

A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa

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Abstract

This paper reports an assessment of the current and potential impacts of invasive alien plants on selected ecosystem services in South Africa. We used data on the current and potential future distribution of 56 invasive alien plant species to estimate their impact on four services (surface water runoff, groundwater recharge, livestock production and biodiversity) in five terrestrial biomes. The estimated reductions in surface water runoff as a result of current invasions were >3000 million m³ (about 7% of the national total), most of which is from the fynbos (shrubland) and grassland biomes; the potential reductions would be more than eight times greater if invasive alien plants were to occupy the full extent of their potential range. Impacts on groundwater recharge would be less severe, potentially amounting to approximately 1.5% of the estimated maximum reductions in surface water runoff. Reductions in grazing capacity as a result of current levels of invasion amounted to just over 1% of the potential number of livestock that could be supported. However, future impacts could increase to 71%. A 'biodiversity intactness index' (the remaining proportion of pre-modern populations) ranged from 89% to 71% for the five biomes. With the exception of the fynbos biome, current invasions have almost no impact on biodiversity intactness. Under future levels of invasion, however, these intactness values decrease to around 30% for the savanna, fynbos and grassland biomes, but to even lower values (13% and 4%) for the two karoo biomes. Thus, while the current impacts of invasive alien plants are relatively low (with the exception of those on surface water runoff), the future impacts could be very high. While the errors in these estimates are likely to be substantial, the predicted impacts are sufficiently large to suggest that there is serious cause for concern.

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1. Introduction

Ecosystems deliver a wide range of services to humanity (e.g. Daily, 1997; Constanza et al., 1997). A 4-year global assessment of the world's ecosystem services (Millennium Ecosystem Assessment, 2005), found that 60% of the services assessed were declining in condition due to a suite of anthropogenic drivers (such as habitat loss and alteration, water abstraction, overexploitation, and invasive alien species). The invasion of ecosystems by alien species has been identified as a large and growing threat to the delivery of ecosystem services (Drake et al., 1989).

Invasive alien species are a product of the ongoing and increasing human re-distribution of species to support agriculture, forestry, mariculture, horticulture and recreation, as well as a result of accidental introductions. They include disease organisms, agricultural weeds, and insect pests. These species are known to 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, global changes in climate and biogeochemical cycling, and increased dissemination of propagules makes ecosystems more susceptible to invasion by alien species (Le Maitre et al., 2004). Besides their impacts on agriculture, forestry and human health, biological invasions are also widely recognised as the

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second-largest global threat (after direct habitat destruction) to biodiversity (Mooney and Hobbs, 2000; Secretariat on the Convention on Biological Diversity, 2001).

Ecosystem services can be grouped into those that meet basic human needs (supporting, regulating, and provisioning services) and those that enhance human well-being (cultural services). Supporting services underpin the basic life-support processes required to sustain all ecosystems, while regulating services control the flow of benefits and treatment of wastes, pests, and diseases. Provisioning services provide products for human use, and cultural services enhance the quality of human life and human well-being. Human well-being, although buffered to some extent against environmental vagaries by culture and technology, is ultimately determined by the continued supply of these services (Millennium Ecosystem Assessment, 2005). Services can be delivered by natural as well as highly managed ecosystems.

Biodiversity plays an important role in the delivery of ecosystem services. It can also be a service in its own right, for example, as the basis of nature-based tourism. In other cases, biodiversity is needed for ecosystems to function effectively, and thus to deliver services (de Groot et al., 2002). Although there is much debate as to which aspects (quantity, variability, distribution, or condition) of genes, species, and ecosystems are important for the continued delivery of ecosystem services, there is general agreement that overall biodiversity is important for ensuring the resilience of ecosystem functions and services (Loreau et al., 2001; Diaz et al., 2006). Ecosystems that retain their full complement of biodiversity are also more resistant to the biological invasions that erode ecosystem services (Diaz et al., 2006).

The impacts of invasive alien species on ecosystem services, and on biodiversity, are significant (estimates vary, but the total costs can be in the order of tens of billions of US\$ each year, McNeely, 2001; Pimentel, 2002; Pimentel et al., 2005). Despite their apparent importance, few studies have sought to estimate the impact of invasive species on the delivery of ecosystem services at a broad-scale. The few studies that have been done have either focussed on a single ecosystem service (for example, on surface water supplies, Le Maitre et al., 2000), or on a single species (for example, the black wattle, De Wit et al., 2001). Broad-scale studies are urgently needed to support the estimation of economic impacts at a level appropriate to policy-makers. They are also needed to provide a basis for deciding on the proper levels of funding for control operations, and to identify priorities for management intervention.

In South Africa, considerable amounts are spent on the control of invasive alien plants. Over the past 10 years, government's contribution to control programmes amounted to over R3 billion (approximately US\$500 million; Anonymous, 2004). A combination of the predicted effects of invasive alien plants on water resources, and the potential for clearing projects to

generate much-needed employment, allowed government to justify this level of expenditure (van Wilgen et al., 2002). However, recent reviews have highlighted the need for better assessments of the problem. Richardson and van Wilgen (2004) concluded that the consequences of invasions for the delivery of ecosystem services are, with the notable exception of impacts on water resources, poorly studied. Another review (Görgens and van Wilgen, 2004) concluded that a good deal of knowledge existed regarding the effects of invasive plants on water resources. This study also showed, however, that there were large gaps in understanding, and challenging problems associated with scaling up the knowledge generated at one level to make predictions at a higher, more meaningful, level. In this paper, we report on a spatially explicit assessment of the current and potential impacts of invasive alien plants on selected ecosystem services and biodiversity in the major terrestrial biomes of South Africa (a biome is a large, regional ecological unit, usually defined by a dominant vegetative pattern). This was conducted to provide a preliminary estimate of the size and location of the impacts, to explore the feasibility of using existing information and data to make such assessments, and to identify areas where information needs to be improved. The assessment is the first attempt to quantify the impacts of more than one ecosystem service in a spatially explicit manner at a national scale in southern Africa.

2. Methods

2.1. Sources of data

We restricted our assessment of impacts to ecosystems within five major terrestrial biomes in South Africa. The biomes were the fynbos (mediterranean shrublands), grassland, savanna (including the thicket biome, *sensu* Vlok et al., 2003), Nama karoo (arid shrublands), and succulent karoo. A range of spatial datasets, captured in a geographic information system, were used to assess the possible impacts of invasions on ecosystem services from each of these biomes (Table 1). The extent of each biome, and the degree of transformation and protection, varies considerably between biomes (Table 2).

