A review of the impacts of biological invasions in South Africa

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Abstract

Compared to other facets of invasion science, the impacts of biological invasions have been understudied, but many studies have been published in the last decade. This paper reviews the growing body of evidence of impacts of invasions in South Africa. We classified information for individual species into ten ecological and four social categories of impact. We also reviewed studies that upscaled this information to larger spatial scales, as well as progress with assigning invasive species to impact severity categories. We identified 123 studies that documented the impacts of 71 invasive alien species, about 5% of the country's naturalized alien biota. The most frequently reported impact category was species interactions (changes to habitat suitability, pollination networks or seed dispersal mechanisms), followed by direct competition, changes to ecosystem functioning (hydrology or nutrient dynamics), hybridization and predation. Trees and shrubs accounted for more than half of the species studied, but there were examples from most other groups of plants and animals. The social consequences of invasions have been less well studied at the level of individual species. Most studies (72%) considered the impacts of a single species, based on data collected on < 1 ha, and were completed in less than a year. Space-for-time substitution was widely used, but widespread collection of data from numerous small plots allowed for reporting impact over larger spatial scales. We also identified seven studies that either monitored impacts over longer periods (up to 40 years), or repeated surveys in the same area to assess change over time. Prominent landscape-scale impacts included reductions in water resources, the attrition of native biodiversity, reductions in rangeland productivity, predation of marine birds and freshwater fishes, and disease organisms affecting native mammals and trees. Nineteen studies at broader scales estimated substantial impacts on landscape-scale water yield, habitats and biodiversity, rangeland productivity, and the economic value of ecosystem services. Despite considerable progress, our understanding remains fragmentary. Impacts are expected to grow as invasions enter exponential phases of spread and densification and as the duration of invasions increases. A robust understanding needs to be developed to provide justification for management costs.

Keywords

Biodiversity; economic impact; EICAT; indicators; SEICAT; tree invasions; water resources

Introduction

The study of biological invasions has grown over the past half century as ecologists built on the foundations laid by Charles Elton in 1958 (Richardson 2011). The field received a major boost with the initiation of the global SCOPE programme on biological invasions in 1982 (Drake et al. 1989). The SCOPE program addressed three main questions: (1) which factors determine whether a species will become invasive?; (2) what are the characteristics of sites that would make them prone to invasion?; and (3) how could this new knowledge be used to develop effective management systems? An important aspect of biological invasions that was omitted from the SCOPE program agenda was the quantification of the impacts of biological invasions on the invaded ecosystems. The systematic study of the impacts of invasive species has lagged behind studies addressing the determinants of invasiveness and invasibility. In reviewing developments in the study of impacts of biological invasions, Pyšek and Richardson (2010) found that the number of studies focusing on impacts, and the proportional contribution of such studies to the overall invasion literature increased steadily between 1990 and 2009 (from c. 14% of studies to c. 27% of studies). They found that information on impacts was unevenly distributed in terms of geography and taxonomy, corresponding to the research biases in invasion ecology in general (Pyšek et al. 2008). Research on invasive mammals, invertebrates and freshwater fishes had focused more clearly on impacts than was the case for other taxonomic groups. The geographical distribution of studies on impact was found to match the magnitude of problems of biological invasions in particular regions of the world and the level of resources available for research. There have also been several important advances in the study of invasion impacts in the last decade. These include assessments of the normative and scientific foundations for the quantification of impacts (Jeschke et al. 2014; Kumschick et al. 2015; Essl et al. 2017) and the development of unified classification frameworks for the classification of environmental (Blackburn et al. 2014) and socio-economic (Bacher et al. 2018) impacts of biological invasions.

Compared to many other countries, South Africa has made a relatively large investment into research on biological invasions (Macdonald et al. 1986; Hill et al. 2020; Richardson et al. 2020a); this provides an opportunity to review advances in the understanding of the impacts of biological invasions at the scale of a single country. Two national reviews of what was known about the impacts of biological invasions were published in 2004 in support of South Africa's programs to manage biological invasions (Görgens and van Wilgen 2004; Richardson and van Wilgen 2004). A more recent review addressed the impact of invasive alien plants on ectothermic animals in South Africa (Clusella-Trullas and Garcia 2017). These reviews all concluded that the consequences of invasions for the delivery of ecosystem goods and services to people had been inadequately studied, and that significant gaps remained. The three reviews also only addressed the impacts of invasive alien plants, and not of all invasive taxa. This paper provides an updated and expanded review of published information on the impacts associated with biological invasions involving all taxonomic groups in South Africa. Our intention was to identify all instances where the impacts of invasive alien species had been examined and/or quantified in South Africa, including attempts to upscale site or plot-level impacts to spatial scales that are more meaningful to managers or policy-makers. Our focus is on invasive alien species in natural, semi-natural and urban areas, and not in production landscapes used for commercial agriculture or forestry. The impacts of alien weeds and pests on crop agriculture has been relatively well studied, and the benefits of control can be relatively easily justified. This is not the case for impacts on biodiversity or ecological functioning in natural ecosystems, which was the focus of this study. The information is intended to provide a benchmark against which developing trends in understanding can be tracked at a national scale.

Methods

Features of the area under review

South Africa covers 1.22 million km^2, with nine terrestrial biomes ranging from desert to rainforest, three marine biogeographic zones (the Indo-Pacific, Atlantic and Antarctic), and inshore islands as well as the sub-Antarctic Prince Edward Island group. South Africa is a mega-diverse country, with high levels of plant and animal endemism; it contains three of the world's recognised biodiversity hotspots: the Cape Floristic Region, the Succulent Karoo and the Maputaland-Pondoland-Albany hotspot (shared with Mozambique and Eswatini, Mittermeier et al. 2004). Major vegetation types include Mediterranean-climate shrublands (fynbos), savannas, arid shrublands (karoo), grasslands and thicket vegetation, with small and scattered areas of Afromontane and coastal forest. South Africa is a relatively arid country with a mean annual rainfall of about 464 mm (compared to a global average of 786 mm). Freshwater ecosystems are mainly in the form of rivers, streams or wetlands, and there are very few natural lakes. The country's environmental and biological diversity provides a varied template upon which biological invasions play out (Wilson et al. 2020). 1422 alien species are known to have established naturalised populations in the country, including 559 terrestrial plant species (over half of which are trees or shrubs), 466 terrestrial invertebrate species, 77 species of freshwater fauna, and 56 marine species, and many of these are invasive (van Wilgen et al. 2020b). Ecologists have for decades expressed concern about the impacts that these species may be having on the country's biodiversity, the productivity of rural farming areas, and on the country's water supplies (van Wilgen 2020). In response to these concerns, the country has implemented national programmes that are attempting to reduce the impact of invasive alien species on natural ecosystems and the services that they deliver to humans (van Wilgen and Wannenburgh 2016).

Inputs for the review

We included studies published before the end of January 2021 that documented the impacts of invasive alien species in South Africa. Our sources included:

- Web of Science and Google Scholar. Our initial searches used the keywords “South* Africa”, “invasive species”, “alien species”, “non-native species”, “invader*”, “biological invasion*”, “bioinvasions*” “impact*”, “effect*” and “consequence*”. We also searched more generally and reviewed the titles, abstracts, and where necessary the full papers of many other publications dealing with invasive species in South Africa to determine whether impacts were examined but not reflected in the titles and abstracts;
- All publications produced by the DSI-NRF Centre for Invasion Biology (1745 peer-reviewed papers between 2004 and 2018; Richardson et al. 2020a);
- Studies cited in a recent comprehensive review of all aspects of biological invasions in South Africa (van Wilgen et al. 2020a);
- Our own knowledge based on four decades of research into biological invasions in South Africa;
- Correspondence with numerous researchers and managers in the country, using the networks of the Centre for Invasion Biology (Richardson et al. 2020a), especially for taxa and life forms with few publications and/or where issues pertaining to impacts were unclear or ambiguous; and
- The reference lists of all publications selected were checked for additional sources, especially sources from the grey literature (i.e. snow-ball sampling).

For species-level impacts, studies were only included if the reported findings were based on measurement of the impact in the field. Studies were excluded if they reported anecdotal rather than quantified accounts of impact, impacts quantified outside of South Africa, or inferred impacts from measurements of the impacts of similar alien species.

