CHAPTER 12

Biological invasions in the Cape Floristic Region: history, current patterns, impacts, and management challenges

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12.1 Introduction

The Cape Floristic Region (CFR) is the most invaded terrestrial area in South Africa in terms of: the conspicuous prominence of (mainly woody) invasive plants (Fig 12.1, Plate 12) (Henderson 2007); the area invaded as surveyed (Kotzé et al. 2010); and the numbers of animal invaders (Picker and Griffiths 2011). At the same time its status as a globally important system for the study of plant invasions is firmly established. Tree invasions in the region provide model systems that have been influential in the development of plant invasion ecology; in particular work on pine species (Richardson et al. 1994) and Australian acacias (Richardson et al. 2011). In fact, the observation of alien trees invading pristine fynbos shows that widespread invasions are not, as suggested by Charles Elton, confined to ecosystems markedly altered by human activities (Elton 1958). This provided part of the stimulus for a major international programme on invasions in the 1980s funded by the Scientific Committee on Problems of the Environment.

So what makes the CFR so highly invaded? For particular plant species in particular systems in the CFR, the answers have largely been determined. The CFR is highly invaded because the natural fire regime creates opportunities for the establishment and proliferation of a suite of woody plants which were introduced and disseminated in huge numbers, providing abundant propagules to launch invasions, and which now occupy a previously empty niche (a tree life form). A range of related traits are associated with invasive success in fynbos, including appropriate seed dispersal mechanisms, the ability to survive or reproduce after fire (persistence is key), and adaptations for survival and proliferation in nutrient-poor soils. Widespread invasions are attributable to interactions between traits (invasiveness), the recipient environment (invasibility), and the processes by which humans have dispersed propagules (introduction dynamics). As such, mechanistic explanations provide tests and examples for understanding fundamental processes in fire ecology, plant–insect interaction, and physiology (Chapters 3, 10, 11).

The CFR has also provided important lessons for invasive species management, in particular the need to incorporate people's perception of invasive species and how interventions need to accommodate particular socio-economic realities. In this respect, probably the biggest development in the CFR (and in South Africa as a whole) has been the establishment of the Working for Water Programme (WfW) in 1995. By focussing on controlling invasive alien plants through job creation, WfW addressed two major issues facing South Africa: unemployment and invasive plants. The resources available for the on-the-ground management of invasions through WfW increased dramatically. R855 million has been spent by WfW in the past 18 years in the Fynbos Biome for clearing invasive trees and shrubs. The publicity and focus on invasion as a public cost was made forcibly and consistently,

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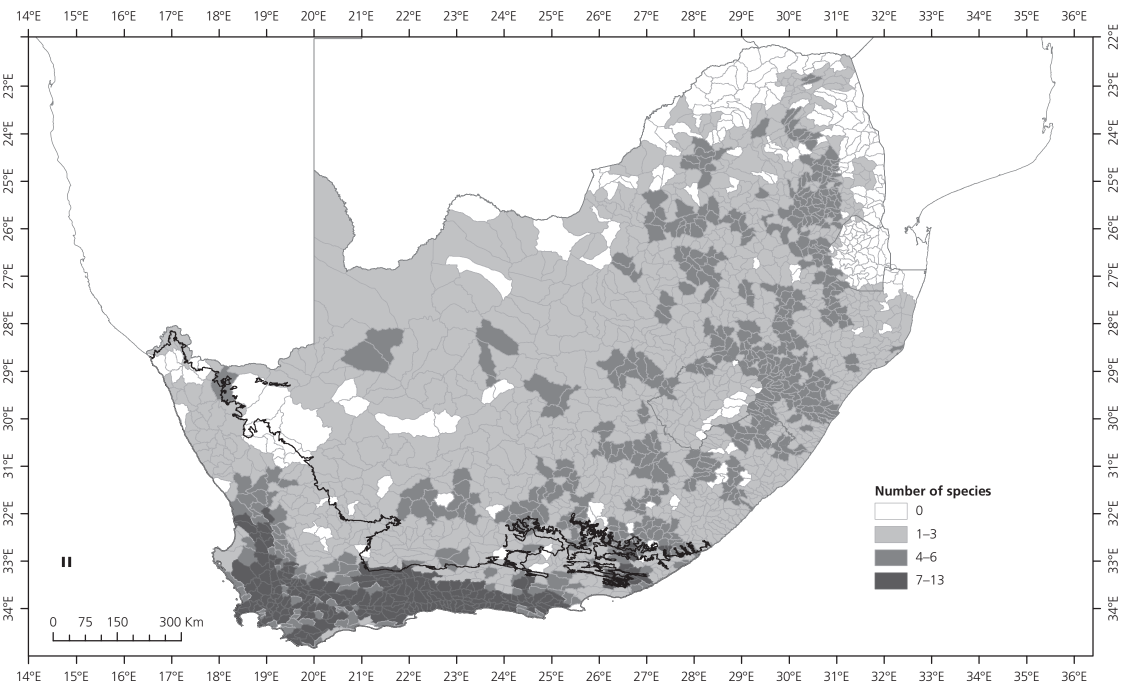


Figure 12.1 The CFR catchments are the most invaded in the country in terms of the species richness of major ecosystem transformers that affect water resources (van Wilgen et al. 2007). The number of species recorded per catchment is shown for thirteen species (*Acacia mearnsii*; *Arundo donax*; *Eucalyptus camaldulensis*; *Hakea sericea*; *Hakea gibbosa; Nerium oleander*; *Pinus patula*; *Pinus pinaster*, *Pinus radiata*; *Populus canescens*; *Prosopis glandulosa*; *Salix babylonica*; *Tamarix chinensis*.)

radically changing public perceptions as to the scale and impact of this as an ecological and economic issue that required urgent intervention (van Wilgen, Khan, et al. 2011). Without this concerted effort, the problems of biological invasions in the region would undoubtedly be much worse.

Funding leveraged through WfW has also been crucial in maintaining the region as a world-leading location for research and implementation of classical biological control of invasive plants. The importation of biological control agents to control invasive plants has recently celebrated its centenary in South Africa, and agents continue to be identified, assessed, and released, making major contributions to control efforts (Klein 2011). The continuity of funding for biological control is the envy of many other countries.

Our knowledge of biological invasions has been strongly influenced by ongoing developments in the South African research environment. In 2004, the South African Department of Science and Technology and the National Research Foundation funded a Centre of Excellence for Invasion Biology with its headquarters in Stellenbosch (http://academic.sun.ac.za/cib/). The centre has served as a catalyst for regular international meetings on all issues of biological invasions in the region, as well as enhancing funding opportunities for both established researchers and their graduate students within this research field.

There are, however, ongoing conflicts of interest (Box 12.1). In the absence of a clear legal framework (regulations governing all invasive species have not yet come into effect as of June 2014), diverse perceptions of the undoubted economic and social value of some alien species (such as shade and timber trees, and angling fish) have been pitted against the severe ecological impacts of invaders. Management is becoming more strategic, however, with more focussed interventions for both plants and animals (Box 12.2). In some cases this involves dramatically increasing the resources spent on specific interventions (Wilson et al. 2013), while in others it is about understanding when interventions will be ineffective. In the latter case, land or river management sometimes needs to focus on getting the best out of novel landscapes (Box 12.3).

12.2 Aims and scope

This chapter provides a background to the history, current status, and possible futures of introduced and invasive plant and animals in the CFR, and details how their impacts and management have changed through time. In line with the observation that the real advances have been made through integrating research and action, we also aim to provide insights for future management.

The geographical scope is the CFR as a whole (see Chapter 1), but coverage for different parts of the CFR differs depending on the availability of data and the particular issues under consideration. Plant invasions are the most studied and iconic, but we also consider the numerous animal invasions in the region, many of which have had major ecological impacts. Arguably, some of the biggest challenges in the future will come from fungi, bacteria, and other microorganisms, but with the difficulties inherent in working on such taxa, there is unfortunately still little to discuss.

Our focus includes terrestrial and freshwater systems but excludes marine invasions, which are subject to different vectors and distribution mechanisms, have different impacts and biogeographic breaks, and have been recently reviewed by Mead et al. (2011). The focus is also on natural and semi-natural ecosystems; we have not provided a detailed analysis of those invasions confined to agricultural or urban landscapes, or of those species introduced as biological control agents for agricultural pests. We have confined our analyses to invasions using the definitions and categories outlined by Blackburn et al. (2011), but see Box 12.4 for an overview of some of the key issues surrounding intra-specific invasions. Experiences and comparison with other mediterranean-type ecosystems (MTEs) are elaborated on in Box 12.5.

12.3 History of introductions

The diversity and abundance of invasive species within the CFR arises, in part, because of a rich history of introductions that accompanied Cape Town's status as one of the most important harbours in the world during the eighteenth and nineteenth centuries.

12.3.1 Plants

Palaeontological records show that hunter-gatherers made extensive use of indigenous plants, but there is no evidence that they introduced any species (Chapter 8, Deacon 1986, 1991). The first large-scale introductions of species (both plants and animals) to the CFR were probably by Khoi pastoralists who arrived in the region about 2000 BP. Early records of crop plant introductions include those of *Medicago polymorpha* (burclover) from 1190 BP and *Ricinus communis* (castor oil) from 1150 BP (Deacon 1986; Macdonald and Richardson 1986; Richardson et al. 1992, 2003). However, there is no evidence that these pre-European introductions had any major ecological impacts.

Invasions essentially began with the establishment of a settlement at Cape Town in 1652 by the Dutch. Early introductions were dominated by woody species for timber (1652 onwards) and dune stabilization (1830 onwards), followed by accidental introductions of crop weeds (1652 onwards), and forage plants (1750 onwards). These were followed in the late nineteenth and twentieth centuries by introductions of many ornamental species (Richardson et al. 2003).

For a range of biological and sociological reasons, most of the invasive species in the CFR come from the southern temperate regions, specifically Australia (Henderson 2006, 2007). First, South Africa and Australia share similar climates and many Australian taxa are well adapted to fire-dominated ecosystems. Second, Cape Town was, until the Suez Canal opened in the late nineteenth century, one of the main stopovers in the sea route between Australia and Europe. Third, both countries had substantial populations of British settlers and so maintained strong cultural, scientific, and, in some cases, familial links.

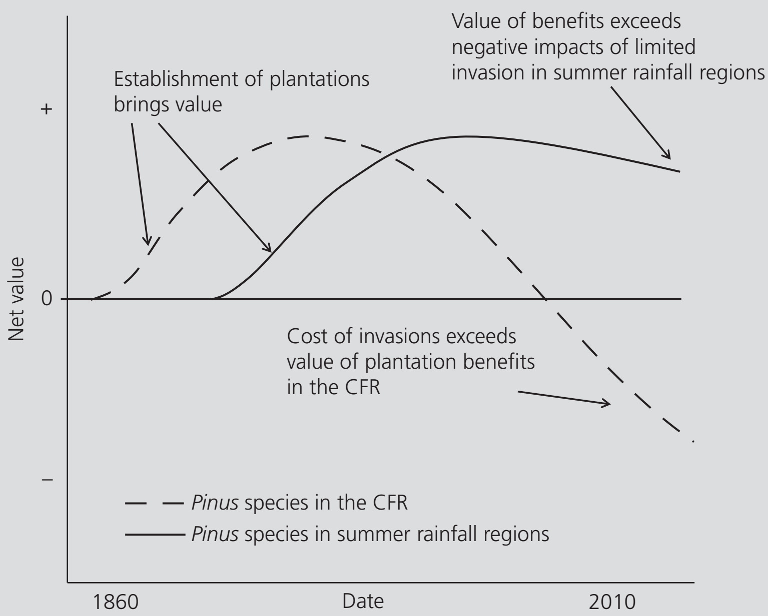
It is anticipated that new plant species will continue to be introduced from around the world, but deliberate introductions now require permitting, and with an increasing appreciation of the consequences of invasions (Box 12.2), the number of new invasive species legally introduced for most purposes should decline. However, strong commercial incentives in some sectors, such as forestry and the emerging biofuels industry, could well override concerns relating to the potential invasiveness of new introductions (Richardson and Blanchard 2011). Given the wide range of alien species already recorded (many of them known either to be invasive elsewhere or to possess traits associated with invasiveness), it is likely that the next cohort of major invaders is already present in the region but have yet to spread significantly into natural habitats (i.e. there is an 'invasion debt' (Wilson et al. 2013)). Moreover, while most plant species that have become invasive in the CFR are also invasive elsewhere in the world, there are a few notable exceptions (e.g. *Acacia stricta* and *Melaleuca parvistaminea* (Wilson et al. 2013)). These species provide unique challenges for management because information on impact, spread, and control is not available from elsewhere.

