Chapter 13
The Role of Environmental Factors in Promoting and Limiting Biological Invasions in South Africa

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Abstract South Africa is a megadiverse country in terms of biodiversity, with continental South Africa composed of nine terrestrial biomes. This diversity is in part due to the wide range of climatic and topographic conditions that exist in the

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country. This chapter explores how these environmental features influence biological invasions (focusing on terrestrial ecosystems). We first discuss broad features of the different landscapes, and then discuss how different environmental factors [geomorphology, soils, climate (including rainfall seasonality), extreme events (specifically droughts and floods), fire, freshwater, and land use] determine which species can establish, spread, and cause adverse impacts. The high diversity of invasive species in South Africa is partly due to the variety of environmental conditions, but some conditions (e.g. fire and aridity) also limit invasions. With reference to plants, invasive species assemblages seem to be co-incident with native species assemblages at a broad-scale (although the driving mechanisms are unclear). However, finer-scale influences of anthropogenic factors (e.g. introduction effort and disturbance) also play important roles in shaping invasive biotas. Together these factors suggest that climate-based species distribution models (with an additional fire filter) can accurately predict the broad-scale potential range of invaders in South Africa. However, at finer scales and for management purposes, we need to understand how humans directly and indirectly influence patterns of invasion.

13.1   What Does South Africa Look Like to an Alien Species?

South Africa is a largely temperate and sub-tropical country covering over 1.2 million km^2. While most of the country is arid to semi-arid, there are significant gradients in rainfall amounts and seasonality (Fig. 13.1). Elevation varies from sea level to over 3000 m asl. Conditions climatically analogous to those that exist in South Africa occur over approximately a fifth of the world's land surface (Richardson and Thuiller 2007; Fig. 1.1 in van Wilgen et al. 2020a, Chap. 1) [in this chapter we only consider continental South Africa, see Greve et al. (2020), Chap. 8 for a discussion of South Africa's sub-Antarctic