

# Invasive alien plants in South Africa: how well do we understand the ecological impacts?

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**This paper examines the evidence for the effects of invasive alien plants in natural and semi-natural ecosystems in South Africa. Invasive alien plants are concentrated in the Western Cape, along the eastern seaboard, and into the eastern interior, but there is a shortage of accurate data on abundance within this range. Most information on site-specific impacts comes from the fynbos biome, and is generally poor for other biomes. The consequences of invasions for the delivery of ecosystem goods and services to people are, with the notable exception of their influence on water resources, inadequately studied. Our understanding of many of the broader aspects of invasion ecology needs to be enhanced, and we identify important challenges for research to address critical gaps in knowledge. Priorities for future research include the development of a predictive understanding of the rates of spread of invasive alien plants, and the development of achievable goals for ecosystem repair after clearing, including measurable criteria for assessing the success of restoration. Climate change could significantly exacerbate problems with invasive species and work is needed to accommodate plausible trajectories in planning and management frameworks. Perhaps the greatest challenge for South African ecologists is to address the twin issues of skills development and social transformation, to ensure that adequate and relevant ecological expertise is maintained to meet future research and management needs. Formal collaboration between organizations to address capacity building and educational transformation in the field of invasion ecology would represent a significant step forward.**

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## Introduction

This account provides a brief overview of alien plant invasions in South Africa, with special emphasis on what is known about their consequences, including those affecting the delivery of ecosystem goods and services. We draw on published and unpublished sources, and highlight some important research challenges in invasion ecology that need to be met if we are to address critical gaps in our understanding. Although South Africa has problems with invasive alien organisms from most major taxonomic groups<sup>1</sup>, here we deal only with alien plant invasions in natural and semi-natural terrestrial and freshwater ecosystems.

Human communities and natural ecosystems worldwide are under siege from a growing number of destructive invasive alien species (including disease organisms, agricultural weeds, and insect pests). These species erode natural capital, compromise ecosystem stability, and threaten economic productivity. The problem is growing in severity and geographic extent as global trade and travel accelerate, and as human-mediated disturbance

and increased dissemination of propagules makes ecosystems more susceptible to invasion by alien species.

Besides their effects on agriculture, forestry and human health, biological invasions are also widely recognized as the second-largest global threat (after direct habitat destruction) to biodiversity<sup>2,3</sup>. In many parts of the world, the most challenging and time-consuming tasks of conservation biologists and managers are those relating to controlling alien species, preventing impacts and, increasingly, repairing systems damaged by aliens<sup>4</sup>.

South Africa has a long history of problems with invasive alien species, and of research and management of biological invasions (Table 1). The Working for Water programme<sup>26–28</sup> was started in 1995 to conduct and coordinate alien-plant management throughout South Africa. The programme initially worked only in watersheds and riparian areas, but now leads alien-plant management initiatives in all natural and semi-natural ecosystems. It has grown into one of the world's biggest programmes dealing with invasive alien species. The enterprise's success has been attributed to its multi-faceted and cross-disciplinary nature that has enabled it to leverage local and international funding and continuing political support. The programme is driven by multi-disciplinary ecological, hydrological, social and economic goals. In practice it has focused on hydrological and social concerns (as embodied in the name of the programme), and its ecological goals are less clearly defined. The extent to which the aim of improving the ecological integrity of natural ecosystems through the control of invasive alien plants has therefore not always been clear to both programme participants and other stakeholders.

In this paper, we examine the ecological evidence for the impacts of invasive alien plants on South African ecosystems. We begin with a brief review of what is known about the extent of invasions and influences of these plants, and then discuss the consequences for the delivery of ecosystem goods and services to people. However, the emerging field of invasion ecology addresses issues beyond the effects of invasive species. The different aspects of invasion ecology can be related to the critical stages of invasion, and these stages also provide a useful framework for classifying the management interventions that are required to deal with the problem (Box 1). Our understanding of many of the broader aspects of invasion ecology needs to improve, and we use this framework to suggest the main challenges for research that will address critical gaps in knowledge and that will serve explicit management needs.

## Components of impact

Appreciation of the effects of invasive alien plants is a multi-scale problem, summarized by the equation  $I = R \times A \times E$ <sup>33</sup>. Impact ( $I$ ) is intuitively the product of the (potential) geographical range of the invader ( $R$ ), its (potential) abundance or density ( $A$ ), and the effect ( $E$ ) of an individual invader or the measurable impacts at the smallest spatial scale. We explore our understanding of each of these components in what follows.

