

An economic assessment of the contribution of biological control to the management of invasive alien plants and to the protection of ecosystem services in South Africa

Willem J. de Lange · Brian W. van Wilgen*

CSIR Natural Resources and the Environment, PO Box 320, Stellenbosch, 7599, South Africa

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*Author for correspondence:
email: bwilgen@csir.co.za;
phone +27 21 888 2400;
fax +27 21 888 2693

Abstract This study is a first attempt at a holistic economic evaluation of South African endeavours to manage invasive alien plants using biological control. Our focus was on the delivery of ecosystem services from habitats that are invaded by groups of weeds, rather than by each individual weed species. We established the net present value of the weed-biological control efforts, and derived benefit:cost ratios by comparing this value (a cost) to the estimated value of ecosystem services protected by weed biological control. We identified four major functional groupings of invading alien plants, and assessed their impact on water resources, grazing and biodiversity. We estimated the area that remained free of invasions due to all historic control efforts in South Africa, and the proportion that remained free of invasion as a result of biological control (which was initiated in 1913). The estimated value of potential ecosystem services amounted to 152 billion South African rands (ZAR – presently, about US\$ 21 billion) annually. Although an estimated ZAR 6.5 billion was lost every year due to invading alien plants, this would have amounted to an estimated additional ZAR 41.7 billion had no control been carried out, and 5 - 75% of this protection was due to biological control. The benefit:cost ratios ranged from 50:1 for invasive sub-tropical shrubs to 3726:1 for invasive Australian trees. Benefit:cost ratios remained positive and our conclusion, that biological control has brought about a considerable level of protection of ecosystem services, remains robust even when our estimates of the economic impacts of key variables (i.e. sensitivity analyses of indeterminate variables) were substantially reduced.

Introduction

Invasive alien plants are a large and growing problem worldwide, as they threaten the integrity of ecosystems and the services that they deliver to humanity. The growth in human populations has been accompanied by unprecedented encroachment on terrestrial ecosystems, and the expansion of global trade has led to the widespread distribution of large numbers of species beyond their native ranges. Both have led to an increase in the number and distribution of invasive alien plant species, causing significant economic losses (Perrings et al. 2009; Pimentel 2002).

Land managers have responded to the threat of invasive alien plants in a variety of ways. Several countries have developed national strategies for dealing with the problem (see, for example, Federal Interagency Committee (1998), and a global strategy has been proposed (McNeeley et al. 2001). All of these approaches support the concept of integrated control, which includes the appropriate use of combinations of mechanical, chemical and biological control, and habitat management.

The biological control of invasive alien plants, using plant-feeding insects and pathogens, (also called “weed biological control”) provides a long-term, self-sustaining solution to many invasive alien plant problems (Moran et al. 2005). Numerous studies (Buhlea et al. 2005; Culliney 2005; De Wit et al. 2001; De Wit et al. 2003; Jarvis et al. 2006; Law 2007; McConnachie et al. 2003; Pimentel et al. 2005; Pringle and Heunis 2006; van Wilgen et al. 2004; van Wilgen et al. 2001; van Wilgen et al. 2000; van Wyk and van Wilgen 2002) have discussed or assessed the economic returns on investments in biological control, but none could be regarded as comprehensive as almost all dealt with single weed species. One of the few more comprehensive reviews of weed biological control was done in Australia (Page and Lacey 2006) and concluded that national weed biological control realised significant long term returns on investments, with benefits far outweighing the total costs. However, this finding was based on a range of individual assessments, which would have led to double-counting of benefits. We are not aware of any study that has attempted to quantify the benefits of biological control in terms of ecosystem services at a landscape (or biome) scale, where numerous species invade the landscape. Such studies are complicated, as the

magnitude of impacts is poorly understood, and the conduct of such studies requires numerous assumptions.

