Biol Invasions (2016) 18:73–87
DOI 10.1007/s10530-015-0990-4

CrossMark

ORIGINAL PAPER

Understanding and managing the introduction pathways of alien taxa: South Africa as a case study

Katelyn T. Faulkner · Mark P. Robertson · Mathieu Rouget · John R. U. Wilson

Received: 18 November 2014 / Accepted: 24 September 2015 / Published online: 27 October 2015

Abstract For the effective prevention of biological invasions, the pathways responsible for introductions must be understood and managed. However introduction pathways, particularly for developing nations, have been understudied. Using the Hulme et al. (J Appl Ecol 45:403–414, 2008) pathway classification, we assessed the South African introduction pathways in terms of the number of introductions, the invasion success of introduced taxa, how the pathways have changed over time, and how these factors vary for vertebrates, invertebrates and plants. Pathway and date of introduction, region of origin, distribution and invasion status data for 2111 alien taxa were extracted from databases. Most alien and invasive taxa were deliberately introduced and subsequently escaped captivity or cultivation. Pathway prominence also varied temporally and across organism types. Vertebrates and plants were largely escapes and although most plant escapes have become invasive, this is not the case for vertebrates. However the number of new plant and vertebrate escapes has increased over time. Invertebrates have been deliberately released or unintentionally introduced as contaminants or stowaways. For invertebrates the number of release, contaminant and stowaway introductions has increased, and most contaminants and stowaways have become invasive. As effective screening procedures are in place for invertebrates released for biological control, the major threats for South Africa are from vertebrate and plant escapes and invertebrate contaminants and stowaways. We recommend improvements to risk assessment and education to prevent escapes, and prioritised inspection strategies to reduce stowaway and contaminant introductions. Finally, as introduction pathways and introduced taxa change temporally, biosecurity decisions need to be informed by information on current and future pathways.

Keywords Biological invasions · Biosecurity · Pre-border control · Invasion success · Mode of introduction · Date of introduction

Electronic supplementary material The online version of this article (doi:10.1007/s10530-015-0990-4) contains supplementary material, which is available to authorized users.

K. T. Faulkner (✉) · J. R. U. Wilson
Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735, South Africa
e-mail: katelynfaulkner@gmail.com

K. T. Faulkner · M. P. Robertson
Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Hatfield 0028, South Africa

M. Rouget
Centre for Invasion Biology, School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa

J. R. U. Wilson
Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

Introduction

Preventing the introduction of alien taxa is often more cost-effective than managing these taxa after introduction (Leung et al. 2002; Puth and Post 2005; Wittenberg and Cock 2005; Simberloff 2006; Simberloff et al. 2013). Most efforts to prevent the introduction of alien taxa into a new region focus on species- or pathway-centred approaches (Hulme 2006). In species-centred approaches, alien taxa that pose a high invasion risk are identified, usually through risk assessments, and then targeted in prevention strategies (Pheloung et al. 1999; Kolar and Lodge 2002; Kumschick and Richardson 2013). Species-centred approaches require a lot of investment (e.g. in taxonomic support and inspection capacity) and are often problematic to employ due to data deficiencies, difficulties associated with the identification of predictive traits, and as risk assessments have not been developed for all taxa (Everett 2000; Hulme 2006; Kumschick and Richardson 2013). Additionally, this approach is often reliant on knowing whether species have become invasive elsewhere, and so is of limited value for organisms that have not had a long and well-studied history of introduction (Williams and Newfield 2002). Consequently, the pathway-centred approach is often more effective (Hulme 2006). This approach uses information on how or why alien taxa are introduced to develop preventative strategies, early detection methods and import regulations that target the most active pathways of introduction (Hulme 2006, 2009). In so doing, available and often limited resources can be distributed effectively (Everett 2000; Bacon et al. 2012). For any targeted pathway, colonisation pressure (i.e. the number of species introduced) and propagule pressure (i.e. the number of individuals introduced and/or the number of introduction events for a specific taxon) should decrease and the probability that introduced taxa will establish and spread will likely diminish (Kolar and Lodge 2001; Simberloff 2009; Pyšek et al. 2011). For example, to decrease the invasion threat posed by shipping to the Great Lakes the mid-oceanic exchange of ballast water has been recommended (MacIsaac et al. 2002). This management technique greatly reduces the number of propagules released by arriving ships and consequently the number of taxa that are successfully introduced decreases (MacIsaac et al. 2002).

Despite the management implications of research on the pathways of introduction, the initial stages of the invasion process (transport and introduction; see Blackburn et al. 2011) have been relatively understudied (Puth and Post 2005). Nevertheless, the body of work on these initial stages has grown over time (Puth and Post 2005) and has demonstrated that the significance of the pathways of introduction varies taxonomically, geographically and temporally (Kraus 2007; Hulme et al. 2008; Lambdon et al. 2008; Wilson et al. 2009; Pyšek et al. 2011; Lehan et al. 2013). It has thus been concluded that pathways of introduction are idiosyncratic in nature and are not only associated with organism traits, but are also shaped by historical social, economic and technological trends (Everett 2000; Lambdon et al. 2008; Hulme 2009; Wilson et al. 2009).

Recent analyses have also demonstrated a link between the pathways of introduction and subsequent invasion success (Pyšek et al. 2011). This association is not likely to be straightforward and may be driven by various processes (Lambdon et al. 2008; Wilson et al. 2009; Pyšek et al. 2011). Firstly, this influence may be attributed to colonisation pressure (Lambdon et al. 2008; Lockwood et al. 2009). The greater the number of species introduced through a pathway, the greater the probability that some will possess the attributes required to successfully invade and the greater the probability that a successful invader will be introduced (Lambdon et al. 2008; Lockwood et al. 2009). Secondly, attributes (e.g. human assistance, propagule pressure, genetic diversity, probability of movement of co-evolved species and pathway duration) that vary across the pathways of introduction may have consequences for the relative success of introduced taxa (Mack 2005; Wilson et al. 2009; Pyšek et al. 2011). Finally, organism traits that facilitate introduction through specific pathways [e.g. larger aquarium fish are more likely to be released by owners (Gertzen et al. 2008)] may confer success during the subsequent stages of invasion (Cassey et al. 2004; Mack 2005; Dehnen-Schmutz et al. 2007). Assessing these processes and determining the relative invasion risk posed by the different pathways would facilitate the development of management strategies that target pathways with a high invasion risk and inform post-introduction management (Pyšek et al. 2011; Essl et al. 2015).