Box 12.1 Conflicts over introduced trees: amenity, forestry, and invasions

Many landscapes support introduced tree populations that simultaneously deliver benefits and have negative impacts. The management of such ecosystems for the sustainable delivery of benefits requires trade-offs to be made between different ecosystem services. For example, the establishment of forestry plantations increases the production of timber but decreases streamflow, grazing for livestock, and other biodiversity-related benefits. Normally, the trade-off would be straightforward in that the benefits could be easily estimated and weighed against the costs for the area converted from one form of land use to another. When the introduced species is also invasive, however, the trade-off becomes more difficult to assess. Such species may not be containable and the dynamics of invasion into adjacent areas and the nature and magnitude of the impacts of such invasions may be unpredictable.

A good example of this problem is provided by pine trees (*Pinus* spp.). Pines are important forestry trees in South Africa but spread rapidly in the CFR (van Wilgen and Richardson 2012). About 6% of South Africa's forest plantations are within the CFR, and 87% of this area is planted to pines. There has not been a comprehensive economic assessment of the costs and benefits of these trees. However, roundwood sales in the fynbos region directly generated R146 million in 2009, and the forest industry is undoubtedly an important employer in rural areas. De Lange and van Wilgen (2010) estimated that the loss of ecosystem services (mainly water) attributable to 'fire-adapted trees' (mainly pines) in the Fynbos Biome was R495 million annually at current levels of infestation. These impacts will increase as invasive pines spread and become denser, leading to water shortages that will constrain development, and lead to severe degradation and loss of unique Fynbos Biome biodiversity. In addition, recurring damage from the ever-escalating frequency of fires (Chapter 3) is currently placing additional burdens on the forestry industry. The evidence suggests that a phasing out of pine-based forestry in the region could deliver the most beneficial outcome, but this is understandably controversial. A more thorough economic assessment of the problem is clearly needed to inform policy in this regard.

The example of pines indicates that the initial benefits arising from the introduction of alien trees often generates an overall loss situation once the associated invasions reach a certain threshold area (Box 12.1 Fig 1). However, by the time this situation comes about, there is a heavy dependence on the planted trees as a resource, and consequently there can be considerable resistance to any attempts to contain or remove the trees (van Wilgen 2012), including resistance to the introduction of classical biological control agents.



Box 12.1 Figure 1 Conceptual illustration showing changing values associated with the trajectory for alien *Pinus* spp. in summer rainfall areas (solid line) and winter rainfall areas (dashed line), based on the scheme by van Wilgen, Dyer, et al. (2011). The hypothetical historic trajectory of net value (sum of benefits minus sum of impacts) is shown over time (adapted from van Wilgen and Richardson (2014)).

12.3.2 Animals

The earliest European settlers also deliberately introduced domestic livestock and household pets and inadvertently imported various pests (e.g. rats and mice) and parasites (both of humans and livestock). During the later colonial era other terrestrial vertebrate species, such as fallow deer, grey squirrels, and a variety of European birds, were deliberately introduced for ornamental purposes, to make the Cape appear more like 'home' to the settlers. There have been no deliberate vertebrate introductions since 1970, although extralimital translocations remain a serious concern (Box 12.4). In contrast, invertebrate introductions were initially almost entirely accidental hitchhikers, either on crop plants or in soil. Only in the last century have deliberate terrestrial invertebrate introductions become commonplace (e.g. biological control agents introduced to stem the spread of alien plants (Klein 2011)). The pattern in aquatic systems is quite distinct, with most alien fish having been deliberately introduced to South Africa (Marr 2012). Some of these species were directly released into the environment for sport, forage, or as pest control agents, while others were kept in captivity (e.g. ornamental species) but subsequently escaped or were released.

For the 108 faunal species for which reliable information exists regarding their date of introduction to the CFR, the number of new introductions was low for the period 1700–1880, after which there was a sharp increase (Fig 12.2), with the numbers of invertebrates increasingly slightly later than the numbers of vertebrates (Picker and Griffiths 2011).

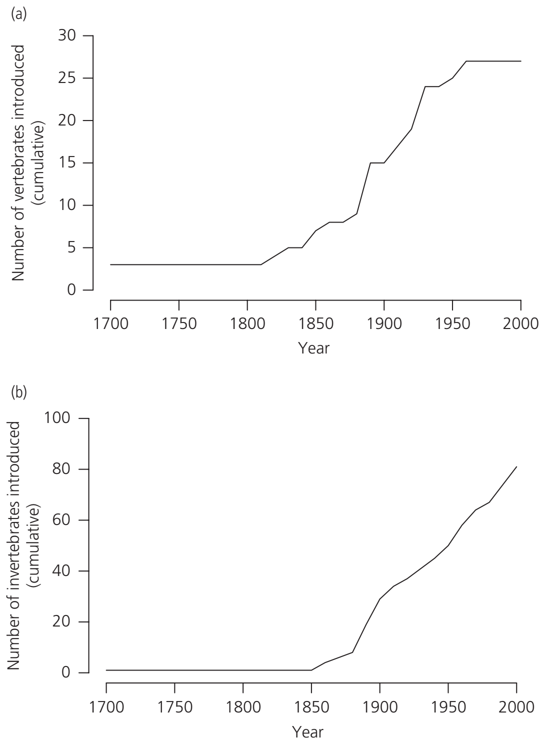


Figure 12.2 Timeline of (a) vertebrate, and (b) invertebrate animal introductions to the region (Picker and Griffiths 2011). Vertebrates tend to have been introduced (or at least recorded) earlier, however, while there have been few new vertebrate introductions recently, the number of invertebrates introduced is climbing rapidly

12.4 Current invasion loads

So what is the current scale of invasions in the region? There is no comprehensive list of introduced species (though see Glen 2002 for cultivated plants), and the status of many introduced species cannot confidently be assigned to an invasion stage according to the Blackburn classification scheme (2011; Table 12.1). However, there are several lists of naturalized and invasive plants, most notably the Southern African Plant Invaders Atlas (Henderson 2001), but only one comprehensive list of animal invaders (Picker and Griffiths 2011).

Importantly, taxa differ in the extent to which they invade untransformed areas. While many invasive plants occur in both transformed and untransformed areas (see Spear et al. 2011 for lists of species in national parks in the CFR), most terrestrial animal introductions are restricted to areas of human habitation or agriculture (e.g. rats, mice, cockroaches, agricultural pests, and pests of stored crops). The majority of freshwater invasions, on the other hand, occur widely in both natural and artificial habitats (i.e. dams and impoundments). Introduced fish were often deliberately released into untransformed locations for sport or food.

The separation between invasive species of transformed areas and those invading natural area is clearly important for management, but the mechanistic reasons limiting distributions are not always clear. For example, while Spanish broom (*Spartium junceum*) is a major invader in other MTEs and is a common roadside invader in the CFR, it has not invaded natural fynbos vegetation. In contrast, Montpellier broom (*Genista monspessulana*) another serious invader of MTEs, has readily invaded natural vegetation despite being found at relatively few sites (Geerts et al. 2013).

Table 12.1 Naturalized alien species per taxon (status according to Blackburn et al. (2011)*). For all species except those known as widespread invaders there is insufficient information available to accurately classify them, and as such classifications are likely to underestimate the invasion stage. Extralimitals are not included (see Box 12.4). The detailed list is available at http://academic.sun.ac.za/cib/supplementary/wilson001.xlsx.

Taxon	Number of species and status	Key ref.
Actinopterygii (fishes)	14 (D2 = 5; E = 9)	4,7
Amphibia (amphibians)	1 (B3)	8
Arachnida (spiders and mites)	16 (11 agricultural/urban) (C3 = 4; D1 = 3; D2 = 6; E = 3)	4
Aves (birds)	8 (B3 = 1; C3 = 1; D2 = 2,4 = E)	4,7
Chilopoda (centipedes)	3 (D1 = 2; D2 = 1)	4
Clitallata (earthworms)	23 (B3 = 4; C3 = 8; D2 = 10; E = 1)	5
Diplopoda (millipedes)	3 (C3 = 1; D2 = 2)	4
Entognatha (springtails)	13 (D2 = 13)	4,7
Gastropoda (snails & slugs)	34 (C1 = 3; C3 = 12; D1 = 8; D2 = 6; E = 5)	2,4
Insecta (insects)	87 (C3 = 4; D2 = 24; E = 59)	4
Malacostraca (woodlice)	5 (C3 = 2; D2 = 3)	4,7
Mammalia (mammals)	15 (B3 = 3; C3 = 5; D2 = 3; E = 4)	4,7
Plantae (plants)	516 (B3 = 167; C3 = 253; D1 = 23; D2 = 30; E = 43)	1, 3, 6, 7
Reptilia (reptiles)	2 (D2 = 2)	8
Secementea (nematodes)	2 (D1 = 1; D2 = 1)	4

[1] Adamson and Salter 1950.
[2] Herbert 2010.
[3] Moll and Scott 1981.
[4] Picker and Griffiths 2011.
[5] Plisko 2010.
[6] Southern African Plant Invaders Atlas; accessed April 2012.
[7] Spear et al. 2011.
[8] van Rensburg et al. 2011.
* B1,individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place); B2, individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them but explicit measures to prevent dispersal are limited at best); B3, individuals transported beyond limits of native range, and directly released into novel environment; C0, individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced but incapable of surviving for a significant period; C1, individuals released into the wild in location where introduced, no reproduction; C2, individuals released into the wild in location where introduced, reproduction occurring, but population not self-sustaining; C3, individuals released into the wild in location where introduced, reproduction occurring, and population self-sustaining; D1, self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction; D2, self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction; E, fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extents of occurrence.

12.4.1 Plant invasions

While the CFR is invaded by a range of different types of plant, species composition and relative importance of growth forms of invaders differs between vegetation types (Table 12.2, Richardson et al. 1997). Tree and shrub species comprise about 40–50% of the species in all the groups, but trees account for a greater proportion records in the Fynbos Biome (~60%) than in the Succulent Karoo Biome (30%). The upland and lowland fynbos have many more invasive herb species than renosterveld, whereas renosterveld and succulent karoo have more invasive succulents, with proportionately more records for the latter in succulent karoo (22%). Invasive graminoids are more common in lowland than in upland fynbos, while few graminoids reach high densities in renosterveld (Le Maitre unpublished data). The densities of invasive trees are high in succulent karoo, but only in riparian areas.

Further, an estimated 25% of the CFR has been transformed by agriculture and urbanization, with certain vegetation types extensively transformed and/or fragmented, particularly the renosterveld (Table 12.3). About half (54%) of the total area of the CFR, largely remote and mountainous regions, is neither transformed nor invaded by plants. An estimated 21% of the untransformed area has been invaded by introduced plants (Fig 12.3, Le Maitre et al. 2000), with strandveld, alluvial vegetation, and wetlands particularly affected (Table 12.3).

Little information is available to quantify how the extent of invasions has changed over time. However, there is evidence that active management combined with biological control has decreased the extent and density of some invasive plants (van Wilgen, Forsyth, et al. 2012). For example, mechanical clearing of hakea has reduced the density and extent of many infestations, while biological control agents have reduced reproductive output, thereby limiting the rate with which cleared sites have been recolonized and new areas invaded (Esler et al. 2010). However, these successes need to be put into the context of dramatic increases in the distribution of other species, particularly pines. In the eastern Fynbos Biome, the cover of invasive pine species more than doubled from 13 to 29% between 1986 and 2007 (Moeller 2010).

Table 12.2 Numbers of invasive alien species and records (a measure of abundance) of different growth forms in subtypes of the Fynbos biome (upland fynbos, lowland fynbos, renosterveld) and Succulent Karoo, based on records from the Southern African Plant Invaders Atlas (SAPIA) database. Only records with a location accurate to 5 × 5 minutes or less were used.

Biome	Fynbos			Succulent Karoo
Sub-type	Lowland Fynbos	Upland Fynbos	Renosterveld	
Number of species				
Aquatic	7	8	5	1
Creeper	11	17	23	2
Graminoid	9	8	2	7
Herb	49	63	5	12
Scrambler	7	7	3	0
Shrub	38	39	10	9
Succulent	75	13	21	11
Tree	55	67	40	18
Number of records				
Aquatic	85	60	38	1
Creeper	46	55	5	8
Graminoid	82	102	95	51
Herb	210	250	61	69
Scrambler	33	64	4	0
Shrub	160	327	137	55
Succulent	15	71	42	83
Tree	970	1711	438	117

Table 12.3 Area invaded by plants in different vegetation bioregions in the CFR according to the National Invasive Alien Plant Survey (Kotzé et al. 2010; see also 12.4). The categories of vegetation are taken from Mucina and Rutherford (2006), and the level of transformed area from the National Land-Cover Database 2000 (CSIR and ARC 2005).