Classification of impacts of individual species

For each study that had quantified the impact of an invasive species, or several species, we noted the species involved, and the nature and magnitude of the impact(s) that had been found. We then assigned the impacts to ecological categories (after Blackburn et al. 2014) as follows:

- Competition: Reductions in the performance or population size of native species through competition with alien species;
- Predation: Declines in the numbers or ranges of native species populations through predation by alien species;
- Hybridization: Declines in the numbers or ranges of native species populations through hybridization with alien species;
- Disease transmission: Declines in the numbers or ranges of native species populations through transmission of disease from alien to native taxa;
- Parasitism: Reductions in the performance or population size of native species through parasitism by alien species, or through disease due to alien pathogens;

- Toxicity: Reductions in the performance or population size of native wildlife through ingestion, inhalation, or contact of toxic alien species, or of native plants through the allelopathic effects of alien species;
- Direct physical disturbance: Reductions in the performance or population size of native species through direct physical disturbance by alien species;
- Herbivory: Reductions in the performance or population size of native species through herbivory by alien species;
- Changes to ecosystem functioning: Changes to ecosystem functioning through changes to nutrient and/or water cycling, geomorphological processes, or disturbance regimes such as fire, brought about by alien species; and
- Indirect impacts through species interactions: Reductions in the performance or population size of native species through habitat modification, disruption of pollination and seed dispersal processes, or mesopredator release brought about by alien species.

In cases where social impacts were involved, the following categories (after Bacher et al. 2018) were used:

- Safety: The alien species results in changes to people's personal safety, their secure access to resources, or protection from disasters;
- Material or immaterial assets: The alien species results in changes to people's material and immaterial assets, including adequate livelihoods, sufficient nutritious food, shelter, and access to ecosystem goods and services;
- Health: The alien species results in changes to people's health, or access to clean air and water; and
- Social, spiritual or cultural: The alien species results in changes to people's social or spiritual wellbeing, or cultural relations.

Scope and spatial and temporal scale of studies

We reviewed all papers to establish their scope in terms of the number of alien species studied, and the habitats where the study was conducted. Where studies were conducted to establish the impacts of multiple species on particular sites, this was noted as multiple co-occurring species. We used the following habitat categories: natural habitats (divided into terrestrial, freshwater, estuarine, marine or island habitats); semi-natural habitats (habitats with most of their processes and biodiversity intact, though altered by human activity relative to the natural state); and urban habitats. We also included studies that quantified the impacts of commercial timber plantations by comparing them to unplanted sites with natural vegetation. These studies were included where the trees involved are known to be invasive, and were categorised as "plantations" in terms of habitat. The spatial scale at which the study was conducted was also noted, along with the duration of the study.

Modelling or other approaches to upscale estimates of impact

We identified studies that attempted to upscale the estimates of impact to larger spatial scales. These approaches included the development of ecological models, assessments of economic impacts (including returns on investment from management interventions), estimates based on expert opinion rather than on measurement in the field, and assessments of the threats posed by alien species to native species of conservation concern ("red-listed" species). For each study, we noted the approach that was used, and the nature and magnitude of the impact.

Formal impact assessments

South Africa has, along with other countries, initiated a process of formally assessing the impact of invasive alien species in the country. This effort is based on systems for assessing both environmental and socio-economic impacts, using the recently-developed Environmental Impact Classification of Alien Taxa (EICAT, Blackburn et al. 2014) and Socio-economic Impact Classification of Alien Taxa (SEICAT, Bacher et al. 2018). These two protocols place invasive species into one of five impact categories: Minimal Concern (MC), Minor (MN), Moderate (MO), Major (MR), and Massive (MA), or Data Deficient (DD) if there is insufficient information to assign them to a category. These studies are needed to justify and guide the regulation of alien species, as well as to provide a basis for prioritizing control measures. EICAT and SEICAT assessments can be conducted at a global level (using all information available from the introduced range of the species), or at a national level (using only the information available from the country concerned). We compiled a list of all species that have been assessed by one or both of these methods at the level of South Africa (i.e. at a national rather than a global level), along with the categories of impact assigned to them. For all species for which impacts had been quantified, or that had been subjected to one or both above assessments, we also noted the impact category that had been assigned to the species using expert opinion (i.e. assessment by one or more experts of the likely degree of impact). The expert opinion approach (reported by Zengeya et al. 2017) also used five categories, which were closely aligned with the EICAT categories, as follows: Negligible, Few, Some, Major, Severe or Data Deficient.

Results

Studies that have quantified the impacts of individual invasive alien species

We identified 123 studies that documented the ecological impacts of 71 invasive alien species in South Africa (Table 1). All papers were in English, which would be expected as no other language has been used in the relevant South African scientific literature in the past. Studies began appearing in the 1980s (following the initiation of the SCOPE programme on biological invasions in South Africa in 1982; Ferrar and Kruger 1983), and the rate of publication increased markedly from the mid-1990s onwards (Fig. 1), when work was increasingly funded by the Working for Water programme (van Wilgen et al. 1998) and the Centre for Invasion Biology (van Wilgen et al. 2014). Since there are over 1400 naturalised alien species in South Africa (van Wilgen et al. 2020b), this represents a sample of 5% of the alien biota that have established populations in the country. In the first national-level status report on biological invasions in South Africa (van Wilgen and Wilson 2018), 107 species were listed as having either major or severe impacts, based on expert opinion (as opposed to assessments of impact in field studies). This review located published accounts describing the impacts of 29 of these 107 species (27%), suggesting that there has been a tendency to study species suspected of having major impacts. Trees and shrubs accounted for more than half of the species studied (Fig. 2A), but there were examples from most other broad taxonomic groupings except for reptiles and marine fish (plants account for just over 50% of the naturalised or invasive alien species in South Africa, and no alien marine fish are known to have established). Most of the published studies (70%) addressed the impacts of terrestrial plants, with more than half of all studies addressing the impacts of invasive trees (Fig. 2B). Other groups that received attention were marine invertebrates (8% of studies) and freshwater fish (7% of studies). Studies on the impacts of alien mammals exclusively addressed the issue of alien cats (*Felis cattus*) and mice (*Mus musculus*) on offshore sub-Antarctic islands, despite the fact that several important alien mammal species are invasive on the mainland (Measey et al. 2020). Other prominent groups that have received relatively little attention included invasive cacti, aquatic plants and terrestrial invertebrates. Several studies have also noted that alien species can reach high densities in some places, and as such suggested that they must have an impact, but the studies did not quantify the impacts [see for example, papers on alien snails by Odendaal et al. (2008) and Appleton et al. (2009)]. In a small number of cases, researchers looked for, but did not detect, any negative impacts associated with invasive alien species [see, for example, Ivanova and Symes (2019) for the impacts of an alien parrot on native bird communities, and van der Merwe et al. (1996) for the impacts of alien pine trees on ground-dwelling spider communities]. In a few other cases, a change was detected, but could not conclusively be attributed to the invasive species that was present (e.g. Rivers-Moore et al. 2013).

Table 1. The number of invasive alien species in South Africa for which ecological or social impacts have been recorded in different impact categories. See Online Resource 1 for a full list of species, impacts, and references to individual studies.

Type of impact	**Impact category**	**Number of alien species involved**	**Mechanisms that lead to impact**	**Life forms involved (with number of species in brackets)**
Ecological	Indirect impacts through species interactions	26	Habitat changes leading to reductions in native species diversity and richness Breakdowns in seed dispersal and pollination mechanisms Increases in above-ground biomass	Trees (16)
				Shrubs (7)
				Marine molluscs (2)
				Terrestrial invertebrate (ant) (1)
	Competition	17	Direct competition for space, nutrients, light or water	Trees (10)
				Grasses (3)
				Shrub (1)
				Freshwater aquatic plant (1)
				Estuarine mollusc (1)
				Terrestrial invertebrate (ant) (1)
	Changes to ecosystem functioning	15	Changes to hydrological or nutrient cycles Increased productivity and biomass accumulation Changes to the occurrence and behaviour of wildfires Changes to sand movement along the coast	Trees (10)
				Shrubs (2)
				Grass (1)
				Marine mollusc (1)
				Estuarine polychaete worm (1)
	Hybridization	8	Hybridization between congeneric alien and native species	Mammals (2)
				Shrubs (2)
				Bird (1)
				Freshwater fish (1)
				Amphibian (1)
				Tree (1)
	Predation	6	Predation of native species by alien species	Mammals (2)
				Freshwater fish (3)
				Marine invertebrate (1)
	Disease transmission	3	Mortality induced in native mammals and plants	Terrestrial Invertebrate (beetle) (1)
				Fungus (1)