In addition to knowledge gaps, implementing pathway-centred prevention strategies and legislation can be challenging due to the sheer number of potential pathways (Hulme et al. 2008; Essl et al. 2015). To facilitate such action Hulme et al. (2008) developed a framework that classifies the pathways of introduction into six categories based on their attributes (e.g. level of human assistance, means of transport and subsequent introduction). In so doing the level of detail that is required for management is retained, while overarching legislation for only six pathways needs be developed (Hulme et al. 2008).

The pathways of introduction for parts of Europe (e.g. for plants in the Czech Republic, see Pyšek et al. 2011) and at a global scale (Hulme et al. 2008) have been comprehensively analysed using this framework. However, research on the introduction pathways for developing nations is lacking, possibly due to data deficiencies driven by economic priorities and practical restrictions (Pyšek et al. 2008). Unfortunately, such research biases are likely hindering our understanding of the early stages of invasion and the overall progress of invasion biology (Pyšek et al. 2008). In South Africa, invasive taxa have significant impacts (van Wilgen et al. 2001). But, assessments of the South African pathways of introduction have been rudimentary and have either focused on specific taxa (e.g. Henderson 2006; Herbert 2010) or a few very specific pathways (e.g. Saccaggi and Pieterse 2013). Finally, due to South Africa's socio-economic history and relatively short introduction record, one would expect that South Africa's pathways of introduction would differ greatly from those of the nations that have already been assessed. Here we utilise the pathway classification framework of Hulme et al. (2008) to evaluate the pathways of introduction for South African alien taxa, and specifically assess: (1) the number of alien taxa that have been introduced through the different pathways, (2) the invasion status of taxa (i.e. their position along the introduction-naturalisation-invasion continuum) introduced through the different pathways, and (3) how the prominence of pathways have changed through time. In each case we explore whether the results differ for plants, vertebrates and invertebrates.

Methodology

Data collection

We assessed recent South African alien species databases and selected the most comprehensive databases with regard to the listed taxa and information content (for full details see Faulkner et al. 2015). Data on taxonomy, pathway of introduction, date of introduction, region of origin, invasion status and distribution for 2111 alien taxa were extracted from the selected databases (for details on the types of data used see Faulkner et al. 2015).

Pathways of introduction were classified using the framework of Hulme et al. (2008). The pathway categories, arranged from greatest to least amount of human assistance, are as follows: (1) release, (2) escape, (3) contaminant, (4) stowaway, (5) corridor and (6) unaided (Hulme et al. 2008). Release is the intentional introduction of a commodity organism for release (e.g. biological control agents). Escape is the intentional introduction of a commodity organism that escapes unintentionally (e.g. pets). Contaminant is an unintentional introduction with a commodity (e.g. commensals on traded plants). Stowaway is an unintentional introduction attached to or within a transport vector (e.g. hull fouling marine taxa). Corridor is an unintentional introduction via human built corridors that link previously unconnected regions (e.g. Lessepsian migrants). Unaided is an unintentional introduction through the natural dispersal of alien taxa across political borders.

Terrestrial, freshwater and marine organisms were considered together, however, we did separate taxa into broad taxonomic categories: vertebrates, invertebrates and plants (these categories are referred to as 'organism type'). Taxa introduced through more than one pathway were assigned to multiple pathway categories (consequently the total number of taxa across the pathways will be greater than the number of taxa analysed). The earliest date of introduction was utilised in instances where multiple introduction events occurred or if, due to uncertainty, a period of time was given. Invasion status data were only recorded if the classifications and definitions of Richardson et al. (2000) or Blackburn et al. (2011) were utilised. These classifications divide the invasion continuum into four stages: transport, introduction, establishment and spread (Richardson et al. 2000; Blackburn et al. 2011). The invasion status (i.e. introduced/casual, naturalised/established or invasive) of alien taxa is determined based on the invasion stage occupied (Richardson et al. 2000; Blackburn et al. 2011). Taxa for which invasion status was not specified or for which a different classification was utilised were assigned an invasion status using distribution data and other useful information (see full methodology below).

Invasion status designation

The framework of Blackburn et al. (2011) divides each invasion status into invasion categories (see Table 1 for definitions). Using this framework we determined, based on the types and level of information found in alien species databases, the evidence required to designate taxa into each invasion category (Table 1). It is important to note that due to the types of data available, organisms classified as D1 were regarded as naturalised but not invasive, this is not the case in Blackburn et al. (2011) in which D1 is classified as naturalised and invasive.

Designations for each alien taxon were made using the data extracted from alien species databases (e.g. distribution data). If invasion status as per Richardson et al. (2000) or Blackburn et al. (2011) was specified this information was utilised and any additional evidence was only employed to assign an invasion category (e.g. naturalised but not invasive taxa as C3 or D1) within the specified invasion status (Table 1). To facilitate invasion category assignments, extracted distribution data were utilised to designate each organism as having a localised, limited or widespread distribution. An organism has a localised distribution if found in only one locality (i.e. one locality point or place name is given) or, for fresh water fish, in small streams or ponds. Taxa with a limited distribution occur in one province (i.e. two or more locality points limited to one province or one province name is given) or river system. Here the term 'province' refers to biogeographical provinces for marine taxa (see Mead et al. 2011) and political provinces for terrestrial taxa. Taxa that occur in multiple provinces or river systems or whose distribution was described as 'widespread' were considered to have a widespread distribution. Taxa with no distribution information had an 'unknown' distribution. Dubious distribution records were not utilised when assigning distribution classifications.

Uncertainty, due to insufficient or vague evidence, often led to taxa being assigned to multiple invasion categories (e.g. D1–D2). A set of rules was developed to standardise invasion category or distribution classification assignments in instances of uncertainty (see Online Resource 1). Additionally, uncertainty was accounted for by rating confidence in invasion status as low, medium or high. Low confidence was assigned if the invasion status of an organism could not be defined (e.g. C1–D1: could be casual or naturalised). If the invasion status of an organism could be determined but the organism's invasion category could not be defined then medium confidence was assigned (e.g. C3 and D1: is naturalised but it is not clear to what extent). A high level of confidence was assigned when the invasion category of an organism could be determined (e.g. C1: casual).