2.2. Selection of important invasive alien plant species

We developed two lists of invasive alien plant species for each biome (Table 3). The first lists the species that are currently of importance in each biome (the “current list”), and the second lists those that would become dominant in each biome if they were allowed to reach their full potential (the “future list”). We used the South African Plant Invaders Atlas (SAPIA) database (Henderson, 1998) to derive the current list. The SAPIA database contains records of alien plant species presence within quarter-degree squares (a grid of approximately $25 \times 25 \text{ km}^2$). We placed all invasive alien plant species that occurred in

Table 1
Salient attributes of spatial datasets used to assess the impacts of invasive alien species on ecosystem services in South Africa

Dataset	Description	Scale	Use	Source
Terrestrial vegetation in South Africa, Lesotho and Swaziland	Map of 68 major vegetation types	1:250,000	Definition of boundaries of major biomes	Low and Rebelo (1996)
	Map of 441 major vegetation types	1: 250,000	Definition of groundwater-dependent ecosystems	Mucina and Rutherford (2004)
Landcover	Satellite-derived classification of land use	1: 250,000	Exclusion of ecosystem services not derived from transformed areas	Thompson (1996)
Protected areas	Boundaries of all protected areas	1: 250,000	Exclusion of ecosystem services not derived from protected areas	Driver et al. (2005)
Invasive alien plant species	Records of presence and abundance of species	Quarter-degree squares (~25 × 25 km ²)	Selection of important species that currently impact on ecosystem services	Henderson (1998)
	Crude maps of extent and density of infestations	1:250,000	Current impact of species on ecosystem services	Le Maitre et al. (2000).
	Estimates of potential distribution (based on climatic modelling)	Grid of 1 km ²	Potential future impact of species on ecosystem services	Rouget et al. (2004)
Mean annual runoff	Estimates of mean annual surface water runoff	Quaternary catchments (varying in size, see text)	Basis for the calculation of impacts on surface water runoff	Midgley et al. (1994); Schulze et al. (1997)
Rivers	Maps of all major rivers	1:500,000	Definition of riparian zones	South African Department of Water Affairs and Forestry
Quaternary catchments	Nested subdivisions within primary, secondary, and tertiary catchments	1: 1 000,000	Basis for the estimation of impacts on water resources	South African Department of Water Affairs and Forestry
Livestock units	The carrying capacity of vegetation types in terms of large livestock units	1: 250,000	Demonstration of consequences of reduction in grazing capacity	Scholes (1998)

Table 2
The extent of five of South Africa's major biomes, showing the extent of transformation and conservation, rainfall and runoff characteristics, and the area of groundwater-dependant vegetation

	Biome				
	Fynbos shrublands	Grassland	Succulent karoo	Nama karoo	Savanna and thicket
Total area (km ²)	71,340	349,190	83,100	360,110	402,870
Area transformed (km ²)	22,700	102,110	4110	4550	59,590
Remaining natural area (km ²)	48,640	247,080	78,990	355,560	343,270
Area under conservation (km ²)	14,840	7430	4450	44,520	44,520
Mean annual precipitation (mm)	503	667	170	225	544
Mean annual runoff (mm)	95	77	4	8	36
Area of groundwater-dependant vegetation (km ²)	3750	2965	974	11,769	9993

>10% of the squares in each biome onto the current list. Examination of the current species distribution reveals that a relatively small number of species occupy >10% of each biome, but that these would account for most of the impacts by virtue of their dominance (Fig. 1). For example, out of 160 species in the fynbos biome, only 34, 17, and 4 species occupied >10%, 20%, and 50% of the quarter-degree squares, respectively. The threshold of 10% would thus capture a small but very important set of species in

each biome. The potential for invasive alien plant species to extend their range has been estimated using climatic modelling at a 1 × 1 km² resolution (Rouget et al., 2004). We used these estimates to derive the future list by including all invasive alien plant species that had the potential to invade >20% of the biome concerned. Only areas classified as highly suitable to a species were used in this assessment. Potentially, many species will occupy a greater area in each biome than they currently do (Fig. 1).

Table 3

Important invasive alien plant species affecting the delivery of ecosystem services in five biomes in South Africa. Impacts on surface water runoff were calculated for landscape or riparian zones, or both, as indicated. See text for a detailed explanation of the classes of impact on grazing potential. Biodiversity impacts were rated as high or moderate if the impact was analogous to that of a plantation, or of degraded areas, respectively. A dash (–) indicates that the species was assumed not to affect the ecosystem service concerned

Species	Life form	Current and future biomes affected	Areas in which surface water is affected	Impact on grazing potential	Estimated impact on biodiversity
<i>Acacia baileyana</i> (Bailey's wattle)	Medium tree	Future: savanna, grassland, fynbos	Landscape and riparian	Very high	High
<i>Acacia cyclops</i> (red eye)	Medium tree	Current: fynbos; Future: fynbos, succulent karoo	Landscape and riparian	Very high	High
<i>Acacia longifolia</i> (longleaved wattle)	Medium tree	Current: fynbos; Future: fynbos, Nama karoo	Landscape and riparian	Very high	High
<i>Acacia dealbata</i> (silver wattle)	Medium tree	Current: grassland; Future: grassland	Landscape and riparian	Very high	High
<i>Acacia decurrens</i> (green wattle)	Medium tree	Current: grassland; Future: grassland	Landscape and riparian	Very high	High
<i>Acacia mearnsii</i> (black wattle)	Medium tree	Current: savanna, grassland, fynbos; Future: savanna, grassland, fynbos	Landscape and riparian	Very high	High
<i>Acacia melanoxylon</i> (blackwood)	Tall tree	Current: fynbos; Future: grassland, fynbos	Landscape and riparian	Very high	High
<i>Acacia saligna</i> (Port Jackson willow)	Medium tree	Current: fynbos; Future: fynbos, succulent karoo	Landscape and riparian	Very high	High
<i>Achyranthes aspera</i> (burweed)	Herb	Future: grassland	–	–	Moderate
<i>Agave americana</i> (American agave)	Succulent	Current: grassland, fynbos; Future: savanna, grassland, fynbos, succulent karoo, Nama karoo	–	Moderate	Moderate
<i>Arundo donax</i> (giant reed)	Tall grass	Current: savanna, grassland, fynbos; Future: grassland, fynbos	Riparian	–	High
<i>Atriplex lindleyi</i> (sponge-fruit saltbush)	Low shrub	Current: fynbos, succulent karoo, Nama karoo; Future: fynbos, succulent karoo, Nama karoo	–	–	Moderate
<i>Atriplex nummularia</i> (old man saltbush)	Low shrub	Current: succulent karoo; Future: fynbos, succulent karoo, Nama karoo	–	–	Moderate
<i>Cortaderia selloana</i> (Pampas grass)	Tall grass	Current: fynbos	–	–	Moderate
<i>Caesalpinia decapetala</i> (Mauritius thorn)	Shrub	Current: savanna	–	Very high	Moderate
<i>Cestrum laevigatum</i> (inkberry)	Shrub	Future: savanna	–	Moderate	Moderate
<i>Chromolaena odorata</i> (triffid weed)	Shrub	Current: savanna, grassland	–	Very high	High
<i>Cuscuta campestris</i> (common dodder)	Parasitic herb	Current: grassland; Future: savanna, grassland	–	–	Moderate
<i>Datura stramonium</i> (common thorn apple)	Annual	Current: fynbos	–	–	Medium
<i>Echinopsis spachiana</i> (torch cactus)	Succulent	Future: savanna, grassland, Nama karoo	–	Very high	Moderate
<i>Eucalyptus camaldulensis</i> (red river gum)	Tall tree	Current: fynbos; Future: grassland, fynbos, succulent karoo	Riparian	–	High
<i>Eucalyptus grandis</i> (rose gum)	Tall tree	Current: grassland	Riparian	–	High
<i>Eucalyptus lehmannii</i> (spider gum)	Medium tree	Future: fynbos	Landscape	High	High
<i>Hakea drupacea</i> (sweet hakea)	Tall shrub	Current: fynbos; Future: fynbos	Landscape	High	High
<i>Hakea gibbosa</i> (rock hakea)	Tall shrub	Current: fynbos	Landscape	High	High
<i>Hakea sericea</i> (silky hakea)	Tall shrub	Current: fynbos; Future: fynbos	Landscape	High	High
<i>Ipomoea indica</i> (morning glory)	Herbaceous climber	Future: savanna, grassland	–	–	Moderate

