is easy or difficult to control without explaining which parameters should be considered to answer this question. All approaches developed to support management decisions should directly address the existence and feasibility of adequate measures, yet our analysis indicates that some do not (e.g. Kil et al. 2004, Weber and Gut 2004).

The approaches also differed significantly in how they considered parameters that influence the feasibility and success of management (Figure 6). As expected, some of these parameters (e.g. number, accessibility and detectability of infestations) played no role in assessment approaches exclusively supporting decisions on the introduction or entry of alien species (n = 7; e.g. Panetta 1993). It is nonetheless striking that, besides 'species traits' and, perhaps, the 'size of (potentially) infested area', approaches rarely considered parameters influencing management. The key question on the availability of effective control or eradication methods for setting priorities in alien species management was only explicitly included in seven approaches (e.g. Feng and Zhu 2010, Nehring et al. 2010). In the same vein, the availability of sufficient funding within the required time frame (including follow-up measures) is a broadly acknowledged premise for management success (Child et al. 2001, Gardener et al. 2010). But only four approaches (e.g. Ou et al. 2008, Skurka Darin et al. 2011) requested information on cost and/or time commitment for managing a given alien species and incorporated a basic estimate of the available financial and personnel resources in the assessment approache.

Management measures can bring about unwanted side effects on biodiversity, e.g. by enhancing the spread of other invasive species (Zavaleta et al. 2001, Jäger and Kowarik 2010, Pearson et al. 2016). Thus, the management of a particular IAS should always take into account the co-occurrence of other alien species (Ballari et al. 2016). Three approaches incorporated this issue by including criteria such as 'impacts of management on native species' (e.g. Randall et al. 2008). Finally, it is important to consider the restorability of native habitats and species communities after management (Zavaleta et al. 2001, Carroll 2011, Panetta et al. 2019). Only Ou et al. (2008) incorporated this concept with their criterion 'cost and time commitment of restoration'. Other studies incorporated information about the irreversibility of impacts (e.g. Olenin et al. 2007, Davidson et al. 2017), and thus, to a certain extent, may endorse conclusions concerning restorability of affected resources.

Management: synthesis

Only half of all studies directly considered prospects for successful management or the efforts to be taken. Additionally, important parameters such as unwanted side effects of management or the restorability of species communities and habitats after successful management were widely ignored. Thus, the majority of the studies lacked essential information to truly support management decisions. Strikingly, this also held for many approaches aimed at prioritisation of management.

Transparency of assessment approaches

Transparency of assessment approaches not only fosters acceptance of assessment results but also improves communication among stakeholders involved in alien species assessment. Here we analysed if (i) the way in which criteria were incorporated into assessment approaches is replicable, (ii) relevant terms were clearly defined, and (iii) underlying values were disclosed.

Transparency of criteria and assessment methods

The transparency of how assessment criteria were incorporated differed among and within the reviewed approaches (Suppl. materials 1, 2). For instance, the approach of Ou et al. (2008) contained quantified criteria (e.g. a percent scale of the 'proportion of current range where the species caused negative impact') as well as qualitative or semi-quantitative, and thus also ambiguous, criteria. One example of the latter is the criterion 'impact on economy and other aspects' which was scaled as follows: one scoring point (SP): 'little or without impact on local economy and other aspects', four SP: 'weak impact on one aspect', six SP: 'significant impact on one aspect', eight SP: 'significant impact on more than two

aspects'. But when is an impact weak or significant? Without explicit explanation, any assessment based on this criterion remains nebulous.

When a quantification of criteria is not possible, questions should have clear and unambiguous explanations and guidelines as to how they should be answered (Weber et al. 2009). In light of this challenge, supplemental guidance addressing questions was published (Gordon et al. 2010) for the well-established Australian Weed Risk Assessment (Pheloung et al. 1999). For the majority of analysed approaches, however, such guiding material is not available.

Transparency is not only crucial in the operationalisation of individual criteria, but also in the way in which the final assessment results are derived. In contrast to the results for individual criteria, nearly all approaches met this requirement.