The various levels and types of information utilised in the invasion status designations were accounted for by rating the content of the information used from 0 to 3. An information content rating of 0 was given if no information was provided. Short descriptions were given a rating of 1 and detailed descriptions were given a rating of 2. Information content was given a rating of 3 if a map of point distribution data with or without additional information was used, or if invasion status at a country wide level was specified.

Analyses

Data analysed

Excluded from all analyses were hybrid taxa, dubious records (for example the mollusc *Vertigo antivertigo* which has only been found as a subfossil, see Herbert 2010), taxa in captivity or under cultivation and those whose region of origin extends into South Africa. Taxa with an uncertain region of origin were excluded unless currently believed not to be of South African origin. Taxa which were listed as alien but for which no information on region of origin was given were assumed to be alien and were included in the analyses. Pathways of introduction were unknown for 1093 of the 1839 alien taxa selected for the analyses (see Online Resource 2 for the types of organisms included in the selected vertebrate and invertebrate taxa). Thus only 746 taxa were included in the statistical analyses. There were no records of the corridor pathway being utilised by alien taxa to enter South Africa and thus

Table 1 Biological invasion categorisations, related definitions and invasion status designations as defined by Blackburn et al. (2011), as well as the evidence required for categorisation

Category	Definition	Status	Evidence
A	Not transported beyond limits of native range	Not introduced	Absent from alien species databases
B1	Individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place)	Casual/introduced	Records of individuals in captivity (e.g. in zoos or in quarantine). No individuals recorded outside captivity
B2	Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them, but explicit measures to prevent dispersal are limited at best)	Casual/introduced	No wild population documented. Individuals kept in cultivation and/or on a ranch or farm
B3	Individuals transported beyond limits of native range, and directly released into a novel environment	Casual/introduced	Records of individuals in the wild. Fate unknown or may be extinct from novel environment
C0	Individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period	Casual/introduced	Failed introductions
C1	Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction	Casual/introduced	Distribution localised and population not reproducing
C2	Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining	Casual/introduced	Distribution localised and population not self-sustaining
C3	Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining	Naturalised/established	Classified as established or naturalised in the literature AND distribution is localised OR population is reproducing and self-sustaining AND distribution is localised
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction	Naturalised/established	Classified as established or naturalised in the literature AND distribution is either limited or widespread
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction	Locally invasive	Classified as locally invasive in the literature OR distribution is limited
E	Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence	Widespread invasive	Classified as invasive in the literature OR distribution is widespread

this pathway was not considered. Analyses were performed in R version 3.0.0 (R Core Team 2013).

The number of taxa introduced through the different pathways

To evaluate how many taxa have been introduced through the different pathways, the counts of taxa were analysed as a two-way (pathway and organism type) contingency table using generalised linear models (Poisson error distribution and log link) to test the association between pathway and organism type (Crawley 2007). Models were checked for overdispersion by dividing the residual deviance by residual degrees of freedom (Crawley 2007; Zuur et al. 2009). No instances of overdispersion were identified. Following Everitt (1977) and Bewick et al. (2004) counts that were significantly lower or higher than expected based on chance alone were identified by calculating the standardised adjusted residuals and comparing these values with critical values of the normal distribution.

Invasion status of taxa introduced by different pathways

To determine whether taxa introduced through the different pathways vary in their invasion success, generalised linear models (Poisson error distribution and log link) were used to analyse a three-way contingency table (pathway, invasion status and organism type) of taxa counts and to determine if invasion status, pathway and organism type are associated (Crawley 2007). The number of taxa that are casual (introduced and outside captivity/cultivation but not naturalised), naturalised but not invasive, and invasive were compared and only taxa with invasion status designations with medium or high confidence (540 taxa) were included. All local and widespread invasive taxa were classified as invasive (Table 1). Models were checked for overdispersion, but no instances were identified (Crawley 2007; Zuur et al. 2009). To determine which counts were significantly different from what was expected based on chance alone, the standardised adjusted residuals were calculated and these values were compared with critical values of the normal distribution (Everitt 1977; Bewick et al. 2004).

Temporal variations in the pathways of introduction

To determine how the pathways of introduction have changed over time, analyses were performed on taxa for which pathway and date of introduction data were available (408 taxa). To determine the pattern of increase over time, the cumulative counts were regressed against date of introduction. As these relationships were not linear, generalised additive models with loess smoothing from the "gam" package (Hastie 2013) were used. Models with varying degrees of span were assessed starting at 0.1 and then increasing the span by small increments. Model selection was based on the Akaike Information Criterion (AIC) and plotting techniques were used to determine whether model assumptions had been met (Zuur et al. 2009). These analyses were not performed for pathways with few (<20) records available (i.e. contaminant, stowaway, unaided and unknown for vertebrates and plants, escape for invertebrates, and release for plants).

Results

The number of taxa introduced varied greatly across the pathways of introduction, but the majority of taxa were escapes (Fig. 1). The number of taxa introduced through the different pathways varied significantly between vertebrates, invertebrates and plants (significant association between pathway and organism type; Table 2). Although significantly more vertebrates and plants were escapes than was expected, significantly more invertebrates were either released or introduced as contaminants or stowaways than was expected by chance. There were a large number of plant and invertebrate taxa for which pathway of introduction is unknown, however, this was not the case for vertebrates.

The invasion status of introduced taxa varied across the pathways of introduction (Fig. 2). The majority of casual, naturalised and invasive taxa were escapes. The association between the pathways of introduction and invasion status varied significantly between vertebrates, invertebrates and plants (significant association between status, pathway and organism type; Table 3). For vertebrates, significantly fewer casual taxa but significantly more naturalised and invasive taxa were released than was expected. Significantly more casual vertebrate taxa were introduced through the escape pathway than expected, and although most invasive vertebrates were escapes this number was not significantly different to what is expected based on chance. Significantly more casual invertebrates were released than was expected, but significantly fewer invasive invertebrates were introduced through this pathway than expected based on chance. For invertebrates, most invasive taxa were introduced through the contaminant and stowaway pathways, but these numbers were not significantly different to what was expected. Significantly fewer plant escapees were casual than was expected, and although there are a large number of invasive plant escapees, this quantity was no greater than what is expected based on chance.