South Africa made significant investments in weed biological control over the past century (Zimmermann et al. 2004). In this paper, we have developed an approach to assess the costs and benefits of South Africa's weed biological research effort. Our focus was on the delivery of ecosystem services from habitats that are invaded by groups of weeds, rather than on single weed species.

Methods

Selection of species

Our study focussed on four groups of invasive alien plant species (Table 1) that invade particular ecosystems, where they create a suite of similar problems. Groups were based on the premise that if one such species were to be removed from the ecosystem concerned (for example by means of effective integrated control), one of the others may simply replace it, with no benefit being gained from the control effort. By using a group approach, questions about the relative contribution of biological control to the alleviation of problems can be addressed more holistically.

Costs of biological control research

Biological control research was initiated in South Africa in 1913, but was most actively pursued from the 1970s onwards. We identified all of the biological control agents that had been investigated for each of the target weed species in each group of weeds (Table 2). We interviewed researchers in all of the major institutes that had conducted research into biological control to establish the time period, number of researchers, and project running costs and salaries associated with each biological control agent (whether or not that agent species was eventually released). The research was mainly conducted at the South African Agricultural Research Council's Plant Protection Research Institute, but also included work at two universities (Cape Town and Rhodes). From this information, we were able to reconstruct the approximate annual research costs related to exploration, to research on safety-screening and other pre-release preliminaries in the laboratory, and as appropriate, to the costs of actual releases, redistribution, monitoring and impact-evaluation of the individual biological control agents in the field. These costs were then inflated to 2008 values, using annual inflation rates. The costs excluded those associated with a unique implementation programme, introduced in 2002, in which certain biological control agents were mass-reared at four facilities, and released in the field (Zimmermann et al. 2004).

Value of ecosystem services

Data on the magnitude of ecosystems services, and the current estimated reductions in the magnitude of these services due to invasive alien plants (van Wilgen et al. 2008) were used as a basis for estimating the value of biological control. These data were provided for five major terrestrial biomes in South Africa: fynbos (mediterranean shrublands); grassland; savanna and thicket; Nama karoo (arid shrublands); and succulent karoo. For each biome, we used the estimates of annual flows of benefits for three major ecosystem services as a basis for estimating monetary values. The services were the provision of water (quantified as mean annual runoff); the provision of grazing for livestock (quantified as livestock stocking rates); and biodiversity (a biodiversity intactness index, see Scholes and Biggs (2005).

We used an estimate of the unit price of water in both in its serviced (64% of total use) and un-serviced (34% of total use) forms, which is sold at 0.143 and 5.395 South African rands (ZAR) per m³ respectively (De Lange and Kleynhans 2008). The volume-based weighted average of ZAR 1.89 per m³ was used to estimate the value of water provision by ecosystems.

We used a weighted average price for livestock in South Africa as a basis for quantifying the impact of invasions on livestock numbers in monetary terms. This amounted to ZAR 2471 per large stock unit (Statistics South Africa 2004).

The unit pricing of biodiversity was based on numerous studies that have attempted to place a monetary value on the ecosystem services derived from biodiversity, including the harvesting of natural products as well as non-use values (Hassan 2003; Higgins et al. 1997; Shackleton and Shackleton 2004; Turpie et al. 2003; Turpie 2003); see Turpie (2004) for a review. We assumed a proportional relationship between biodiversity intactness and the magnitude of ecosystem services. We deducted the value of water and grazing (as these were already accounted for) and then reduced the value of the remaining combined services in each of the major terrestrial biomes separately, using the estimate of the impact of alien plant invasions on the biodiversity intactness in the biome concerned. This yielded values of ZAR 1021, 386, 110, 33 and 33 per ha for fynbos shrublands, savanna and thicket, grassland, succulent karoo and Nama karoo respectively.