Definition of terms

All analysed papers used the term 'invasive', but only ten approaches provided a definition (e.g. Reichard and Hamilton 1997, Magee et al. 2010; see Suppl. material 1). This is a shortcoming as fundamentally different definitions of 'invasive' exist that are either impact-related (Mack et al. 2000) or refer to the spread and population establishment of alien species (Richardson et al. 2000). All assessment approaches applied terms such as 'impact', 'damage' or 'harm' to address effects on relevant resources induced by alien species, yet only six papers explicitly defined those terms (e.g. Kowarik et al. 2003, Nehring et al. 2010, Sandvik et al. 2013). This illustrates the necessity for clarifying ambiguous terms to enhance communication among scientists and other stakeholders (Jeschke et al. 2014).

Disclosure of values

Assessments of impacts are strongly value-laden. Disclosing these values and explaining the reasoning behind them, specifically as they relate to key terms, is crucial for transparency and acceptance (Bartz et al. 2010, Estévez et al. 2015). This especially holds true for the identification of decision-relevant impacts where stakeholders may hold different underlying values. Moreover, the disclosure of underlying values is of vital importance when scaling and calibrating criteria or deriving final assessment results. We found that applied values were disclosed in only a few approaches, resulting in a deficit of transparency. Only four approaches (Kowarik et al. 2003, Nehring et al. 2010, Sandvik et al. 2013, Branquart et al. 2016) explicitly referred to relevant legislation when deriving relevant assessment endpoints or setting thresholds. To some extent, underlying values were revealed by considering the conservation value of affected resources, and a few approaches substantiated their choice of criteria in this way (e.g. Kowarik et al. 2003; Randall et al. 2008). Only one approach went further and directly incorporated views of stakeholders into the assessment procedure (e.g. Kumschick et al. 2012). Transparency of assessment approaches: synthesis

Noticeably, no approach consistently defined all criteria used. Every approach included at least some criteria with a wide scope for interpretation. In part this was certainly due to the fact that not all relevant information can be quantified adequately. Thus, quantified criteria may require data that, in a concrete case, might not be available or may be difficult to collect. This highlights the need for explicit guidelines for the application of criteria. Further, in many approaches, ambiguous or value-laden terms, such as 'invasive', 'impact' or 'damage', were not defined, nor were underlying values revealed.

Conclusions

Over the past 25 years, a wealth of approaches for assessing impacts of alien species has emerged. The scope of the 27 analysed assessment approaches, applicable for alien plant species, covered all relevant assessment purposes, from predictive systems to prioritisation tools for preparing management decisions to information tools. The scale of application ranged from global to national to regional to local assessments. This broad array of assessment approaches provides an adequate basis for supporting decisions on the introduction or management of IAS. With regard to the major topics of our review (i.e. incorporation of impact types, context dependence, management, transparency in assessment approaches), our analysis reveals strengths and weaknesses in all approaches. To further develop assessment approaches, we recommend the following:

- Cover a broad range of environmental impacts at all biodiversity levels. Approaches should consider all possible impacts on biodiversity, including impacts at the levels of genes, species and ecosystems.
- (2) Identify significant environmental impacts. Approaches should disclose the overall magnitude of impacts and consider the value of affected resources to distinguish significant impacts from other changes to environmental features.
- (3) Incorporate context dependence of environmental impacts. Besides a species' ability to induce impacts and its (potential) distribution, the occurrence of (potentially) affected resources should be considered in any risk or impact assessment. Furthermore, approaches should clarify the underlying societal values that direct the differentiation between positive and negative impacts, as well as the assignment of values to resources that are (potentially) affected by alien species.
- (4) Incorporate prospects for successful management. Parameters to be considered include the availability of effective methods and financial resources, information on the magnitude of infestation and target achievement (e.g. unwanted management effects, restorability of affected resources).
- (5) Make assessments transparent. Qualitative approaches in particular should offer clear guidelines for answering questions. Moreover, it is essential that key terms such as 'invasive' or 'impact' be defined and values be disclosed that, for example, play a role in choosing relevant assessment endpoints or setting thresholds.

Along with standards in risk or impact assessment as suggested by Roy et al. (2018), the consideration of these points will strengthen assessment approaches and better support decisions on the introduction and management of invasive alien plants.