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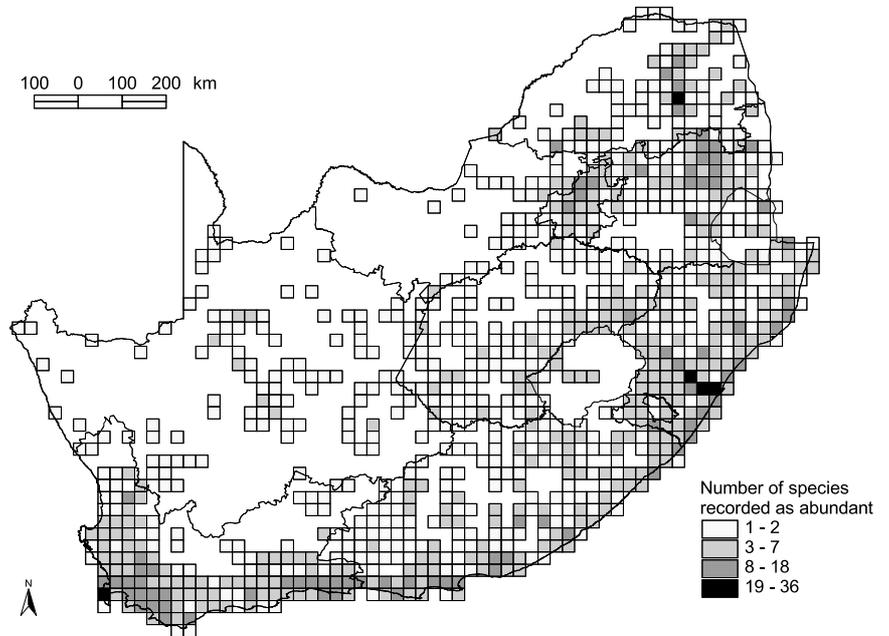
**Table 1.** Main research initiatives on alien plant invasions in South Africa.

Research programmes	Organization(s)	Duration	Examples of important scientific outputs
Biological control of invasive alien plants	Department of Agriculture; Plant Protection Research Institute, Agricultural Research Council; Universities of Cape Town and Rhodes	Initiated 1930 – ongoing.	Synthesis volumes <sup>5,6</sup>
Catchment conservation research programme	South African Forestry Research Institute	1973–1990	Detailed studies on key invaders and invasion processes <sup>7–10</sup>
South African National Programme for Ecosystem Research	Council for Scientific and Industrial Research (CSIR)	1977–1985	Regional syntheses <sup>11–14</sup>
Scientific Committee on Problems of the Environment (SCOPE), programme on biological invasions	CSIR and many participating organizations.	1982–1986	Synthesis volumes <sup>15</sup>
South African Plant Invaders Atlas	Plant Protection Research Institute, Agricultural Research Council	1975 – ongoing	Handbook; and detailed distribution studies <sup>16,17</sup>
Invasive plant ecology programme	Institute for Plant Conservation, University of Cape Town	1994 – ongoing	Synthesis volumes, conceptual contributions and application to management of invasions in the Cape Floristic Region <sup>18–23</sup>
Working for Water programme	Department of Water Affairs and Forestry	1996 – ongoing	First countrywide assessment of extent of woody plant invasions; <sup>24</sup> Best-management practices proceedings <sup>25</sup>

### Geographical range of the problem

Several estimates have been made of the spatial extent of alien plant invasions in South Africa. A rapid reconnaissance in 1996/97<sup>34</sup> suggested that about 10 million hectares of South Africa has been invaded (most of it sparsely) by the approximately 180 species that were mapped. This survey identified mainly woody invaders that impact on water resources. The most comprehensive set of records for the whole country is the South African Plant Invaders Atlas (SAPIA).<sup>16,35</sup> The SAPIA data demonstrate the overall magnitude of the problem, and show that the greatest number of species occurs in the Western Cape, along the eastern seaboard and into the eastern interior (Fig. 1).