Table 3 (continued)

Species	Life form	Current and future biomes affected	Areas in which surface water is affected	Impact on grazing potential	Estimated impact on biodiversity
<i>Jackaranda mimosifolia</i> (jackaranda)	Tall tree	Current: savanna, grassland; Future: savanna, grassland	Landscape and riparian	Moderately high	High
<i>Lantana camara</i> (lantana)	Shrub	Current: savanna, grassland, fynbos; Future: savanna	–	Very high	High
<i>Leptospermum laevigatum</i> (Australian myrtle)	Medium tree	Current: fynbos; Future: fynbos	Landscape	Very high	High
<i>Macfadyena unguis-cati</i> (cat's claw creeper)	Climber	Future: savanna	–	–	High
<i>Melia azedarach</i> (Persian lilac)	Tall tree	Current: savanna, grassland, fynbos; Future: savanna, grassland	Landscape and riparian	Moderately high	High
<i>Nicotiana glauca</i> (wild tobacco)	Shrub	Current: savanna, fynbos, succulent karoo, Nama karoo; Future: savanna, grassland, fynbos, succulent karoo, Nama karoo	–	–	Moderate
<i>Paraserianthes lophantha</i> (stink bean)	Medium tree	Current: fynbos; Future: fynbos	Landscape and riparian	–	High
<i>Pennisetum clandestinum</i> (Kikuyu grass)	Grass	Current: fynbos	–	–	Moderate
<i>Pinus elliottii</i> (slash pine)	Tall tree	Future: savanna, grassland	Landscape	High	High
<i>Pinus halepensis</i> (Aleppo pine)	Tall tree	Future: savanna, grassland, fynbos, Nama karoo	Landscape	Very high	High
<i>Pinus patula</i> (patula pine)	Tall tree	Current: grassland; Future: grassland	Landscape	High	High
<i>Pinus pinaster</i> (cluster pine)	Tall tree	Current: fynbos; Future: fynbos	Landscape	Very high	High
<i>Pinus radiata</i> (Monterey pine)	Tall tree	Future: fynbos	Landscape	Very high	High
<i>Populus alba</i> (white poplar)	Tall tree	Current: grassland	Riparian	–	High
<i>Populus canescens</i> (grey poplar)	Tall tree	Current: grassland, fynbos	Riparian	–	High
<i>Prosopis glandulosa</i> (mesquite)	Tall tree	Current: fynbos, succulent karoo, Nama karoo; Future: savanna, Nama karoo	Landscape and riparian	High	High
<i>Prunus persica</i> (peach)	Medium tree	Current: savanna	–	–	Moderate
<i>Psidium guajava</i> (guava)	Medium tree	Current: savanna, grassland; Future: savanna	–	High	Moderate
<i>Pyracantha angustifolia</i> (yellow firethorn)	Tall shrub	Current: grassland	–	Moderately high	Moderate
<i>Robinia pseudoacacia</i> (black locust)	Tall tree	Future: savanna, grassland	Landscape and riparian	Moderately high	High
<i>Rubus cuneifolius</i> (American bramble)	Shrub	Current: grassland	–	Very high	Moderate
<i>Rubus fruticosus</i> (European blackberry)	Shrub	Current: grassland, Fynbos; Future: fynbos	–	Very high	Moderate
<i>Salix babylonica</i> (weeping willow)	Medium tree	Current: grassland; Future: grassland	Riparian	–	High
<i>Senna didymobotrya</i> (peanut butter cassia)	Shrub	Current: savanna; Future: savanna	–	Low	–
<i>Senna occidentalis</i> (wild coffee)	Shrub	Future: savanna	–	Low	–
<i>Solanum mauritianum</i> (bugweed)	Medium tree	Current: savanna, grassland, fynbos; Future: savanna, grassland	–	Low	Moderate
<i>Solanum seafortianum</i> (Potato creeper)	Climber	Future: savanna	–	Low	–
<i>Solanum sisymbriifolium</i> (wild tomato)	Shrub	Future: grassland	–	–	Moderate
<i>Xanthium strumarium</i> (large cocklebur)	Annual	Current: savanna; Future: savanna, grassland	–	Moderate	–