Acknowledgements

Many thanks to Johannes Kollmann, Jan Pergl, Jan Thiele and an anonymous reviewer for helpful comments on an earlier version of the manuscript. We further thank Kelaine Vargas Ravdin for improving our English, and providing stimulating comments.

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Supplementary material I

Assessment results

Authors: Robert Bartz, Ingo Kowarik

Data type: measurement

- Explanation note: Information on how the approaches reviewed were assessed in terms of their purpose, assessment methodology, transparency and in how far they meet certain requirements regarding the assessment of impacts, the consideration of context dependence, and the support of management decisions.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.43.30122.suppl1

Supplementary material 2

Assessment criteria

Authors: Robert Bartz, Ingo Kowarik

Data type: description

- Explanation note: Information and examples of how the evaluation criteria and parameters were applied in the analysis.
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Link: https://doi.org/10.3897/neobiota.43.30122.suppl2

RESEARCH ARTICLE



Differential germination strategies of native and introduced populations of the invasive species *Plantago virginica*

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Academic editor: M. von der Lippe | Received 7 October 2018 | Accepted 19 December 2018 | Published 19 March 2019

Citation: Xu X, Wolfe L, Diez J, Zheng Y, Guo H, Hu S (2019) Differential germination strategies of native and introduced populations of the invasive species *Plantago virginica*. NeoBiota 43: 101–118. https://doi.org/10.3897/ neobiota.43.30392

Abstract

Germination strategies are critically important for the survival, establishment and spread of plant species. Although many plant traits related to invasiveness have been broadly studied, the earliest part of the life cycle, germination, has received relatively little attention. Here, we compared the germination patterns between native (North America) and introduced (China) populations of Plantago virginica for four consecutive years to examine whether there has been adaptive differentiation in germination traits and how these traits are related to local climatic conditions. We found that the introduced populations of P. *virginica* had significantly higher germination percentages and faster and shorter durations of germination than native populations. Critically, the native populations had a significantly larger proportion of seeds that stayed dormant in all four years, with only 60% of seeds germinating in year 1 (compared to >95% in introduced populations). These results demonstrate striking differences in germination strategies between native and introduced populations which may contribute to their successful invasion. Moreover, the germination strategy of *P. virginica* in their native range exhibited clear geographical variation across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that P. virginica may have experienced strong selection for earlier life history characteristics. Our findings highlight the need to examine the role of rapid evolution of germination traits in facilitating plant invasion.

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Keywords

Adaptation, germination strategy, native and introduced populations, invasive species, Plantago virginica

Introduction

Invasive species have become a severe threat to terrestrial ecosystems and human society owing to their impacts on biodiversity, ecosystem functioning (Kolar and Lodge 2001) and economies (Strayer et al. 2006). Understanding the mechanisms that promote invasion success is critical for predicting the emergence and expansion of an invasion and determining strategies for mitigating their impacts (Kolar and Lodge 2001; Strayer 2012). Several decades of research has identified plant traits such as size, growth rate and competitive ability that often correlate with invasion success (van Kleunen et al. 2010). In contrast, the earliest part of the life cycle, germination, has received relatively little attention. (Udo et al. 2017; Gioria and Pyšek 2017).

As the first phase in the life cycle of plants, germination is pivotal for the establishment and expansion of populations, especially for annual species under competitive conditions (Donohue et al. 2010; Hirsch et al. 2012; Leiblein-Wild et al. 2014). Several germination characteristics have been found to be related to invasive potential (Baker 1974; Radford and Cousens 2000), but successful germination strategies may vary amongst ecosystems. For example, comparative experimental studies between invasive and non-invasive congeners under experimental conditions showed that invaders tended to germinate earlier and took shorter time to reach the highest germination percentages (Muñoz and Ackerman 2011). In an Argentina desert community where the native annual flora is mainly composed of summer annual species, the late germination niche of the alien winter annual grass *Schismus barbatus* contributes to its successful invasion (Pucheta et al. 2011). In California grasslands, earlier germination phenology has been shown to yield competitive advantages for invasive species (Godoy and Levine 2014).