Of South Africa's eight terrestrial biomes, fynbos is the best-studied and clearly the most invaded biome. There are dense invasions in the mountains and lowlands and along all the major river systems<sup>36,37</sup>. The principal invaders are trees and shrubs in the genera *Acacia*, *Hakea* and *Pinus*. Several studies have also produced very detailed distribution maps at finer scales for regions within the biome<sup>19,23</sup>. The forest biome has been heavily invaded but the extent cannot be accurately quantified<sup>36</sup>. The grassland and savanna biomes have also been extensively invaded. Important species here include Australian wattles (*Acacia* species), other tree species, and a variety of woody scramblers (notably trifid weed, *Chromolaena odorata*, and brambles, *Rubus* species). Invasions are densest along the banks and in the beds of the rivers; few, if any, river systems have not been extensively invaded. Invading trees such as jacaranda (*Jacaranda mimosifolia*) and syringa (*Melia azedarach*) have spread into semi-arid savanna by spreading along perennial rivers. In the Nama Karoo woody invaders, notably mesquite (*Prosopis* species), have invaded large areas of alluvial plains and seasonal and ephemeral watercourses. Several cacti (*Opuntia* species) and saltbushes (*Atriplex* species) have invaded large areas of the Nama Karoo and Succulent Karoo biomes<sup>38</sup>



**Fig. 1.** The distribution of invasive alien plant species in South Africa. Data are from the South African Plant Invaders Atlas.<sup>16,35</sup> Shading indicates the number of species listed as 'abundant' in each quarter-degree cell.

and the thicket biome in the Eastern Cape<sup>36</sup>. Information on the distribution of invasive alien grasses in South African ecosystems is poor<sup>39</sup>.

Data from the South African Plant Invaders Atlas<sup>35</sup> provides some quantification of the extent of invasions in forest, fynbos, grassland, karoo (no distinction was made between Nama and Succulent Karoo biomes in the SAPIA database) and savanna biomes. Most invasive species have been recorded from savanna (294 species in 653 quarter-degree squares) and grassland biomes (293 in 624 squares). The smallest biomes, fynbos and forest, stand out as having fewer recorded invasive species (156 in 153 squares and 191 in 165 squares, respectively), but many more invasive species in these biomes were recorded as abundant (44% and 51%, respectively). SAPIA has 113 species records assigned to 'karoo' (480 squares; 25% of species have been recorded as abundant).

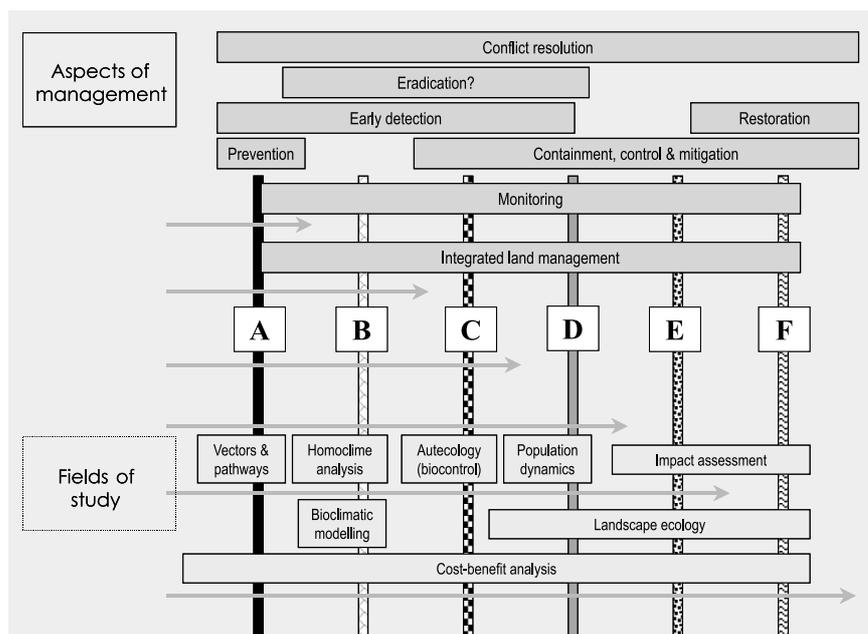
### Box 1. Elements of invasion ecology.

**INVASION ECOLOGY IS THE STUDY OF THE** human-mediated introduction of organisms, especially introductions to areas outside the potential range of given organisms as defined by their natural dispersal mechanisms and biogeographical barriers. The field addresses all aspects relating to the introduction of organisms, their ability to establish, naturalize and invade in the target region, their interactions with resident organisms in their new location, and the consideration of costs and benefits of their presence and abundance with reference to human value systems.