For vertebrates, invertebrates and plants the number of taxa introduced through the pathways has changed temporally (Fig. 3). The number of vertebrate escapees has increased over time and has accelerated since

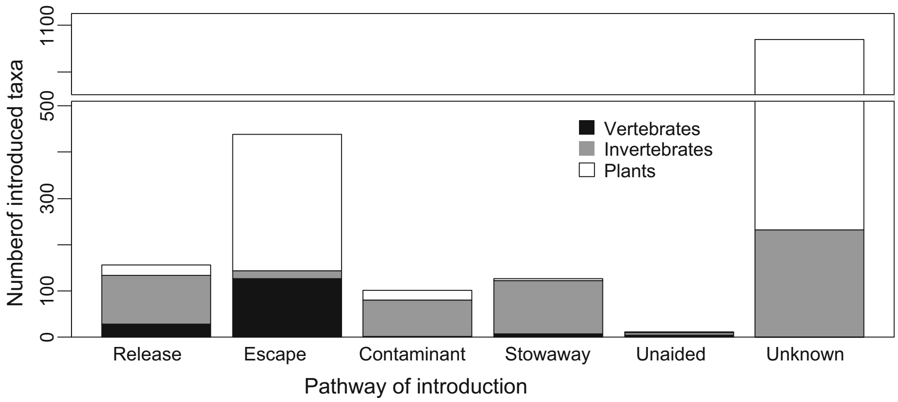

Fig. 1 The number of alien vertebrates, invertebrates and plants introduced to South Africa through the pathways of introduction. The break in the y-axis extends from 510 to 950

Table 2 Observed counts and expected values from a generalised linear model testing the association between organism type and pathway of introduction ($df = 8$, $\chi^2 = 608.6$, $P < 0.001$) for taxa introduced to South Africa

Pathway of introduction	Organism type					
	Vertebrates		Invertebrates		Plants	
	Observed	Expected	Observed	Expected	Observed	Expected
Release	28	31.8	106*	60.0	22*	64.3
Escape	127*	89.4	16*	168.8	296*	180.9
Contaminant	2*	20.8	79*	39.2	21*	42.0
Stowaway	8*	25.9	115*	48.8	4*	52.3
Unaided	5*	2.2	5	4.2	1*	4.5

Values that are significantly higher or lower than expected by chance are indicated using an asterisk. Taxa for which the pathways of introduction are unknown were not included in the statistical analysis

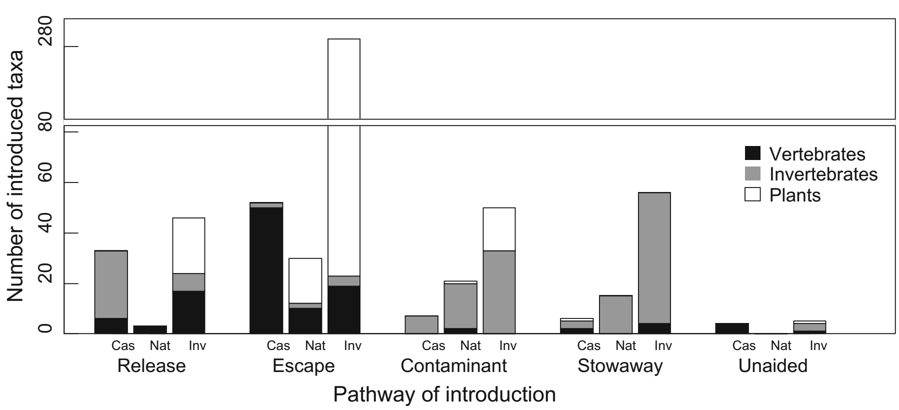

Fig. 2 The invasion status of alien vertebrates, invertebrates and plants introduced to South Africa through the pathways of introduction. Taxa that are casual (Cas) have been introduced but are neither naturalised nor invasive, naturalised taxa (Nat) are naturalised but not invasive and invasive taxa (Inv) are naturalised and invasive. The break in the y-axis extends from 80 to 250

Table 3 Observed counts and expected values from a generalised linear model testing the association between invasion status, pathway of introduction and organism type ($df = 16$, $\chi^2 = 63.0$, $P < 0.001$) for taxa introduced to South Africa

Organism type	Pathway of introduction	Invasion status					
		Casual		Naturalised		Invasive	
		Observed	Expected	Observed	Expected	Observed	Expected
Vertebrates	Release	6*	13.2	3*	1.3	17*	11.4
	Escape	50*	45.8	10	11.7	19	21.5
	Contaminant	0	0.2	2*	0.7	0	1.1
	Stowaway	2*	0.4	0	1.3	4	4.4
	Unaided	4*	2.4	0	0.0	1*	2.6
Invertebrates	Release	27*	19.7	0	1.4	7*	12.9
	Escape	2*	5.2	2	0.9	4*	1.9
	Contaminant	7	6.8	18	19.0	33	32.2
	Stowaway	3*	5.6	15	13.7	52	50.7
	Unaided	0*	1.6	0	0.0	3*	1.4
Plants	Release	0	0.0	0	0.3	22	21.7
	Escape	0*	1.0	18	17.4	264	263.7
	Contaminant	0	0.0	1	1.3	17	16.7
	Stowaway	1*	0.0	0	0.0	0*	1.0
	Unaided	0	0.0	0	0.0	1	1.0

Values that are significantly higher or lower than expected by chance are indicated using an asterisk. Taxa for which the pathways of introduction are unknown were not included in the statistical analysis

1950. In contrast, few new vertebrate taxa have been released since the 1950s, and no new releases have been recorded since 1980. For invertebrates the number of stowaways, contaminants and releases has increased over time. The number of released invertebrates has increased sharply since 1970. In contrast, the increase in invertebrate contaminant and stowaway introductions in the 1900s was more gradual, particularly since the early 1900s for contaminants and the 1950s for stowaways. However, invertebrate contaminant and stowaway introductions accelerated in the 2000s. The number of plant escapees has gradually increased over time. The number of invertebrates and plants for which pathway of introduction is unknown has increased over time, and for invertebrates has accelerated since the 1990s.

Discussion

The innate idiosyncrasies of the pathways of introduction (e.g. geographical, taxonomic and temporal variations) for alien taxa have been demonstrated in various global and country-level analyses (Kraus 2007; Hulme et al. 2008; Lambdon et al. 2008; Wilson et al. 2009; Pyšek et al. 2011; Lehan et al. 2013). Consistent with these analyses, the South African pathways of introduction vary in their significance across organism types, in their influence on invasion success and temporally.

