

direct effects, for example, by providing more resources to one species than to another [25], and potentially through indirect effects, such as by the transfer of resources and fixed carbon between individuals [26].

Another positive facilitation effect is the interaction between the introduced *S. molle* and native trees observed in semi-arid savanna of South Africa [27], where the establishment of the fleshy-fruited *S. molle* occurs predominantly under tree canopies, resulting in the formation of clumps around a single indigenous tree. This probably because by perching and nesting in trees, frivorous birds direct seeds of *S. molle* to subcanopy sites [27, 28]. Some studies have demonstrated that subcanopy microsites conditions are favourable for seed germination and seedling establishment [29]. This process is known as nucleation [30] whereby the clumps tend to grow around a single founder tree.

Conclusion

There is clear evidence that biological invasions are one of most damaging phenomena that humans have ever generated on ecosystems. Despite intensive research into causes and consequences of biological invasion, we are still far from understanding the full complexity of the phenomenon. This is partly because so many different aspects need to be considered when trying to develop a general theory. This chapter has shown that no single trait can predict invasion success; those that seem to be correlated with invasiveness are to a large extent habitat specific. The chapter has highlighted that successful invasion appears to depend on number of factors that facilitate the surmounting of invasion barriers. Those factors include habitat features, recent disturbances and distance from putative source populations, life history traits and seed biology that may interact to facilitate invasions. It is also important to understand the links between traits of alien plants and features of the environment in mediating invasiveness.

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INVASIVE ALIEN SPECIES

Are invasive aliens a real threat to biodiversity in South Africa?

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South Africa has abundant biodiversity, but also has many invasive alien species, especially plants and fish, that can transform ecosystems. Invading alien trees and shrubs impact on fynbos and threaten up to a quarter of the nation's plant species. Freshwater ecosystems are often dominated by alien fish, while invasive alien plants invade the catchments of major rivers, riparian zones and open water surfaces. Invasive alien pathogens and diseases, such as the rinderpest that decimated wildlife and livestock at the end of the 19th century, pose a constant potential threat to biodiversity. Uncertainties in monitoring and predicting trends, and rehabilitating priority conservation areas are important challenges.

Introduction

Biodiversity is a term that encompasses the full range of variation in life on Earth. It is more than just a count of species, because it refers to the variety of ways those species co-exist in communities at different scales [1]. With its savanna, grassland, thicket, karoo, desert, forest and fynbos vegetation, South Africa is endowed with more than its fair share of the world's biodiversity. Each vegetation type has its own distinctive fauna, flora and ecological functioning and some have remarkably high concentrations of species. The country also has two internationally recognised biodiversity hotspots: the Cape Floral Kingdom and the Succulent Karoo (the only arid land hotspot in the world). With its extraordinary levels of biodiversity, South Africa is considered one of the 'megadiversity' countries in the world [2]. South Africa also has an abundance of invasive alien species, particularly alien plants and alien freshwater fish, and these pose significant threats to the continued survival of our remarkable biodiversity [3].

How invasive species affect biodiversity

Invading alien organisms are widely regarded as the second-largest threat to biodiversity, after direct habitat destruction. Invasive alien species simply out-compete many of our indigenous species and they come to dominate many areas if left to spread unchecked. Often, their ability to do this is because of the phenomenon of 'ecological release' – a term coined to describe the behaviour of introduced plants and animals when they are 'released' from the hosts of diseases, parasites and predators that keep them in check in their native ranges. They can transform the structure of vegetation, thus making it unsuitable as habitat for birds, insects and mammals, change the nature of veldfires, use excessive amounts of water and change the nature of nutrient cycles.

How has South Africa's biodiversity been affected?

Not all of our ecosystems have been equally affected by invasions. In the Western and Eastern Cape provinces, the fynbos shrublands have been literally over-run with alien plants, possibly because they have been settled for much longer than other areas. Freshwater ecosystems, too, are highly invaded, as alien plants and fish can rapidly spread along rivers once they are introduced. That is not to say that other ecosystems will not become invaded, given enough time. In the sections that follow, we have outlined three examples – the fynbos, freshwater ecosystems, and an introduced cattle disease – that illustrate the kinds of impacts that invasive species have had on our biodiversity.