				Bacterium (1)
	Parasitism	3	Reduction in fitness in native freshwater fish populations	Protozoan (2)
				Invertebrate (tapeworm) (1)
	Toxicity	2	Lethal effects on native mammals Allopathic effects on native plants	Annual herb (1)
				Virus (1)
	Herbivory	2	Consumption of native plants	Terrestrial invertebrate (snail) (1) Freshwater fish (1)
	Direct physical disturbance	1	Injury to livestock	Grass (1)
Social	Safety	4	Increased severity and intensity of wildfires	Trees (4)
	Material or immaterial assets	4	Declines in economic returns from stock farming Damage to infrastructure in urban areas	Shrubs (2)
				Tree (1)
				Herbaceous plant (1)
	Health	1	Allergic reactions	Tree (1)

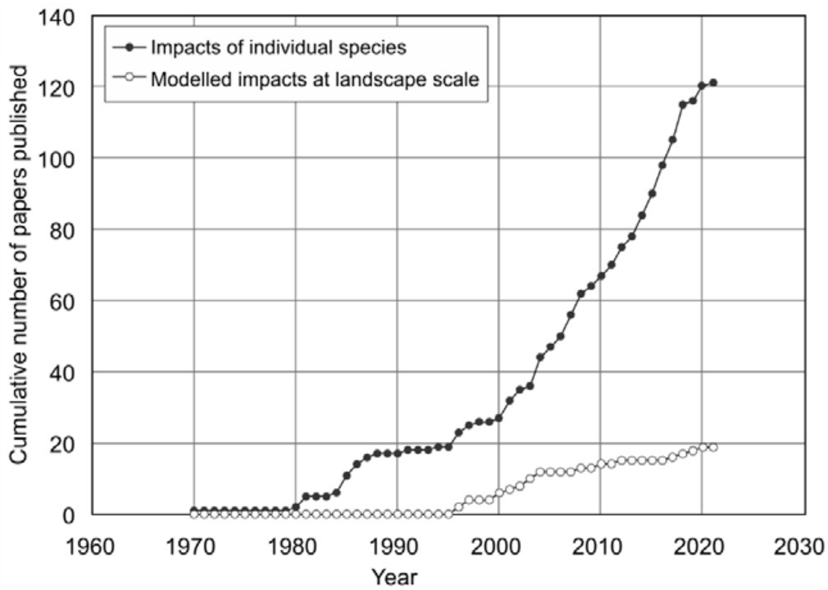

Fig. 1. Cumulative number of papers published between 1970 and 2020 which describe the impacts of (1) individual invasive alien species and (2) the modelled impacts of multiple invasive species in South Africa.

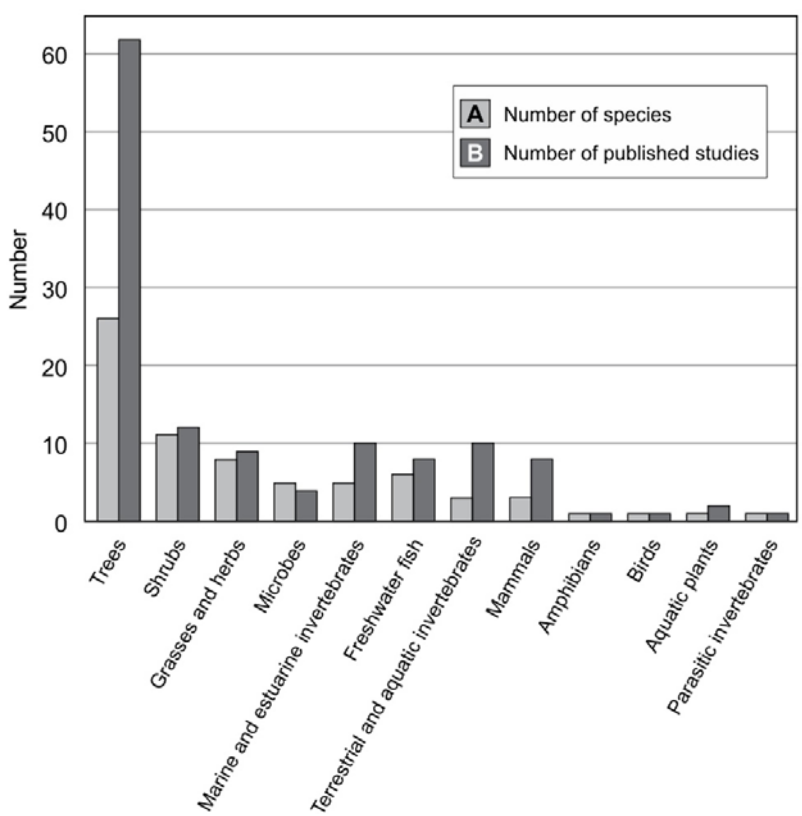

Fig. 2. The number of (A) invasive alien species across broad taxonomic and life-form groupings for which ecological impacts have been quantified in South Africa; and (B) the number of published studies on each group.

Indirect impacts through species interactions was the impact category most frequently reported (Table 1), and this was mainly associated with changes to habitats that made the environment less suitable for a range of native species, including birds, terrestrial and marine invertebrates, mammals, amphibians and reptiles (see Online Resource 1 for details of all studies identified). This type of impact also included disruptions to pollination networks (Gibson et al. 2012; 2013; Grass et al. 2014; Hansen et al. 2017) and seed dispersal mechanisms (Bond and Slingsby 1984). Impacts that came about through competition were also important, and were mainly associated with alien trees that shaded out native plants and reduced the richness and abundance of native plant communities (Online Resource 1). Changes to ecosystem functioning have also been documented largely for trees and shrubs. Increases in evapotranspiration by evergreen alien trees have arguably been the most important impact recorded, as this impact has influenced environmental policy in South Africa (van Wilgen et al. 2016), but other impacts include increases in above-ground biomass, litterfall and soil nitrogen, and decreases in soil carbon (Online Resource 1). We found evidence of impact in all other ecological impact categories (Table 1). In contrast to ecological studies, we found very few studies that quantified the social impact categories of safety, material or immaterial assets, or health (Table 1).

Brief synopsis of the prominent impacts of invasive alien species

Studies on the effects of invasive alien species in South Africa have highlighted a number of important impacts (see Online Resource 1 for brief accounts of all individual studies summarised in this section). Prominent among these are the reductions in water resources brought about by invasive alien trees, the attrition of native biodiversity, reductions in rangeland productivity, predation of marine birds on islands and of freshwater fishes in rivers and streams, and the impacts of alien disease organisms on native mammals and trees. The social consequences of these impacts have been less well studied at the level of individual species, but a few studies have indicated that invasions by certain species have affected people's safety, material wellbeing and health. The most prominent of these impacts are discussed briefly below.

South Africa is an arid country, and economic growth is constrained by inadequate water resources (Blignaut and van Heerden 2009). Large increases in evapotranspiration have been quantified for evergreen alien trees in the genera *Acacia*, *Eucalyptus*, *Pinus* and *Prosopis*, but were less severe for deciduous trees in the genus *Populus*. These increases are additional to the baseline water use by the invaded native grassland or shrubland vegetation, and range from 200 – 600 mm/yr rainfall equivalent. The increased water use can lead to decreases in streamflow of between 300 and 500 mm/yr (van Lill et al. 1980; van Wyk 1987; Dzikiti et al. 2016). The magnitude of the impact increases with the density of the invasion as well as with the mean annual rainfall. Groundwater resources are also reduced in arid areas because some alien tree species draw water from aquifers at a rate in excess of replenishment (Dzikiti et al. 2013). In the case of alien deciduous trees, studies have indicated substantially lower increases in evapotranspiration of around 20 mm/yr (Ntshidi et al. 2018).

South Africa is one of the world's mega-diverse countries, and invasive alien species pose threats (both immediate and insidious) to this biodiversity. Impacts of invasive species on biodiversity have been demonstrated for a range of native taxa. Decreases in the richness and abundance of native plant communities have arisen due to competition and environmental modifications caused by invasive plants. It has also been widely reported that habitat changes have resulted in decreased abundance and diversity of native terrestrial invertebrate and bird assemblages (Online Resource 1). A smaller number of studies have reported similar impacts on native reptiles, earthworms, amphibians and large mammals (Online Resource 1). Native freshwater fish populations have been severely reduced, in many cases to local extinction, through predation by introduced bass (genus *Micropterus*) and trout (genera *Oncorhynchus* and *Salmo*) (Woodford et al. 2005; Shelton et al. 2015a). Predation on offshore islands by alien mice (*Mus musculus*) and cats (*Felis catus*) has had severe impacts on nesting sea bird populations, resulting in at least one local extinction (the common diving petrel *Pelecanoides urinatrix*) from the sub-Antarctic Marion Island (Watkins and Cooper 1986; McClelland et al. 2018). There is also evidence that disruptions to seed dispersal (Bond and Slingsby 1984) and pollination (Gibson et al. 2012; 2013; Hansen et al. 2017) mechanisms have been brought about by invasive alien species, potentially threatening the continued existence of many rare and/or endemic native plant species.