The number of taxa introduced through the different pathways

In line with global trends (Hulme et al. 2008), most introduced taxa in South Africa are escapes. However, as shown here and in studies on global (Kraus 2007; Hulme et al. 2008), European (Hulme et al. 2008) and Chinese (Xu et al. 2006) data, the relative importance of different pathways of introduction varies across organism types. Similar to our results, escapes are important for the introduction of vertebrates globally (Kraus 2007; Hulme et al. 2008) and plants in China (Xu et al. 2006), the USA (Lehan et al. 2013) and Europe (Hulme et al. 2008; Lambdon et al. 2008; Pyšek et al. 2011). Additionally as shown here for South Africa, in global and European studies invertebrate introductions are dominated by contaminants

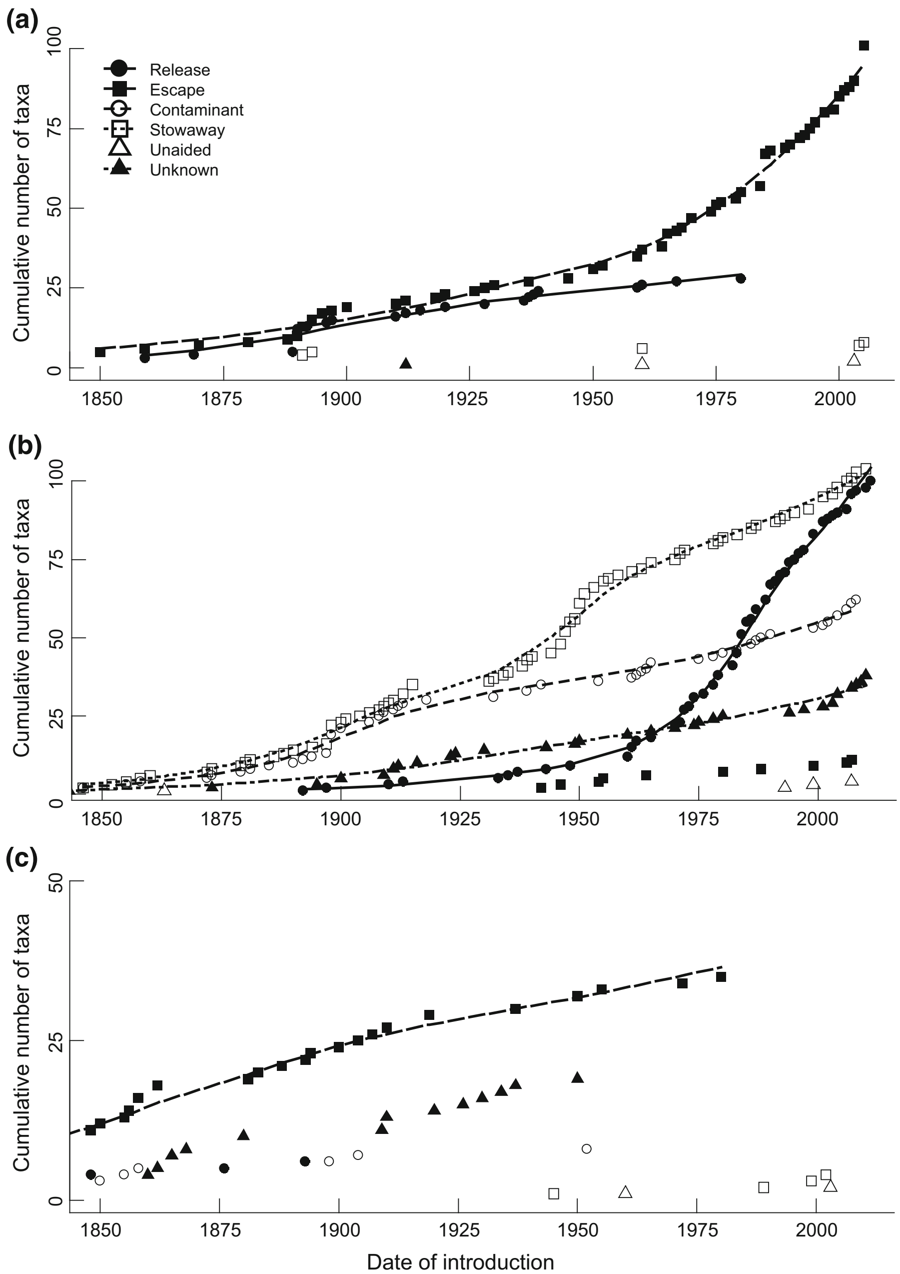

Fig. 3 Temporal pathway of introduction patterns for **a** vertebrates, **b** invertebrates and **c** plants introduced to South Africa. Fitted lines are loess best regression curves selected using AIC. Curves were not fitted to pathways with less than 20 introduction records

and stowaways (Kenis et al. 2007; Hulme et al. 2008) and the unaided pathway plays a small role (Hulme et al. 2008; Pyšek et al. 2011). However, due to difficulties in recognising and reporting unaided introductions, the importance of this pathway is likely underestimated in most assessments (Hulme et al. 2008; Essl et al. 2015).

In contrast to our findings for South Africa, in Europe vertebrates are more commonly released than escape (Hulme et al. 2008), and plants are more often unintentionally introduced (e.g. as contaminants (Lambdon et al. 2008; Pyšek et al. 2011); see Lehan et al. (2013) for similar results for the USA). These differences could be because South Africa is a developing nation with a relatively short introduction history. For instance, Europe's long history of agriculture would have provided many chances for the deliberate and accidental introduction of plants (Mack and Erneberg 2002). Despite the large role that releases play in invertebrate introductions in South Africa, this pathway plays a relatively small role globally and in Europe (Kenis et al. 2007; Hulme et al. 2008). In South Africa alien invertebrates are released for the biological control of alien organisms, and the importance of this pathway demonstrates the significance of South African biological control projects (Moran et al. 2005; Klein 2011; Moran et al. 2013). Finally, while the corridor pathway plays an important role in some regions (e.g. Lessepsian migrants in Europe, see Katsanevakis et al. 2013), this pathway does not facilitate the introduction of taxa to South Africa. However, in South Africa human-made corridors do aid the spread of alien taxa (e.g. human made tunnels allow fish to disperse) once introduced (Richardson et al. 2003).