Similar to interspecific comparisons, examining the differentiation in germination patterns of an invasive species between its native and introduced ranges can also provide insights into the ecological and evolutionary mechanisms of invasion. Several studies have shown that seeds, originating from introduced populations, germinated at greater percentage, earlier and/or faster (Blair and Wolfe 2004; Erfmeier and Bruelheide 2005; Maron et al. 2007). Studies of intraspecific variation in germination can help explain species' range expansions (Blair and Wolfe 2004; Erfmeier and Bruelheide 2005; Kudoh et al. 2007; Maron et al. 2007).

In addition to seasonal timing of germination, seed dormancy is also an important component of a species temporal niche and life history strategy (Baskin and Baskin 2014). However, relatively few studies have examined how seed dormancy strategies could contribute to the success of invasive species. Kudoh et al. (2007) found that Japanese (introduced) populations of *Cardamine hirsuta* exhibited stronger initial dormancy and more persistent seed banks than European (native) populations, both of which can increase the probability of survival in the novel range. An opposite pattern

of seed dormancy was reported for introduced populations of *Ulex europaeus* which showed less physical dormancy, perhaps selected by decreased seed predation in the introduced range (Udo et al. 2017).

The variation in seed germination and dormancy could be driven by geographical variation in environmental factors, such as temperature and precipitation (Blair and Wolfe 2004; Sax et al. 2007) and further lead to population differentiation. For example, germination timing and rates of *Campanula americana* showed adaptive responses to local temperatures across its latitudinal range (Zettlemoyer et al. 2017). The rapid adaptation of introduced plants to the local environments plays a fundamental role in the expansion of species' geographical ranges and invasion success in introduced ranges. Hence, understanding intraspecific variation in germination characteristics across geographic and environmental gradients is important for interpreting invasion mechanisms and predicting the distribution of exotic species in future.

The goal of this study was to use a set of four-year germination experiments to build a better understanding of how seed germination traits may contribute to plant invasiveness. We used, as a case study, *Plantago virginica*, a species native to North America that has invaded China (Wang et al. 2015). Specifically, we compared germination percentages, timing and speed and rates of dormancy of seeds collected from native and introduced populations under controlled experimental conditions. We also used widespread seed collection sites in order to evaluate whether germination characteristics exhibit adaptation to local climatic conditions. The germination experiments were conducted for consecutive four years to test how seed dormancy, a critical part of the plant species' life history strategy, is different in the introduced versus native range.

Materials and methods

Study Species

Plantago virginica is an annual herb native to eastern North America that was introduced by accident and first reported in Jiangxi Province in the southeast of China in 1951. Since that time, it has spread extensively to eastern and southern China (Guo et al. 1996; Wang et al. 2015) and, more recently, north and west in Hunan, Henan and Chongqing Provinces (Fang et al. 2004; Guo et al. 1996; Wang 2016). The species' primary habitats in the introduced range include abandoned farmlands, orchards and lawns.

P. virginica is a winter annual. It germinates in the autumn, grows vegetatively through the winter and flowers, sets seeds and dies in the following spring and summer. It consists of a rosette of basal leaves, from which one or more cylindrical flowering spikes develop, densely covered with small flowers and their bracts. The species produces dimorphic flowers that exhibit a mixed mating system: cleistogamous (permanently closed, self-pollinated, i.e. selfing) and chasmogamous (wind or insect-pollinated, i.e. outcrossing) flowers (Xu et al. 2017). One individual usually produces

200–500 seeds (Guo et al. 1996). The seeds are often dispersed by animals or humans (Fang et al. 2004). Due to its strong reproductive ability and fast dispersal, *P. virginica* in the introduced range has caused substantial effects on native species and ecosystems and was listed as an invasive plant by China (Database of Invasive Alien Species in China (http://www.chinaias.cn).

Seed collections

Seeds for this study were collected in 2012 from 12 native (USA) and 10 introduced (China) populations (Fig. 1, Suppl. material 1: Table S1). The seeds from each population were collected from at least 30 individuals representing different maternal families (growing at least 1 m apart) and placed in separate paper envelopes and stored at 4 °C before the experiments.