Example 1: Invasive alien plants and the fynbos

The impacts of invasive alien species (especially invasive plants) on biodiversity are currently most keenly felt in the Cape Floral Kingdom (CFK), which covers 90 000 km² of southwestern South Africa. This area, barely 4% of the land surface of southern Africa, contains 45% of the subcontinent's plant species. There are almost 8 600 species of flowering plants and ferns, of which almost 70% (5 850 species) are endemic (that is, they are found nowhere else) [4]. The CFK is also the smallest of six such Kingdoms into which the world's vegetation is subdivided, and is the only one which is

found entirely within the borders of a single country. Almost one-third of the Kingdom has already been lost to urbanisation, agriculture and forestry, and the remaining areas (mainly in the mountains) are under severe threat from invading alien plants.

There are few detailed studies on the extent of the problem, but where these have been done they confirm what can generally be observed. For example, a study in 1996 [5] showed that almost 40% of the Cape Peninsula has been transformed by agriculture and urbanisation. Of the remaining area, 10.7% was under dense stands of alien plants and another 32.9% was lightly invaded. The prognosis for the future of the Kingdom under a scenario of limited or no funding for the control of invading alien plants is grim [6]. Alien plants spread as a result of regular fires, as well as increasing levels of agriculture, road building, forestry and development. While spread rates are not fully understood, there are plenty of examples that illustrate the extent to which areas have become invaded. Indications are that southern Africa could lose almost a quarter of its plant species from this region alone due to invading alien plants.



Figure 3.54 Pines trees invading fynbos vegetation in the Eastern Cape. A forestry plantation (right centre) provides the initial source of seeds, from where the trees invade pastures (foreground) and upper catchment areas, displacing native species and reducing streamflow from the catchments. [B.W. van Wilgen]

Example 2: Invasive aliens and freshwater ecosystems

Freshwater ecosystems face significant threats from nutrient enrichment, chemical pollution, drainage and water extraction, erosion and dams. Invasion by alien species exacerbates these problems significantly [7]. Internationally, alien fish species top the list of threats to indigenous fish populations [8], and this is certainly true for the unique indigenous freshwater fishes of the CFK [9]. Most of our river systems now contain alien fishes that were introduced for angling and fish farming purposes in the 1900s. These species originate from both outside South Africa (mainly USA and Europe), as well as South African species stocked outside their natural distribution range (for example, Mozambique tilapia and sharp-toothed catfish). Alien fish species dominate CFK rivers, both in area occupied and numbers, with 16 species recorded to date [10]. Once common and widely distributed, indigenous fish species, such as the Berg-Breede whitefish and Clanwilliam sawfin, are now restricted to mountain streams and a few large dams where predatory alien fishes are absent or uncommon. The worst invaders are rainbow trout in the upper reaches of rivers and smallmouth bass, carp, Mozambique tilapia and sharp-toothed catfish in the middle and lower reaches of rivers of the CFK.

The predatory and competitive impacts of invasive alien fishes on South African fishes have been severe. There are 45 IUCN (International Union for the Conservation of Nature) red-listed fish species in South Africa, of which 24 are endemic or near-endemic to the CFK [9]. Invasive alien fish species (mainly predatory species like smallmouth bass) are listed as the primary threat for 23 of the 24 indigenous fish species in the CFK. Predation on fish is not the only impact alien fish have on indigenous biota; they impact on aquatic plants and invertebrates, removing the source of food for native fishes and affecting the ability of rivers to absorb and decompose organic material. Carp are internationally renowned for causing water quality problems through their bottom-feeding habits and destruction of freshwater plants [11].



Figure 3.55 Smallmouth bass. This alien fish of North American origin is now established in many South African rivers, especially those of the Cape Floral Kingdom, where it is responsible for sharp declines in the numbers of native fish species. [Dean Impson]

The catchments and banks of many rivers are invaded by alien trees (gums, pines, wattles, willows and others), which use excessive amounts of water and reduce the flow of rivers. Invasive alien trees along riparian habitats have led to the elimination of shade-intolerant dragonflies and damselflies; this is of especial concern where the species are endemic. Invasive alien plants, especially Australian *Acacia* trees along water-courses, are by far the most important threat to these dragonflies and damselflies in South Africa. Removal of the invasive alien trees has led to the recovery of several species that had previously been thought to be extinct [12].