Impacts of invasive alien plant groups on ecosystem services

As the invasive alien plants groups occurred in more than one biome, we used spatial cover data from Le Maitre et al. (2000) to determine the proportion of the cover of each group that was found in each biome. The loss of ecosystem services due to invasion by each group was expressed in monetary terms using the above unit prices, and the relative cover of the group in the biome concerned. The estimated reduction in the value of ecosystem services was in direct proportion to the relative cover of each of the invasive alien plant groups in each biome. The invasive succulent and subtropical shrub groups do not have any noticeable impact on water resources (van Wilgen et al. 2008), so the impact of these groups on water resources was taken to be zero.

Contribution of biological control to reducing impacts on ecosystem services

Three estimates of the value of ecosystem services were available at the start of this study (Fig). These were (i) the value that could be expected from ecosystems that were unaffected by alien plants; (ii) the current values, which reflect the extent of invasion as well as the contribution of past control efforts; and (iii) the future value when invasive alien plants occupy all of the available suitable habitat (van Wilgen et al. 2008). To estimate the contribution of biological control to the overall control of alien plants, and therefore to the protection of ecosystem services, estimates for two key variables were still required.

The first key variable was the relative proportion of the prevention of loss of services attributable to biological control relative to other forms of control (the ratio B:C in Fig. 1). We used expert opinion to estimate this proportion. We conducted one-on-one two-hour discussions with recognised experts for each of the alien plant groups. Following that, we held broader discussions with larger workshops, typically with five or more experts who had in excess of 100 years of combined experience in biological control research and practice in South Africa.

The second key variable was the proportion of land that would have remained uninvaded had invasive alien plants not been subjected to any form of control (D + E in Fig. 1).

To derive an-approximation of this proportion, we relied on historical records (Richardson et al. 1997) that suggest that invasive plant spread began in 1700 in the fynbos, and in 1850 in the karoo, grassland and savanna biomes (fynbos has a much longer history of alien plant introductions), and that the weeds would achieve their maximum densities and land 'occupation' by about 2150. The time from the start of the spread of the invasive plants to the present (2009) was expressed as a percentage of the time between the start of spread and 2150, assuming that the alien plant species expanded at a linear rate until they occupied all suitable habitats in given area. The total possible level of ecosystem services at risk from invasion (A + B + C + D) was multiplied by this percentage to estimate the value of D + E (Fig. 1).

Benefit:cost estimation and sensitivity analyses

We estimated a benefit:cost ratio (the value of ecosystem services protected compared to the cost of biological control research) for each group of weeds. Net present values for ecosystem services were estimates from future annual benefit flows, discounted at 8% over 140 years. As the potential errors in the estimates of both of the above-mentioned key variables could be large, we performed sensitivity analyses with respect to the effect of these estimates on our findings. We first reduced our estimate of the value of ecosystem services protected by all forms of historic control to a much lower values (ranging from 85 down to 25% of the estimated value). For each of these values, we then calculated the ratio of the proportion of the control attributable to biological control as compared to. other forms of control that would have delivered a benefit: cost ratio of 1:1.

Results

Costs of biological control research

The total cost of biological control research on the four invasive alien plant groups amounted to ZAR 102 million, expressed in 2008 values (Table 3). The cost for individual groups covered an approximate five-fold range, from ZAR 10 million for fire-adapted trees to ZAR 50 million for subtropical shrubs.

Value of ecosystem services

The estimated potential annual value of ecosystem services from extant un-transformed ecosystems amounted to ZAR152 billion (Table 4). Most of this value (63%) was derived from water, while grazing and biodiversity contributed 22 and 15%, respectively. Of the total value, ZAR6.5 billion was estimated as having been lost due to current levels of alien plant infestation, and ZAR41.7 billion was estimated to have been saved by the complete range of control efforts.

Contribution of alien plant groups to impacts in biomes

The relative impacts of the various groups of invasive alien plants varied between the different biomes (Table 5). Fire-adapted trees (pines and hakeas) contributed 20% of the relative impact in fynbos ecosystems, and relatively little elsewhere. Invasive Australian trees dominated in all ecosystems except savanna and thicket, contributing between 78 and 96% of the impact. Savanna ecosystems suffered impacts from all groups of plants.