Bioregion	Area (ha)	Transformed area (% of total area)	Untransformed area invaded by alien plants (% of total area)	Untransformed area not invaded by alien plants (% of total area)
Albany Thicket	1 196 000	7	40	53
Alluvial Vegetation	96 000	52	25	23
East Coast Renosterveld	852 000	69	3	28
Eastern Fynbos–Renosterveld	1 716 000	17	37	46
Eastern Strandveld	40 000	14	43	43
Estuarine Vegetation	14 000	41	19	40
Freshwater Wetlands	7 000	23	37	40
Inland Saline Vegetation	108 000	34	4	62
Karoo Renosterveld	30 000	9	1	90
Knersvlakte	112 000	23	1	76
Namaqualand Hardeveld	11 000	0	1	99
Namaqualand Sandveld	906 000	5	10	85
Northwest Fynbos	1 474 000	20	19	61
Rainshadow Valley Karoo	566 000	7	1	92
Seashore Vegetation	29 000	16	5	79
South Coast Fynbos	304 000	19	45	36
South Strandveld	84 000	23	37	40
Southern Fynbos	338 000	17	14	69
Southwest Fynbos	1 111 000	34	33	34
West Coast Renosterveld	603 000	88	1	11
West Strandveld	234 000	46	32	22
Western Fynbos–Renosterveld	1 031 000	6	6	88
Zonal & Intrazonal Forests	97 000	13	39	49
Total	**10 959 000**	**25**	**21**	**54**

12.4.2 Animal invasions

In their review of alien and invasive animals in South Africa, Picker and Griffiths (2011) listed 571 species in South Africa (452 terrestrial, 79 marine, and 40 freshwater), of which half (287) of those with adequate distributional data occur in the CFR. This is a large number given that the CFR represents only 4% of South Africa's surface area. The majority are terrestrial, with only 8% occurring in freshwater systems, mostly fish. However, alien freshwater fish have been introduced into all but a few minor river catchments (Marr et al. 2012).

The listing of alien invertebrates is certainly incomplete, as the taxonomy of many invertebrate taxa remains insufficient for alien species to be recognized. Moreover, within the better-known groups, additional introductions are continually being discovered (Herbert 2010). Most alien animals present in the CFR are invasive elsewhere. In fact 45% are invasive on all other continents except Antarctica, but very few (3%) have invaded Africa alone (Picker and Griffiths 2011).

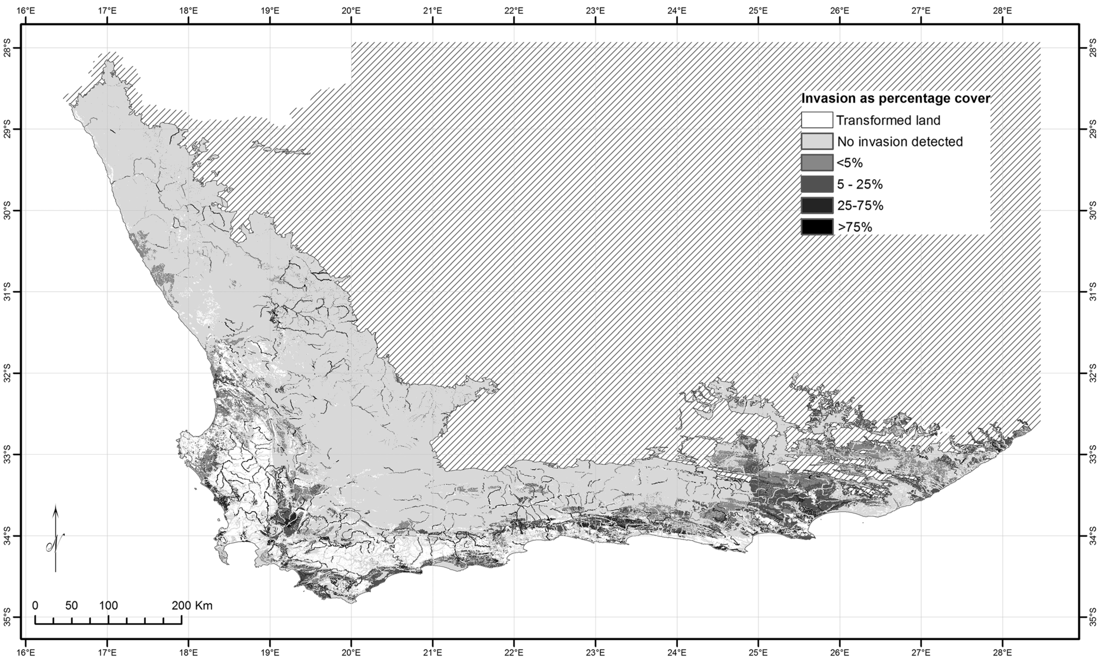


Figure 12.3 The extent of alien plant invasions in the CFR as determined by the National Invasive Alien Plant Survey (Kotzé et al. 2010). The choice of classes for the different levels of invasion are as per Le Maitre et al. (2000). In many of the drier areas, invasions are largely confined to linear strips along rivers or river floodplains. Invasions on land considered transformed (National Land-Cover Database 2000 (CSIR and ARC 2005)) are not considered.

12.5 Impacts

12.5.1 Impacts from plant invasions

Plant invasions alter species and community diversity as well as ecosystem processes in the CFR. This alters the generation and delivery of ecosystem services both directly (e.g. pollination, food, and fibre production), and indirectly, by altering biotic controls of ecosystem processes (e.g. primary production, nutrient cycling, and water fluxes). A few studies have quantified the economic consequences of these impacts on fynbos, but only one has done so for succulent karoo (Table 12.4). The economic impacts in the CFR as a whole are likely to be millions of rands annually.

Tree invaders have the greatest impacts on community composition and water resources in the CFR (Gaertner et al. 2009 ; Le Maitre et al. 2000), with the severity of impacts increasing with the degree and duration of the conversion from shrub vegetation to woodland or forest. Given the lack of competitors, if nothing is done, plant invasions will continue to expand until they occupy all available natural lands. Here we discuss four cases: acacia invasions in fynbos, pine invasions in fynbos, *Prosopis* invasion in succulent karoo, and grass invasions in renosterveld.

Increasing dominance by Australian acacias alters native community composition, structure, and biomass (van Wilgen and Richardson 1985), changing soil nutrient pools and cycling (Yelenik et al. 2004), suppressing native vegetation, and depleting native soil seed banks (Holmes et al. 2000; Le Maitre, Gaertner, et al. 2011). Long-standing acacia invasions result in degradation beyond structural and functional thresholds, complicating restoration (Le Maitre, Gaertner, et al. 2011). In many cases, such ecosystems have changed to such a degree that they are in an alternative stable state (i.e. a novel ecosystem sensu Hobbs et al. 2006; Box 12.3).

Pines, in contrast, change community composition and structure by eventually replacing species but do not establish feedback loops through changes to nutrient cycling. As invasion intensifies, pines change abiotic conditions (e.g. they have a much higher biomass than fynbos and use more water, shade out native vegetation, and can cause higher intensity fires). Restoration after pine invasion is still feasible but requires the reintroduction of key functional native species (Gaertner et al. 2012).

Distinguishing different degrees of ecosystem degradation can guide decisions on whether restoration is feasible and affordable, and, if so, how it should be approached (Richardson and Gaertner 2013). However, identifying the degree of ecosystem degradation resulting from invasion is a major challenge for researchers and managers. Recently the concepts of resilience and novel ecosystems have been applied, elucidating invasion dynamics and identifying practical management strategies (Gaertner et al. 2012; Richardson and Gaertner 2013).

Species of the genus *Prosopis* have major effects on ecosystem functioning in arid ecosystems (Le Maitre et al. 2007) and they have thus been identified as priorities for control. The trees tend to invade low-lying areas where ground water is close to the surface and hence, most accessible. *Prosopis* invasions can lead to changes in vegetation structure and alteration of the spatial distribution of nutrients in the landscape (Schlesinger et al. 1990). Dense stands of *Prosopis* can access groundwater and under certain conditions, significantly increase water extraction rates (Wise et al. 2012). This could depress groundwater levels and aridify soils, complicating restoration efforts.

Grass invasions in renosterveld hamper the return of native vegetation to abandoned fields. Even decades after they have been abandoned, the ability of indigenous vegetation to re-recolonize these areas seems to be limited by competition mainly from invasive alien grasses, even where these fields are in close proximity to natural vegetation (Iponga et al. 2005; Krug and Krug 2007). Invasive grasses are favoured by nutrient enrichment from adjacent agricultural lands (Milton 2004; Krug and Krug 2007), overgrazing, and frequent burning (van Rooyen 2004).

Table 12.4 Impacts of alien plants on ecosystem services and the potential benefits of control operations. Values prior to 2011 taken from Le Maitre, de Lange, et al. (2011) and converted back to Rand, using an exchange rate appropriate at the time (R7 = US$1).

Impact	Effects on services and cost	Source
Reduced mean annual runoff	up to 87 M m^3/yr of water, 34% of Cape Town's water resource; R1.2 million/yr at R0.014/m^3, R164.4 million/yr at R1.89/m^3 for 5 quaternary catchments	Le Maitre et al. 1996; de Lange and van Wilgen 2010
Reduced mean annual runoff	clearing could yield water at 14% of the cost of delivery from a new dam [sub-quaternary]	van Wilgen et al. 1996
Loss of value of land	clearing could increase the purchase value of catchment land 16 fold [hypothetical area]	Higgins et al. 1997
Reduced mean annual runoff	clearing could yield cost–benefit ratios of 1:6 to 1:12 [Kromme, Kouga, Baviaanskloof river systems]	Hosking and du Preez 1999
Various costs of invasion in fynbos	losses of harvestable products of R16.1–67.9/ha (e.g. flowers), R7.0–58.1/ha for recreation, and R9787/ha for water [biome]	Turpie and Heydenrych 2000
Reduction in mean annual runoff (current)	Fynbos: 1064 M m^3/yr, R 2010 million at R1.89/m^3 [biome] Succulent Karoo: 98 Mm^3/yr, R186 million [biome]	van Wilgen et al. 2008; de Lange and van Wilgen 2010
Reduction in groundwater recharge (current)	Fynbos: 4.4 M m^3/yr, R8 million [biome] Succulent Karoo: 0.2 M m^3/yr, R0.4 million [biome]	van Wilgen et al. 2008; de Lange and van Wilgen 2010
Reduction in large stock units (grazing)	Fynbos: 74 000 large stock units, R203 million at R2471/large stock unit [biome] Succulent Karoo: 40 000 large stock units, R10 million [biome]	van Wilgen et al. 2008; de Lange and van Wilgen 2010
Biodiversity intactness (excluding land transformation & degradation)	Fynbos: 3% (of Biodiversity Intactness Index) R219 million at R1021/ha [biome] Succulent Karoo: <0.1%, R2 million at R33/ha [biome]	van Wilgen et al. 2008; de Lange and van Wilgen 2010

12.5.2 Impacts from animal invasions

Most non-insect invertebrate species introduced to terrestrial ecosystems are confined to urban environments or agricultural landscapes. Some of these are significant economic pests of stored products and crop plants, or are biological control agents, but they have little impact on natural systems. While there is little evidence that the species that do occur in natural landscapes (e.g. earthworms, woodlice, and millipedes) have major impacts (Picker and Griffiths 2011), they have been poorly studied to date.

A list of invasive alien animals ranked on the severity of known impacts in the CFR would be dominated by fish. Invasions by the common carp (*Cyprinus carpio*) cause turbidity, biodiversity loss, and competition; whereas smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), rainbow trout (*Onchorhynchus mykiss*), and brown trout (*Salmo trutta*) all change community dynamics through predation (Marr 2012). The negative ecological impact of introduced fish on indigenous fish of the CFR was first recognized soon after the introduction of North American bass (*Micropterus* spp.) in the late 1930s, but fish continued to be stocked throughout the CFR until the 1980s (Coke 1988). The initial impact of introduced fishes was poorly recorded, because the indigenous fish were not considered to be of any value. There is, however, a strong correlation between the presence of predatory introduced fish and the absence of indigenous taxa (Marr et al. 2012). Alien fish affect the behaviour and composition of indigenous fish assemblages in the CFR (Impson 2007), as well as affecting lower trophic levels, including aquatic invertebrates and algae (Lowe et al. 2008). The 2007 IUCN assessment lists 23 of the CFR's 24 endemic primary freshwater fish taxa as threatened by alien fish (Tweddle et al. 2009). Therefore, the remaining indigenous fish populations can only be conserved, and their ranges increased, through the elimination of introduced species from rivers identified as conservation priorities (Impson 2007).

The impacts of other invasive vertebrates include mallard ducks possibly hybridizing with native congeners (nine species in southern Africa, including the yellow-billed duck (*Anas undulata*), the African black duck (*Anas sparsa*), and the Cape shoveler (*Anas smithii*); see Box 12.4 for other examples); Indian house crows raiding nests and eating fledglings and eggs of indigenous birds; and feral pigs degrading ecosystems through rooting, trampling, and consumption of plants, animals, and soil organisms, particularly in renosterveld.