In some cases, though, habitat changes brought about by alien plants have benefitted native species. The widespread proliferation of invasive trees (e.g. *Eucalyptus* species) has provided nesting and roost sites for at least 21 species of native raptors in regions where native trees that provide such habitat are scarce (Hirsch et al. 2020). Commercial afforestation of native grasslands with invasive alien trees led to reductions in the populations of 90 species of native grassland birds, but also led to simultaneous increases in 65 bird species associated with woodland and forest habitats (Allen et al. 1997). It has also been noted that effective conservation of the Vulnerable endemic Knysna Warbler (*Bradypterus sylvaticus*) would require the retention of invasive alien brambles (*Rubus* species) as nesting sites (Pryke et al. 2011; Visser et al. 2002). These cases are not always examples of quantified impact; they illustrate that impacts may not always be exclusively negative, and this may necessitate nuanced approaches to management in order to accommodate trade-offs.

Rangelands cover >70% of the land surface of South Africa, and they support over 43 million head of domestic livestock and wildlife of considerable economic importance (O'Connor and van Wilgen 2020). Rangelands have been impacted either because invasive alien trees shade out palatable grasses, or because alien herbs and shrubs replace palatable plants with unpalatable, harmful or toxic plants. Invasive alien trees have been shown to reduce the capacity of the land to support livestock by between 34 and 75% (Ndhlovu et al. 2011; Yapi et al. 2018), but the impacts of herbs and shrubs have not been demonstrated in this regard.

Invasive alien disease-causing microorganisms have also had serious consequences in some cases. The most dramatic of these was the rinderpest epidemic that resulted from the introduction of an alien *Morbillivirus* virus in 1896 (De Vos et al. 2001; Rodwell et al. 2001; Renwick et al. 2007). This virus laid waste to cattle and wildlife populations across southern and eastern Africa, with severe ecological and economic consequences. It is estimated that 2.5 million cattle died in South Africa alone, with up to 95% mortality in some districts (van Helden et al. 2020). Bovine tuberculosis (caused by the alien bacterium *Mycobacterium bovis*, which was introduced with cattle from Europe) has infected many wild mammals, including herbivores and carnivores. The long-term effects on wild mammal populations are not well understood, but in the case of threatened species such as lions (*Panthera leo*) the effects of the disease may be compounded by other threatening factors such as habitat loss, poaching and feline immunodeficiency virus. This could have devastating consequences for the survival of lions in the wild (van Helden et al. 2020). In a more recent development, the polyphagous shothole borer (*Euwallacea fornicatus*) and its fungal symbiont (the pathogen *Fusarium euwallaceae*) are known to have infected and killed individuals of at least 80 tree species, 35 of them native species (Paap et al. 2018; Department of Agriculture, Forestry and Fisheries 2020).

South Africa has many fire-prone ecosystems, and invasion by fire-adapted alien species can alter the frequency and intensity of wildfires, and cause feedback loops that promote the further spread of fire-promoting alien species at the expense of native species. These phenomena, although known to occur, have been poorly studied at a global scale (Aslan and Dixon 2020). Studies in South Africa have shown that invasions can increase fuel loads (van Wilgen and Richardson 1985) or even introduce fire into previously fire-free environments (Rahlao et al. 2009). In one case, remote sensing suggested that invasions by alien trees and shrubs increased the impact and difficulty of control of wildfires (Kraaij et al. 2018).

Enrichment of soil nitrogen by nitrogen-fixing alien plants has been found to be a persistent impact, lasting for many years after clearing of the invasive trees in some areas. This in turn has been found to facilitate secondary invasion by alien or native weedy grass species, which compromises the restoration of functional native ecosystems (Nsikani et al. 2017).

Hybridization between alien and native species can break up gene complexes co-adapted to local environments, leading to the loss of well-adapted genotypes (Simberloff 1996). Instances of hybridization between invasive alien and native species have been reported for four native plant species, two mammal species, and one each for bird, freshwater fish and amphibian species (Online Resource 1).

In the coastal and marine environment, three invasive alien species (two mussels and a barnacle) have become dominant along the country's west coast, and are spreading eastwards (Robinson et al. 2020). These three species have become markedly abundant, increasing the biomass of intertidal communities substantially. While these invasions have displaced native species on certain substrates, the overall abundance of native species has not been significantly reduced. However, mass mortality has been noted in a native species of swimming crab, where mussel larvae attach to the eyes of the crabs, blinding them (Branch and Steffani 2004). The main impact that has been seen as potentially positive is that mussel invasions have increased the food supply and breeding success of African Black Oystercatchers (*Haematopus moquini*) (Loewenthal et al. 2016). These birds were assessed as Near Threatened in 2000, but the species has been downlisted to Least Concern currently (Taylor et al. 2015). Care should nonetheless be taken where the apparent positive effects are on a single native species, while other species or ecosystem processes may be negatively impacted.

Social impacts have been far less extensively studied at the level of individual alien invasive species. Attempts to stabilise naturally mobile coastal sand dunes by planting the invasive Australian tree *Acacia cyclops* has halted natural sand movement, leading to substantial beach erosion which threatens many housing developments along the south coast (Lubke 1985). Human safety is threatened in fire-prone areas through the extensive planting (and subsequent invasion) of alien trees in the genera *Acacia*, *Eucalyptus* and *Pinus*. These trees increase fuel loads and the severity of fires (Kraaij et al. 2018), leading to increases in the difficulty of controlling fires and to the damage that they do. In the 1920s, invasions of semi-arid rangelands by the cactus *Opuntia ficus-indica* led to severe hardship and in some cases the abandoning of farms (van Sittert 2002). Declines in the income of cattle farmers have also been demonstrated where rangeland become invaded by the alien shrubs *Parthenium hysterophorus* and *Chromolaena odorata* (Wise et al. 2008).

Scope and scale of studies

Most studies (61%) were conducted in natural terrestrial habitats (Fig. 3), and a further 12% were conducted in plantation habitats. The invasive alien tree species used in plantation forestry are routinely planted into natural grassland or shrubland (fynbos) vegetation, where they rapidly become dominant. Thus, almost three quarters of all studies have been conducted in terrestrial habitats. Studies in freshwater and marine natural habitats accounted for a further 12 and 6% of studies respectively. Two studies were conducted in semi-natural habitats (impoundments on inland rivers, and an estuarine marina). We found only one study that could be classified as having been undertaken in an urban habitat. In this study (Seymour et al. 2020), the predatory impacts of domestic and feral cats (*Felis catus*) were quantified, although the impact was quantified for adjacent natural areas as well.

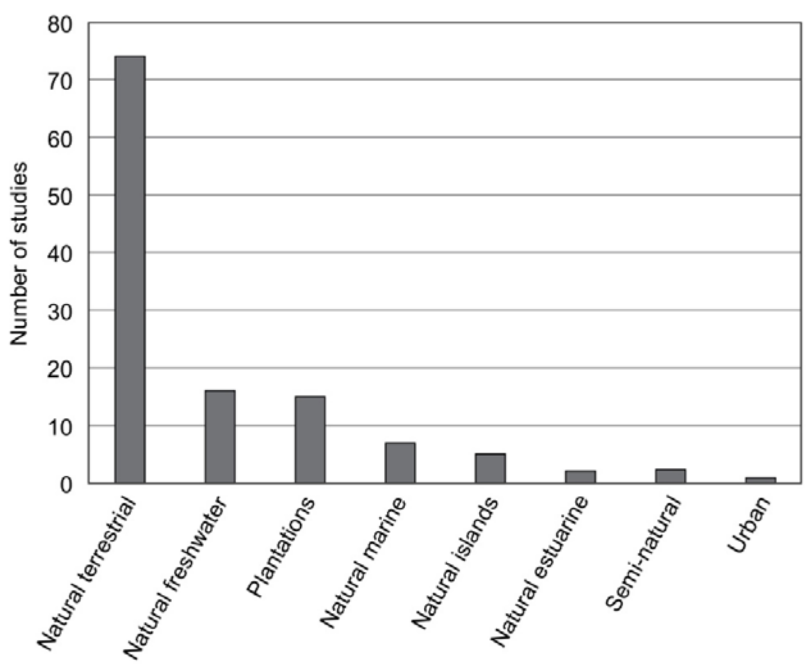

Fig. 3. The number of studies of the impact of biological invasions conducted in various habitats in South Africa.