Biological control was estimated to have resulted in substantial levels of protection for these ecosystem services (Table 6). The annual value of services from ecosystems that would have been invaded by invasive Australian trees amounted to ZAR 8.3 billion, with savings of ZAR 2.6 billion and ZAR 1.1 billion arising from the protection of water and grazing resources in grasslands, and ZAR 1.5 billion from the protection of biodiversity in the fynbos. The biological control of invasive succulents was also estimated to have protected services that deliver a value of ZAR 2.9 billion, mostly in the savanna and thicket biomes.

Contribution of biological control to protecting ecosystem services

Experts estimated that biological control had contributed 5% to the overall control of fire-adapted trees. In the case of *Hakea* shrubs, mechanical control had a large impact on reducing the extent of invasions, and biological control prevented re-colonisation (Esler et al. 2009). No biological control is currently available for *Pinus* trees, which re-invade cleared areas, and may even be occupying areas cleared of *Hakea*. There is however, a time-lag between mechanical clearing and re-infestation during which an increase in ecosystem service delivery is realised, resulting in a small degree of protection for ecosystem services.

The biological control of invasive Australian trees is aimed at reducing seed output which will slow or stop further spread. Past control has relied to some degree on mechanical clearing, and this effort has varied between the biomes. The expert group therefore allocated separate percentages to biomes. They agreed on values of 70, 28, 24, 24 and 30% for the contribution of biological control to the protection of ecosystems services derived from the fynbos, grassland, succulent karoo, Nama karoo and savanna and thicket biomes respectively.

Invasive succulents posed a significant threat to rangelands before biological control was introduced. For example, the area invaded by *Opuntia aurantiaca* could have been 15 times greater had it not been for biological control (Zimmermann et al. 2004), and *Opuntia ficus-indica* had invaded over 1 million hectares the early 20th century, but is now under sustained (> 60 years), satisfactory control (the cactus now infests <10% of the area originally colonized (Annecke and Moran, 1978; Moran and Zimmermann 1991). Also, among several other cactus species, *Opuntia stricta* var. *stricta* (Hoffmann et al. 1999) and *Cereus jamacura* (Klein, 1991) were brought under substantial control after the introduction of biological control. The expert group agreed that biological control had contributed 75% to the overall control of this group.

Biological control within the subtropical shrub group has been less successful. Both *Chromolaena odorata* and *Caesalpinia decapetala* remain invasive despite the release of agents. The level of biological control against *Lantana camara* has been highly variable (depending on the agents(s) used, the area invaded, and the considerable varietal differences of *L. camara* itself, Baars and Naser 1991) but overall has been rated as substantial (Zimmermann et al. 2004), so that the need for additional control measures has been significantly reduced. However, because *Ch. odorata* and *Ca. decapetala*-and perhaps other invasive species have the potential to replace *Lantana*, it was agreed that the proportion of benefit attributable to biological control should be estimated at only 5% for the group as a whole.

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control. The expert group agreed that biological control had contributed 75% to the overall control of this group.

Biological control within the subtropical shrub group has been less successful. Both *Chromolaena odorata* and *Caesalpinia decapetala* remain invasive despite the release of agents. The control success against *Lantana camara* has been rated as substantial (Zimmermann et al. 2004), so that the need for additional control measures has been significantly reduced. However, given that the first two weed species remain invasive and may even replace *Lantana*, it was agreed that the proportion of benefit attributable to biological control should be 5% for the group as a whole.

Cost:benefit estimation and sensitivity analyses

The estimated net present value of protected benefits attributable to biological control, using the above proportions, ranged from ZAR 840 million in the case of fire-adapted trees to ZAR 104 billion in the case of invasive Australian trees (Table 7). The benefit:cost ratios associated with the four groups were all positive, and ranged from 50:1 in the case of subtropical shrubs to 3726:1 in the case of invasive Australian trees (Table 7).