Transition from 'native' in a given locality to 'alien' in another place involves a number of stages that may be illustrated with reference to a series of barriers, depicted by A–F in the figure. Few introduced species overcome all potential barriers; most alien species do not become widespread and abundant in new habitats and have little or no measurable impact. Those that overcome the barriers may have substantial effects. These species are the subject of this paper.

The development of an understanding of the relationship between the species concerned and the barrier in question, can be used to define fields of study, indicated at the bottom of the diagram. Similarly, aspects of invasive alien plant management can be related to the phases of the invasion process, and these are indicated at the top of the diagram. Information generated by research in the various fields of study can be used to support the development and improvement of management approaches.

Fundamental research questions in invasion ecology<sup>15,31</sup> can also be related to this scheme. These questions include: 1) why are some species more successful invaders



Schematic representation of the phases between introduction to a locality and establishment and proliferation in natural (undisturbed) environments. The ability of a given species to overcome a series of barriers in the new environment defines its current (not necessarily ultimate) status as an alien. Barriers indicated in the diagram are: A, main geographical barriers; B, local environmental barriers; C, reproductive barriers; D, dispersal barriers; E, environmental barriers (disturbed habitats); and F, environmental barriers (undisturbed habitats). This scheme objectively defines 'casual', 'naturalized' and 'invasive' species. Some species that overcome barrier F may become 'transformers'<sup>29,30</sup> and are of principal concern to managers

than others? [all barriers]; 2) why are some systems more susceptible to invasions than others? [barriers B–F]; and 3) how can the harmful impacts of invasions be prevented, reduced or mitigated? [mainly barriers C–F]. Consideration of ecosystem-level impacts in natural and semi-natural ecosystems (the

focus of this paper) is mainly relevant for species that overcome barrier F. Since prevention of invasions is the best way of avoiding the consequences,<sup>32</sup> all preceding phases and transitions (indicated by arrows) must also be considered when assessing impacts.

Five major aquatic weeds have spread over large areas in South Africa. These are water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*), Kariba weed (*Salvinia molesta*), parrot's feather (*Myriophyllum aquaticum*) and red water fern (*Azolla filiculoides*). Of these, water hyacinth is the most significant and damaging weed. It is widespread throughout South Africa and severely affects rivers in the Western and Eastern Cape, KwaZulu-Natal, Mpumalanga and on the Vaal River in the Gauteng and Free State provinces.

In addition to the existing invasions, that many invasive species already here have not fully occupied the potential suitable habitat,<sup>17</sup> and new species are regularly being added to the list of invaders. South Africa has one of the biggest problems with alien plant invasions of any country in world.

#### Abundance and density

Data on the geographical distribution of invasive alien plant species provide information at one level. However, it is important to know, at finer scales, how abundant or dense invasive species can become. The only systematic source of data on species abundance comes from the SAPIA database, which records the abundance of species in different categories. These

data confirm what can readily be observed — 68 species were recorded as 'abundant' (the highest category) in more than 15% of the quarter-degree squares where they were mapped. It is also known that many species form closed-canopy stands in many ecosystems. These include pines and hakeas (*Pinus* and *Hakea* species) in fynbos, wattles (especially *Acacia mearnsii*), eucalypts (especially *Eucalyptus camaldulensis*), and giant reed (*Arundo donax*), along rivers, mesquite (*Prosopis* species) in dry riverbeds in arid areas, and lantana (*Lantana camara*) in Eastern Cape grasslands. Many aquatic weeds form dense closed mats in freshwater ecosystems. Our understanding of the extent of invasions at different densities is poor, however, and this limits our ability to predict impacts for the whole country.

#### Impacts of alien invasive plants

Global reviews of the effects of plant invasions suggest that the most damaging species transform ecosystems by using excessive amounts of resources (notably water, light and oxygen), by adding resources (notably nitrogen), by promoting or suppressing fire, by stabilizing sand movement and/or promoting erosion, by accumulating litter or by accumulating or redistributing salt.<sup>29</sup> Such changes potentially alter the flow, availability

or quality of nutrient resources in biogeochemical cycles; they modify trophic resources within food webs; and they alter physical resources such as living space or habitat, sediment, light and water.<sup>40</sup> Invaders are most likely to have substantial effects on ecosystems (acting as 'ecosystem engineers'<sup>41</sup>) by rapidly changing disturbance regimes.<sup>42</sup> We explore the evidence from South African ecosystems here by examining the known consequences of invasive alien plants on ecosystem structure, composition and processes — the building blocks of biodiversity.<sup>43</sup>