Germination experiments

Germination trials were conducted with seeds from the same initial seed collection for four consecutive years (2012–2015), in order to compare the effect of seed dormancy amongst populations (see populations we used in each experiment in the Suppl. material 1: Table S1). The first experiment was in autumn 2012 in Shanghai, China, consisting of 10 native and 10 introduced populations, with 6 replicates per population (a Petri dish containing 50 seeds was the replicate). The 50 seeds of each replicate were weighed to the nearest 0.0001 g. The second experiment was conducted in spring 2013 in Statesboro, GA, USA and used 20 seeds from each of 10 native and 10 introduced populations. The final two experiments were conducted in autumn 2014 and 2015, in Nanjing, China with each experiment comprising of six native and six introduced populations and each population containing 25 replicates and 30 seeds per replicate. In 2015, additional 5 replicates were used to investigate the proportion of mouldy seeds in both native and introduced populations. All the seeds representing each population were thoroughly mixed while being selected for germination.

For each germination trial, seeds were placed on moistened filter papers in Petri dishes and incubated in illumination incubators with a photoperiod of 12 h cold white light and 12 h darkness under 25 °C. Petri dishes were watered daily and the number of germinated seeds was counted as their visible radicles reached a length of 2 mm. Since a preliminary experiment revealed that the seeds of *P. virginica* typically germinate in two weeks, the present experiments lasted between 2–3 weeks, allowing one week to ensure that no more seeds germinated. The germination percentage (the proportion of germinated seeds), the days to germination (the day of the first occurrence of germination in each replicate) and the duration of germination (the period from the first to the last seed germinating) were calculated.



Figure 1. Locations of *P. virginica* in the native range (**a**) and introduced range (**b**). Grey dots represent GBIF data as a background representation of the species' approximate range and the blue asterisks show the locations of populations sampled for seeds.

Statistical analyses

Data of germination characteristics were analysed by generalised linear mixed models (GLMM) and mixed-effects Cox models, with region and year as fixed factors and population within region as a random factor. We validated the use of GLMMs with the restricted maximum likelihood (Laplace Approximation) estimation method (REML) based on the normalised scores of standardised residual deviance of response variables: germination percentage and duration of germination. The level of significance of each fixed factor was determined by an F-ratio test. The analyses were performed with statistical package "Ime4" in R. For the analysis of days to germination, we used a mixed-effects Cox model fit by maximum likelihood to examine the differences in timing of germination between native and introduced regions and amongst years. The level of significance of each fixed factor was determined using γ^2 -test. The analysis was performed with statistical package "coxme" in R. We also examined the differences in germination characteristics (germination percentages, days to germination and duration of germination) of each region amongst years using the least significant difference (LSD) test. Due to the lack of data on "days to germination" and "duration of germination" in 2013, data from three years (2012, 2014 and 2015) of these two variables were used in the generalised linear mixed models, mixed effects Cox model and the LSD test. Since seed mass may affect the germination characteristics, especially germination percentage, data for germination characteristics in our first experiment (2012) were independently analysed by GLMM and mixed-effects Cox models, with region as a fixed factor and seed mass and population within region as random factors, to test for the effects of region while controlling for seed mass. The differences in proportion of mouldy seeds between native and introduced regions were tested using another generalised linear mixed model, with region as a fixed factor and population as a random factor.

Relationships between climate and germination characteristics were analysed using GLMMs. Monthly mean temperature and precipitation values for each sampling site were extracted using QCIS 2.18 (Becker et al. 2016), from WorldClim 2.0, a global climate database (www.worldclim.org) with a spatial resolution of 1 km. Mean annual temperature and precipitation of each site were used to test for relationships between germination characteristics of seeds and environmental conditions using mixed models that accounted for population as a random effect and estimated temperature, precipitation and latitude as fixed effects. Models were fitted using all covariates alone and in combination as a multiple regression, as well as allowing for interaction between temperature and precipitation. Model comparison was conducted using AIC.

Results

Germination characteristics of native and introduced populations

Introduced populations of *P. virginica* displayed significantly higher germination percentages (96.76 \pm 0.36) than native populations (84.21 \pm 1.29) in the four-year experiments (Fig. 2a) and germination percentages were significantly different amongst years (*P* < 0.001; Table 1; Fig. 3a). For native populations, germination percentage increased through the four years (from 61.14 \pm 5.00 in 2012 to 94.24 \pm 1.00 in 2015). For introduced populations, there was no such significant change in germination over time (Fig. 3a).