Sensitivity analyses revealed that benefit:cost ratios would remain positive even if the estimates of the two key variables were substantially reduced (Fig. 2). For example, the estimate of the proportion of benefit attributable to biological control could be reduced by between 98 and 99% without the benefit:cost ratios becoming negative. If the approximation of the area that would have been invaded had there been no control in the past (the second key variable) was also reduced (by up to 75%), benefit:cost ratios remained positive and remained so even when the first key variable was reduced by between 85 and 99%, depending on the group of weeds.

Discussion

Biome-scale impacts of invasive alien plants

Most previous studies of the economic value of weed biological control have focussed on a single invasive alien plant species, but in this paper we have studied groupings of invasive alien plant species. The main problem with single-species approaches is that they do not address the problem of substitution, where an alien species that is brought under control can, and often is, replaced by another alien species that can have similar impacts. Attempts to estimate the combined value of weed biological control by aggregating the benefits of single-species control programs can lead to double-counting (eg. Page and Lacey 2006), and this will compromise the integrity of the estimates. Our study has attempted to overcome this approach by grouping species that have similar impacts and can replace each other in the landscape. In our examples, a degree of success has been achieved with *Hakea* and *Lantana* shrubs in fynbos and savanna ecosystems respectively. However, it is likely that *Pinus* species will replace *Hakea* species in fynbos, and *Chromolaena odorata* will replace *Lantana camara* in savannas. For this reason, the contribution of biological control to the protection of ecosystem services in these biomes was estimated as being very small (5%). The full economic potential of biological control can only be realised if the entire suite of similar invasive alien plants is brought under control. This highlights the need for further research to identify additional biological control agents for the full suite of alien plants that invade particular ecosystems.

Estimating the value of biological control of invasive alien plants

The evaluation, in monetary terms, of the benefits of biological control is necessary, *inter alia*, for deciding on appropriate levels of funding to support research. The input data for this paper were derived from a study that quantified non-monetary benefits (van Wilgen et al. 2008). While that study was useful, the analysis presented here makes it possible to compare input costs with benefits, and can be used to demonstrate the return on investment offered by biological control. Our finding that biological control has brought about a substantial level of protection of ecosystem services is subject to potential errors in the estimation of two key variables, but the errors in our estimates would have to have been extremely large to reach a different conclusion. The approach proposed here has exposed the need for more accurate estimates of the effectiveness of different forms of control, as well as the plausible rates of spread. If these data become available, which is highly unlikely, they will considerably increase the levels of confidence in the results reported here. Otherwise, it would seem that these are the best estimates that are achievable at present, and that the main conclusions drawn from them are, in broad principle, if not in detail, unambiguous and compelling.

Risks and benefits associated with biological control of invasive alien plants

The use of biological control to address the problems of invasive species is controversial. On the one hand it can and has conferred significant benefits, but on the other it is seen by many as too risky to consider as a serious part of integrated control measures. Published opinions on these matters often appear in the scientific literature (for example Moran et al. 2005; Simberloff and Stiling 1996; Louda and Stiling 2003) further promoting the perception of large risks. At best, this leads to excessively stringent requirements for the introduction of biocontrol agents, and at worst to the total avoidance of the use of biological control as an option (McFadyen 2004; Sheppard et al. 2006).

The arguments for the use of biological control include that it is cost effective and very safe compared with the expense and risks associated with herbicide development and deployment; that biological control can be successfully integrated with other management practices; and, most compelling of all, that biological control is self-sustaining (Moran et al. 2005). The arguments against biological control maintain that the outcomes of an introduction cannot be predicted precisely enough *a priori* to know with any certainty that the benefits will outweigh the environmental costs. Proponents of this view often point to examples of unintended consequences, such as impacts on non-target species, and the disruption of food webs, in support of their views.