The majority of studies (72%) considered the impacts of a single species, and only 6% considered more than three species (Fig. 4). A further 6% of papers considered the impacts of multiple co-occurring species over large areas (see, for example, Kraaij et al. 2018 who compared fire impacts in invaded and un-invaded areas).

Almost all studies were conducted at a spatial scale of < 1 ha, and were completed in less than a year. However, although many studies were based on observations on small plots, the number of plots was quite large in some cases, and this approach was routinely used to estimate potential impacts over larger areas. For example, in the terrestrial environment, Shackleton et al. (2015) assessed native plant cover and composition on 894 plots of 50m^2 each distributed over the Northern Cape province so that impacts could be assessed over an area of > 1 million ha. In the freshwater environment, most studies assessed impact at point locations along single or multiple rivers or streams (see, for example, Shelton et al. 2015a; Woodford et al. 2005), again allowing for impacts to be reported for river stretches of several km.

The data used to assess impact were collected over less than one year in almost all studies. Given the challenges of monitoring impacts over several decades, most studies have adopted an approach of space-for-time substitution, in which invaded sites are compared to un-invaded sites, assuming that the observed differences are due to changes on the invaded site as a result of invasion over time. We did however find six studies that either monitored impacts over longer periods, or repeated surveys in the same area to assess change. The duration of these studies ranged from eight to 40 years (Table 2).

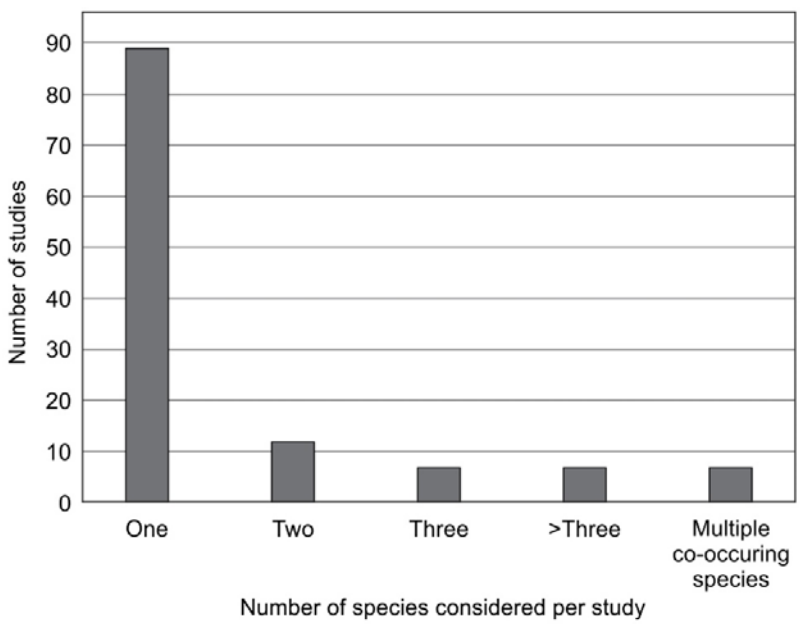

Fig. 4. The number of species considered in individual studies of the impact of biological invasions in South Africa.

Table 2. Salient features of long-term (> 5 years) studies (listed in chronological order of publication) of the impact of biological invasions in South Africa.

Study	**Habitat**	**Invasive alien species investigated**	**Duration and sampling interval**	**Source**
Impact of invasive alien trees on surface water discharge from catchments	Plantation	*Eucalyptus grandis Pinus patula*	Continuous gauging of streamflow from experimental catchments between 1956 and 1977 (21 years). Catchments were afforested with *E. grandis* in 1969 and with *P. patula* in 1971)	van Lill et al. (1980)
Impacts of an invasive alien tree on native vegetation	Plantation	*Pinus radiata*	Initial survey of natural vegetation in 1945, repeated in 1984 after 35 years of afforestation	Richardson and van Wilgen (1986)
Impact of invasive alien pines on surface water discharge from catchments	Plantation	*Pinus radiata*	Continuous gauging of streamflow from six experimental catchments between 1940 and 1980 (40 years). Catchments were afforested in 1940, 1948, 1956, 1964, and 1972, and one was left unplanted as a control	van Wyk (1987)
Impact of bovine tuberculosis on buffalo (*Syncerus caffer*)	Natural terrestrial	*Mycobacterium bovis*	Annual sampling between 1991 and 1998 (8 years)	Rodwell et al. (2001)
Impacts of invasive alien mussels on native intertidal species	Natural marine	*Mytilus galloprovincialis Semimytilus algosus*	Six repeated surveys between 1980 and 2016 (36 years)	Robinson et al. (2007) Sadchatheeswaran et al. (2018)
Impacts of invasive mice on native invertebrates	Natural island	*Mus musculus*	Three repeated surveys of mouse density and invertebrate communities in 1976, 1996 and 2006 (30 years)	McClelland et al. (2017)

Studies that have modelled the consequences of invasion at broader scales

We identified 19 studies that have estimated the impacts of invasive alien species on the ecosystems that they invade (Table 3). These studies commenced in the mid-1990s, and have accumulated steadily since then (Fig. 1). These studies have been based at least in part on the recorded impacts of invasive alien species, but have also had to make assumptions to scale impacts up to levels where the estimates could be used to inform policy and the prioritization of management interventions. Those aspects that have been studied can be divided into four broad categories: reductions in runoff from the catchments of important rivers and dams, or in the levels of groundwater sources; reductions in the economic value of ecosystem services at various scales; reductions in habitat and biodiversity at landscape scales; and reductions in the productivity of rangelands. The broad findings are summarised briefly below.

Several studies have attempted to estimate the impacts of invasive alien trees on water supplies. The first study (Le Maitre et al. 1996) estimated that invasion of a 35 000 ha catchment by alien trees and shrubs would decrease water runoff by 10.6% on average over a 100-year period, resulting in substantial threats to the sustainable supply of water to the city of Cape Town. Studies using similar models and assumptions estimated that invasive alien trees reduced river flows by between 7.2 and 22.1% in four catchments ranging in size from 13 000 to 63 000 ha (Le Maitre et al. 2002). The models used in these and subsequent studies have been refined and improved over time. Estimated reductions in runoff are scale-dependent and vary with the average rainfall over the catchment, the degree of invasion, and the species involved. The most recent review (Le Maitre et al. 2020) concluded that, at a national scale, invasive alien plants are currently reducing South Africa's surface water runoff by an estimated 2.9% (ranging between 1 and 45% in different catchments), and that this could increase to 5.2% (ranging between 4 and 64%) if the invasions are not contained.

Biological invasions have economic consequences because they can substantially reduce the flow of ecosystem services from invaded areas. Attempts to quantify the monetary value of these impacts began in 1996, when it was estimated that more water could be delivered, at a lower unit cost, by integrating alien plant control with the maintenance of water supply infrastructure, than without control (van Wilgen et al. 1996). At about the same time, Higgins et al. (1997) estimated that ecosystem services arising from a hypothetical 4 km^2 area of mountain fynbos vegetation would be worth US$ 3 million with no management of invasive species, compared to US$ 50 million with effective alien plant management. Further studies focussed on single alien plant species, but scaled the impacts up to a landscape scale (see De Wit et al. 2001 for *Acacia mearnsii*; McConnachie et al. 2003 for *Azolla filiculoides*; and Wise et al. 2012 for *Prosopis* species), and all of these studies estimated substantial economic losses arising from invasions. De Lange and van Wilgen (2010) estimated the economic losses due to invasive alien plants arising from a loss of water resources (US$ 773 million per year), rangeland productivity (US$ 45 million per year), and biodiversity (conservatively estimated to be US$ 57 million per year). This is the only study to date that has provided economic estimates at a national scale.