All assessments of the pathways of introduction are limited by the quality and scope of the available data (Mack and Erneberg 2002; Lambdon et al. 2008). In South Africa, pathway of introduction information was not available for a large proportion of alien plants (71 %) and invertebrates (42 %). In comparison, these data were not available for ~30 % of plants in the USA (Mack and Erneberg 2002; Lehan et al. 2013) and for between 2 and 8 % of invertebrates in Europe (Hulme et al. 2008). The availability of pathway of introduction data may depend on how well-known the alien taxa are. For example, these data may be available for taxa that are widespread invasive species, but may not be available for those that have a limited distribution. Indeed for South Africa, these data are available for many invasive plants, but for few casual plant taxa (Fig. 2). Pathway of introduction data may also be more easily recorded for organisms that are intentionally introduced than for those that are introduced unintentionally (Lehan et al. 2013). Thus although most introduced invertebrates were stowaways and contaminants, in this assessment the importance of these pathways for invertebrates may be underestimated. For plants, the number of taxa introduced as contaminants may also be underestimated, however, of the plants that do not have data available most are likely to have escaped from cultivation. Although these data gaps could be due to diffused or inaccessible data and may be remedied through directed action (Faulkner et al. 2015), additional data may therefore strengthen the observed patterns for invertebrates and plants (i.e. most invertebrates are contaminants or stowaways and most plants are escapees), and would thus not influence the final conclusions of this work.

Invasion status of taxa introduced by different pathways

To our knowledge the contribution of different pathways to the numbers of invasive (as opposed to simply introduced) taxa has not been previously explored for vertebrates and invertebrates, however, this aspect has been investigated for plants (see Pyšek et al. 2011). Our results show that plants introduced through the release or escape pathways in South Africa are no more likely to be successful invaders than plants introduced through any of the other pathways. In line with these results, ornamental plants (escapes) in the Mediterranean have a low average invasibility (low probability of becoming naturalised on a randomly selected island; Lambdon et al. 2008). However in contrast to our findings, released plants in the Czech Republic have a high likelihood of being successful invaders (Pyšek et al. 2011).

If colonisation pressure (the number of species introduced, see Lockwood et al. 2009) was the absolute driver behind invasion success, one would expect the escape pathway for plants and vertebrates, and the release, contaminant and stowaway pathways for invertebrates to be associated with invasiveness. However, this was not the case, and the identified associations, or lack thereof, may instead be due to pathway attributes and in particular to the degree of human assistance involved in introductions. The high degree of human assistance associated with releases may have aided vertebrates introduced through this pathway by acting as a buffer against hazards (e.g. environmental stochasticity; Mack 2005). Additionally, taxa that are intentionally introduced are often selected based on traits that may aid their success, and are often introduced in high numbers during multiple introduction events (Mack 2005). Pathway attributes and in particular human intention have also determined the level of success attained by released invertebrates. As these invertebrates are biological control agents, they are unlikely to have large-scale negative impacts due to the competency of pre-release screening protocols (Moran et al. 2005; Klein 2011; Moran et al. 2013). In contrast, invertebrate contaminants and stowaways receive little human assistance and thus although a large number of invertebrates were introduced through these pathways, there was no significant association between these unintentional introductions and invasion.

Temporal variations in the pathways of introduction

In South Africa, as in other parts of the world, the pathways of introduction vary temporally, and while some pathways increase in importance over time, others decline in significance (Hulme et al. 2008; Lambdon et al. 2008; Wilson et al. 2009; Pyšek et al. 2011). For alien vertebrates in South Africa the decline in releases is due to a decrease in aesthetic and angling releases, while the pet trade could be facilitating the increase in escapes. Since 1975 there has been a dramatic increase in the number of reptiles (individuals and species) imported into South Africa for the pet trade (van Wilgen et al. 2010). The increasing number of plant escapes (until ~1980) likely reflects the prominent role of the ornamental plant trade (Foxcroft et al. 2008; Martin and Coetzee 2011). Although no new plant escapes have been recorded since ~1980, this result does not reflect a decline in the importance of the escape pathway for plants, but is rather due to a deficiency in date of introduction data for alien plants in South Africa (see Faulkner et al. 2015). These trends are not unique and globally there has been a decline in the release pathway for vertebrates (since ~1900; Hulme et al. 2008) and an increase in the escape pathway for vertebrates (~1940s; Kraus 2007) and plants (from ~1780; Hulme et al. 2008). The dramatic increase in the importance of the release pathway for invertebrate introductions mirrors an increase, from 1970, in the number of biological control agents released (Moran et al. 2005; Klein 2011). Regulatory process complications resulted in a decline in the number of biological control agents released between 2000 and 2011 (Klein 2011). However, as these complications have been remedied we expect a future increase in invertebrate releases (Klein 2011).

A relationship between the amount of trade and accidental introductions has been demonstrated (Levine and D'Antonio 2003; Westphal et al. 2008). Each ship or container will not bring with it the entire species pool but rather a sample of species, some of which would have already been introduced (Levine and D'Antonio 2003). Thus, over time the number of new species introduced will not accumulate at the same rate as the number of visiting ships or the value of imports. Consequently, the relationship between trade and the number of introductions is not linear, and as trade increases the per unit (e.g. ship or container) probability of introducing a new species decreases (Levine and D'Antonio 2003). In South Africa, the number of unintentional invertebrate introductions (contaminants and stowaways) has increased over time, and although this increase slowed in the twentieth century, since 2000 the number of contaminant and stowaway introductions has accelerated (Fig. 3). Additionally, although the value of merchandise imports has accumulated exponentially over time, there has been a linear accumulation of new accidental introductions (Fig. 4). This uncoupled increase in trade and accidental introductions (from ~1975) may indicate that a large proportion of the taxa associated with South Africa's trading partners have already been introduced. There has, however, been a recent shift in South Africa's trading partners and countries like India, China and Brazil have become more prominent (Gonzalez-Nuñez 2008). As these countries will expose South Africa to new pools of alien species it is likely that the number of new unintentional introductions will continue to accelerate (Levine and D'Antonio 2003). Finally, although accidental introductions have played a relatively small role in the introduction of plants to South Africa, these pathways are playing an increasing role for alien plants in the USA and Europe (Lambdon et al. 2008; Lehan et al. 2013). In the USA this increase has been attributed to the import of contaminated seed (Lehan et al. 2013). A number of plant species have been introduced to South Africa as contaminants (e.g. *Cosmos bipinnatus*) and thus this pathway should not be neglected.