In an increasingly risk-averse world, the problem that arises is that, more and more, a precautionary approach is taken, and biological control agents are not released, or in some cases not even considered as a possible option for control (see McFadyen 2004; Sheppard et al. 2006). However, avoiding biological control and relying on mechanical and chemical methods alone, is both expensive and unsustainable

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Table 1 Groups of invasive alien plant species in South Africa, and ecosystems impacted upon by each group

Invasive alien plant species group	Genera of invasive plants	Principal ecosystems impacted	Other ecosystems impacted
Fire-adapted trees	<i>Pinus</i> <i>Hakea</i>	Fynbos shrublands	Savanna and grasslands
Perennial invasive Australian trees	<i>Acacia</i> <i>Leptospermum</i> <i>Paraserianthes</i>	Fynbos shrublands Grassland Savanna	Riparian zones in all biomes
Invasive succulents (cacti)	<i>Opuntia</i> <i>Cereus</i> <i>Harrisia</i>	Karoo arid shrublands Grassland Savanna	None
Subtropical shrubs	<i>Lantana</i> <i>Chromolaena</i> <i>Caesalpinia</i>	Savanna Grassland	None

Table 2 Numbers of weed species in selected groups, and associated biological control agents studied in South Africa between 1913 and 2008

Genus	Number of weed species investigated	Number of biological control agent species investigated	Number of biological control agent species released	Release dates
<i>Pinus</i>	1	1	0	-
<i>Hakea</i>	2	6	6	1970 – 2006
<i>Acacia</i>	8	10	10	1986 – 2004
<i>Paraserianthes</i>	1	1	1	1989
<i>Leptospermum</i>	1	2	2	1994 – 1996
<i>Opuntia</i>	11	10	10	1913 – 1985
<i>Cereus</i>	1	2	2	1990
<i>Harrisia</i>	1	2	2	1983 – 1990
<i>Lantana</i>	1	21	21	1961 – 2002
<i>Chromolaena</i>	1	3	3	1990 – 2001
<i>Caesalpinia</i>	1	2	1	1999
Totals	34	77	68	1913 - 2006

Table 3 Net present (2008) value of the cost of biological control research for five groups of invasive alien plants (see Table 1 for alien plant groups; ZAR = South African rands)

Invasive alien plant species group	Estimated costs (ZAR)
Fire-adapted trees	10 320 124
Perennial invasive Australian trees	27 941 017
Invasive succulents (cacti)	13 626 030
Subtropical shrubs	50 563 394
Total	102 450 565

Table 4 The estimated annual value of ecosystem services (million ZAR; ZAR = South African rands) derived from five terrestrial ecosystems in South Africa under a scenario of no invasion, at current levels of infestation with invasive alien plants, and estimates of the value saved due to invasive alien plant control efforts in the past

Ecosystem service	Biome	Pristine un-invaded ecosystems	Current levels of infestation	Protected by historic control efforts
Water	Fynbos	12 832	10 814	1 230
	Grassland	50 486	48 896	11 909
	Succulent Karoo	694	508	42
	Nama karoo	5 243	4 971	569
	Savanna and thicket	27 137	25 401	6 049
	Total	96 393	90 592	19 801
Grazing	Fynbos	1 194	992	348
	Grassland	13 155	13 103	R 5 089
	Succulent Karoo	1 233	1 222	243
	Nama karoo	8 112	8 112	3 197
	Savanna and thicket	10 030	9 959	3 778
	Total	33 726	33 389	12 656
Biodiversity	Fynbos	5 320	5 101	2 579
	Grassland	2 745	2 706	1 071
	Succulent Karoo	239	237	124
	Nama karoo	1 063	1 051	608
	Savanna and thicket	12 782	12 626	4 847
	Total	22 151	21 723	9 232
All ecosystem services		152 271	145 705	41 690

Table 5 The relative importance (%) of four groups of invasive alien plants in five terrestrial biomes in South Africa. Fig.s are based on spatial distribution data from Le Maitre et al. (2000)