Invasive alien plants can transform landscapes and reduce biodiversity. Rouget et al. (2003) predicted that between 23 and 27% of remaining landscapes in the Cape Floristic Region would become transformed by invasion, while Latimer et al. (2004) estimated that invasive alien plants may pose the greatest continuing threat to rare Proteaceae in the same region. Turpie and Heydenrych (2000) estimated that annual losses of ecosystem services caused by alien plant invasions were around US$ 5/ha for both wildflower harvests and recreational use, and $163/ha for water supplies at the scale of a 21000 ha national park. An attempt was also made to model the current and potential impacts of alien plant invasions at a national scale by van Wilgen et al. (2008). They estimated that current invasions had almost no impact on biodiversity intactness (the remaining proportion of pre-modern populations) except in the Cape Floristic Region, but that biodiversity intactness could decrease substantially in future as invasive alien plants continued to spread. This work provided the basis for De Lange and van Wilgen's (2010) estimate of the value of lost biodiversity cited above. Biological invasions are also one of 12 factors taken into account when native species are listed in the IUCN Red Lists. Zengeya et al. (2020) reported that 17% of 23 609 native species (across all taxa) had alien species listed as a major component of their extinction risk. The proportion of threatened species that were imperilled by alien species varied across threat categories, being higher for Endangered (61%) and Vulnerable species (48%) and lower for Critically Endangered species (40%). For these three categories, the proportion of species that are being threatened by alien species was highest for fishes, amphibians and plants. Zengeya et al. (2020) noted that alien species were rarely considered to be the sole threat for most native species, but that aliens exacerbated the effects of anthropogenic activities such as pollution, water abstraction and altered flow regimes through predation, competition and physical alteration of ecosystems.

The potential impacts of invasive alien plants on rangeland productivity were modelled at a national scale by van Wilgen et al. (2008). They used the current and predicted future range of 57 invasive alien plant species (including trees, shrubs, herbs, annuals, climbers, grasses and succulents) to estimate the impact of invasions on livestock numbers. They concluded that livestock numbers were currently reduced by only 1%, but that this could increase substantially as invasions spread.

Table 3. Methods and findings of studies (listed in chronological order) that have attempted to upscale assessments of the impacts of invasive alien species to broader spatial scales in South Africa.

Study	Approach	Findings	Source
Modelling the impact of invasive trees on water runoff from an individual catchment	Hydrological model based on afforestation experiments; alien plant spread linked to periodic fires	Invasion caused an estimated decrease in runoff of 347m^3/ha/yr, potentially equating to losses of > 30% of the water supply to Cape Town	Le Maitre et al. (1996)
Cost effectiveness of removing invasive alien plants from an individual catchment	Economic model of returns on investment (water yielded per unit expenditure) from catchments with and without alien plant control	Unit cost of water production was lower when alien plants were cleared and the catchment maintained in alien-free condition	van Wilgen et al. (1996)
Valuation of ecosystems services from fynbos vegetation with and without invasive alien plants	Quantified the value of water production, wildflower harvest, hiker visitation, ecotourist visitation, endemic species and genetic storage over time with and without removal of invasive alien plants	Substantial increases in value gained from removal of invasive alien plants, mainly due to water production and genetic storage, providing economic justification for management	Higgins et al. (1997)
Effect of alien plant control on the cost of delivering water from a large dam and water supply scheme	Delivery cost of water was estimated by discounting the future costs and benefits of the water supply scheme with and without alien plant control, to estimate the relative efficiency of two approaches	The unit cost of delivering water from the dam was lower if maintenance costs for the scheme were broadened to include removal of invasive alien plants from the catchment	van Wilgen et al. (1997)
Preliminary assessment of the impact of invading alien plants on surface water resources in South Africa	Used crude mapping to estimate the density of invading alien plants at a national scale, and the estimated reductions in surface water flow based on increases in above-ground biomass	Alien plants, mainly trees and woody shrubs, were estimated to have invaded 10.1 million ha of South Africa and Lesotho, and that this resulted in an incremental increase in plant water use of 3 300 million m^3 of water per year	Le Maitre et al. (2000)
Effects of invasions on ecosystem services at the scale of a large protected area	Estimation of losses in ecosystem services (wildflower harvest, recreational use, pollination services, and water supply) due to invasion of fynbos ecosystems on the Agulhas Plain	Losses amount to 2.3–9.7 US$/ha for wildflowers, 1–8.3 US$/ha for recreational use, and 163 US$/ha for water	Turpie and Heydenrych (2000)

Study	Approach	Findings	Source
Estimates of the costs and benefits of an invasive tree species (*Acacia mearnsii*) at a national scale	Estimation of the net present value of benefits (timber and other products, and carbon sequestration) and costs (losses of water and biodiversity, fire damage and decreases in grazing capacity) under different management scenarios	Failure to manage invasions spreading from plantations yielded a benefit–cost ratio of 0.4, indicating that continuing with commercial growing without dealing with invasions spreading from plantations would not be sustainable. Combining physical clearing and plant-attacking biological control delivered the best outcome, yielding a benefit-cost ratio of 7.5:1	De Wit et al. (2001)
Estimates of the impacts of alien tree invasions on water runoff in the catchments of four major rivers	Alien plant invasions were mapped at a scale of 1:50 000, and water use was estimated from streamflow reduction models based on above-ground biomass of alien trees	Invasive alien trees reduced the natural river flows by 7.2, 22.1, 6.0 and 9.4% in each of the catchments respectively	Le Maitre et al. (2002)
Returns on investment from biological control of *Azolla filiculoides* at a national scale	The cost of stock losses, replacing water pumps, setting up an alternative water supply, and the loss of recreational activities were compared to the costs of biological control that reduced these losses to zero for all practical purposes	The net present value of the biological control was US$206 million for South Africa as a whole. For the year 2000, the benefit–cost ratio was 2.5:1, increasing to 13:1 in 2005, and 15:1 in 2010	McConnachie et al. (2003)
Assessment of the extent of current and potential future habitat transformation in the Cape Floristic Region	Used rule-based and regression tree models to predict the spread and potential impact of alien trees and shrubs across the Cape Floristic Region	Models predicted that between 27.2 and 23% of untransformed area are would become invaded by alien plants, but that further work would be needed to confidently predict the impacts of this	Rouget et al. (2003)
Assessed the effects of various forms of land transformation on populations of native Proteaceae	Compared the effects of invasive alien species with other forms of transformation using Bayesian hierarchical regression models	Transformation for agriculture or plantation forestry have had the largest effects, but invasive alien plants may pose the greatest continuing threat to rare Proteaceae if they continue to spread at current rates	Latimer et al. (2004)

Study	Approach	Findings	Source
Returns on investment from biological control of six invasive alien plant species at a national scale	The impact on water resources, the value of land, and ecosystem services attributed to biodiversity was estimated at current levels, and at counterfactual levels that would have prevailed in the absence of biological control	Benefit:cost ratios from slowing, halting or reversing the rate of spread of the six species ranged from 8:1 to 709:1 at the time of the study	van Wilgen et al. (2004)
Impact of invading alien plants on water yield at national and biome scales	Used current and potential future distribution of the more widespread invasive alien plants to assess current and future impact on water resources	Current reductions in surface water runoff amounted to about 7% of the national total; potential reductions would be eight times greater if invasive alien plants occupied the full extent of their potential range	van Wilgen et al. (2008)
Impact of invading alien plants on rangeland productivity at national and biome scales	Used current and potential future distribution of the more widespread invasive alien plants to assess current and future impact on rangeland productivity	Current reductions in livestock numbers were small (1% of the potential number), but could increase substantially if invasive alien plants occupied the full extent of their potential range	van Wilgen et al. (2008)
Impact of invading alien plants on biodiversity intactness at national and biome scales	Used current and potential future distribution of the more widespread invasive alien plants to assess current and future impact on biodiversity intactness	With the exception of the fynbos biome, current invasions have almost no impact on biodiversity intactness (the remaining proportion of pre-modern populations), but intactness could decrease substantially if invasive alien plants occupied the full extent of their potential range	van Wilgen et al. (2008)
Economic impact of invading alien plants at a national scale	Reductions in water yield, livestock numbers and biodiversity were combined with the unit price of water, the average price of livestock, and estimates of the monetary value of biodiversity	Approximately 4% of the value of national ecosystem services derived from water, rangelands and biodiversity was currently lost due to invasive alien plants	De Lange and van Wilgen (2010)
Estimates of the costs and benefits of an invasive tree species (*Prosopis glandulosa* and hybrids with other *Prosopis* species) at a provincial scale	Estimation of the net present value of benefits (firewood and fodder) and costs (losses of water and biodiversity, and decreases in grazing capacity) under different scenarios of spread and economic returns	Current (2009) estimated net value was positive, but was predicted to become negative within 4 - 22 years, depending on the realised rate of spread	Wise et al. (2012)