The impacts of invasive invertebrates in the CFR have been poorly studied to date, but given experiences in other countries, several species are likely to be having important effects. Invasions by Argentine ants (*Linepithema humile*) disrupt food webs through predation and competition, altering native ant assemblages and leading to the collapse of mutualisms, such as the burial and protection of large proteaceous seeds (Chapter 10, Bond and Slingsby 1984; Christian 2001; Lach 2007). They also reduce seed set in *Protea* species by excluding native pollinators from inflorescences (Lach 2007). German wasps (*Vespula germanica*) sting people, damage agricultural crops (e.g. grapes) and, as voracious predators, likely influence invertebrate communities (Kenis et al. 2009; Veldtman et al. 2012). The harlequin ladybird (*Harmonia axyridis*) is a recent invasion (Stals and Prinsloo 2007), but in other parts of this predator's introduced range it has severely impacted other coccinellids causing substantial negative cascade effects in ecosystem (Kenis et al. 2009). The varroa mite (*Varroa destructor*) has caused massive economic impacts on the honey industry and pollination of crops and native plants worldwide, but local bees (in particular the Cape honey-bee (*Apis mellifera capensis*)) appear to have developed some natural resistance in the absence of the application of any varroacide, suggesting South Africa will be less impacted (Allsopp 2006). These four invertebrate species tend to nest or aggregate in areas where there is human activity, and it remains to be seen whether, in time, they will become widespread invaders in pristine vegetation. However, one of the most abundant introduced invertebrates in the CFR, the dune or white garden snail (*Theba pisana*) can reach densities of hundreds per square metre in natural coastal habitats (Odendaal et al. 2008). While its ecological impacts remain unstudied, there can be little doubt that such intense and selective grazing pressure must impact competitive interactions amongst plant species, overall plant biomass, and as a major protein resource, the dynamics of their predators (e.g. mice and birds). These interactions are in urgent need of further investigation.

12.6 Historical and current management and policy responses

12.6.1 Responses to plant invasions

The threat invasive alien plants pose to fynbos ecosystems was already recognized by Peter MacOwan in 1888 and in 1908 Rudolf Marloth raised concerns that alien plants would replace natural vegetation (Stirton 1978). A landmark publication in 1945 stated that 'one of the greatest, if not the greatest, threats to which the Cape vegetation is exposed, is suppression through the spread of vigorous exotic plant species' (Wicht 1945). Nonetheless, attempts at control were largely ineffective until the 1970s (Macdonald et al. 1989), when two separate initiatives arose to address the problem: co-ordinated mechanical clearing operations on mountain catchment land, managed by the Department of Forestry (Fenn 1980); and a resurgence in the acquisition of biological control agents.

The Department of Forestry's ambitious campaign aimed to control infestations from the mountain areas between Cape Town and Port Elizabeth using a fell-and-burn approach over a period of 15 yr (Fenn 1980). The clearing programme was integrated with a policy of prescribed burning on a 12 yr cycle (Bands 1977) and was closely adhered to during the late 1970s. However, the impetus was lost in the 1980s as a result of declining funding and seasonal restrictions on the use of prescribed burning (van Wilgen et al. 1997).

Large-scale mechanical clearing operations were resumed in 1995 under the auspices of WfW, which combined the need to protect ecosystem services (especially water resources) through controlling invasive alien plants with the opportunities to create employment for impoverished people in rural areas (van Wilgen, Khan, et al. 2011). A recent assessment (van Wilgen, Forsyth, et al. 2012) revealed that the combined effects of mechanical clearing and biological control have reduced the extent of some (e.g. Australian acacias and hakea species) but not all (e.g. pine species in mountains, and *Eucalyptus camaldulensis* along lowland rivers) of the major invasive plant species (summarized in Table 12.5; see also Fig 12.4). Gains made in the control of hakea species are being offset by invasion by pine species, which are equally successful invaders of the same areas. Invasion by pine species continues to pose the most significant threat to the integrity of fynbos ecosystems, in particular in rugged and inaccessible mountain areas, where control is costly (Box 12.1).

Another assessment, at a finer scale (McConnachie et al. 2012), found that at the prevailing rates of clearing it would take between 54 and 695 years to clear the catchments of the Krom and Kouga Rivers, assuming no further spread. The study concluded that invasive alien plant control projects must make fundamental changes to their approach in order to progress (cf. Fig 12.4).

The use of biological control agents to control plants specifically invading the fynbos region began in the 1960s, when insects were introduced to first combat *Hypericum perforatum* (which was largely an agricultural weed) and then *Hakea sericea* (a much larger threat to natural vegetation). The programme was later expanded to include several other alien plant species, with substantial funding from WfW (Zimmermann et al. 2004). To date, two terrestrial species are under complete control (i.e. no other management interventions are required to restrict impacts to acceptable levels), and eight under a substantial degree of control (Table 12.5). For other invasive species research into new biological control agents remains ongoing, in particular,

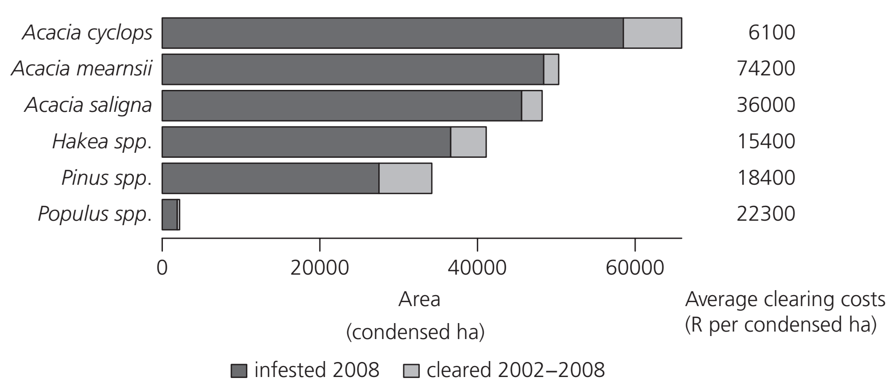


Figure 12.4 Infestation size and area manually cleared by WfW teams for five major invaders in the Fynbos Biome as of 2008. Clearing data are from WfW Information Management System (WIMS) records, accessed June 2012, and infested area from the work by Kotzé et al. (2010). Clearing costs (in rand (R) per condensed ha) were converted to 2008 values using the consumer price index. Note that the cleared area count may reflect the same area cleared twice (initial clearing and follow up) and that cleared area could have been reinvaded. Consequently the rather minor impact of mechanical clearing shown here could actually be smaller.

Table 12.5 Current status and trends for some of the historically major plant invaders in the Cape Floristic Region.

Plant species	Date of introduction	Declaration as a weed[1]	Prominence value[2]	Trend[3]	Resources spent on physical control[4]	Degree of biological control achieved[5]
Acacia cyclops	1845	R028 of 2001, C2	48 400 ha (2008 condensed area)	reducing	R45.3M (WfW 1995–2008)	substantial
Acacia longifolia	1827	R028 of 2001, C1	no longer of major concern	reducing		substantial
Acacia mearnsii	1858	R028 of 2001, C2	Major riparian invader; 27 500 ha (condensed area)	increasing slightly	R141M (WfW 1995–2008)	not determined, but recently released agents look promising
Acacia melanoxylon	1848	R028 of 2001, C2				substantial
Acacia pycnantha	1892	R028 of 2001, C1		no major increase		substantial
Acacia saligna	1848	R028 of 2001, C2	major monocultural stands ~45 600 ha (condensed area)	decreasing	R93.7M (WfW 1995–2008)	substantial
Ageratina adenophera						negligible
Cylindropuntia imbricata	unknown but early	Proclamation 161/1938				
Cylindropuntia fulgida	<1900	Proclamation 171/1940				
Eucalyptus camaldulensis				increasing	negligible	
Hakea drupacea	1830s	Proclamation 161/1938				
Hakea gibbosa	1830s	Proclamation 161/1938	36 600 ha (condensed area all *Hakea* spp.)		R69.3M all *Hakea* spp. (WfW 1995–2008)	negligible
Hakea sericea	1830s	Proclamation 161/1938		decreasing		substantial
Hypericum perforatum	1942	Proclamation 62/1948	few scattered infestations in largely disturbed areas	not recorded	negligible	complete
Lantana camara	1858	Proclamation 37/1954				negligible to substantial
Leptospermum laevigatum	1850	R028 of 2001, C1				negligible
Nasella trichotoma	Boer War fodder	Proclamation 260/1976				
Nerium oleander	1811	R028 of 2001, C1				
Nicotiana glauca	Late 1800s	R028 of 2001, C1				
Opuntia aurantiaca	<1856	Proclamation 171/1940				

continued

Table 12.5 *Continued*

Plant species	Date of introduction	Declaration as a weed[1]	Prominence value[2]	Trend[3]	Resources spent on physical control[4]	Degree of biological control achieved[5]
Opuntia ficus-indica	late 1600s	Proclamation 161/1938		low levels	negligible	substantial
Paraserianthes lophantha	1835	R028 of 2001, C1				substantial
Pinus pinaster	1680	R028 of 2001, C2	58 500 ha (condensed area for all *Pinus* spp.)	increasing rapidly	R123.3M all *Pinus* spp. (WfW 1995–2008)	none (release being considered at the time of writing)
Populus species			1 900 ha	stable if reducing	R6.7M (WfW 1995–2008)	
Prosopis glandulosa	1900	R028 of 2001, C2				
Sesbania punicea	<1900	R028 of 2001, C1		small cyclical outbreaks controlled by biocontrol agents	negligible	complete
Solanum mauritianum						negligible
Aquatics						
Eichhornia crassipes	1884	Proclamation 170/1937 under Weeds Act No 42 of 1937				substantial in South Africa as a whole, though less in the CFR
Myriophyllum aquaticum	1921	Proclamation 252/1956				substantial
Salvinia molesta	unknown	Proclamation 252/1956				complete

[1] Declaration as a weed is as per the Conservation of Agricultural Resources Act No 42 of 1983, revised in 2001. C1 = Category 1, C2 = Category 2 (as per definition in section 'Responses to plant invasions').
[2] Area from van Wilgen, Forsyth, et al. (2012) and Kotzé et al. (2010).
[3] Trend is the overall trend in relative value of invasions over last 10 years.
[4] Clearing costs are expressed as 2008-equivalent Rand.
[5] Biological control agents released for the control of important invasive alien plant species in the CFR (Klein 2011). The degree of biological control is as follows: none, no biological control agents have been released; complete, no other control measures are needed to reduce the weed to acceptable levels; substantial, other methods are needed to reduce the weed to acceptable levels, but less effort is required; negligible, despite damage, control of the weed remains entirely reliant on the implementation of other control measures.

for pine species, but there is substantial resistance to the introduction of pine biocontrol agents from the forestry industry (Hoffmann et al. 2011; Moran and Hoffmann 2012). In contrast to other countries (Louda et al. 2003), no substantial non-target effects have been recorded in South Africa, and substantial governmental and self-regulatory procedures are in place to keep it that way.

South Africa's legislation with regard to the management of invasive alien plants was strengthened in parallel with the implementation of WfW. The Conservation of Agricultural Resources Act was broadened in 2001 to include three categories of invasive alien plants. Category 1 weeds are invasive species that must be controlled or eradicated where possible. Category 2 invaders have commercial importance and may be grown by permit in demarcated areas, and their products can be traded, provided that steps are taken to prevent spread. Category 3 invaders have ornamental value and are allowed by permit to remain in demarcated areas, but further trade and plantings are prohibited, and steps must be taken to prevent spread. However, implementation of the act has been limited to isolated instances, and it remains to be shown whether it has succeeded in curbing the spread of invasive species.

One of the biggest changes in the region has been around how people perceive invasive species (Carruthers et al. 2011). For example, alien plants were introduced in the nineteenth century in response to the perception that mobile dunes needed stabilizing. However, such stabilization led to beach erosion. In the past decades there has been a shift in policy. Aliens have been removed and shifting dunes restored (Lubke 1985). Similarly, the potential need for post-control restoration is becoming increasingly appreciated and acted upon (Box 12.3).

Box 12.2 The invasive alien species strategy for the Greater CFR and other initiatives

In response to alien plant invasions reaching crisis proportions in the CFR, the Cape Action for People and the Environment (C.A.P.E.) commissioned the development of a comprehensive invasive alien strategy with funding from the Global Environmental Facility and the World Bank. Following an extensive series of stakeholder workshops under the aegis of the C.A.P.E. Invasive Alien Species Task Team, the resulting strategy was published in 2009 (C.A.P.E. 2009). The vision outlined was that by 2020 the negative impacts of invasive alien species on the economic, ecological, and social assets of the Greater CFR will have been significantly reduced; in the future no indigenous species will be driven to extinction by invasive alien species; and sustainable programmes will be in place to minimize any future impacts. Specifically the strategy aimed to

a) ensure invasive alien species are managed within appropriate policy and legislative frameworks, legal mandates are assigned and/or delegated, incentives and disincentives are in place to encourage compliance, and conflicts are minimized;
b) improve collaboration and harmonization between all role players through strategic planning and prioritization at appropriate scales;
c) enable a better understanding of the impacts of invasive species through awareness-raising and education, optimize the implementation of the strategy through appropriate institutional arrangements, adequate capacity, and technical expertise;
d) prevent new introductions, and detect and eradicate species before they establish and become widespread;
e) ensure the integration of control measures; and
f) promote adaptive management informed by research, monitor progress, and evaluate efficacy of control methods.