Biome	Fire- adapted trees	Invasive Australian trees	Invasive succulents	Subtropical shrubs
Fynbos	20.3	79.5	0.1	0
Grassland	0.8	77.6	2.6	18.9
Succulent Karoo	4.8	94.4	0.8	0
Nama karoo	0	95.6	4.4	0
Savanna and thicket	2.3	21.6	42.2	34.0

Table 6 The value of annual flow of benefits (ZARm; ZAR = South African rands) attributable to the biological control of four groups of invasive alien plants in five biomes in South Africa

Ecosystem service	Biome	Invasive alien plant group			
		Fire-adapted trees	Invasive Australian trees	Invasive succulents	Subtropical shrubs
Water	Fynbos	12.50	683.12	0	0
	Grassland	4.89	2602.65	0	0
	Succulent Karoo	0.10	9.79	0	0
	Nama karoo	0	132.38	0	0
	Savanna and thicket	6.82	395.93	0	0
	Total	24.32	3823.86	0	0
Grazing	Fynbos	3.54	193.57	0.33	0.01
	Grassland	2.09	1112.35	99.59	48.16
	Succulent Karoo	0.58	55.79	1.37	0
	Nama karoo	0	743.19	104.72	0
	Savanna and thicket	4.26	247.25	1194.48	64.23
	Total	10.48	2325.13	1400.49	112.39
Biodiversity	Fynbos	26.21	1432.47	2.47	0.01
	Grassland	0.44	234.12	20.96	10.14
	Succulent Karoo	0.30	28.62	0.70	0
	Nama karoo	0	141.47	19.93	0
	Savanna and thicket	5.47	317.52	1532.68	82.41
	Total	32.42	2153.92	1576.75	92.56
Total		67.22	8329.91	2977.23	204.95

Table 7 Estimated net present values (ZAR millions; ZAR = South African rands) of ecosystem service benefits attributable to biological control of four groups of invasive alien plants in five terrestrial biomes in South Africa. Benefit:cost ratios compare the net present value (at 8% discount rate) of benefits to the net present value of the costs of biological control

Biome	Fire-adapted trees	Invasive Australian trees	Invasive succulents	Subtropical shrubs
Fynbos	528	28 863	35	< 1
Grassland	93	49 363	1506	729
Succulent Karoo	12	1177	26	0
Nama karoo	0	12 713	1558	0
Savanna and thicket	207	12 005	34 089	1833
Total	840	104 122	37 215	2562
Benefit:cost ratio	81:1	3726:1	2731:1	50:1