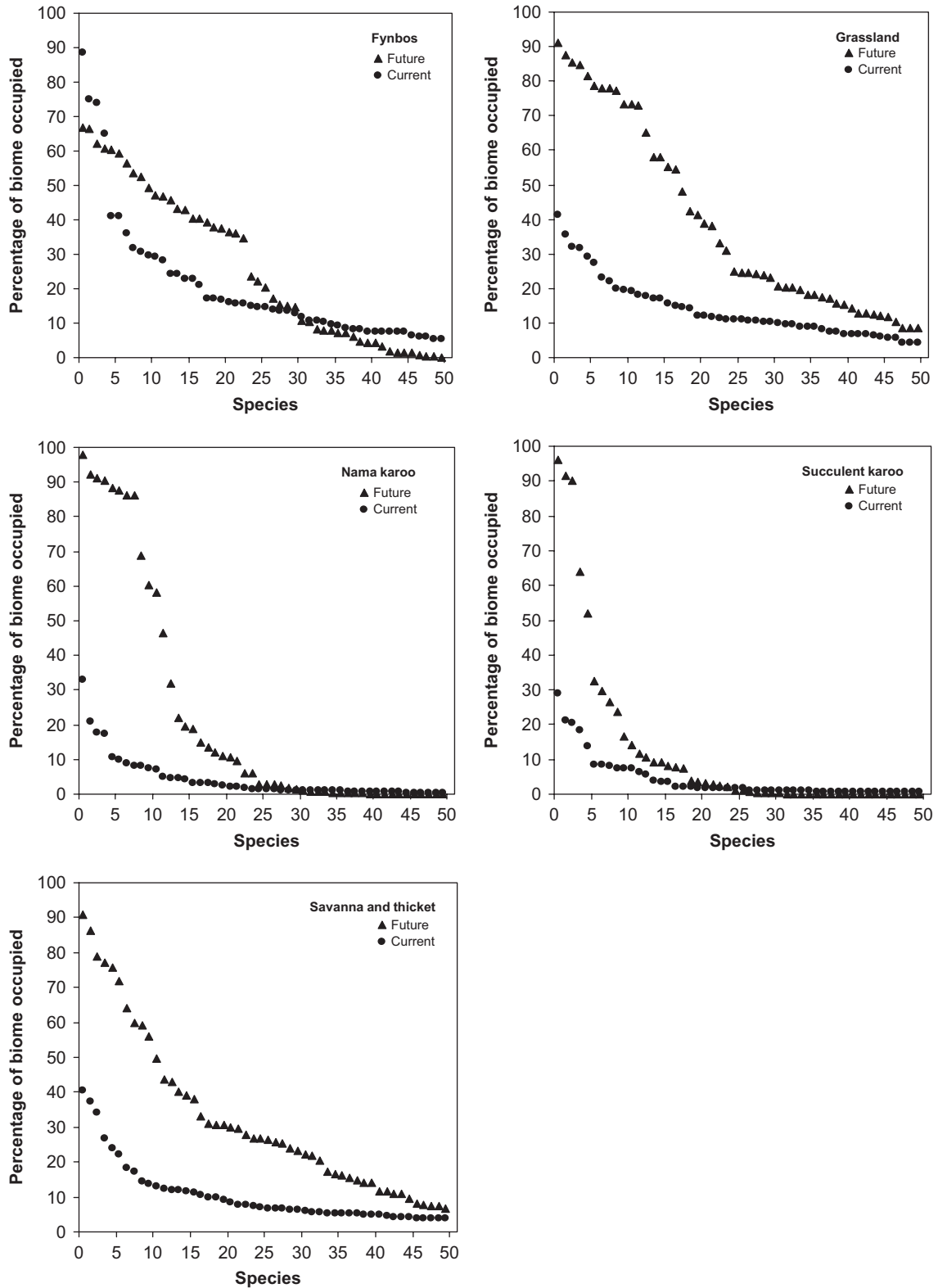


Fig. 1. Percentage of the biome occupied by the 50 most abundant invasive alien plant species in five biomes in South Africa. The current distribution was estimated from records of presence in quarter-degree squares, and the future distribution from climatic suitability modelling.

We used 20% as a threshold for selecting species for inclusion in the future list, and not 10% as in the case of the current list, given the greater degree of uncertainty involved.

For each biome, we created subsets of the current and future lists, consisting of those invasive alien plant species that would have an impact on each of the ecosystem services assessed. We also eliminated invasive species that

were known to be under complete or substantial biological control (Zimmermann et al., 2004), as well as those that were known to be naturalised but not to be aggressively invasive in the biome concerned, or that were known to colonise disturbed areas only.

2.3. Selection of important ecosystem services

Many ecosystem services and categories of ecosystem services exist (Daily, 1997; de Groot et al., 2002; Millennium Ecosystem Assessment, 2005). In a similar fashion to the Southern African Millennium Ecosystem Assessment (Biggs et al., 2004), we limited our study to the provisioning ecosystem services—a category with good available data and high relevance to decision-makers. Within this category we selected ecosystem services that are supplied by largely untransformed natural areas and where we have sound knowledge of the impacts of invasive alien plants. These were the generation of surface water runoff, the recharge of groundwater, and the provision of grazing to domestic livestock. These services provide significant benefits to South African society and have been well studied and documented. Besides being a basic need for survival, water underpins agriculture, forestry, mining, and industry in South Africa, and is a limiting resource; in addition, many rural towns in western South Africa are dependent on groundwater (van Tonder, 1999). Grazing provided by natural vegetation also contributes significantly to livestock production in the country (Scholes, 1998).

This list of ecosystem services is not exhaustive and misses some key services where we do not have adequate data on their supply or on the impact of alien plants. Examples include fuel wood harvesting, medicinal plant supply, soil protection, and climate regulation, as well as ecosystem services generated by human-modified systems (such as crop production).

This study, like the Millennium Ecosystem Assessment (2005), sees biodiversity and its status as a necessary precondition to sustained ecosystem service supply. Thus, an assessment of the current and future impacts of alien plant invasions on biodiversity integrity was conducted to assess the integrity of the ecosystems and their ability to continue supplying other ecosystem services not assessed. Although there are circumstances where biodiversity can be a service itself, we did not consider it further in this way.

2.4. Impacts on surface water runoff

The species listed as being of importance to surface water runoff included species that could be classified as tall trees, medium trees or large shrubs according to the definitions given by Le Maitre et al. (2000). Each list was further subdivided, based on habitat records in the SAPIA database, and published lists (Nel et al., 2004), into those tree and shrub species that invade riparian areas, those that

invade landscapes away from riparian areas (“drylands”), and those that invade both.