Several research projects were undertaken and tools developed to give effect to the strategy, such as the development of a spatial decision support tool for prioritization and scheduling of invasive alien plant interventions (Roura-Pascual et al. 2009) and the prioritization of species and primary catchments for the purposes of guiding the invasive plant operations in the terrestrial biomes of South Africa (van Wilgen et al. 2007).

But does this strategy represent a better approach to management than the 'strategy of hope' that characterizes most control operations (van Wilgen, Dyer, et al. 2011)? Although the strategy provides the framework for reducing the impacts posed by invasive alien species, without buy-in at the highest level to implement the strategy and a functional co-ordination body, the situation will not be turned around. The key lies in the co-ordination of management practices between the relevant role players, clear time-based targets, and application of the available tools (van Wilgen, Forsyth, et al. 2012).

There have, however, been some successes already. The development of a nursery partnership programme between the South African Nursery Association and the Department

continued

Box 12.2 *Continued*

of Environmental Affairs' National Resource Management Programme enabled key players to collaborate and regulate the industry to prevent the importation of listed or potentially invasive plant species.

An early detection and rapid response unit has been established within the City of Cape Town with support from the South African National Biodiversity Institute's Invasive Species Programme (through funding from the Department of Environmental Affairs' National Resource Management Programme; Wilson et al. 2013). Having an early detection and rapid response programme in a major centre such as Cape Town provides the necessary impetus to garner public support, follow up on new sightings, and ensure that pressing problems are dealt with as soon as they are identified.

Another ongoing initiative is the C.A.P.E. Invasive Animal Working Group. This improves information sharing, co-operation and synergy amongst stakeholders, provides strategic direction, and sets priorities for invasive animal management in the Greater CFR. Through this working group much-needed funding was obtained to control priority invasive animals (e.g. the Rondegat fish eradication project; Weyl et al. 2013). Programmes are in place for controlling mallards (*Anas platyrhynchos*), feral pigs (*Sus scrofa*), Indian house crows (*Corvus splendens*), and the guttural toad (*Amietophrynus gutturalis*) which, although indigenous to other parts of South Africa, is not native to Cape Town and poses a threat to the endemic western leopard toad (*Amietophrynus pantherinus*).

12.6.2 Responses to animal invasions

In comparison to other MTEs, the control of animals in the CFR is less developed and extensive. A small population of house crows (*Corvus splendens*) established in the vicinity of Cape Town harbour in the late 1990s. Unfortunately control measures were not immediately introduced, resulting in a rapid population increase to approximately 10 000 birds in 2008. Since 2009, around 9 000 birds had been removed, but around 2 000 remain currently, and control aimed at eradication is ongoing. A pair of tahrs (*Hemitragus jemlahicus*) that escaped from an encampment on Devil's Peak founded a population on Table Mountain, with their numbers peaking at ~600 in the mid-1970s. South African National Parks instituted a controversial culling programme, ending in 2005. However, a very small residual population still persists there. A feral pig control programme started in 2011 in the West Coast mainly in the Riebeeck Kasteel area. Around 500 pigs have been either shot or trapped since the start of the programme. Finally, a programme is ongoing to eradicate the guttural toad (*Amietophrynus gutturalis*) from the City of Cape Town, though control operations are complicated by the urban setting of the invasion.

The only documented successful eradication programme (of any taxon) in South Africa was against the white-lipped milk snail (*Otala punctata*; Wilson et al. 2013) which was discovered in a small suburban area near Cape Town and in the Cape Town docks in 1986. Both populations were eliminated by 1989 using a combination of baiting with molluscicide, hand picking, and spraying with herbicide (Herbert and Sirgel 2001). Less intensive control efforts were employed in an attempt to eradicate the vermiculate snail (*Eobania vermiculata*) from Port Elizabeth. These efforts failed, resulting in the species becoming an established pest in the area. With greater administrative support and better communication of the needs of control (Box 12.2), there is reason to be optimistic that the management of animal invasions will improve in future.

One area that is particularly promising is a recent project aimed at eradicating alien fish from a stretch of river. The Rondegat River in the Cederberg was the first river selected for treatment using the piscicide rotenone because there was a discrete 4 km stretch that was heavily invaded. Above this stretch, separated by a natural barrier, were healthy populations of indigenous fish, while downstream a weir was upgraded to prevent natural reinvasion (Marr et al. 2012). Proposed in 2002 by CapeNature and following an extensive environmental impact assessment and protracted public participation process, the river was treated in March 2012 and again in March 2013. A comprehensive programme is currently in place to monitor the recovery of fish and invertebrate taxa. Initial findings indicate that the eradication was successful and that the river ecosystem is recovering rapidly (Weyl et al. 2013).

12.7 Where to next with management?

It is clearly important to continue control programmes aimed at reducing or containing impacts as far as possible. In particular, it is important to conserve the unique biodiversity of the CFR, and to protect the integrity of its catchment areas, so that they can continue to deliver vital ecosystem services (Turpie et al. 2003). Invasions are driven by features, processes, and events that characterize the CFR (e.g. lack of trees, particular fire regimes, and specific human activities), and management options are also constrained by particular factors. In order to design the most effective solutions, these drivers and constraints need to be considered (Roura-Pascual et al. 2009). There have been various reviews of the management of invasive organisms in the CFR and South Africa more generally (for some recent examples see van Wilgen et al. 2010; McConnachie et al. 2012; van Wilgen, Cowling, et al. 2012; van Wilgen, Forsyth, et al. 2012; Wilson et al. 2013). In this section we highlight some of the emerging management recommendations (see also Box 12.2).

12.7.1 Plants: future management and research needs

The most important constraint to effective management is the lack of sufficient funding and trained human capacity to address the problem (van Wilgen, Forsyth, et al. 2012). Although substantial amounts have been allocated to the control of invasive alien plants in fynbos areas, it has only been possible to reach a relatively small proportion of the invasions, and in many areas invasive alien plants continue to spread (McConnachie et al. 2012; van Wilgen, Forsyth, et al. 2012). Most extant fynbos occurs in mountain areas (Table 12.3), and the rugged and inaccessible nature of these areas further complicates the task of control and follow-up. Many invasive alien plant species are spread by fires in fynbos, yet regular, unplanned wildfires are a feature of these areas (van Wilgen et al. 2010). The unpredictable nature of fires often upsets plans for control operations and demands a level of flexibility from managers that is not always attainable. This is complicated by the dual mandate of WfW to (a) protect ecosystem services, and (b) provide employment and build capacity (van Wilgen, Khan, et al. 2011). Having dual goals can be a double-edged sword, as it requires trade-offs between job creation and effective management, leading in some cases to a reduction in the effectiveness of control operations.

Because several important invasive alien species also have value, there are often conflicting views on how they should be treated, and this means that in some cases other trade-offs have to be made (Box 12.1). There are also significant challenges associated with land ownership. Co-operative landowners are required for effective control to be achieved at a landscape scale (Urgenson 2011).

Several recommendations to improve the efficiency of management have been made (McConnachie et al. 2012; van Wilgen, Forsyth, et al. 2012). These include:

a) Prioritization of areas to be cleared (Fig 12.5). Since current levels of funding do not allow for all areas to be cleared, available funding should focus on priority areas (Forsyth et al. 2012). This is an unpleasant reality, because areas assigned a lower priority may then have to be abandoned; but the alternative of spreading the available resources thinly is likely to result in inefficient control everywhere.
b) Improved planning, monitoring, and evaluation. The development of management plans with time-based goals, and monitoring progress towards these goals, should form an essential part of management but is currently not adequately done. In particular there should be follow-up control after fire events.
c) Directing a greater proportion of the available funding to biological control. Mechanical and chemical controls are, at best, holding actions, and biological control can offer the most sustainable solutions at very attractive rates of return on investment (de Lange and van Wilgen 2010). Currently, expenditure on biological control is insufficient and only accounts for 3% of total expenditure on control (van Wilgen, Forsyth, et al. 2012). In particular, attention should be paid to finding biological control solutions for invasive pine species (Hoffmann et al. 2011).
d) Improving the qualifications of field managers, and the foremen and/or contractors facilitating the clearing. Currently, very few managers have qualifications in ecosystem management, and this lack of trained capacity impacts on the effectiveness of control programmes. The establishment of an appropriate training course in alien plant management, the provision of bursaries, and employment of graduates would go a long way to addressing this need. The failure of previous field programmes due to this shortcoming was identified long ago (Macdonald et al. 1989).
e) Dealing with conflicts. The economic benefits of some invasive plant species can be outweighed by negative impacts, and in such cases it may not be justifiable to place constraints on control options to protect benefits. In such cases, political courage and sustained commitment would be required to ensure sustainable outcomes through, for example, allowing expansion of biological control options to more damaging agents, (van Wilgen, Dyer, et al. 2011), or even phasing out pine-based plantation forestry in fynbos regions

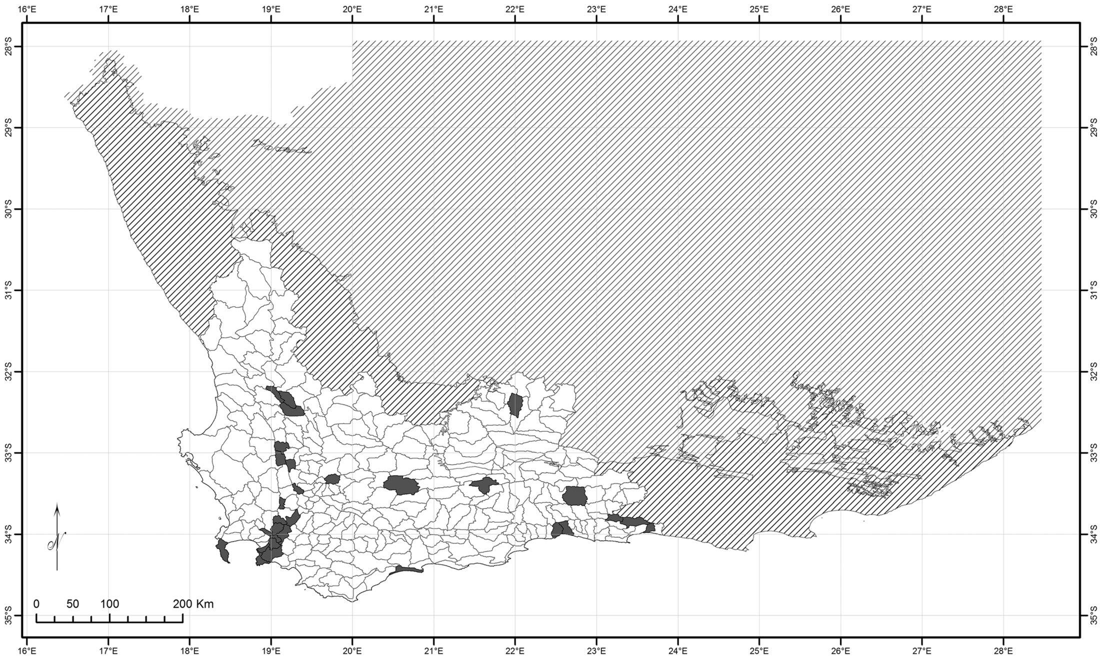


Figure 12.5 The results of a prioritization exercise for WfW's Western Cape water management region, showing the quaternary catchments (shaded areas) in each primary catchment that were rated as the highest priority (Forsyth et al. 2012). Invasive alien plant clearing projects should focus on these areas to ensure the best use of limited resources. Note these water management areas do not correspond exactly to vegetation types, and some of the area involved in the prioritization was outside the CFR.

(Box 12.1; van Wilgen and Richardson 2012). There needs to be a clear, agreed process in place to deal with such issues if they arise with new introductions.

f) Promoting the more widespread use of schemes of payment for ecosystem services. It is possible for municipalities to levy charges on water supplies to support alien plant control operations in catchment areas, thereby protecting the source of water (Turpie et al. 2008). The practice is not currently widespread and could be expanded, though the commodification of ecosystem services can lead to undesirable outcomes.

g) Managing perceptions. The threats associated with invasive alien plants are not particularly well or widely understood, and many control programmes are opposed in part because of misconceptions (van Wilgen 2012). Public support can be improved by raising awareness of the rationale and benefits of clearing, particularly in the context of widespread private ownership of land.

h) Pre-emptive management and research. Species can be and are identified as problems long before they are widespread (Wilson et al. 2013). In such circumstances, eradication is a feasible goal providing there is the continuity to make this happen. The establishment of an early detection and rapid response unit for the City of Cape Town is a major step towards this (Box 12.2). The scientific evidence on which to base legislation and to inform discussions with stakeholders equally requires detailed information on such invasions and the potential for different control options. This information can and should be collected before impacts are severe.