Figure 3.56 Invasive alien black wattle trees along the Rondergat River, in the Cederberg, Western Cape. These trees dominate the riparian zone, completely replacing native trees, and make the habitat unsuitable for other organisms such as dragonflies. [Dean Impson]

In addition to alien fish, other introductions include invasive alien snails, mussels and freshwater crayfish, although their impacts are not yet clearly understood. Freshwater snails will almost certainly compete with native species for both food and physical space. They may also act as intermediate hosts for liver flukes that infect livestock (as they do where they are invasive in other parts of the world).

Floating aquatic weeds also take their toll. One study [13] was able to show that the red water fern formed dense mats (5-20 cm thick), on dams of up to 10 ha and on slow-moving water bodies in South Africa. The weed seriously affected the biodiversity of freshwater ecosystems and had severe implications for all aspects of water utilisation. These effects were considered to be most severe in the agricultural sector, where the weed increased siltation of dams and rivers, reduced the quality of water for agricultural and domestic use, clogged irrigation canals and pumps and caused drowning of livestock that were unable to differentiate between pasture land and a weed-covered dam.

Example 3: Rinderpest and large mammals

Diseases represent a potentially devastating aspect of invasive organisms, as modern scares such as avian flu have amply demonstrated. One such devastating invasion has already occurred in Africa in the form of the rinderpest epidemic that took place at the end of the 19th century [14]. Early in February, 1896, large numbers of cattle and wildlife were reported to be dying from an obscure disease on both sides of the Zambezi River. By March it had reached Bulawayo, where a diagnosis of rinderpest was made. From there the plague was rapidly conveyed southwards by means of transport oxen and migrating wildlife. As it spread southwards it caused ruin and devastation, killing the majority of domestic animals in the region, as well as countless thousands of wild ungulates. Serious attempts were made to stop the disease at the Orange River by erecting a 1 000-mile long fence, but this, too, proved ineffective. By 1897, an effective inoculation was developed, and before the end of 1898 more than two million head of cattle had been successfully inoculated. By the end of 1898 rinderpest was under control and temporarily disappeared from South Africa. Although rinderpest's stay in the region was relatively short, its effects on large grazing and browsing ungulates was immense and their numbers were so reduced that it took decades for them to recover.



Figure 3.57 The rinderpest epidemic at the end of the 19th century caused enormous losses of both domestic stock and wildlife. [15]

What does the future hold?

Invasive alien species are a large and growing problem of the environment. Attempts have been made to predict the future impact of these species, but predictions are difficult as both the rate at which these species spread and the extents to which they will come to dominate ecosystems are critical unknowns. However, if we simply project what is known about invasive species and their ability to colonise and dominate areas, the consequences could be staggering [6]. Whether or not the predicted levels of invasion are possible is a matter of conjecture, but there are indicators that we can use to assess the seriousness of the threat. Many of South Africa's remaining natural ecosystems are relatively free of significant infestations of invasive alien plants at present (with the notable exception of the Fynbos Biome, where infestations of invasive plants are at much higher levels). The fact that many invasive plant species already occur in many areas at low densities, and are known to be able to develop into dense closed stands over time, suggests that an ongoing escalation in the level of infestations can be expected. The situation can also be expected to worsen as new invasive species become established. New invasive species will continue to arrive, and many potential invasive species are probably already here – but not yet invading. Many serious invasions have exhibited a 'lag period' in which the introduced species may occur at very low population levels for several decades before becoming invasive, sometimes suddenly. This could be the result of exponential population growth, a period of selection of genotypes suited to the newly invaded environment, or the occurrence of a change in environmental conditions that constrain invasions. With the rapid growth in the rate of introduction of new species, most introductions of alien species have occurred recently. It is therefore likely that a large number of invaders are currently in their 'lag period' and the rate of new invasive species problems will increase dramatically in future. Global changes, such as changes in climate and in the rates and magnitudes of biogeochemical cycles, may further worsen the situation by bringing about conditions that would make some benign alien species suddenly become invasive.

Science has an important role to play in mitigating the effects of invasive alien species. Awareness needs to be raised about the problem and regular and effective monitoring will be required to detect new introductions or

spread of alien species. Effective means of control also need to be developed and successfully implemented, preferably with the support and assistance of landowners and other key stakeholder groups. Regulations for alien plant and animal species that are currently being developed under the National Environmental Management: Biodiversity Act (NEMBA) will hopefully lead to more effective management of alien species.