Most South African research on alien-plant impacts has focused at small spatial scales (plots or communities), and much of this work has been in the fynbos biome. This research has shown that dense stands of alien trees and shrubs in fynbos can rapidly reduce abundance and diversity of native plants at the scale of small plots.<sup>44,45</sup> As regards mechanisms for this attrition, studies in dense stands of Port Jackson willow (*Acacia saligna*) have documented the decline of soil-stored seed banks of native plants, leading to the local extinction of native species.<sup>46,47</sup> Such invasions also greatly increase biomass<sup>48,49</sup>, and change litterfall dynamics<sup>50</sup> and nutrient cycling<sup>51–55</sup>. These changes have marked, and varied, effects on fire regimes.<sup>42,56</sup> In the lowlands, alien annuals reduce small-scale diversity of native herbs.<sup>57</sup> Tree and shrub invasions in fynbos change many aspects of faunal communities.<sup>58</sup> Studies have documented altered abundance and composition in native ant communities, with implications for the seed dispersal functions of native plants.<sup>59</sup> The altered feeding behaviour of native generalist birds that disperse seeds, with likely detrimental effects on native species, has also been described.<sup>60,61</sup>

Studies from other biomes have produced scattered information on impacts. In arid savannas, the widespread replacement of native *Acacia*-dominated communities by alien *Prosopis* species radically changes bird habitats, leading to reduced species richness and diversity. These changes include the elimination of raptors and reductions in frugivores and insectivores.<sup>62</sup> In mesic savannas, *Chromolaena odorata* invasions in riparian areas increase shading on riverbanks, leading to altered sex ratios of native Nile crocodiles due to reduced soil temperatures in nests.<sup>63</sup> In the coastal zone (on Robben Island in Table Bay), invasive *Acacia cyclops* provides nesting opportunities for rare African penguins.<sup>64</sup> Our understanding of the extent and effects of alien grass invasions in South Africa is poor.<sup>39</sup>

Despite widespread concern over the significant ecosystem-level consequences of invasive alien plants, impacts at this scale are inadequately studied in South Africa. For example, the very dense stands of prickly pear (*Opuntia ficus-indica*) that covered large areas of central South Africa in the first part of the 20th century drove ranchers off their land,<sup>65</sup> but no data are available to describe processes leading to these outcomes, nor have the impacts themselves been adequately documented.

In aquatic ecosystems, dense mats of invasive water hyacinth are often quoted as resulting in the deterioration of aquatic biodiversity and changes to water chemistry and oxygen levels.<sup>66</sup> However, systematic studies of these impacts are lacking in South African ecosystems, and much of the evidence is based on undocumented observations.

Other consequences likely to be significant, but not thoroughly studied, in South Africa include the increased availability (amount and diversity) of seed resources for frugivorous birds, and reduced food supplies for insectivorous birds. Such effects are probably very common, with effects that ripple through trophic levels.

At a national scale, several studies have documented the effects of alien plants (usually without a clear distinction

between planted and invasive stands) on habitats for vertebrate animals. Patterns for several bird species are most dramatic. These include range expansions of the hadeda ibis (*Bostrychia hagedash*),<sup>67</sup> acacia pied barbet (*Tricholaema leucomelas*),<sup>68</sup> southern masked weaver (*Ploceus velatus*),<sup>69</sup> and many tree-nesting raptors.<sup>70</sup> Replacement of grasslands with plantations of alien trees has reshuffled abundances of bird species at the regional scale. For example, in Mpumalanga, where 90 bird species are characteristic of grasslands and 65 characteristic of woodlands, woodland species have benefited from afforestation (conversion of grassland and woodland to forest).<sup>71</sup> On the other hand, species diversity of grassland birds, and globally threatened grassland birds in particular, was significantly reduced in proportion to the extent of conversion from grassland to stands of alien trees. This study dealt largely with plantations of alien trees, but the results are indicative of changes due to alien tree invasions in these systems. Although these investigations have focused largely on the dynamics and dimensions of the range of the bird species, such range changes indicate pervasive alterations to many ecosystem features. For example, transformation of grassland and shrublands into thickets of alien trees alters soil properties, with substantial effects on herbivores and soil fauna.