12.7.2 Animals: future management and research needs

Given the lack of knowledge of the alien fauna within the CFR, the initial need is for a comprehensive list of the species involved, and their current distributions. The most comprehensive listing to date (Picker and Griffiths 2011) is far from complete in its cover of invertebrates. The involvement of a wide range of taxonomists, both local and international, would be essential to achieve this. Although a comprehensive listing of all alien animals would be extensive and likely ever growing,

Box 12.3 Managing change

WfW management operations were traditionally based on the assumption that native vegetation will 'self-repair' and that ecosystems will be set on a trajectory towards restoration of pre-invasion structure and function, once dense stands of alien invaders have been removed (Esler et al. 2008). However, the likelihood of successful passive restoration (through autogenic recovery) decreases rapidly as the intensity and/or duration of invasion increases (Le Maitre, Gaertner, et al. 2011). Secondary invasion, resource alteration, or long-lasting 'legacy effects' prevent the re-establishment of native species for decades (Galatowitsch and Richardson 2005; Reinecke et al. 2008; Le Maitre, Gaertner, et al. 2011). In some cases active restoration strategies need to be integrated with existing alien clearing programmes. To guide decisions on whether active restoration is required and ecologically and economically feasible, it is important to identify certain patterns in the invasion process (Richardson and Gaertner 2013). A concept that has shaped thinking in this regard in the CFR is that of novel ecosystems (Gaertner et al. 2012; Richardson and Gaertner 2013).

Novel ecosystems are ecosystems that contain combinations of species that have not coexisted before. They arise through human action, environmental change, and the impacts of the deliberate or inadvertent introduction of species from other parts of the world (Hobbs et al. 2006). According to the three-threshold model (Plate 12) an invaded ecosystem can be considered a novel ecosystem once fundamental alterations in structure and functioning of the ecosystem have occurred that changes internal ecosystem feedbacks. While such ecosystems are not natural, they can still have significant ecological roles. For example, Australian acacia thickets in the CFR support an avifauna of similar richness and density to natural vegetation (Rogers and Chown 2014), but crucially they do not support many nectar-feeding birds that are common elsewhere in the region.

Converting such a novel ecosystem back to a more natural state is very difficult to achieve. Major management interventions, for example the introduction of fynbos species of at least the main functional guilds, and in some cases soil restoration, will be required. Follow-up control of the same or secondary invaders will be necessary for several years. Whether restoration at this stage is justifiable depends on the conservation status of the vegetation type, the site location (proximity to native remnants and sources of reinvasion) and the availability of resources. The high conservation value of fynbos will count in favour for restoration, but in certain cases it might be more cost-effective to use available resources on limiting invasion and densification in more intact areas, and seeking to optimize selected ecosystem functions and services in novel ecosystems.

The novel ecosystem concept is, however, controversial. While it can be viewed as an expedient measure, there needs to be a debate about how far to take it, and in particular, whether it provides a route out for decision makers unwilling to spend more money on invasions.

without such a list it is not possible to identify potential species of concern or to implement monitoring and possible management programmes for them. These species could then be ranked using information from known impacts in other regions of the world, and target species identified for further study and management. This is especially relevant to the alien invertebrates, which also make up the bulk of the alien fauna. Concurrently, a protocol needs to be developed to prevent further introductions nationally, as well as translocations within the country. This should be aligned with existing phytosanitary regulations. For example, a very wide range of spiders, aquarium fish, and reptiles are imported into South Africa without proper risk assessments or evaluations. To date few alien reptiles or aquarium fish have established, but a substantial risk exists that requires better legislation and implementation. The roles and responsibilities of the respective stakeholders concerned with non-native fishes in the region need to be clarified, and a comprehensive conservation plan that identifies priority conservation actions and highlights key management and research needs should be drawn up.

There is little regulation and even less enforcement with respect to the importation (pet trade) and subsequent translocation of introduced invertebrates, most of which were accidentally imported along with wood, stored products, soil, host plants, and animals. Internal translocation continues to occur in the same way and includes accidental or deliberate release of aquarium and angling fish and snails, trade and exchange of composting earthworms, and interprovincial movement of horticultural and agricultural products. This is in sharp contrasts to the tight national regulation restricting the movement of agricultural goods between states in Australia. In a similar scenario for plants, there is a need both for better regulation, planning, and capacity to implement plans.

Box 12.4 Extralimitals, assisted migration, and genetic pollution

The designation of species as alien depends on the geographical scale considered. This chapter focusses mostly on one scale (species are defined as alien if their historical distribution range is outside South Africa) but species can also be translocated outside their natural distribution ranges within geopolitical boundaries (i.e. extralimital introductions) and indigenous species can be translocated within their natural distribution ranges.

We have recorded 47 extralimital plant species and more than 25 extralimital animal species introduced to (or within) the CFR (Box 12.4 Table 1), although for some species their range expansions into the region are due to human modification of the environment rather than human-mediated dispersal (e.g. urban areas watered during summer provide resources throughout the year for hadedas; Macdonald et al. 1986).

Assisted migration has been suggested for species that will not be able to move or adapt fast enough to changes in climate (Hoegh-Guldberg et al. 2008). Extralimital species, however, can have the same impacts as alien species. They can compete with indigenous species through exploitation and habitat change, introduce novel pathogens and parasites, and hybridize with indigenous species. Translocations within the CFR (mostly for horticultural or ornamental purposes) pose a major threat to the integrity of several Proteaceae species, with substantial risks of both genetic homogenization and genetic pollution (i.e. the loss of genetic population structuring and therefore the ability to adapt to changing conditions; Greig 1979). Any proposals for translocation (or assisted migration) need to be assessed with the potential for undesirable impacts in mind (Richardson et al. 2009).

Extralimital species also pose a major practical problem for legislators. Species restrictions might need to encompass specific areas, but such detail is not encapsulated in current legislation. For example, the translocation of freshwater fish (e.g. smallmouth yellowfish, sharptooth catfish, Mozambique tilapia, and banded tilapia) within the CFR cannot be prohibited by the local conservation authority on account of these species being endemic to South Africa. As such, extralimitals pose both practical problems for conservationists, and raise scientific questions about how to define species.

Box 12.4 Table 1 Extralimital plant and animal species introduced to the Cape Floristic Region that cause or could cause unintended adverse impacts.

Group and species	Main issues	Reference
Plants (47): including 14 proteas, 6 asteraceae, 4 ericas	hybridization	
Ungulates (13): *Tragelaphus angasii*, *Aepyceros melampus*, *Tragelaphus strepsiceros*, *Antidorcas marsupialis*, *Connochaetes gnou*, *Connochaetes taurinus*, *Damaliscus pygargus*, *Equus burchellii*, *Giraffa camelopardalis*, *Hippotragus niger*, *Oryx gazella*, *Redunca fulvorufula*, *Kobus ellipsiprymnus*	hybridization, competition, herbivory on plants (that are not adapted to herbivory), introduction of pathogens	Spear and Chown 2008, 2009
Birds (5): *Accipiter melanoleucus*, *Bostrychia hagedash*, *Bubulcus ibis*, *Dicrurus adsimilis*, *Numida meleagris*	often either a nuisance (e.g. hadeda) or potential competitors	Altwegg et al. 2008; Curtis et al. 2007
Fishes (5): *Clarias gariepinus*, *Labeobarbus aeneus*, *Oreochromis mossambicus*, *Tilapia sparrmanii*, *Pseudocrenilabrus philander*	predation, altering food webs	Marr et al. 2012
Amphibians (3): *Xenopus laevis*, *Amietophrynus gutturalis*, *Hyperolius marmoratus*	hybridization, predation	van Rensburg et al. 2011
Reptiles (2): *Lygodactylus capensis*, *Stigmochelys pardalis*		van Rensburg et al. 2011
Insects (1): Agapanthus borer	major threat to commercial production, potential impacts on native range	Picker and Krüger 2013

Box 12.5 Comparisons with other mediterranean-type ecosystems

The Mediterranean Basin has by far the longest history of annual and perennial crop cultivation of any MTE and has been radically altered by extensive human settlement over millennia (di Castri 1989; Kruger et al. 1989). Many species have been introduced there, including several South African (e.g. *Carpobrotus edulis*, *Oxalis pes-caprae*) and Australian (e.g. *Acacia saligna*) plants that have become invasive (Gimeno et al. 2006; Traveset et al. 2008). Mediterranean islands have also seen many species introduced for the public good becoming invasive (Lambdon and Hulme 2006). Notwithstanding these examples, invasive alien plants in the Mediterranean Basin seem to have been much less damaging than in other MTEs.

Colonization by people of California (~15 000 BP), Chile (~13 000 BP), and Australia (~40 000 BP) occurred before Europeans arrived but, as for South Africa, species introductions and impacts were probably limited until European settlers arrived (Kruger et al. 1989). Invasions in MTEs also still show significant signals of their colonial history. For example, California has more naturalized alien species from a wider range of source areas than Chile (Arroyo et al. 2000; Jiménez et al. 2008), arguably due to difference in the trade links set up by their respective colonizers, Britain and Spain (Kruger et al. 1989).

The Spanish reached Chile in 1540. Chilean matorral, like garrigue and maquis in the Mediterranean Basin, is dominated by evergreen shrubs and low trees. These ecosystems are highly susceptible to invasions by grasses and other herbaceous species but seem relatively resistant to invasions by woody plants. Unlike in other MTEs, fires in Chile were rare but are increasing as invasions by flammable species expedite fires or increase fire frequencies (Arroyo et al. 2000; Pauchard et al. 2008). Large-scale introduction of alien trees to Chile occurred much later than to Australia or South Africa. Widespread invasions by alien acacias and pines have only occurred there in the past few decades (Simberloff et al. 2010).

Coastal areas in California were colonized by Europeans in 1697, with interior regions not colonized until 1848, when it became part of the United States. Californian chaparral is dominated by evergreen shrubs, some of which are fire killed. Herbaceous invaders are present but are rarely abundant in the post-fire flora and are absent from mature stands (Kruger et al. 1989). Coastal regions, however, have a different fire regime, and invasions by cosmopolitan herbaceous weeds, especially grasses from the Mediterranean Basin, have almost completely replaced the native flora (Kruger et al. 1989; Seabloom et al. 2003).

The British colonized Australia in 1786 and actively introduced a wide range of species, with organizations dedicated to introducing European species, 'naturalization societies', playing a large role (Murray and Phillips 2012). Given South Africa's and Australia's shared colonial history, many species were introduced to both regions at similar times, and species were often transferred from one region to the other. However, while the natural vegetation types of the MTEs in South Africa and in Australia are characterized by a similar mix of growth forms, albeit with greater dominance of taller sprouters in Australia (Richardson and Cowling 1992; Cowling and Witkowski 1994), the growth forms of the major invaders differ markedly: herbaceous species, particularly South African geophytes, are invasive in Western Australia (e.g. *Gladiolus caryophyllaceus*, *Romulea rosea*), while woody Australian species are invasive in the CFR. The other MTEs all include desert shrublands, but none are as species rich or diverse as the succulent karoo (Desmet 2007). These environments seem to be subject to invasions by similar species: trees and other woody species along rivers, and succulents and annual herbaceous species elsewhere (Milton and Dean 2010). All the MTEs now have more introduced freshwater fish species than endemic species (Marr et al. 2010), with a strong overall tendency towards more similar fish faunas. However, terrestrial vertebrate invasions have had little impact in the CFR, certainly when compared to Australia and to some extent Chile.

Management of invasive species is perhaps where there are some of the biggest differences between MTEs. Classical biological control of plants has been used extensively in Australia, California, and South Africa, but there is only a single very recent example from Europe (Shaw et al. 2011) and a very limited case from the Chilean MTE (the use of fungi for the control of *Rubus* spp.). Programmes like WfW are not found in any of the other MTEs reflecting, in part, different socio-economic conditions. Labour costs are relatively high in Australia and California, but there are several grassroots environmental movements involved in control (e.g. LandCare) and high-tech approaches are more commonly applied. Given the more recent history of introductions to Chile, the hope is that lessons learned in other regions can be transferred there (Simberloff et al. 2010).

12.8 Conclusions

Over the past 20 years, invasion science has developed as a distinct discipline, with over five specialist international journals and a rise in scientific articles greater than the general growth in science output (Pysek et al. 2006). In this rapidly developing field, the CFR continues to provide textbook examples of invasions. While the CFR has been a valuable testing ground for developing the practice and management of biological invasions, we hope that much greater progress will be made in implementing control over the next 20 years. This will required greater engagement with the public (Box 12.1), better implementation (Box 12.2), occasionally a more pragmatic approach (Box 12.3), and an understanding of the risks of all types of species translocations (Box 12.4). However, for many groups we still know little about which species are potential invasives in the CFR, what impacts they cause, and what the major future risks are likely to be. While the invasions seen in the CFR share similarities with invasions elsewhere (including other MTEs; Box 12.5), the unique interactions between species, environment, and humans in the CFR means that there is still a need to work group by group, and system by system, in order to limit the impacts that introductions cause to this area.