We used maps of the extent of invasive alien species infestations in each biome to estimate impacts on surface water runoff. These infestations were mapped at a scale of 1:250,000, and are a crude approximation of the extent and density of invasions of each species in the late 1990s (Le Maitre et al., 2000). The cover of each species on the current list was used to estimate the impacts in terms of reductions in surface water runoff, using the methods described by Dzvukamandja et al. (2005). This approach divides invaded areas into riparian strips and drylands. Invaders in riparian strips potentially have access to additional water from the river itself, to groundwater in the riparian strip and to lateral discharges of groundwater into the riparian zone. Their transpiration, and thus their impact on surface water flows, is limited only by the atmospheric vapour demand and by the physiology of the plant. The physiological limitations were catered for by assuming that the plant could only transpire at a proportion of the atmospheric demand. Transpiration by dryland invaders (and thus the reduction in surface water flows) was limited to a proportion of the pre-invasion runoff. The proportions were determined by the invader size class as defined by Le Maitre et al. (2000), and were 78%, 60%, and 23% for tall trees, medium trees, and tall shrubs, respectively. The reductions in surface water flows were calculated at the level of quaternary catchments (quaternary catchments are nested subdivisions within primary, secondary, and tertiary catchments, ranging in size from 5000 to 180,000 ha), and these were summed to determine the combined impact of all species in each biome.

The potential impact of future invasions was determined using a similar procedure, adapted to be compatible with the scale at which potential future invasions had been mapped. Estimates of reductions in surface water runoff were calculated for cells of one minute by one minute (approximately $1.8 \times 1.8 \text{ km}^2$). The mean annual runoff within each cell was obtained from Midgley et al. (1994). Reductions were estimated as above for those alien plant species designated as landscape invaders on the future list. As many species could potentially occupy the same grid cell in future, summing the estimated reductions for all species would result in an over-estimate of impacts. We therefore estimated the reduction associated with the single species that would cause the largest reduction in the grid cell concerned, and summed these estimates for each biome. Riparian zones were assumed to cover 1% of each grid cell in which rivers were located (the cover of riparian zones across the country amounted to this area on average, assuming that each riparian strip was 20 m wide). For each grid cell that contained at least one riparian invasive species, surface water runoff reduction was assumed to be 500 mm more than that of the vegetation that was replaced from the 1% deemed to be within the riparian zone. A reduction of 500 mm represents the estimated average

annual water use from areas invaded by alien trees that have constant access to river water via bank storage. The estimates for the landscape and riparian reductions were combined to obtain an estimate of overall reduction.

2.5. Impacts on groundwater recharge

We confined our analysis of impacts on groundwater recharge to a subset of vegetation types mapped by [Mucina and Rutherford \(2004\)](#). These types included those with a high likelihood of groundwater dependence (riparian vegetation, alluvial and aeolian deposits where the groundwater is believed to be potentially within the rooting depth of at least the woody plant species, dolomitic and limestone areas, and dune vegetation). Deep-rooted invasive alien trees and shrubs would effectively reduce the recharge of groundwater aquifers in these vegetation types, assuming that they have access to water that would, under normal circumstances, filter through to groundwater rather than form part of surface water runoff. We assumed that invasive alien plants classified as tall trees, medium trees, and tall shrubs ([Le Maitre et al., 2000](#)) would reduce groundwater recharge by 20% of the mean annual runoff in the area concerned. This magnitude of reduction was based on comparisons of groundwater recharge rates between dune areas with no vegetation, natural vegetation and infestations of Australian wattles ([Zhang et al., 2004](#)). Estimates of current impacts were based on areas where groundwater-dependent vegetation and infestations of invasive alien plants (as mapped by [Le Maitre et al., 2000](#)) overlapped. Those associated with potential future impacts were based on the future potential distributions as mapped by [Rouget et al. \(2004a\)](#).

2.6. Impacts on grazing

The species listed as being of importance to grazing excluded those that would have little or no impact on grazing (for example, those species that only invade highly disturbed areas). Each species record in the SAPIA database is designated as very abundant, abundant, frequent, occasional, present, or rare, depending on the density of plants where the record was made. From the current list for each combination of species and abundance class, we used expert opinion to estimate the percentage by which an infestation of the species would reduce the grazing capacity of pristine vegetation. In order to do this, several experts familiar with the species and their effects in the field were consulted; these included field ecologists from the Centre for Invasion Biology (www.sun.ac.za/cib/) as well as researchers with decades of field experience in the biological control of invasive species. Species were classified into five broad types with regard to impact:

i. Very high—species that reduce the grazing potential by 80% when very abundant, by 20–50% when abundant or frequent, and by 5% when occasional.

- ii. High—species that reduce the grazing potential by 60% when very abundant, by 15–30% when abundant or frequent, and by <5% when occasional.
- iii. Moderately high—species that reduce the grazing potential by 40% when very abundant, by 10–25% when abundant or frequent, and by <2% when occasional.
- iv. Moderate—species that reduce the grazing potential by 30% when very abundant, by 5–20% when abundant or frequent, and by <2% when occasional.
- v. Low—species that reduce the grazing potential by 15% when very abundant, by 3–7% when abundant or frequent, and by <2% when occasional.

The impacts of these invasions in each of the biomes was assumed to be restricted to untransformed natural vegetation, excluding areas transformed by crop agriculture, plantation forestry, urban development, and protected areas (where livestock production for commercial purposes does not take place).

We used estimates of the mean livestock production (in large livestock units per km²) to represent the potential of un-invaded vegetation to support livestock production ([Scholes, 1998](#)). The impact of current invasions of alien plant species on potential livestock production was estimated using maps of the extent of invasive alien species in each biome ([Le Maitre et al., 2000](#)). We estimated the impact of each species based on the density in which it was recorded, at a 1-min grid cell resolution (1.8 × 1.8 km²). The impact was then assumed to be that associated with the one species predicted to have the greatest impact on grazing in the grid cell concerned, and these estimates were summed for the biome as a whole. The potential impact of future invasions was estimated by assuming that the areas identified as highly suitable for a species (in terms of climatic suitability; [Rouget et al. \(2004\)](#)) would become densely invaded by that species. The impact was assumed to be that associated with the species with the highest potential impact predicted to occur in each grid cell, and these reductions in grazing potential were summed across each biome.

2.7. Impacts on biodiversity

The impacts of alien invasive plants on biodiversity are poorly understood ([Richardson and van Wilgen, 2004](#)). For the purposes of this study, we needed a spatially explicit estimate of changes in biodiversity integrity with changes in alien distributions. For this purpose the biodiversity intactness index (BII) developed by [Scholes and Biggs \(2005\)](#) proved useful. This index translates expert estimates of land use impacts on vertebrate and plant populations into a spatial estimate of biodiversity integrity. It is an aggregate index that combines information on ecosystem distribution, species richness and the extent and impact of major land uses on biodiversity. It is intended to provide an easy-to-understand overview of the

state of biodiversity for policy-makers and the public. In essence, BII is a richness and area-weighted average of the impact of a set of land use activities on populations of plants, mammals, birds, reptiles, and frogs in a given area. If the population impact (I_{ijk}) is defined as the relative population of taxon i (as compared to the reference state) under land use activity k in ecosystem j , then BII gives the average remaining fraction of the populations of all species considered:

$$\text{BII} = \frac{\sum_i \sum_j \sum_k R_{ij} A_{jk} I_{ijk}}{\sum_i \sum_j \sum_k R_{ij} A_{jk}},$$

where R_{ij} is the richness (number of species) of taxon i in ecosystem j and A_{jk} is the area of land use k in ecosystem j .