Seeds from introduced populations started to germinate significantly earlier than those of native populations in all three years (P < 0.001; Table 1; Fig. 3b). The days to germination differed significantly amongst years (P < 0.001; Table 1) and gradually got shorter in later years for both native and introduced populations (7.37 ± 0.07 to 4.14 ± 0.07 and 7.00 ± 0.00 to 3.44 ± 0.07 , respectively; Fig. 3b).

Native populations displayed longer durations of germination than introduced populations in all years (Table 1; Fig. 2c), but the magnitude of this difference varied amongst years (Table 1; Fig. 3c). The duration of germination of native populations diminished over years (from 3.24 ± 0.25 to 2.60 ± 0.11) (Fig. 3c).

The impact of seed mass on germination characteristics

There was no difference in seed mass between the native and introduced ranges, but seed mass was significantly different amongst populations within each region (See Suppl. material 2: Figure S1). Overall germination percentages, the days to germination and the duration of germination were all significantly different between regions, even when controlling for the effects of seed mass (Table 2).



Figure 2. Box plots of introduced (China) and native (USA) populations of *Plantago virginica* across years: **a** germination percentage **b** days to germination **c** duration of germination.



Figure 3. Mean trait values (\pm SE) of native (USA) (blue triangles) and introduced (China) (red symbols) populations of *Plantago virginica*: **a** germination percentage **b** days to germination **c** duration of germination. Days to germination and duration of germination were not measured in 2013. Within each panel, means labelled with the same letter (capital: introduced populations; lower case: native populations) do not differ at *P* = 0.05 based on LSD test.
		C						
	Germination percentage (%)			Days to germination (d)		Duration of germination (d)		
Fixed effects	df	Residual df	F	df	χ^2	df	Residual df	F
Region	1	718	7.096*	1	193.862***	1	694	18.328***
Year	3	718	27.26***	2	534.160***	2	694	5.342**
Region ×Year	3	718	21.02***	2	20.868***	2	694	4.880**
Random effects			SD		SD			SD
Population (Region)			0.962		0.805			0.060

Table 1. Summary of generalised linear mixed models analyses of germination percentage and duration of germination and mixed-effects Cox model of days to germination of *P. virginica* from introduced (China) and native (USA) regions.

Variables of germination percentage and duration of germination were analysed with generalised mixed-effects models and the fixed effects were tested with numerical approximations of the *F*-statistic. Variables of days to germination were analysed with a mixed-effects Cox model and the fixed effects were tested with deviance differences as χ^2 -statistic. † *P* < 0.1, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Table 2. Summary of generalised linear mixed models analyses of germination percentage and duration of germination and mixed-effects Cox model of days to germination of *P. virginica* from introduced (China) and native (USA) regions in the experiment conducted in 2012.

	Germination percentage (%)			Days to germination (d)		Duration of germination (d)		
Fixed effects	df	Residual df	F	df	χ^2	df	Residual df	F
Region	1	116	3.9801*	1	124.74***	1	110	1.0709*
Random effects			SD		SD			SD
Seed mass			2.4186		0.0132			0.1220
Population (Region)			1.0650		1.3737			0.1741

Variables of germination percentage and duration of germination were analysed with generalised mixed-effects models and the fixed effects were tested with numerical approximations of the *F*-statistic. Variables of days to germination were analysed with a mixed-effects Cox model and the fixed effects were tested with deviance differences as χ^2 -statistic. † *P* < 0.1, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001

The proportion of mouldy seeds in native and introduced populations

The proportion of mouldy seeds in introduced populations (22.53 ± 7.99 (%)) was significantly higher than in native ones (4.80 ± 1.70 (%)) after being subjected to a four-year storage period (Suppl. material 3: Figure S2).

Relationships between germination characteristics and environmental variables

None of the germination characteristics (germination percentage, days-to-germination, nor germination duration) was significantly related to mean annual temperature, precipitation and latitude (Suppl. material 5: Figure S4; all P > 0.1). Lowest AIC values supported models only including population-level random effects. However, there was significantly more variability in germination percentages amongst populations in the native range compared to the introduced range, suggesting greater population differentiation (std = 1.55 in native range and std < 0.1 in the introduced range).