Supplementary Material: List of alien species recorded as naturalized or invasive in the fynbos region with status according to the scheme proposed by Blackburn et al. (2011). Available at: <http://academic.sun.ac.za/cib/supplementary/wilson001.xlsx>.

References

Adamson, R.S. and Salter, T.M. (1950). *Flora of the Cape Peninsula*. Juta & Co. Cape Town.

Allsopp, M.H. (2006). *Analysis of* Varroa destructor *infestation of southern African honeybee populations*. MSc thesis, University of Pretoria, Pretoria.

Altwegg, R., Wheeler, M., and Erni, B. (2008). Climate and the range dynamics of species with imperfect detection. *Biology Letters*, **4**, 581–4.

Arroyo, M.T.K., Marticorena, C., Matthei, O., and Cavieres, L.A. (2000). Plant invasions in Chile: present patterns and future predictions. In H.A. Mooney and R.J. Hobbs, eds. *Invasive species in a changing world*, pp. 385–421. Island Press, Covelo.

Bands, D.P. (1977). Prescribed burning in Cape fynbos catchments. In H.A. Mooney and C.E. Conrad, eds. *Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems*. Palo Alto California, August 1977. USDA Forest Service General Technical Report WO-3, pp 245–56.

Blackburn, T.M., Pyšek, P., Bacher, S., et al. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, **26**, 333–9.

Bond, W. and Slingsby, P. (1984). Collapse of an ant–plant mutualism—the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology*, **65**, 1031–7.

C.A.P.E. (2009). *Invasive alien species strategy for the Greater Cape Floristic Region*. CapeNature, Cape Town.

Carruthers, J., Robin, L., Hattingh, J.P., Kull, C.A., Rangan, H., and van Wilgen, B.W. (2011). A native at home and abroad: the history, politics, ethics and aesthetics of acacias. *Diversity and Distributions*, **17**, 810–21.

Christian, C.E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, **413**, 635–9.

Coke, M. (1988). Freshwater fish conservation in South Africa: a rising tide. *Journal of the Limnological Society of Southern Africa*, **14**, 29–34.

Cowling, R.M. and Witkowski, E.T.F. (1994). Convergence and non-convergence of plant traits in climatically and edaphically matched sites in mediterranean Australia and South Africa. *Australian Journal of Ecology*, **19**, 220–32.

CSIR and ARC (2005). *National land-cover database 2000*. CSIR and the Agricultural Research Council, Pretoria.

Curtis, O.E., Hockey, P.A.R., and Koeslag, A. (2007). Competition with Egyptian geese *Alopochen aegyptiaca* overrides environmental factors in determining productivity of black sparrowhawks *Accipiter melanoleucus*. *Ibis*, **149**, 502–8.

Deacon, H.J. (1991). Historical background of invasions in the southern African mediterranean region. In F. Groves RHDC, ed. *Biogeography of mediterranean invasions*. pp. 51–7. Cambridge University Press, Cambridge.

Deacon, J. (1986). Human settlement in South Africa and archaeological evidence for alien plants and animals. In I.A.W. Macdonald, F.J. Kruger, and A.A. Ferrar, eds. *The ecology and management of biological invasions in southern Africa*, pp. 3–19. Oxford University Press, Cape Town.

de Lange, W.J. and van Wilgen, B.W. (2010). 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. *Biological Invasions*, **12**, 4113–24.

Desmet, P.G. (2007). Namaqualand—a brief overview of the physical and floristic environment. *Journal of Arid Environments*, **70**, 570–87.

di Castri, F. (1989). History of biological invasions with special emphasis on the Old World. In J.A. Drake, H.A. Mooney, F. di Castri et al. eds. *Biological invasions: a global perspective*, pp. 1–30. John Wiley and Sons, Chichester.

Elton, C.S. (1958). *The ecology of invasions by animals and plants*. Methuen, London.

Esler, K.J., Holmes, P.M., Richardson, D.M., and Witkowski, E.T.F. (2008). Riparian vegetation management in landscapes invaded by alien plants: insights from South Africa. *South African Journal of Botany*, **74**, 397–400.

Esler, K.J., van Wilgen, B.W., te Roller, K.S., Wood, A.R., and van der Merwe, J.H. (2010). A landscape-scale assessment of the long-term integrated control of an invasive shrub in South Africa. *Biological Invasions*, **12**, 211–8.

Fenn, J.A. (1980). Control of *Hakea* in the Western Cape. In S. Neser and A.L.P. Cairns, eds. *Proceedings of the Third National Weeds Conference of South Africa*. pp. 167–73. Balkema, Cape Town.

Forsyth, G.G., Le Maitre, D.C., O'Farrell, P.J., and van Wilgen, B.W. (2012). The prioritisation of invasive alien plant control projects using a multi-criteria decision model informed by stakeholder input and spatial data. *Journal of Environmental Management*, **103**, 51–7.

Gaertner, M., Den Breeyen, A., Hui, C., and Richardson, D.M. (2009). Impacts of alien plant invasions on species richness in mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319–38.

Gaertner, M., Holmes, P.M., and Richardson, D.M. (2012). Biological invasions, resilience and restoration. In J. Andel and J. Aronson eds. *Restoration ecology: the new frontier*, pp. 265–80. Wiley-Blackwell, Oxford.

Galatowitsch, S. and Richardson, D.M. (2005). Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. *Biological Conservation*, **122**, 509–21.

Geerts, S., Botha, P.W., Visser, V., Richardson, D.M., and Wilson, J.R.U. (2013). Montpellier broom (*Genista monspessulana*) and Spanish broom (*Spartium junceum*) in South Africa: an assessment of invasiveness and options for management. *South African Journal of Botany*, **87**, 134–45.

Gimeno, I., Vila, M., and Hulme, P.E. (2006). Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* L. in the western Mediterranean. *Journal of Biogeography*, **33**, 1559–65.

Glen, H.F. (2002). *Cultivated plants of southern Africa*. Southern African National Biodiversity Institute and Jacana, Johannesburg.

Greig, J.C. (1979). Principles of genetic conservation in relation to wildlife management in southern Africa. *South African Journal of Wildlife Research*, **9**, 57–78.

Henderson, L. (2001). *Alien weeds and invasive plants. Plant Protection Research Institute Handbook No. 12*. Agricultural Research Council, Pretoria.

Henderson, L. (2006). Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. *Bothalia*, **36**, 201–22.

Henderson, L. (2007). Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). *Bothalia*, **37**, 15–248.

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

Herbert, D.G. and Sirgel, W.F. (2001). The recent introduction of two potentially pestiferous alien snails into South Africa and the outcomes of different pest management practices: an eradication and a colonization. *South African Journal of Science*, **97**, 301–4.

Higgins, S.I., Turpie, J.K., Costanza, R., et al. (1997). An ecological economic simulation model of mountain fynbos ecosystems—dynamics, valuation and management. *Ecological Economics*, **22**, 155–69.

Hobbs, R.J., Arico, S., Aronson, J., et al. (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., et al. (2008). Assisted colonization and rapid climate change. *Science*, **321**, 345–6.

Hoffmann, J.H., Moran, V.C., and van Wilgen, B.W. (2011). Prospects for the biological control of invasive *Pinus* species (Pinaceae) in South Africa. *African Entomology*, **19**, 393–401.

Holmes, P.M., Richardson, D.M., van Wilgen, B.W., and Gelderblom, C. (2000). Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecology*, **25**, 631–9.

Hosking, S.G. and du Preez, M. (1999). A cost-benefit analysis of removing alien trees in the Tsitsikamma Mountain catchment. *South African Journal of Science*, **95**, 442–8.

Impson, N.D. (2007). Freshwater fishes. In: *Western Cape state of biodiversity report 2007*, pp. 18–35. CapeNature Scientific Services, Stellenbosch.

Iponga, D.M., Krug, C.B., and Milton, S.J. (2005). Competition and herbivory influence growth and survival of shrubs on old fields: implications for restoration of renosterveld shrubland. *Journal of Vegetation Science*, **16**, 685–92.

Jiménez, A., Pauchard, A., Cavieres, L.A., Marticorena, A., and Bustamante, R.O. (2008). Do climatically similar regions contain similar alien floras? A comparison between the mediterranean areas of central Chile and California. *Journal of Biogeography*, **35**, 614–24.

Kenis, M., Auger-Rozenberg, M.A., Roques, A., et al. (2009). Ecological effects of invasive alien insects. *Biological Invasions*, **11**, 21–45.

Klein, H. (2011). A catalogue of the insects, mites and pathogens that have been used or rejected, or are under consideration, for the biological control of invasive alien plants in South Africa. *African Entomology*, **19**, 515–49.

Kotzé, J.D.F., Beukes, B.H., van den Berg, E.C., and Newby, T.S. (2010). *National Invasive Alien Plant Survey*. Report Number: GW/A/2010/21.). Agricultural Research Council: Institute for Soil, Climate and Water, Pretoria.

Krug, C.B. and Krug, R.M. (2007). Restoration of old fields in renosterveld: a case study in a mediterranean shrubland of South Africa. In V.A. Cramer and R.J. Hobbs, eds. *Old fields: dynamics and restoration of abandoned farmland*, pp. 265–85. Island Press, Washington, DC.

Kruger, F.J., Breytenbach, G.J., Macdonald, I.A.W., and Richardson, D.M. (1989). The characteristics of invaded mediterranean-climate regions. In J.A. Drake, H.A. Mooney, F. di Castri, et al. eds. *Biological invasions. A global perspective*, pp. 181–214. John Wiley and Sons, Chichester.

Lach, L. (2007). A mutualism with a native membracid facilitates pollinator displacement by Argentine ants. *Ecology*, **88**, 1994–2004.

Lambdon, P.W. and Hulme, P.E. (2006). Predicting the invasion success of mediterranean alien plants from their introduction characteristics. *Ecography*, **29**, 853–65.

Le Maitre, D.C., de Lange, W.J., Richardson, D.M., Wise, R.M., and van Wilgen, B.W. (2011). The economic consequences of the environmental impacts of alien plant invasions in South Africa. In D. Pimentel, ed. *Biological invasions: economic and environmental costs of alien plant, animal and microbe species*, pp. 295–323. CRC Press, Boca Raton.

Le Maitre, D.C., Gaertner, M., Marchante, E., et al. (2011). Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions*, **17**, 1015–29.

Le Maitre, D.C., Milton, S.J., Jarmain, C., Colvin, C.A., Saayman, I., and Vlok, J.H.J. (2007). Linking ecosystem services and water resources: landscape-scale hydrology of the Little Karoo. *Frontiers in Ecology and the Environment*, **5**, 261–70.

Le Maitre, D.C., van Wilgen, B.W., Chapman, R.A., and McKelly, D.H. (1996). Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology*, **33**, 161–72.

Le Maitre, D.C., Versfeld, D.B., and Chapman, R.A. (2000). The impact of invading alien plants on surface water reources in South Africa: a preliminary assessment. *Water SA*, **26**, 397–408.

Louda, S.M., Pemberton, R.W., Johnson, M.T., and Follett, P.A. (2003). Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annual Review of Entomology*, **48**, 365–96.

Lowe, S.R., Woodford, D.J., Impson, N.D., and Day, J.A. (2008). The impact of invasive fish and invasive riparian plants on the invertebrate fauna of the Rondegat River, Cape Floristic Region, South Africa. *African Journal of Aquatic Science*, **33**, 51–62.

Lubke, R.A. (1985). Erosion of the beach at St. Francis Bay, Eastern Cape, South Africa. *Biological Conservation*, **32**, 99–127.

Macdonald, I.A.W., Clark, D.L., and Taylor, H.C. (1989). The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941–87. *South African Journal of Botany*, **55**, 56–75.

Macdonald, I.A.W. and Richardson, D.M. (1986). Alien species interrestrial ecosystems of the Fynbos Biome. In I.A.W. Macdonald, F.J. Kruger, and A.A. Ferrar, eds. *The ecology and management of biological invasions in southern Africa*, pp. 93–108. Oxford University Press, Cape Town.

Macdonald, I.A.W., Richardson, D.M., and Powrie, F.J. (1986). Range expansion of the hadeda ibis *Bostrychia hagedash* in southern Africa. *South African Journal of Zoology*, **21**, 331–42.

Marr, S.M. (2012). *Conservation of the native freshwater fishes of the Cape Floristic Region (South Africa): management of non-native species*. University of Cape Town.

Marr, S.M., Impson, N.D., and Tweddle, D. (2012). An assessment of a proposal to eradicate non-native fish from priority rivers in the Cape Floristic Region, South Africa. *African Journal of Aquatic Science*, **37**, 131–42.