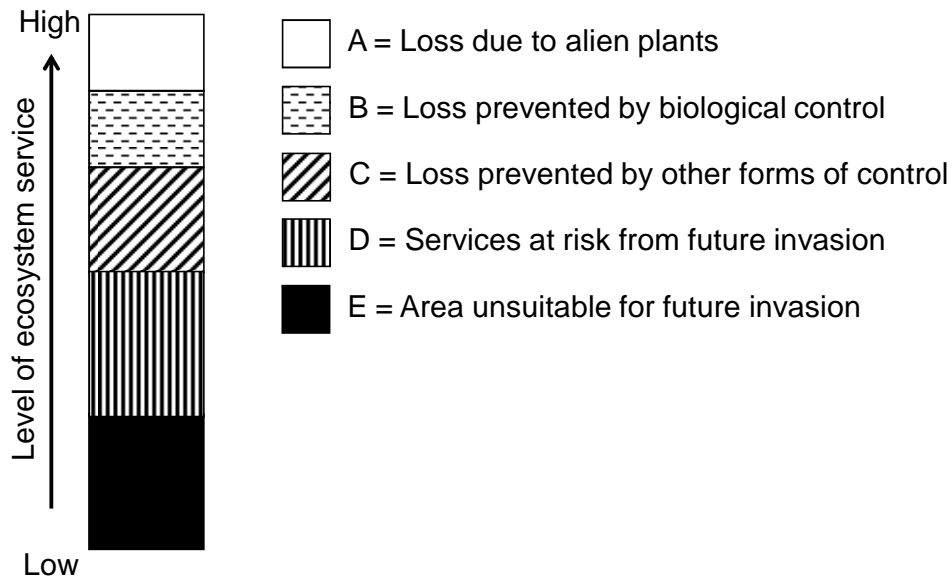


Fig 1. Apportioning of ecosystem services according to the impact of invading alien plants and their control. Estimates of services from an ecosystem unaffected by alien plants ($A + B + C + D + E$), and for services from an ecosystem affected by alien plants and control operations ($B + C + D + E$) were available, and A was obtained by subtraction. The proportion unsuitable for future invasion (E) was also known. Estimates for the proportion that would have been affected by alien plants had no control taken place ($D + E$), and the proportion of prevention of loss of services attributable to biological control and other forms of control (the ratio $B:C$) were key variables that required quantification (see text).

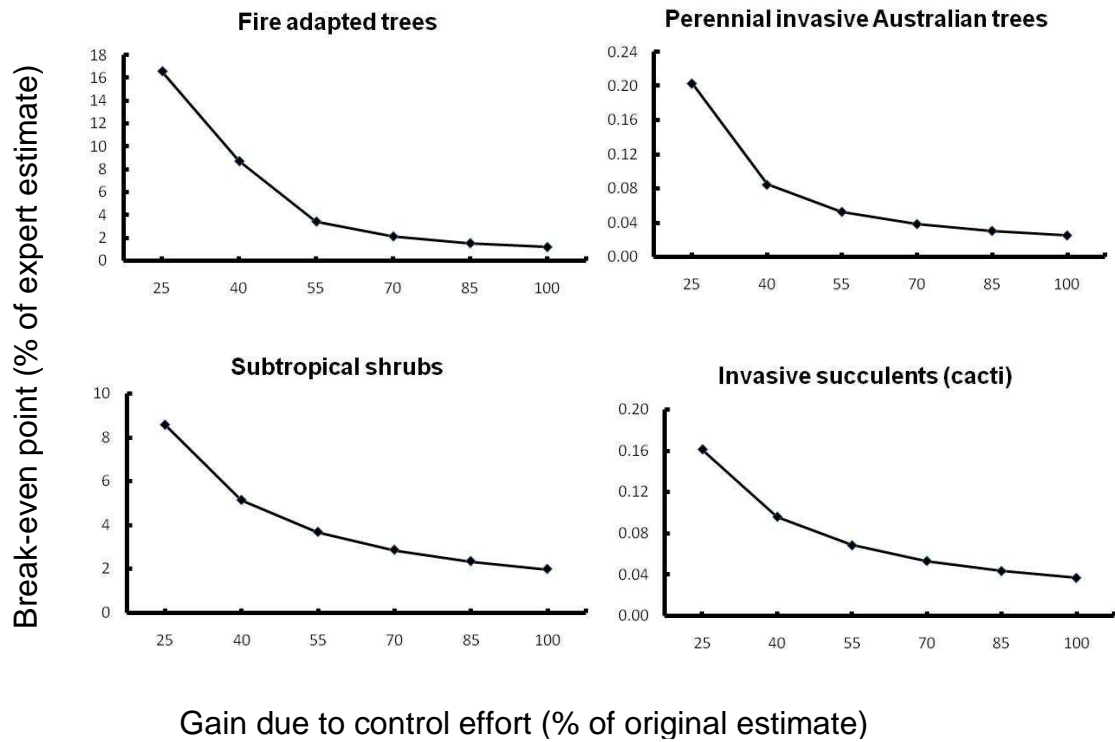


Fig. 2. Break-even points of the proportion of control attributable to biological control (expressed as a % of an expert estimate) for a range of gains in the value of ecosystems services due to overall control effort (gains are expressed as % of the base estimate made in this study).