Data on the population impact (I_{ijk}) are currently not available, so Scholes and Biggs (2005) consulted three or more taxonomic specialists for each taxon to produce expert estimates of impact per land use per taxon per biome. These estimates were generated for protected areas, light use, cultivation, plantations, and urban and degraded areas. The index has been applied to South Africa by Biggs et al. (2006) based on the 1996 national land cover data which recognises areas of cultivation, plantations, urban development, protected areas, degraded areas and natural areas (equivalent to areas of light use). This data layer represents biodiversity intactness without invasive alien plants.

The lists of alien invasive plant species were then divided into two categories per biome. These were species which in dense stands would have impacts equivalent to those associated with plantations, or with degraded areas. As described above, several experts familiar with the species and their effects in the field were consulted when assigning species to the two categories.

The current extent of dense infestations per species was assessed using the estimates of Le Maitre et al. (2000). If the polygon of dense infestation was found to include any species from list above, it was categorised as a degraded area or plantation area depending on the species present. If both categories of species were present then the area was classified as a plantation. These areas were merged with the national land cover data layer and used to calculate the changes in biodiversity intactness. A similar procedure was used for the estimated future impacts of invasions, using data from Rouget et al. (2004).

3. Results

3.1. Determination of area at risk from invasion

The extent of terrestrial biomes in South Africa ranges from <7.5 to >40 million ha (Table 2). Our assessment sought to quantify the impacts of invasive species on ecosystem services arising from the untransformed areas of the biomes. The two karoo types are the least transformed

of these biomes, with between 1% and 5% transformed by agriculture and urban development. About one third of the grassland and fynbos biomes, and 15% of the savanna biome, have been transformed. The savanna, fynbos, and Nama karoo biomes are reasonably well represented in the national network of protected areas, while the succulent karoo (5%) and grassland (2%) biomes have relatively little area under formal conservation. The fact that some biomes have only small areas under formal protection could have implications for their management. For example, clear and co-ordinated invasive alien plant control policies would be required to ensure their widespread implementation by larger numbers of landowners in biomes where levels of formal protection are low.

3.2. Selection of important invasive alien plant species

A total of 56 species were listed in the current and future lists as having important impacts on the delivery of ecosystem services (Table 3). Tall and medium trees (28 species) and shrubs (16 species) made up the bulk of species, while herbs, annuals and climbers (7 species), grasses (3 species) and succulents (2 species) accounted for the remainder. Many succulents from the genus *Opuntia* (cacti) were eliminated from the lists—although they are widespread, they are under effective biological control. We also eliminated many species that were widespread, or potentially widespread, either because they are invaders of disturbed areas only, or because they are known not to be aggressive invaders. Finally, the paucity of grasses in our lists is remarkable. Grasses are important, but often overlooked, elements of the South African invasive flora. Milton (2004) lists over 100 invasive alien species in South Africa, for example; these are, however, not adequately captured in the SAPIA database (which lists only 9 grass species), because of the difficulty of identifying such species.

3.3. Impacts on surface water runoff

The estimated annual reductions in surface water runoff as a result of current infestations of invasive alien plants ranges from 0.4 mm (rainfall equivalent) in the dry Nama karoo, to 15.2 mm in the fynbos shrublands. These estimated reductions amount to over 3000 million m³ of surface water runoff annually (Fig. 2), most of which is from the fynbos and grassland biomes, and which represents approximately 7% of the runoff of the country (Le Maitre et al., 2000). If infestations of invasive alien plants were to reach their full potential, these impacts could increase to between 2.3 mm in the dry Nama karoo, and 38.5 mm in the grassland biome; the potential reductions could be more than eight times greater, at about 25,000 million m³ of surface water runoff (approximately 58% of the surface water runoff of the country; Fig. 2). Most of this impact would be felt in the grassland biome.

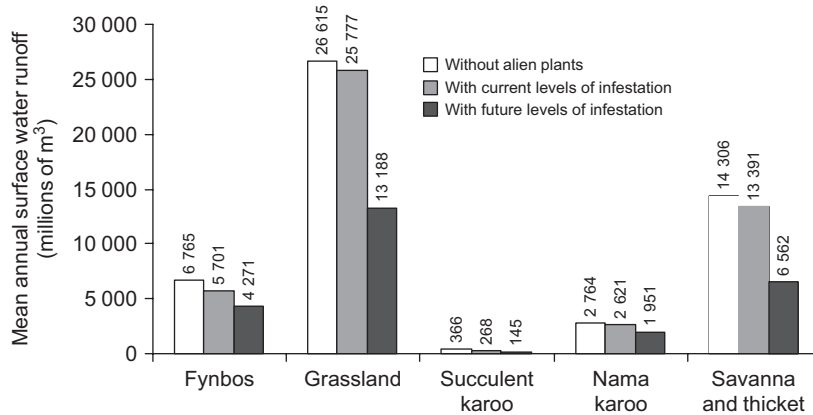


Fig. 2. Estimates of the current and potential impacts of invasive alien plants on surface water runoff in five biomes in South Africa.

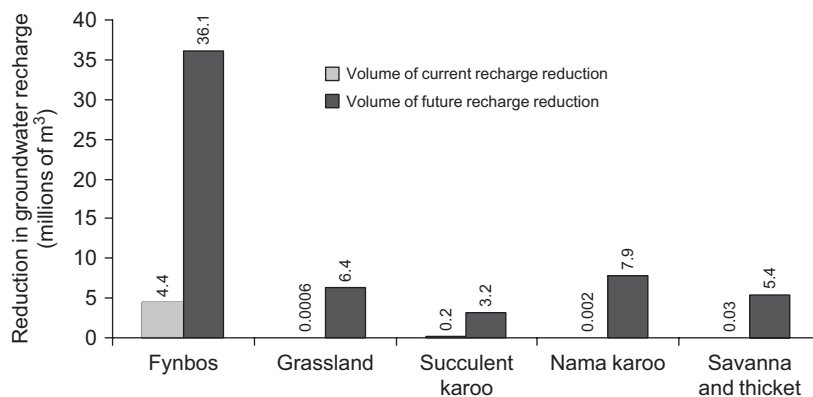


Fig. 3. Estimates of the current and potential impacts of invasive alien plants on groundwater recharge in five biomes in South Africa.