Marr, S.M., Marchetti, M.P., Olden, J.D., et al. (2010). Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem? *Diversity and Distributions*, **16**, 606–19.

McConnachie, M.M., Cowling, R.M., van Wilgen, B.W., and McConnachie, D.A. (2012). Evaluating the cost-effectiveness of invasive alien plant clearing: a case study from South Africa. *Biological Conservation*, **155**, 128–35.

Mead, A., Carlton, J.T., Griffiths, C.L., and Rius, M. (2011). Revealing the scale of marine bioinvasions in developing regions: a South African re-assessment. *Biological Invasions*, **13**, 1991–2008.

Milton, S.J. (2004). Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69–75.

Milton, S.J. and Dean, W.R.J. (2010). Plant invasions in arid areas: special problems and solutions: a South African perspective. *Biological Invasions*, **12**, 3935–48.

Moeller, J. (2010). *Spatial analysis of pine tree invasion in the Tsitsikamma region, Eastern Cape, South Africa: a pilot study*. BSc (Hons) thesis, Rhodes University, Grahamstown.

Moll, E.J. and Scott, L. (1981). *Trees and shrubs of the Cape Peninsula: a comprehensive field guide to over 230 indigenous and naturalized species*. University of Cape Town, Cape Town.

Moran, V.C. and Hoffmann, J.H. (2012). Conservation of the Fynbos Biome in the Cape Floral Region: the role of biological control in the management of invasive alien trees. *Biocontrol*, **57**, 139–49.

Mucina, L. and Rutherford, M.C., eds. (2006). The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.

Murray, B.R. and Phillips, M.L. (2012). Temporal introduction patterns of invasive alien plant species to Australia. *Neobiota*, **13**, 1–14.

Odendaal, L.J., Haupt, T.M., and Griffiths, C.L. (2008). The alien invasive land snail *Theba pisana* in the West Coast National Park: Is there cause for concern? *Koedoe* **50**, 93–9.

Pauchard, A., Garcia, R.A., Pena, E., Gonzalez, C., Cavieres, L.A., and Bustamante, R.O. (2008). Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. *Biological Invasions*, **10**, 547–53.

Picker, M. and Griffiths, C. (2011). *Alien and invasive animals: a South African perspective*. Struik Nature, Cape Town.

Picker, M.D. Krüger, M. (2013). Spread and impacts of the Agapanthus borer (*Neuranethes spodopterodes* (Hampson, 1908), comb. nov.), a translocated native moth species (Lepidoptera: Noctuidae). *African Entomology*, **21**, 172–6.

Plisko, J.D. (2010). Megadrile earthworm taxa introduced to South African soils (*Oligochaeta: Acanthodrilidae*, *Eudrili-*

dae, *Glossoscolecidae*, *Lumbricidae*, *Megascolecidae*, *Ocnerodrilidae*). *African Invertebrates*, **51**, 289–312.

Pysek, P., Richardson, D.M., and Jarosik, V. (2006). Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. *Preslia*, **78**, 437–68.

Reinecke, M.K., Pigot, A.L., and King, J.M. (2008). Spontaneous succession of riparian fynbos: is unassisted recovery a viable restoration strategy? *South African Journal of Botany*, **74**, 412–20.

Richardson, D.M. and Blanchard, R. (2011). Learning from our mistakes: minimizing problems with invasive biofuel plants. *Current Opinion in Environmental Sustainability*, **3**, 36–42.

Richardson, D.M., Cambray, J.A., Chapman, R.A., et al. (2003). Vectors and pathways of biological invasions in South Africa—past, present and future. In G. Rui and J. Carlton, eds. *Invasive species: vectors and management strategies*, pp. 292–49. Island Press, Washington, DC.

Richardson, D.M., Carruthers, J., Hui, C., et al. (2011). Human-mediated introductions of Australian acacias—a global experiment in biogeography. *Diversity and Distributions*, **17**, 771–87.

Richardson, D.M. and Cowling, R.M. (1992). Why is mountain fynbos invasible and which species invade? In B.W. van Wilgen, D.M. Richardson, F.J. Kruger, and H.J. van Hensbergen, eds. *Fire in South African mountain fynbos*, pp. 161–81. Springer-Verlag, Berlin.

Richardson, D.M. and Gaertner, M. (2013). Plant invasions as builders and shapers of novel ecosystems. In R.J. Hobbs, E.C. Higgs, and C.M. Hall, eds. *Novel ecosystems: intervening in the new ecological world order*, pp. 102–14. Wiley-Blackwell, Oxford.

Richardson, D.M., Hellmann, J.J., McLachlan, J.S., et al. (2009). Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences USA*, **106**, 9721–4.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., and Henderson, L. (1997). Alien plant invasions. In R.M. Cowling, D.M. Richardson, and S.M. Pierce, eds. *Vegetation of southern Africa*, pp. 535–70. Cambridge University Press, Cambridge.

Richardson, D.M., Macdonald, I.A.W., Holmes, P.M., and Cowling, R.M. (1992). Plant and animal invasions. In R.M. Cowling, ed. *The ecology of fynbos*, pp. 271–308. Oxford University Press, Cape Town.

Richardson, D.M., Williams, P.A., and Hobbs, R.J. (1994) Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography*, **21**, 511–27.

Rogers, A.M. and Chown, S.L. (2014). Novel ecosystems support substantial avian assemblages: the case of invasive alien *Acacia* thickets. *Diversity and Distributions*, **20**, 34–45.

Roura-Pascual, N., Richardson, D.M., Krug, R.M., et al. (2009). Ecology and management of alien plant invasions in South African fynbos: accommodating key complexities in objective decision making. *Biological Conservation*, **142**, 1595–604.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., et al. (1990). Biological feedbacks in global desertification. *Science*, **247**, 1043–8.

Seabloom, E.W., Borer, E.T., Boucher, V.L., et al. (2003). Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications*, **13**, 575–92.

Shaw, R.H., Tanner, R., Djeddour, D., and Cortat, G. (2011). Classical biological control of *Fallopia japonica* in the United Kingdom—lessons for Europe. *Weed Research*, **51**, 552–8.

Simberloff, D., Nunez, M.A., Ledgard, N.J., et al. (2010). Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. *Austral Ecology*, **35**, 489–504.

Spear, D. and Chown, S.L. (2008). Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *Journal of Biogeography*, **35**, 1962–75.

Spear, D. and Chown, S.L. (2009). The extent and impacts of ungulate translocations: South Africa in a global context. *Biological Conservation*, **142**, 353–63.

Spear, D., McGeoch, M.A., Foxcroft, L.C., and Bezuidenhout, H. (2011). Alien species in South Africa's national parks. *Koedoe*, **53**, 1–4.

Stals, R. and Prinsloo, G. (2007). Discovery of an alien invasive, predatory insect in South Africa: the multicoloured Asian ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *South African Journal of Science*, **103**, 123–6.

Stirton, C.H. (1978). *Plant invaders: beautiful*, *but dangerous*. Department of Nature and Environmental Conservation, Cape Town.

Traveset, A., Brundu, G., Carta, L., et al. (2008). Consistent performance of invasive plant species within and among islands of the Mediterranean basin. *Biological Invasions*, **10**, 847–58.

Turpie, J. and Heydenrych, B. (2000). Economic consequences of alien infestation of the Cape Floral Kingdom's vegetation. In C.W. Perrings, M. Williamson, and S. Dalmazzone, eds. *The economics of biological invasions*, pp. 152–82. Edward Elgar, Cheltenham.

Turpie, J.K., Heydenrych, B.J., and Lamberth, S.J. (2003). Economic value of terrestrial and marine biodiversity in the Cape Floristic Region: implications for defining effective and socially optimal conservation strategies. *Biological Conservation*, **112**, 233–51.

Turpie, J.K., Marais, C., and Blignaut, J.N. (2008). The Working for Water Programme: evolution of a payments for ecosystem services mechanism that addresses both poverty and ecosystem service delivery in South Africa. *Ecological Economics*, **65**, 788–98.

Tweddle, D., Bills, R., Swartz, E., et al. (2009). The status and distribution of freshwater fishes. In W.R.T. Darwall, K.G. Smith, D. Tweddle, and P.H. Skelton, eds. *The status and distribution of freshwater biodiversity in Southern Africa*, pp. 21–37. IUCN, Gland, Switzerland and South African Institute for Aquatic Biodiversity, Grahamstown.

Urgenson, L.S. (2011). *Ecological and social aspects of riparian restoration and non-native plant invasions: studies from the Pacific Northwest, .S. and the Western Cape, South Africa*. School of Environmental and Forest Sciences, University of Washington.

van Rensburg, B.J., Weyl, O.L.F., Davies, S.J., et al. (2011). Invasive vertebrates of South Africa. In D. Pimentel, ed. *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*, pp. 326–78. CRC Press, Boca Raton.

van Rooyen, S. (2004). *Factors affecting alien grass invasion into west coast renosterveld fragments*. MSc thesis, University of Stellenbosch, Stellenbosch.

van Wilgen, B.W. (2012). Evidence, perceptions, and trade-offs associated with invasive alien plant control in the Table Mountain National Park, South Africa. *Ecology and Society*, **17**.

van Wilgen, B.W., Cowling, R.M., and Burgers, C.J. (1996). Valuation of ecosystem services: a case study from South African fynbos ecosystems. *BioScience*, **46**, 184–9.

van Wilgen, B.W., Cowling, R.M., Marais, C., Esler, K.J., McConnachie, M., and Sharp, D. (2012). Challenges in invasive alien plant control in South Africa. *South African Journal of Science*, **11/12**, 108–10.

van Wilgen, B.W., Dyer, C., Hoffmann, J.H., et al. (2011). National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. *Diversity and Distributions*, **17**, 1060–75.

van Wilgen, B.W., Forsyth, G.G., de Klerk, H., Das, S., Khuluse, S., and Schmitz, P. (2010). Fire management in mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology*, **47**, 631–8.

van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., et al. (2012). An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. *Biological Conservation*, **148**, 28–38.

van Wilgen, B.W., Khan, A., and Marais, C. (2011). Changing perspectives on managing biological invasions: insights from South Africa and the Working for Water Programme. In D.M. Richardson, ed. *Fifty years of invasion ecology: the legacy of Charles Elton*, pp. 377–93. Wiley-Blackwell, Oxford.

van Wilgen, B.W., Little, P.R., Chapman, R.A., Görgens, A.H.M., Willems, T., and Marais, C. (1997). The sustainable development of water resources: history, financial costs and benefits of alien plant control programmes. *South African Journal of Science*, **93**, 404–11.

van Wilgen, B.W., Nel, J.L., and Rouget, M. (2007). Invasive alien plants and South African rivers: a proposed approach to the prioritization of control operations. *Freshwater Biology*, **52**, 711–23.

van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M., and Schonegevel, L. (2008). A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management*, **89**, 336–49.

van Wilgen, B.W. and Richardson, D.M. (1985). The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands—a simulation study. *Journal of Applied Ecology*, **22**, 955–66.

van Wilgen, B.W. and Richardson, D.M. (2012). Three centuries of managing introduced conifers in South Africa: benefits, impacts, changing perceptions and conflict resolution. *Journal of Environmental Management*, **106**, 56–68.

van Wilgen, B.W. and Richardson, D.M. (2014). Managing invasive alien trees: challenges and trade-offs. *Biological Invasions*, **16**, 721–734.

Veldtman, R., Addison, P., and Tribe, G.D. (2012). Current status and potential future impact of invasive vespid wasps (*Vespula germanica* and *Polistes dominulus*) in South Africa. *IOBC/wprs Bulletin*, **75**, 217–21.

Weyl, O.L.F., Ellender, B.R., Woodford, D.J., and Jordaan, M.S. (2013). Fish distributions in the Rondegat River, Cape Floristic Region, South Africa, and the immediate impact of rotenone treatment in an invaded reach. *African Journal of Aquatic Science*, **38**, 201–9.

Wicht, C.L. (1945). *Report of the committee on the preservation of the vegetation of the South Western Cape*. Special Publication of the Royal Society of South Africa, Cape Town.

Wilson, J.R.., Ivey, P., Manyama, P., and Nänni, I. (2013). A new national unit for invasive species detection, assessment and eradication planning. *South African Journal of Science*, **109**, 1–13.

Wise, R.M., van Wilgen, B.W., and Le Maitre, D.C. (2012). Costs, benefits and management options for an invasive alien tree species: the case of mesquite in the Northern Cape, South Africa. *Journal of Arid Environments*, **84**, 80–90.

Yelenik, S.G., Stock, W.D., and Richardson, D.M. (2004). Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology*, **12**, 44–51.

Zimmermann, H.G., Moran, V.C., and Hoffmann, J.H. (2004). Biological control in the management of invasive alien plants in South Africa, and the role of the Working for Water Programme. *South African Journal of Science*, **100**, 34–40.