Although we know something about how invasive alien plants influence ecosystem structure and functioning, few studies have explored the dynamics of links between those properties, or how such changes affect the capacity of ecosystems to deliver goods and services to people. In the next section we address the need for improving our understanding of such links, and the challenge of scaling up.

### Impacts of alien plant invasions on the delivery of goods and services

Large parts of South Africa still have natural or semi-natural vegetation.<sup>72</sup> Even in areas where human activities have degraded or transformed habitats, goods and services provided by these ecosystems still contribute substantially to human well-being.<sup>26,73</sup> Invasive alien plants affect, via the altered functioning of ecosystems, the capacity of the latter to deliver goods and services. It is becoming increasingly important for ecologists to be able to express the benefits of expenditure on ecosystem management and conservation in terms of such goods and services. This is particularly relevant in South Africa, where, given the emphasis on social benefits embodied in the new constitution, limited government funding is available for direct allocation to alien-plant management. Assessing effects on goods and services has not been an explicit focus of studies on invasion ecology (Box 1). This needs to be addressed if ecologists are to make meaningful contributions to policy debates.

Most South African research that has explicitly addressed the links between alien plant invasions and ecosystem goods and services has dealt with water resources. These studies are reviewed elsewhere,<sup>28,74–77</sup> but there are other examples of goods and services that are influenced by invasions (Table 2). In the absence of documented links between invasions, ecosystem integrity, and goods and services, this discussion can only highlight a few obvious cases where such connections can be observed. The need for detailed studies remains.

Besides direct effects in the form of reduced streamflow, invasive alien plants have clear consequences for the ecological integrity of catchment areas. For example, invasion of fynbos catchment areas increases biomass and fuel loads, leading to enhanced fire hazard and soil erosion.<sup>78</sup> As a result, the ability of catchments to store water for steady release throughout the year

**Table 2.** Examples of goods and services provided by South African ecosystems and ways in which they are influenced (or potentially so) by invasive alien plants.

Goods and services offered	Biomes or zones	Invasive alien species impacting on goods and services	Impact of invasive species
Water discharge	Fynbos, grassland	Wattles ( <i>Acacia</i> species), pines ( <i>Pinus</i> species) and gums ( <i>Eucalyptus</i> species).	Reduced streamflow, and reduced yields from dams
Maintenance of soil stability in fire-prone catchments	Mountain catchments	Hakeas ( <i>Hakea</i> species) and pines ( <i>Pinus</i> species).	Increased fire intensity induces water repellency and increased erosion.
Replenishment of sand on beaches	Coastal zone	Rooikrans ( <i>Acacia cyclops</i> )	Binding of sand, beach erosion
Timber	Indigenous forest and woodlands	Triffid weed ( <i>Chromolaena odorata</i> ) Cat's claw creeper ( <i>Macfadyena unguis-cati</i> )	Provides 'ladder fuels' carrying fire to tree canopies Destruction of forest/woodland canopy
Grazing for livestock and wild-life	Grassland, savanna, karoo	Wattles ( <i>Acacia</i> species), tussock grasses ( <i>Nasella</i> species), cacti ( <i>Opuntia</i> species), mesquite ( <i>Prosopis</i> species)	Reduced grazing potential
Recreation	Aquatic, riparian	Aquatic weeds, mainly water hyacinth ( <i>Eichhornia crassipes</i> )	Reduced capacity for boating, canoeing, water-skiing, fly fishing
Fishing	Estuaries	Wattles ( <i>Acacia</i> species), pines ( <i>Pinus</i> species) and gums ( <i>Eucalyptus</i> species).	Reduced freshwater input to estuaries and altered frequency of mouth breaching

(an ecosystem service) is compromised. Invaded and burnt watersheds are denuded of soil, and runoff after rain is rapid, causing flooding, damage to property and infrastructure, and siltation.<sup>78,79</sup> The extent and consequences of these impacts at regional scales are poorly understood.

In coastal zones, stabilization of naturally mobile sand dunes through increased plant cover and root biomass of planted and invasive rooikrans (*Acacia cyclops*) has altered coastal sediment movements (an ecosystem service that replenishes sand on beaches subject to continuous marine erosion). This has led to massive beach depletion that threatens coastal developments in the Eastern and Western Cape provinces.<sup>80</sup>

The provision of recreational opportunities is another important ecosystem service that is often adversely affected by invasion. For example, recreational fishing is a pastime of large numbers of people, and supports a significant economic sector. Opportunities for fishing are affected by invasion of waterbodies by floating aquatic species, and of riverbanks by alien trees. Such impacts have potentially significant knock-on effects for the creation of ecotourism opportunities, which can be significant (J.A. Cambray, pers. comm.).