Discussion

The potential importance of germination characteristics for biological invasions has been hypothesised for decades (Baker 1974) and, because of their crucial consequences for fitness, germination traits are thought to undergo strong environmental selection (Cohen 1966; Donohue et al. 2005; Hierro et al. 2009; Venable 2007). Nonetheless, few comparative studies of invaded and native ranges have been conducted. Here, we found that the introduced populations of *P. virginica* had significantly higher germination percentages and faster and shorter durations of germination than native populations. Specifically, the seeds of introduced populations germinated more rapidly and reached a higher germination percentage in a shorter time, whereas the seeds of native populations germinated more slowly and took a longer time to complete germination. Critically, the native populations had a significantly larger proportion of seeds that stayed dormant in all four years, with only 60% of seeds germinating in year 1 (compared to >95% in introduced populations). These results demonstrate striking differences in germination strategies between native and introduced populations which may contribute to their successful invasion.

Germination percentages, speed and timing

Recent studies have reported that the introduced populations can have higher germination percentages than native populations, often arguing that the higher germination percentages in many cases were due to higher seed mass in invasive populations (Beckmann et al. 2011; Leiblein-Wild et al. 2014). In this study, we also found that the germination percentages in introduced populations were higher, but the differences in germination percentages between regions were independent of seed mass.

The timing and speed of germination play important roles in determining the successful establishment of exotic species when they arrive in novel environments (Baskin and Baskin 2014; Donohue et al. 2010; Gioria and Pyšek 2017; Gioria et al. 2018). Rapid germination gives plants a size advantage in early season (van Kleunen and Johnson 2007) and the subsequent asymmetric competition may then thwart establishment or reduce growth and reproduction of the ones with later germination (Schlaepfer et al. 2010; Weiner and Thomas 1986). For example, it has been reported that the seeds of introduced populations of *Ambrosia artemisiifolia, Rhododendron ponticum* and *Ulmus pumila* germinated earlier and faster than those of native populations (Erfmeier and Bruelheide 2005; Hirsch et al. 2012; Leiblein-Wild et al. 2014). Such pattern was also found in other species such as *Eupatorium adenophorum* (Li and Feng 2009), *Echium* and *Verbascum* species (Hock et al. 2015). Our results are consistent with these findings, showing that seeds of introduced populations germinated earlier and faster than those of native populations of *P. virginica* may be explained by the Evolution of Increased

Competitive Ability hypothesis (EICA). Due to a lack of native enemies, the introduced plants may reallocate resources from defence mechanisms into growth and gain a greater fitness than their native counterparts (Blossey and Nötzold 1995; Callaway and Ridenour 2004; Joshi and Vrieling 2005). Although the introduced plants always performed better than native ones, we cannot rule out other mechanisms (such as phenotypic plasticity) due to the lack of direct evidence showing the rapid evolution of competition ability of plants in introduced populations.

Furthermore, genetic-based variation in germination has recently been demonstrated in invasive species. Based on a quantitative trait-loci analysis, Huang et al. (2010) showed that germination phenology of *Arabidopsis thaliana* was linked to particular regions on chromosomes. In addition, other factors such as founder effects, random genetic drift and maternal effects could also be responsible for differences in germination traits between native and introduced regions. Therefore, it remains an open question in most cases whether differences in germination percentages have been selected by the environments in introduced region and therefore are an important determinant of invasiveness (Gioria et al. 2018) or are a by-product of the genetic bottleneck and/or random chance associated with the invasion process (Sakai et al. 2001).

Seed dormancy

Amongst other germination characteristics, seed dormancy represents an important component of a germination strategy (Baskin and Baskin 2014) and is often a bethedging and/or risk-reducing strategy in temporally unfavourable conditions and/ or unpredictable environments (Venable 2007; Venable and Brown 1988). The strategy of low germination percentage with deep dormancy can reduce the risk of extinction during unfavourable conditions. In our study, we found that seeds of native populations had significantly deeper dormancy, i.e. the germination percentage of seeds collected from native populations increased with storage time. This result suggests that the conditions of plant growth in introduced populations are more favourable or the seedlings in introduced populations had higher ability to tolerate unsuitable conditions (Gioria et al. 2018). Higher tolerance of seedlings with higher germination percentage and speed can further facilitate the success of invasion (Leiblein-Wild et al. 2014).