Management implications and recommendations

To obtain a more reliable indication of the pathways that require management, the idiosyncrasies discussed above must be taken into account. For instance, although the majority of alien and invasive taxa (vertebrates and plants) introduced to South Africa are escapes, and the number of taxa introduced through this pathway has increased over time, this is not the

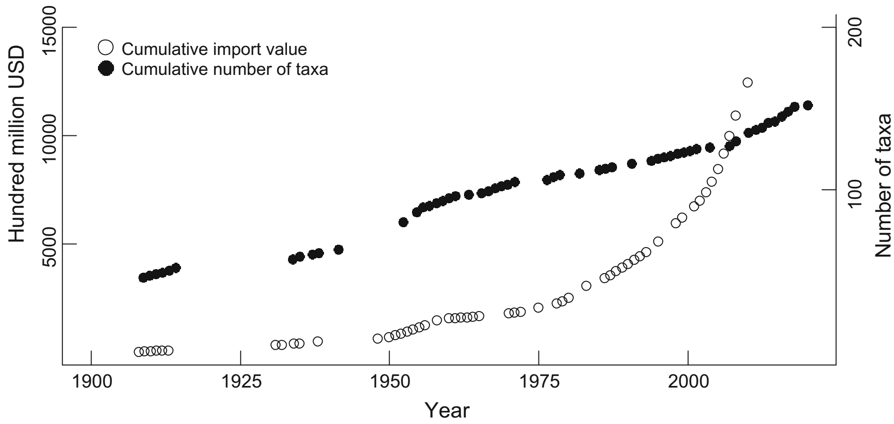

Fig. 4 Temporal trends in the value of South African merchandise imports and the number of taxa introduced unintentionally to South Africa. Import data for 1908–1959 were obtained from the United Nations, and data for 1960–2012 were obtained from the World Bank. All import values were converted to 2010 US dollars

only pathway that should be a priority for management and legislation. For invertebrates the association between the contaminant and stowaway pathways and invasion was not significant, however, a high number of invasive invertebrates have been introduced through these pathways. Additionally the contaminant and stowaway pathways have increased in importance over time, and the emergence of new trading partners may significantly increase the risk of these unintentional introductions. Thus the contaminant and stowaway pathways also pose a biosecurity risk and must be a priority for management. Finally, despite the release pathway's apparent importance for vertebrate and invertebrate introductions, as vertebrate releases have declined over time and invertebrate releases are biological control agents, this pathway actually poses little risk to South Africa.

In South Africa intentional introductions are managed under the National Environmental Management Biodiversity Act (No 10 of 2004). Under this act 168 vertebrate entities and 240 plant entities are prohibited from import. Although such legislation is a start, to prevent introductions through the escape pathway the problem must be tackled from numerous fronts. Firstly, before importation all taxa should be evaluated using a full risk assessment (Pheloung et al. 1999; Simberloff 2006; Kraus 2007). Those involved in the trade of alien taxa (e.g. pet store or nursery owners) as well as the general public need to be educated on the risks posed, existing protocols and the identification of banned taxa (Reichard and White 2001; Martin and Coetzee 2011). To decrease propagule pressure (abundance in trade) and in turn the likelihood of escape, the sale price of high risk taxa could be increased (Dehnen-Schmutz et al. 2007; van Wilgen et al. 2010). For vertebrates, restrictions on how and where individuals are kept need to be developed and enforced, and owners must be identifiable (e.g. through microchip implants) and held to account if escapes occur (Hulme et al. 2008). Finally, the attention of management and policy makers must be drawn to new, inconspicuous introductions that facilitate escapes, e.g. internet and traditional medicine trade (see Martin and Coetzee 2011; Wojtasik 2013).

Contaminant introductions are managed under The Agricultural Pests Act (Act No 36 of 1983), which requires that all consignments of plant materials are inspected before import to South Africa and upon arrival by officials from the Department of Agriculture, Forestry and Fisheries. Despite this, between 2004 and 2011, 24 % of all budwood (dormant cuttings for propagation) inspected after import was contaminated (Saccaggi and Pieterse 2013). Unfortunately the effectiveness of South Africa's inspection protocols is unknown, and the increasing number of unintentional introductions indicates that quarantine services do not have the resources to properly police ports of entry (Giliomee 2011). Following the polluter pays principle, companies exporting consignments that are contaminated should be held accountable (Hulme et al. 2008). More resources should be allocated for inspections and detailed records of inspection outcomes, be they positive or negative, must be kept. Inspection records can be used to evaluate the efficacy of current protocols and to develop prioritised inspection strategies (Areal et al. 2008; Bacon et al. 2012). To prevent stowaway introductions ballast water legislation is currently being developed (Draft Ballast Water Bill, 2013). However, to further tackle stowaways the polluter pays principle could again be instituted, whereby the owner of the vector (e.g. shipping company) is liable if either the vector or the transported goods are contaminated (Hulme et al. 2008).

Conclusions

In South Africa, the pathways of introduction for alien taxa are idiosyncratic in nature, and vary in the number of taxa introduced, in their influence on invasion success and temporally. Additionally, the number of taxa introduced and the success of introduced taxa varies across organism types. These idiosyncrasies have consequences for decision making, and to be effective pathway-centred prevention strategies must be informed by context-specific studies. Additionally, through the utilisation of temporal introduction and trade data, as well as trade predictions, an indication of the future significance of unintentional pathways may be obtained (Levine and D'Antonio 2003). Unfortunately due to geographical variations in the pathways of introduction, the results of detailed studies in one part of the world are unlikely to be applicable in other regions, thus making it necessary for each nation or region to undertake assessments. We believe that further work on the link between the pathways of introduction and subsequent invasion success and impact, particularly focussing on the underlying drivers, is required and that this may be a particularly fruitful avenue of research.