Study	Approach	Findings	Source
Estimating impacts at a national scale through expert opinion	Opinions were sought from experts on different taxonomic groups to rank 552 regulated invasive alien species in terms of social or ecological cost and benefits. Species were broadly classified as either inconsequential, destructive, beneficial or conflict-generating	107 species were assessed as generating major or severe impacts. Most of these (80) were terrestrial or freshwater plants	Zengeya et al. (2017)
Predicted impact of failing to control invasive alien plants from the catchments of two dams	Estimates of plant cover and spread rates were used to model reductions in water supply over 45 years	The two dams were estimated to be at risk of losing up to 44 and 51% of their mean annual inflows respectively	Preston et al. (2018)
Estimating returns on investment from clearing invasive alien plants from Cape Town's water catchment areas	Estimates of plant cover, spread rates and clearing costs were used to model returns on investment in alien plant control over 30 years	For every 1000 South African Rands invested, between 400 and 500 m^3 of water would be generated	Turpie et al. (2019)
Estimating impacts using red-listing processes	Examination of red data lists to identify cases where invasive alien species constituted a contributing threat to Vulnerable, Endangered, and Critically Endangered species	48% of 1641 Vulnerable, Endangered, or Critically Endangered species were threatened by invasive alien species	Zengeya et al. (2020)

Formal impact assessments

In South Africa, national-level EICAT assessments have been completed for 49 species, but in 53% of the cases the assessment was Data Deficient due to a lack of information (Table 4). Eighteen species were assessed as having major or massive impacts. These include two grass species (*Arundo donax* and *Glyceria maxima*) that competitively displace native species (Visser et al. 2017) and ten tree or shrub species. The massive or major impacts associated with trees or shrubs include the formation of dense thickets by *Eucalyptus camaldulensis* along waterways that dominate and exclude native vegetation (Tererai et al. 2013, Hirsch et al. 2020), the competitive displacement of native vegetation and native bird and invertebrate communities by two species of *Prosopis* (Steenkamp and Chown 1996; Dean et al. 2002; Schachtschneider and February 2013), or displacement of native invertebrates by *Lantana camara* and *Chromolaena odorata* (Samways et al. 1996, Mgobozi et al. 2008). Five Australian *Acacia* species were also assessed as having Major impacts (Jansen 2020). The remaining species included the Argentine ant (*Linepithema humile*) which competitively displaces and reduces the abundances of native ants (Schoeman and Samways 2011), four freshwater fish species that prey on native fauna (*Micropterus dolomieu*, *M. salmoides*, *Oncorhynchus mykiss* and *Salmo trutta*), and the Nile tilapia (*Oreochromis niloticus*) that hybridises with native tilapia species (D'Amato et al. 2007). The species assessments using the EICAT and SEICAT frameworks were not necessarily based on rigorous measurement of impacts in the field, as was required for including the species summarised in Table 1. The EICAT and SEICAT frameworks cater for the quality of input data by assigning a level of confidence to the impact assessments.

Table 4. The number of species alien to South Africa that have been assessed in terms of the Environmental Impact Classification for Alien Taxa (EICAT) for the level of impact within South Africa.

Broad taxonomic group	**Data Deficient**	**Minimal Concern**	**Minor**	**Moderate**	**Major**	**Massive**	**Total**
Grasses	5	0	2	2	2	0	11
Other plants	2	0	0	1	10	0	13
Invertebrates	3	0	0	0	1	0	4
Freshwater fish	16	0	0	0	4	1	21
All species	26	0	2	3	17	1	49

In South Africa, SEICAT has only been applied to 11 species of mammals (Hagen and Kumschick 2018), 43 gastropod species (Kesner and Kumschick 2018), and four Australian *Acacia s*pecies (Jansen 2020) (Table 5). Additional alien species that occur in South Africa have been assessed at a global scale (i.e. including all records of impact of a given species in its global alien range), but here we report only the species that have been assessed for impacts observed in South Africa alone.

Table 5. The number of species alien to South Africa that have been assessed in terms of the Socio-Economic Classification of Alien Taxa Scheme (SEICAT) for the level of impact within South Africa.

Broad taxonomic group	Data deficient	Minimal Concern	Minor	Moderate	Major	Massive	Total
Gastropods	12	2	17	3	0	0	34
Mammals	0	0	3	7	1	0	11
Australian *Acacia* species	0	1	3	0	0	0	4
Total	12	3	23	10	0	1	49

Discussion

Current levels of understanding

Studies of impacts of plant invasions in South Africa cover the full spectrum of impact-generating mechanisms revealed in the global review of Levine et al. (2003). Indeed, South Africa examples are cited as key evidence of impacts of plant invasions through effects on plant community structure, nutrient cycling, hydrology and fire regimes. Our understanding of the impacts of biological invasions in South Africa has also grown substantially over the past two decades (Fig. 1), but it remains limited despite more than three decades of relatively well-funded research. The impacts generated by invasion have been documented for only 5% of known established species, and fewer than 20 studies have attempted to estimate the magnitude and consequences of invasion at scales broader than individual research sites. In addition, the impacts are set to grow because extensive invasions by many species are relatively recent, and the majority of the impacts reviewed in this paper have been caused by alien species that only established dense populations over the past few decades. The impacts of individual species increases with their abundance or density, and the area that they occupy (Parker et al. 1999), and there is also clear evidence that the magnitude and permanence of the impact is strongly affected by the duration of invasion (e.g. Le Maitre et al. 2011; Holmes et al. 2020).There is good evidence from many parts of the world that impacts of invasive alien plants may only manifest decades or more after dense invasive stands have established (Downey and Richardson 2016). Thus, while there is some understanding of well-established species whose impacts have accumulated over decades, little has been done to determine thresholds of range, density and duration at which impacts become measurable or influential. Such insights are urgently needed as there is clearly a substantial invasion debt in South Africa. Rouget et al. (2016) defined “impact debt” as the additional environmental and socio-economic impact that could result as invasive species already in a region increase in abundance, density, geographical range, and residence time. Many invasive species in South Africa, even those that have already invaded large areas, have potential for further expansion (Rouget et al. 2004). At least one study predicted increases in impact that could be orders of magnitude greater than current levels if invasive species increased in density and spread further to occupy all suitable habitat (van Wilgen et al. 2008).

Most studies have reported on the impacts of a single species, and on a single selected feature of the invaded environment. However, interactions between different alien species on the same site, and between alien and native species, could produce additional or more marked effects, some of which may change in a non-linear fashion with different degrees or combinations of invasion (Kuebbing et al. 2016). A lack of understanding of these interactions limits our ability to predict impacts on sites invaded by multiple species. The situation is further complicated by the fact that biological invasions do not act in isolation when causing impact. A review of South Africa's global-change research effort revealed that fewer than 4% of 1149 studies considered how biological invasions interacted with three or more other drivers of global change (e.g. climate change, habitat transformation, pollution or overharvesting), and concluded that this was a key gap in understanding (van Wilgen et al. 2020c). The magnitude of such impacts is likely to increase in a non-linear fashion over time. Developing capacity to assess the current magnitude, and to project the long-term consequences, of invasions on South Africa's diverse ecosystems should therefore be a key research priority for the future. The country currently spends over a hundred million US dollars on control measures annually (Zengeya and Wilson 2020) in an environment where such levels of funding will increasingly have to be justified in terms of returns on investment. Given the relative paucity of information on impacts locally, it seems prudent to make use of insights on the full suite of impacts of particular invaders gleaned from global evidence, in order to more rapidly generate a robust picture of impact. For example, Australian *Acacia* species, and trees in the family Pinaceae, have major impacts as invaders in many parts of the world, many of which are relevant in South Africa (Le Maitre et al. 2011; Nuñez et al. 2017). Given the magnitude of invasions, the number of invasive species, and the limited resources available for research in South Africa, guidelines on how to utilize research from other regions (and the risks associated with such transfers of knowledge) would be useful.