Alternatively, high germination percentages can serve as an escape from unfavourable conditions in the seed bank. If predators or pathogens attack seeds more than seedlings, rapid germination rather than dormancy could be advantageous (Baskin and Baskin 2014; Xiao et al. 2007). Indeed, we investigated the proportion of mouldy seeds after storage for four years and found that the proportion of mouldy seeds was higher in introduced populations than in native ones (See Suppl. material 3: Figure S2), which is consistent with previous reports (Baskin and Baskin 2014).

Geographical differentiation in seed germination

Geographical variation in local adaptation to climates or environments can enable a species to inhabit a large ecological breadth and range. For instance, Meyer et al. (1995) found that more widely distributed *Penstemon* species exhibited more variable germination patterns across their range, suggesting that ecotypic differentiation in germination itself may contribute to the geographic range of widespread species. A recent study also reported a geographical pattern of seed germination in *Gladiolus gueinzii* (Tabassum and Leishman 2018). It found that the seeds from the range edge populations had significantly faster germination times and greater dispersal ability which may be a key factor in promoting further range expansion of this species (Tabassum and Leishman 2018). Alternatively, a wide germination niche of species could simply result from very broad germination requirements for all populations of that species (Baskin and Baskin 2014; Donohue et al. 2010). In at least one case study, species with a wider range of germination temperatures also had larger geographic ranges (Brändle et al. 2003).

In the present study, the germination strategy of *P. virginica* in their native range exhibited clear geographical variations across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation (Suppl. material 5: Figure S4). Although these relationships were not statistically significant, the clear differences amongst populations suggest selection for germination strategies due to other local habitat factors. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that *P. virginica* may have experienced strong selection for earlier life history characteristics and /or not enough time for subsequent evolution to occur.

The more limited range of germination traits in introduced populations may also be ascribed to the more homogenous genetic background and lower genetic loads than in native populations caused by the genetic bottleneck and Allee effect during the range expansion (Sakai et al. 2001). Thus, it is possible that lower genetic diversity of *P. virginica* in the introduced range may have led to weaker responses to geographical variation in environmental factors and further limited the expansion of distribution range in a short invasive history (Xu et al. 2017). Moreover, the sampling range in China was not as broad as that in the U.S., which may influence these inferences about population differentiation, but these sampling sites represented almost all habitats across most of the distribution of *P. virginica* in China.

Conclusions

There was significant differentiation in germination strategies and dormancy patterns between native and introduced populations in *P. virginica*. Seeds of introduced populations exhibited less dormancy and higher germination percentage and germinated earlier and faster than those of native populations. The germination

strategy of *P. virginica* in their native range exhibited clear geographical variations across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that *P. virginica* may have experienced strong selection for earlier life history characteristics. These differences in seed germination characteristics are likely to impact the individual plant fitness, biotic interactions, as well as the species' success with invasion. Our findings highlight the need to further examine the role of rapid evolution of germination traits in facilitating plant invasions.

Acknowledgements

We thank Teresa E. Popp, Shuaihua Zhong, Jiawei Wang, Fengyao Yuan, Jiaqi Cheng, Hui Dong, and Dening Kong for helping to conduct the experiments. This work was supported by National Key R&D Program of China (2017YFC1200105), Natural Science Foundation of Jiangsu province (BK20161445) and Project of National Natural Science Foundation of China (No. 31100298).

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Supplementary material I

Table S1. Source populations of *P. virginica* seeds used in germination experiments

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: species data

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Link: https://doi.org/10.3897/neobiota.43.30392.suppl1

Supplementary material 2

Figure S1. Box plots of seed mass

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: statistical data

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Supplementary material 3

Figure S2. Proportion of moldy seeds

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: species data

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Supplementary material 4

Figure S3. Photos of introduced population of P. virginica

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: media

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Link: https://doi.org/10.3897/neobiota.43.30392.suppl4

Supplementary material 5

Figure S4. Relationships between the germination traits and environmental variables

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: statistical data

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Link: https://doi.org/10.3897/neobiota.43.30392.suppl6

Supplementary material 6

Coordinates

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu Data type: occurrence

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