Besides services, ecosystems deliver tangible goods in the form of food and fibre for consumption by humans or their domestic livestock. Some examples of direct consequences for the production of these goods include the invasion of palatable rangelands by unpalatable alien plants (for example, jointed cactus, *Opuntia aurantiaca*, and mesquite, *Prosopis* species), which reduce grazing potential; the displacement of native flora suitable for flower harvesting (for instance, the invasion of fynbos by pines, hakeas and wattles); or the potential destruction of timber resources from indigenous forests by invasive creepers such as cat's claw creeper (*Macfadyenia unguis-cati*).<sup>81</sup> Although these outcomes are readily observable, few studies have quantified them in terms of the regional-scale delivery of ecosystem goods. The indirect or secondary impacts of invasions on goods and services are even more difficult to quantify. For example, reductions in runoff resulting from the invasion of upper watersheds by alien trees will affect the discharge of fresh water into estuaries. This, in turn, will affect the dynamics of estuaries (such as the frequency of opening and closing of the mouth and resultant sediment dynamics<sup>82</sup>), with consequences for the suitability of estuaries as

nursery sites for important marine fish species. It is thus possible that invasion of mountain catchment areas could have consequences for fish yields from marine ecosystems, but the links have not been clearly demonstrated.

In aquatic ecosystems, thick mats of water hyacinth sometimes have serious consequences and cause problems for all aspects of water utilization<sup>66</sup>. These outcomes include: reduced quality of drinking water owing to bad odours, taste, colour and turbidity; promotion of waterborne, water-based and water-related diseases (such as malaria, encephalitis and filariasis); increased siltation of rivers and dams; diminished areas for fishing and water transport; deterioration of aquatic biodiversity; blocking and preventing anchorage; clogging of irrigation canals and pumps; and enhanced flood damage to road and rail bridges and hydro-electric power schemes. For these, quantitative studies at appropriate scales are lacking.

The above examples, although few in number and not representative of all the ecosystems affected by alien plant invasions in South Africa, indicate that the consequences for ecosystem goods and services are widespread and profound. Further work is required to enable us to scale-up our understanding of these invasions, in general and in detail, in terms of their implications for the benefits that these systems deliver. Such insights are crucial for 'mainstreaming'<sup>83</sup> concerns about the effects of invasive alien species on local, regional and national economies to ensure appropriate management actions.

Studies of the impacts of invasive alien plants should also acknowledge that some invasive alien species (including those that cause significant changes to natural ecosystems) may also have considerable value. This has resulted in conflicts of interest in several spheres. Conflicts are most pronounced where invasive species underpin large commercial activities, such as plantation forestry (*Pinus* species);<sup>84-86</sup> where they provide firewood (many *Acacia* species),<sup>87</sup> food (*Opuntia* species),<sup>88</sup> fodder (*Prosopis* species), building materials (*Arundo donax*, *Acacia saligna*), agroforestry components,<sup>89</sup> or nectar for bees (*Eucalyptus* species);<sup>90</sup> and where they have aesthetic or utilitarian value (ornamentals, shade trees or windbreaks). The science of invasion ecology (Box 1) has a role to play in informing these (often polarized) debates,<sup>91,92</sup> but has only recently begun to do so.<sup>85,86,89</sup>

## Conclusions

Considerable research effort has been expended on studying the impacts of invasive alien plants in South Africa. As is the case worldwide, most studies have documented changes to ecosystem properties, less often to processes and functions. We have highlighted many areas where the understanding of invasion ecology in a South African context is tenuous. On the other hand, South African research has made a disproportionately large contribution to invasion ecology considering the limited resources available to do so.<sup>93</sup> Local ecologists have played important roles in many research, synthesis, and implementation initiatives, including the SCOPE programme on biological invasions,<sup>94,95</sup> the Global Invasive Species Programme<sup>96</sup> and through pivotal contributions leading to the establishment of the Working for Water programme.<sup>26,27</sup> Advances in our understanding of invasion ecology (Box 1) have had, as is the case worldwide<sup>97</sup>, rather limited effect on management initiatives. We are inadequately equipped to prevent the introduction of new species, to detect and eradicate potentially dangerous organisms before they become major problems. And, at best, we are only partially equipped to deal with the full suite of species that are already a problem. More focused attention must be given to those aspects of invasion ecology that are most directly relevant to management. In this section, we discuss some aspects that seem to qualify for priority treatment in South Africa.