Consequences of biological invasions

The consequences of biological invasions of natural ecosystems include social and economic impacts arising from changes to the composition, structure and functioning of natural ecosystems. The full suite of impacts associated with biological invasions is clearly greater than the direct impacts of individual species that have been highlighted in this review. Many studies have shown that invasion by alien species can change diverse aspects of ecosystems, causing a wide range of indirect effects, some of which potentially have profound implications for ecosystem structure and functioning in the longer term. As in other parts of the world, several invasive species in South Africa have caused regime shifts – alterations to the state of ecosystem structure and function that are difficult or impossible to reverse. In some cases, regime shifts change the ability of natural ecosystems to sustainably support economic activity and subsistence livelihoods. There are already well-documented warnings in this regard arising from the South African experience. Scarce and vital water resources are being depleted in areas of relatively high rainfall (e.g. the catchments of Cape Town, invaded by alien trees and shrubs, Le Maitre et al. 1996), as well as in more arid areas where people are almost totally dependent on groundwater (e.g. in the case of invasions by *Prosopis* in arid regions, Dzikiti et al. 2017; Wise et al. 2012). The invasion of shrublands by alien trees can also change fire regimes, increasing the risks associated with wildfires (Kraaij et al. 2018), diminishing the water-retention capacity of catchments due to soil damage and erosion (van Wilgen and Scott 2000), and hastening the extinction of hundreds of endemic plant and animal species (Raimondo et al. 2009). In freshwater ecosystems, introduced predatory fish can lead to fundamental changes to the structure of benthic communities (Shelton et al. 2015b). Invasion of landscapes by Australian *Acacia* species can fundamentally alter the seed bank composition and nutrient status of the soil (Yelenik et al. 2004;

Richardson and Kluge 2008; Nsikani et al. 2017), leading to irreversible changes. These and changes to seed dispersal and pollination networks, and communities of invertebrates and micro-organisms in the soil could alter the nature of ecosystems and their ability to retain native species and to support ongoing economic and social activities. These activities include livestock and wildlife ranching, the harvesting of natural products, and ecotourism, recreation and cultural experiences. The development of a full appreciation of the impacts of biological invasions at these levels is still in its infancy, as elsewhere globally. A recent review of the impacts of biological invasions on ecosystem services (Vilà and Hulme 2017) revealed a patchy understanding, due in most cases to a paucity of adequate information on which to base reliable estimates. At this stage, it appears that the consequences of biological invasions would in all probability be substantial, but quantifying them will require the development of robust models using multidisciplinary approaches.

Tracking trends in impact

South African legislation requires a formal assessment of the status of biological invasions every three years, and two such reports have been produced to date (van Wilgen and Wilson 2018; Zengeya and Wilson 2020). A set of 20 indicators was developed to provide a framework for reporting on the status of biological invasions at a national level (Wilson et al. 2018). Two of the indicators in this framework address impacts, namely the impact of individual species on the environment, and the degree of impact from multiple species present on particular sites.

With regard to the impact of individual species, the first attempt at rating was done by soliciting expert opinion (Zengeya et al. 2017). Even though it was recognised at the time that the formal EICAT and SEICAT systems would provide more reliable assessments, hardly any assessments had been done by the time the first status report had to be submitted. It was subsequently decided that all future status reports would be done in terms of the formal EICAT and SEICAT assessments, because they provide a consistent and objective method for rating impacts across different mechanisms. The intention is to assess all naturalised or invasive species in South Africa using these frameworks. This will require the collation of all available information on the impact of individual species, and because such information is currently limited to around 5% of the species, most will likely be assessed as data deficient. However, this will provide a baseline which can be regularly updated as new information becomes available, and the information collated here can be used to establish the initial baseline.

While the impact of individual species can be assessed within the EICAT and SEICAT frameworks, there is no accepted, unified system of classification to account for impacts on sites. The issue is currently addressed in South Africa using an indicator based on invasion-induced reductions in the flow of ecosystem services (Zengeya and Wilson 2020; Wilson et al. 2018). These impacts are estimated at a site level, and would have to include the cumulative impacts of all invasive alien species present on the site. In addition, it is possible that invasive species outside of the site being considered could have impacts on the site, for example by invading an upstream catchment and changing hydrological dynamics. Assigning values to the indicator requires information on the spatial distribution and magnitude of ecosystems services, and on the impact of all relevant invasive species on that service. Ecosystem services can be mapped, but reliable information on the magnitude of impacts is scarce, so that currently the indicator can only be estimated with a relatively low level of confidence.

Do impacts of invasion in South Africa differ from those reported elsewhere?

Each region of the world is unique in terms of the dimensions of biological invasions and the impacts that they cause. Our review has confirmed that a number of aspects of impact in South Africa differ from those in other countries of similar size. For plant invasions, South Africa is unique in the overall scale of invasions by alien trees and in the obvious impacts that such invasions have wrought (Richardson et al. 2020b). Impacts on biodiversity are likely to be more pronounced in South Africa than in other countries of similar size, given the above-average levels of diversity and endemism in the country (van Wilgen et al. 2020b). Unlike the situation in rangelands in many other parts of the world, impacts as a result of radical changes to fire regimes caused by invasions of alien plants are not a major problem in South Africa, because alien grasses have not invaded widely (Visser et al. 2017). The very limited success of introduced vertebrates (except for mammals on a few islands) has also shaped perspectives on the impacts of biological invasions in South Africa (Measey et al. 2020). More than half of the studies in South Africa addressed the impacts of plants, which is slightly more than the global figure of 44% (Pyšek et al. 2008). Nonetheless, non-plant taxa could ultimately have the greatest impacts. For example, the recently-detected polyphagous shothole borer (*Euwallacea fornicatus*) is arguably the most damaging tree pest to ever arrive in South Africa (Paap et al. 2020). This invasion could have similar consequences to those associated with the arrival of Dutch elm disease in North America (Strobel and Lanier 1981), illustrating that impacts across continents may converge as new species establish.

Challenges

Despite the steady increases in the understanding of the impact of invasive alien species in South Africa, much remains to be done. A robust and defensible understanding of impacts is necessary to formulate evidence-based strategies to deal with invasions now and in the future. This is important because effective mitigation of impacts will be costly, and will have to be justifiable in a country that faces many challenges, and that has limited means to address them. It is necessary to develop a better understanding of invasive species traits and processes that could potentially generate regime shifts, as these often tip ecosystems to new states that are very difficult if not impossible to reverse. There is also an urgent need for objective protocols for dealing with conflicts of interest that arise when invasive alien species have both benefits and costs (van Wilgen and Richardson 2012; Woodford et al. 2016; Zengeya et al. 2017). Objective assessments, involving the quantification of costs and benefits will be crucial for the development of sustainable management strategies (e.g. for *Prosopis*, see Shackleton et al. 2017). Further work is also needed to ensure that those invasive species that have the greatest impact (current and potential) receive priority attention.

To date, the invasive alien species that are perceived to have had the largest impacts have been among those most studied. These include many tree species, as well as aquatic plants. However, other problematic plant taxa, such as the Cactaceae, have not been well researched in terms of their impact. In addition, some species received attention because of an interest in particular environments (for example, freshwater ecologists have studied invasive predatory fish, and marine ecologists have focussed on intertidal mussels). Groups that have not received much attention include vertebrate taxa, as they have had few known or obvious impacts, and invertebrate taxa whose environmental impacts may be less easily observed. Research effort will in all likelihood remain reactive to perceived impact, but a shift towards less conspicuous taxa (such as invertebrates, fungi and soil organisms) may well reveal impacts that have not been obvious until now.

Most studies have taken place in terrestrial ecosystems. Plantations of invasive alien trees and protected areas were frequently used as study sites, while some other studies clearly focussed on productive rangelands or riparian areas. Making recommendations regarding which ecosystems should receive priority in terms of their vulnerability to impacts by biological invasions is also not straightforward, given the diversity of ecosystems in South Africa and their importance for different reasons. Previous work aimed at prioritising areas for invasive alien species management exercises (e.g. Forsyth et al. 2012) have recognised the relative importance of primary water source areas, biodiversity hotspots, protected areas and productive natural rangelands. These management prioritization exercises have only focussed on terrestrial ecosystems, possibly because all studies to date that have attempted to upscale estimates of impact have been in terrestrial environments (Table 3). A focus on terrestrial environments is likely to remain, unless new and important impacts become apparent in freshwater, estuarine, marine or offshore island ecosystems.

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Conflicts of interest or Competing interests

The authors declare no conflicts or competing interests.

Availability of data and material

This review is based on published information, and all studies that were included are listed in the supplementary tables.

Authors' contributions

BvW and DMR initiated the review. BvW sourced material, conducted the classifications and wrote the paper. DMR and TZ sourced additional material and worked on various drafts of the paper. All authors read and approved the final version before submission.

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