Acknowledgments This work was supported by the South African National Department of Environment Affairs through its funding of the South African National Biodiversity Institute's Invasive Species Programme. Additional funding was provided by the DST-NRF Centre for Invasion Biology. MR acknowledges funding from the South African Research Chairs Initiative of the Department of Science and Technology and National Research Foundation of South Africa. We thank Dian Spear for advice on data collection as well as Hildegard Klein and Angela Bownes for their help with additional information on biological control agents.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Areal FJ, Touza J, MacLeod A, Dehnen-Schmutz K, Perrings C, Palmieri MG, Spence NJ (2008) Integrating drivers influencing the detection of plant pests carried in the international cut flower trade. J Environ Manag 89:300–307

Bacon SJ, Bacher S, Aebi A (2012) Gaps in border controls are related to quarantine alien insect invasions in Europe. PLoS One 7:e47689

Bewick V, Cheek L, Ball J (2004) Statistics review 8: qualitative data—tests of association. Crit Care 8:46–53

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

Cassey P, Blackburn TM, Russell GJ, Jones KE, Lockwood JL (2004) Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. Glob Chang Biol 10:417–426

Crawley MJ (2007) The R Book. Wiley, Chichester

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

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

Everett RA (2000) Patterns and pathways of biological invasions. Trends Ecol Evol 15:177–178

Everitt BS (1977) The analysis of contingency tables. Chapman and Hall Ltd, London

Faulkner KT, Spear D, Robertson MP, Rouget M, Wilson JRU (2015) An assessment of the information content of South African alien species databases. Bothalia: Afr Biodivers Conserv 45:1–11. doi:10.4102/abc.v45i1.1103

Foxcroft LC, Richardson DM, Wilson JRU (2008) Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. Environ Manag 41:32–51

Gertzen E, Familiar O, Leung B (2008) Quantifying invasion pathways: fish introductions from the aquarium trade. Can J Fish Aquat Sci 65:1265–1273

Giliomee JH (2011) Recent establishment of many alien insects in South Africa—a cause for concern. African Entomol 19:151–155

Gonzalez-Nuñez X (2008) 15-year review: trade policy in South Africa. Trade and Industrial Policy Strategies, Pretoria

Hastie T (2013) gam: generalized additive models. http://cran.r-project.org/package=gam. Accessed 3 July 2014

Henderson L (2006) Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. Bothalia 36:201–222

Herbert DG (2010) The introduced terrestrial mollusca of South Africa. South African National Biodiversity Institute, Pretoria

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. J Appl Ecol 43:835–847

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

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

Katsanevakis S, Zenetos A, Belchior C, Cardoso AC (2013) Invading European seas: assessing pathways of introduction of marine aliens. Ocean Coast Manag 76:64–74

Kenis M, Rabitsch W, Auger-Rozenberg M-A, Roques A (2007) How can alien species inventories and interception data help us prevent insect invasions? Bull Entomol Res 97:489–502

Klein H (2011) A catalogue of the insects, mites and pathogens that have been used or rejected, or are under consideration, for the biological control of invasive alien plants in South Africa. African Entomol 19:515–549

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236

Kraus F (2007) Using pathway analysis to inform prevention strategies for alien reptiles and amphibians. Manag Vertebr Invasive Species 21:94–103

Kumschick S, Richardson DM (2013) Species-based risk assessments for biological invasions: advances and challenges. Divers Distrib 19:1095–1105

Lambdon PW, Lloret F, Hulme PE (2008) How do introduction characteristics influence the invasion success of Mediterranean alien plants? Perspect Plant Ecol Evol Syst 10:143–159

Lehan NE, Murphy JR, Thorburn LP, Bradley BA (2013) Accidental introductions are an important source of invasive plants in the continental United States. Am J Bot 100:1287–1293

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc R Soc Lond B 269:2407–2413

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers Distrib 15:904–910

MacIsaac HJ, Robbins TC, Lewis MA (2002) Modeling ships' ballast water as invasion threats to the Great Lakes. Can J Fish Aquat Sci 59:1245–1256

Mack RN (2005) Predicting the identity of plant invaders: future contributions from horticulture. HortScience 40:1168–1174

Mack RN, Erneberg M (2002) The United States naturalized flora: largely the product of deliberate introductions. Ann Missouri Bot Gard 89:176–189

Martin GD, Coetzee JA (2011) Pet stores, aquarists and the internet trade as modes of introduction and spread of invasive macrophytes in South Africa. Water SA 37:371–380

Mead A, Carlton JT, Griffiths CL, Rius M (2011) Introduced and cryptogenic marine and estuarine species of South Africa. J Nat Hist 45:2463–2524

Moran VC, Hoffmann JH, Zimmermann HG (2005) Biological control of invasive alien plants in South Africa: necessity, circumspection, and success. Front Ecol Environ 3:77–83

Moran VC, Hoffmann JH, Zimmermann HG (2013) 100 years of biological control of invasive alien plants in South Africa: history, practice and achievements. S Afr J Sci 109:1–6

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. J Environ Manag 57:239–251

Puth LM, Post DM (2005) Studying invasion: have we missed the boat? Ecol Lett 8:715–721

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

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

R Core Team (2013) R: a language and environment for statistical computing. http://www.r-project.org/. Accessed 23 April 2014

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

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

Richardson DM, Cambray JA, Chapman RA, Dean WRJ, Griffiths CL, Le Maitre DC, Newton DJ, Winstanley TJ (2003) Vectors and pathways of biological invasions in South Africa—past, present and future. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, pp 292–349

Saccaggi DL, Pieterse W (2013) Intercepting aliens: insects and mites on budwood imported to South Africa. J Econ Entomol 106:1179–1189

Simberloff D (2006) Risk assessments, blacklists, and white lists for introduced species: Are predictions good enough to be useful? Agric Resour Econ Rev 35:1–10

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

van Wilgen BW, Richardson DM, Le Maitre DC, Marais C, Magadlela D (2001) The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. Environ Dev Sustain 3:145–168

van Wilgen NJ, Wilson JRU, Elith J, Wintle BA, Richardson DM (2010) Alien invaders and reptile traders: what drives

the live animal trade in South Africa? Anim Conserv 13:24–32
Westphal MI, Browne M, MacKinnon K, Noble I (2008) The link between international trade and the global distribution of invasive alien species. Biol Invasions 10:391–398
Williams PA, Newfield M (2002) A weed risk assessment system for new conservation weeds in New Zealand. Department of Conservation, Wellington
Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24:136–144
Wittenberg R, Cock MJW (2005) Best practices for the prevention and management of invasive alien species. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Wage JK (eds) Invasive alien species: a new synthesis. Island Press, Washington, pp 209–232
Wojtasik EM (2013) Richness and diversity of alien ethnomedicinal plant taxa used and sold for traditional medicine in South Africa. Dissertation, University of Witwatersrand
Xu H, Qiang S, Han Z, Guo J, Huang Z, Sun H, He S, Ding H, Wu H, Wan F (2006) The status and causes of alien species invasion in China. Biodivers Conserv 15:2893–2904
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York