Our review has emphasized the paucity of well-documented accounts of the impacts of invasions, and of robust models enabling us to scale-up our predictions of consequences for goods and services. The development of such models demands a better understanding of the results of invasions at fine scales. Such outcomes vary with species, soil type, and disturbance regime. There is some potential for improved prediction based on well-studied invasions in other parts of the world, but local studies at carefully selected sites are essential. We need to determine the possible ranges of the invasive species already present, as well as the potential extent of species with a high risk of invading in the future.<sup>17</sup> Alien grasses have been inadequately studied in South Africa. Their importance as invaders is increasing in many parts of the country,<sup>39</sup> and this is likely to be exacerbated by climate change.<sup>98</sup> Further studies here are also a priority. For realistic scenario development, we need to improve our understanding of rates of naturalization and spread. Some previous attempts to predict impacts of invasion have used rather simplistic approaches for simulating spread.<sup>99–101</sup> Estimates of the economic outcomes of invasion at a national scale have been found to be sensitive to assumptions relating to rates of spread,<sup>101</sup> indicating that greater understanding of this aspect of invasion ecology would improve the accuracy of impact predictions. Good progress has been made with mechanistic modelling of plant invasions.<sup>22,23,102,103</sup> Such advances have, however, yet to be incorporated into policy and have thus had limited effect on management to date.

The issue of ecosystem repair after clearing also requires attention. Many ecosystems, especially when sparsely invaded or even densely invaded for a short time, can recover after clearing without further management intervention, but others cannot. Some work on restoration ecology has been conducted in the fynbos biome,<sup>104</sup> but more research is needed in all areas affected by invasions. Given the scale at which clearing operations are being conducted, we require improved understanding of how to manage ecosystem recovery. This is especially critical for riparian systems, which are usually densely invaded, and subject to erosion after clearing. Such research should define achiev-

able goals for repair, provide measurable criteria for assessing its success, and develop protocols for the incorporation and monitoring of repair goals into management programmes.

Climate change also needs to be addressed. Altered climate patterns could have significant consequences for the distribution of alien plant species.<sup>98</sup> Some alien species that are currently non-invasive or only naturalized and/or which persist as isolated populations could become (more) invasive as climates change. Interactions among the many factors mediating invasion dynamics, and the interactions between alien and native biota, are extremely difficult to predict under changed climatic conditions. The complexity of understanding how climate change might affect the dynamics of invasion in South Africa was recently illustrated for *Prosopis*.<sup>98</sup> This study showed that the factors affecting potential trajectories for *Prosopis* species are so numerous, and uncertainties so great, that very little confidence could be placed in any predictions. Careful consideration should be given to defining research priorities in this arena to avoid wasted effort. An overarching aim of any research in this field should be to identify those species that pose the greatest risks and the areas likely to face the greatest pressure from invasive species. This would improve our ability to take pre-emptive action.

Along with the daunting challenges outlined above, is the socio-political dimension. The Working for Water programme has been acclaimed internationally for its innovative approach to leveraging funding for invasive-plant management by addressing environmental and socio-political priorities to the benefit of both.<sup>93,97</sup> Further strategic innovations are needed to direct appropriate research in the field of invasion ecology while giving attention to capacity building and social transformation. The current generation of experienced ecologists in South Africa were largely trained under the auspices of the South African Cooperative Scientific Programmes of the CSIR<sup>105</sup> and their associated activities. There is no obvious successor to these programmes, and the country's ability to address ecosystem management will be compromised unless new ecologists can be trained and find gainful employment.<sup>106</sup> At the same time there is a need to diversify the ranks of South African ecologists so that they better reflect the demographics of the country. The country is fortunate in having a small but vibrant body of ecologists on which such diversification can build.<sup>107</sup> It is imperative that these scientists collaborate to address the challenges that lie ahead. Progress in dealing with the mounting problems caused by invasive alien species demands innovative, multidisciplinary collaboration. There is currently no national centre in South Africa with the mission of addressing all facets of invasion ecology. What expertise there is, is thinly spread between a few universities and the science councils. Formal collaboration between organizations to address all component issues, within a clear framework of capacity building and transformation, would be a huge step forward.

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