3.4. Impacts on groundwater recharge

The extent of groundwater-dependant vegetation was the greatest in the fynbos biome, where it accounted for >5% of the total area of the biome (Table 2). About 3% and 2.5% of the Nama karoo and savanna biomes, respectively, were designated as groundwater dependant, while the proportion of the succulent karoo and grassland biomes was about 1%. The estimated potential reductions in groundwater recharge are correspondingly highest (36 million m³ annually) in the fynbos biome. The actual volumes are small, however, when compared to the estimates for surface water runoff, amounting to only 1.5% of the potential reductions in surface water runoff due to invasive alien plants (Fig. 3). The estimated potential reductions in the grasslands are relatively small compared to the potential reductions in surface water runoff. Similarly, the reductions in groundwater recharge in the two karoo biomes are small, but arguably more significant given that the importance of water in these arid ecosystems.

3.5. Impacts on grazing

The grassland, Nama karoo and savanna biomes would potentially support the largest number of livestock units in

the country (Fig. 4). The estimated current reductions in the potential for these ecosystems to support grazing stock, as a result of invasive alien plant infestations, amount to between 200 (in the Nama karoo) and 74,500 (in the fynbos) large stock units (Fig. 4). This amounts to just over 1% of the potential number of livestock that can be supported by these ecosystems. However, if infestations of invasive alien plants are allowed to reach their full potential, these impacts could increase to 71% of the potential.

3.6. Impacts on biodiversity

Current estimates of the BII range from 71% to 89% for the five biomes analysed (Fig. 5). These estimates take into account the conversion of natural landscapes by means of agriculture, forestry or urban development, as well as land degradation, but they do not account for the impacts of invasive alien plants. When the additional impacts of invasive alien plants are considered, estimates of the current levels for the BII only declined in the fynbos biome (from 73% to 70%; Fig. 5). This finding reflects the fact that the fynbos biome currently has the highest levels of alien plant infestations; this, in turn, is probably due to the considerably longer period of colonial settlement in the

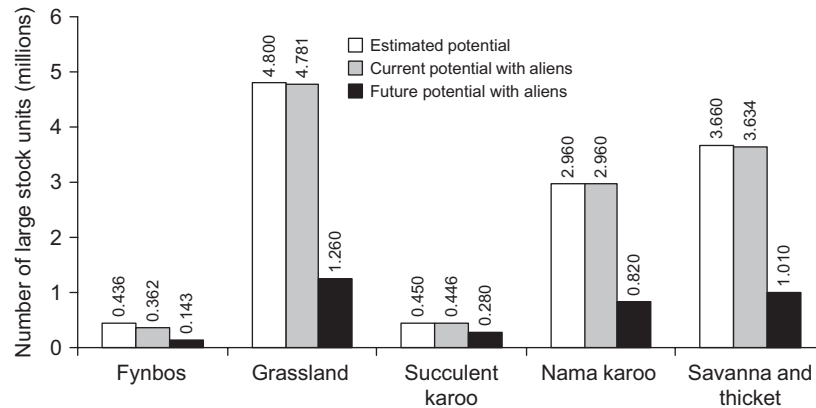


Fig. 4. Estimates of the potential numbers of large stock units that could be supported in five biomes in South Africa, the degree to which these numbers are currently and potentially reduced by invasive alien plants.

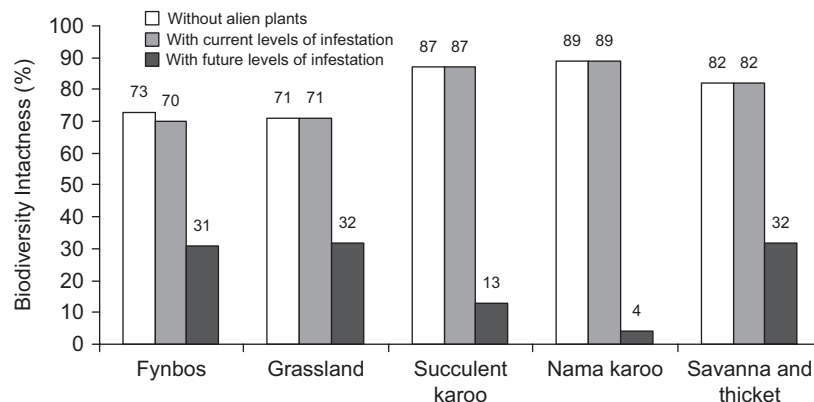


Fig. 5. Estimates of the current and potential impacts of invasive alien plants on biodiversity in five biomes in South Africa. Data are expressed as a “biodiversity intactness index” (Scholes and Biggs, 2005), which is the estimated proportion of remaining populations of vertebrates and vascular plants.

area. Under a scenario where invasive alien plants are allowed to reach their full potential, however, the values decline dramatically, to around 30% for the savanna, fynbos and grassland biomes, but to even lower values (13% and 4%) for the two karoo biomes, suggesting significant potential population declines of >90% in places.

4. Discussion and conclusions

4.1. The importance of large-scale assessments

Economic evaluations of the impacts of invasive alien plants are required for the formulation of appropriate approaches to the problem. Such evaluations must in turn be based on good estimates of the consequences in terms of ecosystem services. Many of the studies that have been done in this regard have been focussed at smaller spatial scales where good data are available (e.g., van Wilgen et al., 1997; Turpie and Heydenrych, 2000), or on a single species (e.g., de Wit et al., 2001; McConnachie et al., 2003). While these studies are useful, they do not support the

higher-level estimates that would be required to formulate appropriate national policies for dealing with invasive species. Our study has provided estimates, albeit preliminary ones, at a biome-scale, demonstrating the feasibility of such approaches. The limited number of datasets available to do this evaluation also illustrates the difficulties facing those who wish to attempt higher-level assessments. First, good datasets on many ecosystem services are not available. Where they are available, they have not always been collected at the same scale, with the same degree of accuracy, or for a common purpose. These shortcomings require assessors to make assumptions that could compromise the reliability of estimates, or confuse comparisons.

Our results suggest that, while the current impacts of invasive alien plants are relatively low (with the exception of those on surface water runoff), the future impacts could be very high. In all likelihood, the current impacts have been underestimated, while future impacts may well have been overestimated because of our assumptions that all climatically suitable areas would become invaded. The data on the current extent of invasions are very coarse and incomplete, while those for the future are modelled using

climatic suitability, and this approach produces a large estimate for cover. In addition, any analysis at a national level has to involve broad assumptions, as we have made in this study. These included, for example, the assumptions that only certain species would impact on ecosystem services; that all climatically suitable areas would become invaded; that particular levels of impact on grazing and groundwater recharge could be assumed; and that reductions in biodiversity resulting from invasions would be similar to those associated with other forms of degradation. The approach, however, has allowed us to produce estimates, albeit unsophisticated ones, at a national level.

4.2. The serious nature of the problem

Reductions in the provision of ecosystem services of the magnitude estimated in this study would generate significant, negative economic consequences. Whether or not they materialise depends to a large degree on whether or not the ecosystems at risk will suffer from the predicted levels of invasion. Are such levels possible? A number of points can be made in this regard. In the first place, many of South Africa's remaining natural ecosystems are relatively free of significant infestations of invasive alien plants at present (with the notable exception of the fynbos biome, where infestations of invasive plants are at much higher levels). The fact that many invasive plant species already occur in many areas at low densities, and are known to be able to develop into dense closed stands over time, suggests that an ongoing escalation in the level of infestations can be expected over time. The situation can also be expected to worsen as new invasive species become established. New invasive species will continue to arrive, and many potential invasive species are probably already here—but not yet invading. Many serious invasions have exhibited a “lag period” in which the introduced species may occur at very low population levels for several decades before becoming invasive, sometimes suddenly (Crooks, 2005; Pyšek and Hulme, 2005). This could be the result of exponential population growth, a period of selection of genotypes suited to the newly invaded environment, or the occurrence of a change in environmental conditions that constrain invasions. With the rapid growth in the rate of introduction of new species, most introductions of alien species have occurred recently. It is therefore likely that a large number of invaders are currently in their “lag period”, and the rate of new invasive species problems will increase dramatically in future. Global changes, such as changes in climate and in the rates and magnitudes of biogeochemical cycles, may further worsen the situation, by bringing about conditions more favourable for invasions (Dukes and Mooney, 1999; Baruch and Jackson, 2005). Finally, our study has also only focussed on four ecosystem services, and the potential is there for the addition of many more; this would probably also increase the levels of estimated impacts on ecosystem services (even if some of these were positively affected by invasions), and

situation could worsen as new species arrive and become invasive. We believe, therefore, that this problem is significant, growing in importance, and demanding of serious scientific attention at an appropriate level.

The seriousness of the predictions of impact can be illustrated with reference to water supplies. South Africa is a dry country, and like many others the demand for water resources often exceeds the capacity of ecosystems to provide them. While the country as a whole still has a water surplus, recent studies have shown that demand already exceeds supply in more than half of the 87 water management areas in South Africa (van Wilgen et al., 2007). Thus, any further reduction in water supplies as a result of watershed areas becoming invaded by trees and shrubs will seriously retard the prospects for economic growth. Similar statements could be made with regard to livestock production. Although estimates are difficult to make at a national level, livestock production from natural ecosystems generates in the order of R1.25 billion annually in South Africa (Department of Agriculture, 2005). A significant proportion of this economic benefit may well be lost as a result of invasion of rangelands by trees, shrubs, succulents, and unpalatable grasses. The impacts of reductions in biodiversity on the delivery of ecosystem services would require further study to be able to understand the important links.

Our assessment has attempted to quantify the impacts of invasive species (and, by proxy, the benefits of control) at a biome level. Managers of alien plant infestations would like to know, more exactly, where they should focus their efforts to maximise the benefits in terms of improved protection of ecosystem services. We have not attempted to address this issue here, but the dataset created as part of this project could feed into decision-support products developed for this purpose. For example, van Wilgen et al. (2007) used data on the distribution and impacts of alien plants to examine where such priorities should lie. Their approach identified priority areas that had not been identified as such, and predicted that their approach would provide decision-makers with an objective and transparent method with which to prioritise areas for the control of invasive alien plants. The explicit mapping of impacts on ecosystem services would provide important material in this regard.

4.3. Levels of confidence in predictions

Our data and approaches do not allow for the calculation of error estimates associated with predicted impacts. While the errors in these estimates could be large, the predicted impacts are of sufficient magnitude to suggest that, even with significant over-estimates, there is cause for serious concern; for example, even if the levels of impact are one tenth of those predicted, they would result in significant losses of benefit.

Future studies of this kind would be improved by the inclusion of a sensitivity analysis. There would be a number

of ways in which this could be done. We have chosen those species that were expected to have the largest impacts on the ecosystem service concerned. In the event that the particular species did not prove to be invasive, sensitivity analysis could examine the impacts of species in declining order of predicted impact. For example, we assumed that future impacts on grazing would be associated with the one species predicted to have the greatest impact. This could result in an under-estimate (in cases where additional areas may be invaded by other species), or an overestimate (if the selected species fails to invade, and the impact reverts to the next-worst species). The levels of expected impact could also be varied in a sensitivity analysis (for example, by using categories for high, medium and low levels of impact). Finally, the possibility that future invasions could cover varying areas within the estimated climatically suitable habitat could be explored.

4.4. Challenges for future research

Conducting assessments at a national level will pose significant challenges for researchers. This assessment has highlighted some of these, which include:

- i. the need for robust, comprehensive estimates of the distribution of invasive alien species, accompanied by approximations of the density of invasions. The development of such datasets would require a co-ordinated, national effort involving different land management agencies and other significant landowners. This underscores the importance of a holistic view of invasions and co-operation between authorities;
- ii. the development of simple models that will allow for the estimation of impacts of invasions on important ecosystem services. The models should incorporate the ability to scale up from studies at smaller scales to produce estimates at, for example, the level of biomes or provinces;
- iii. the development of techniques to estimate the rate at which invasive alien plants will spread. Our estimates of the potential future impacts of invasive alien plants are large, but there is no way of knowing when these levels of impact would be reached, given the inability to estimate rates of spread. One solution could be combine our findings with the opinions of an expert panel on probable spread rates and other important relevant variables to arrive at estimates; and
- iv. the likely replacement of one invasive species by another. For example, if an important species is cleared from an area, or brought under biological control, the area may simply be invaded by another species, which could nullify the net benefits gained from control operations. Competition between different invasive alien plant species is also important in this regard. Relatively un-invaded areas may be threatened by several invasive species, each of which could have different impacts. The relative degree to which one or

some of these species will eventually dominate a given area needs to be estimated to assess potential impacts.

We believe that addressing these issues is important. Accurate estimates of the ecological consequences (in terms of ecosystem services at a broad-scale) can only be made if the challenges outlined above are overcome. They can then form the basis for a rigorous economic assessment of consequences, the development of science-founded policies, and serve to ensure that adequate attention is paid to the issue at national levels.

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