islands]. There are nine terrestrial biomes within continental South Africa (Mucina and Rutherford 2006), with each biome largely contiguous to itself. Importantly, the major points of entry of goods coming into the country are in different biomes [Cape Town's ports and airports are in the Fynbos Biome, Durban's in the Indian Ocean Coastal Belt, Port Elizabeth's in the Thicket; the airports in Gauteng (i.e. Johannesburg/Pretoria) are in the Grassland; the land borders of both Beit Bridge and Lebombo are in the Savanna; and the land borders with Namibia are in the Desert] (Fig. 12.1 in Faulkner et al. 2020, Chap. 12) chapter. While human population density is much lower in the more arid biomes (the Desert, Nama-Karoo, and Succulent Karoo Biomes), even in these biomes alien species have been introduced due to farming, as ornamentals and pets, or due to mining activities (e.g. construction, the movement of equipment, and phytoremediation). This means there is a large pool of potential invaders, many opportunities for introduction and dissemination, and a range of environmental factors that can promote or limit invasions.
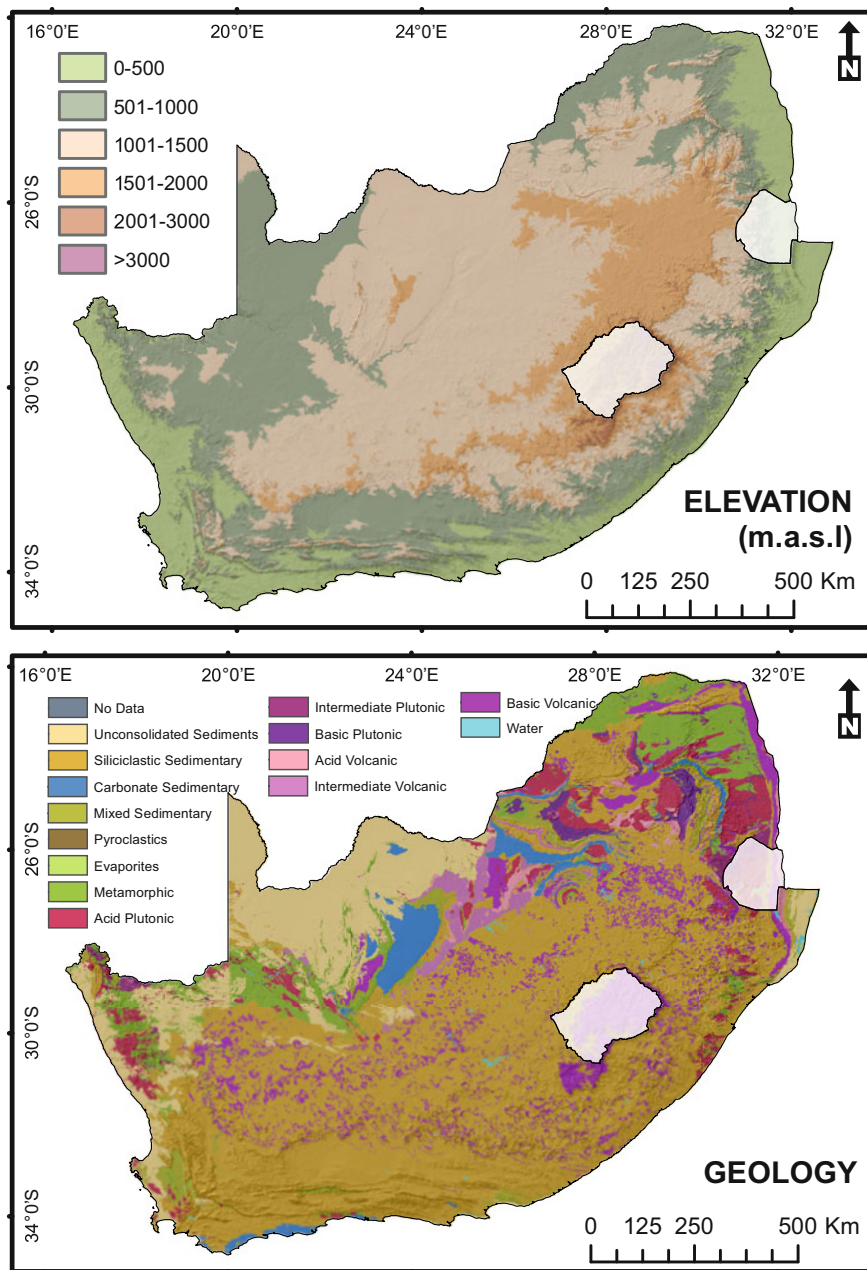
Fig. 13.1 Key environmental conditions of South Africa. ELEVATION: Data obtained from the Shuttle Radar Topography Mission (SRTM; USGS 2014) illustrate how South Africa's terrain varies from zero along the coastline to well over 3000 m above sea level in the Drakensberg mountains. GEOLOGY: Hartmann and Moosdorf (2012) describe 15 dominant rock types in a global lithology and geology (GLiM) assessment. South Africa has 12 of these 15 types, with siliciclastic sedimentary properties dominating (53%) followed by unconsolidated sediments (13%).
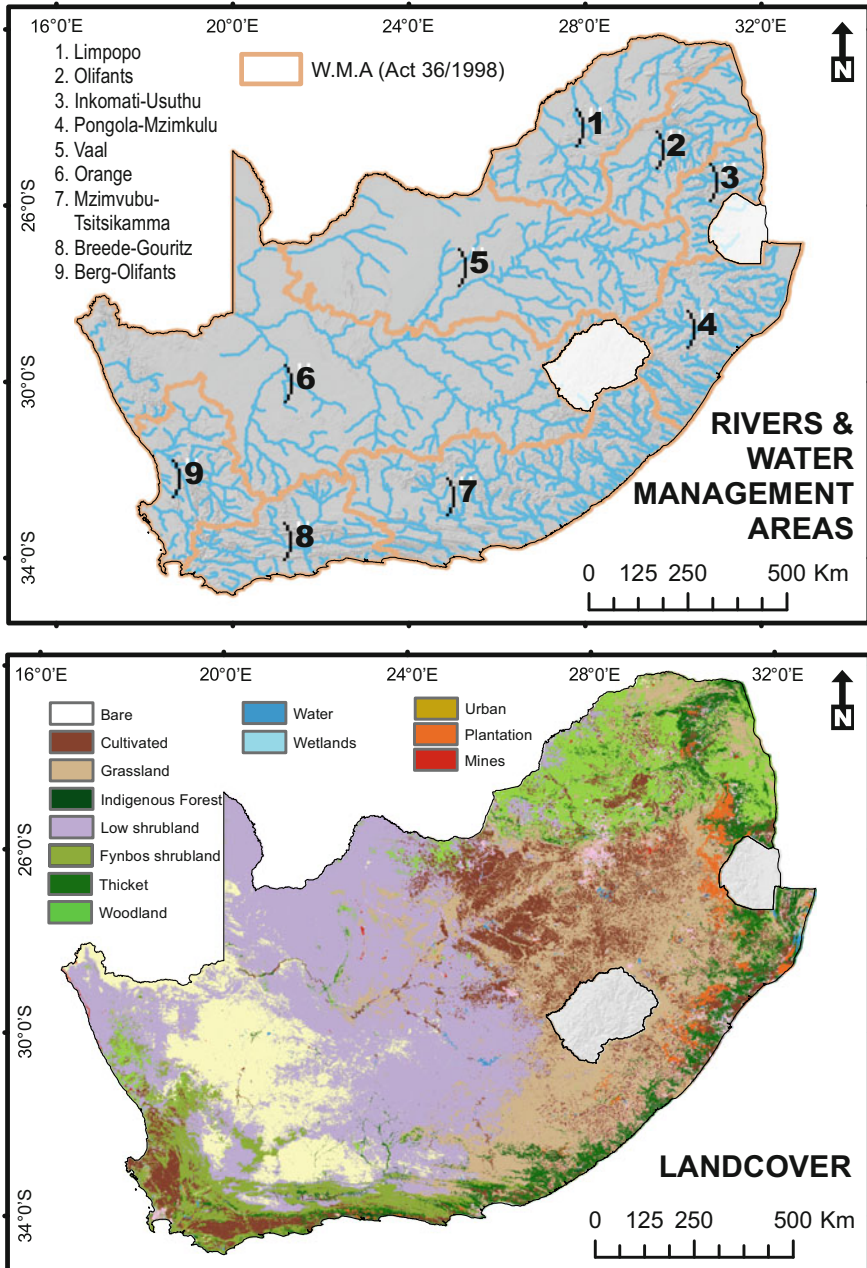
Fig. 13.1 (continued) RIVERS AND WATER MANAGEMENT AREAS (WMA): South Africa has over 1500 km of rivers and streams. To improve integrated water systems management, nine WMA were described in a recent revision of the National Water Act (36/1998) (Department of Water and Sanitation 2016): (1) Limpopo, (2) Olifants, (3) Inkomati-Usuthu, (4) Pongola-Mzimkulu, (5), (6) Orange, (7) Mzimvubu-Tsitsikamma, (8) Breede-Gouritz and (9) Berg-Olifants. LANDCOVER: The 2013–2014 national land-cover dataset was modelled from multi-seasonal Landsat 8 imagery and describes 72 landcover classes summarised down to 14 classes for broad scale visualisation (Department of Environmental Affairs 2015).
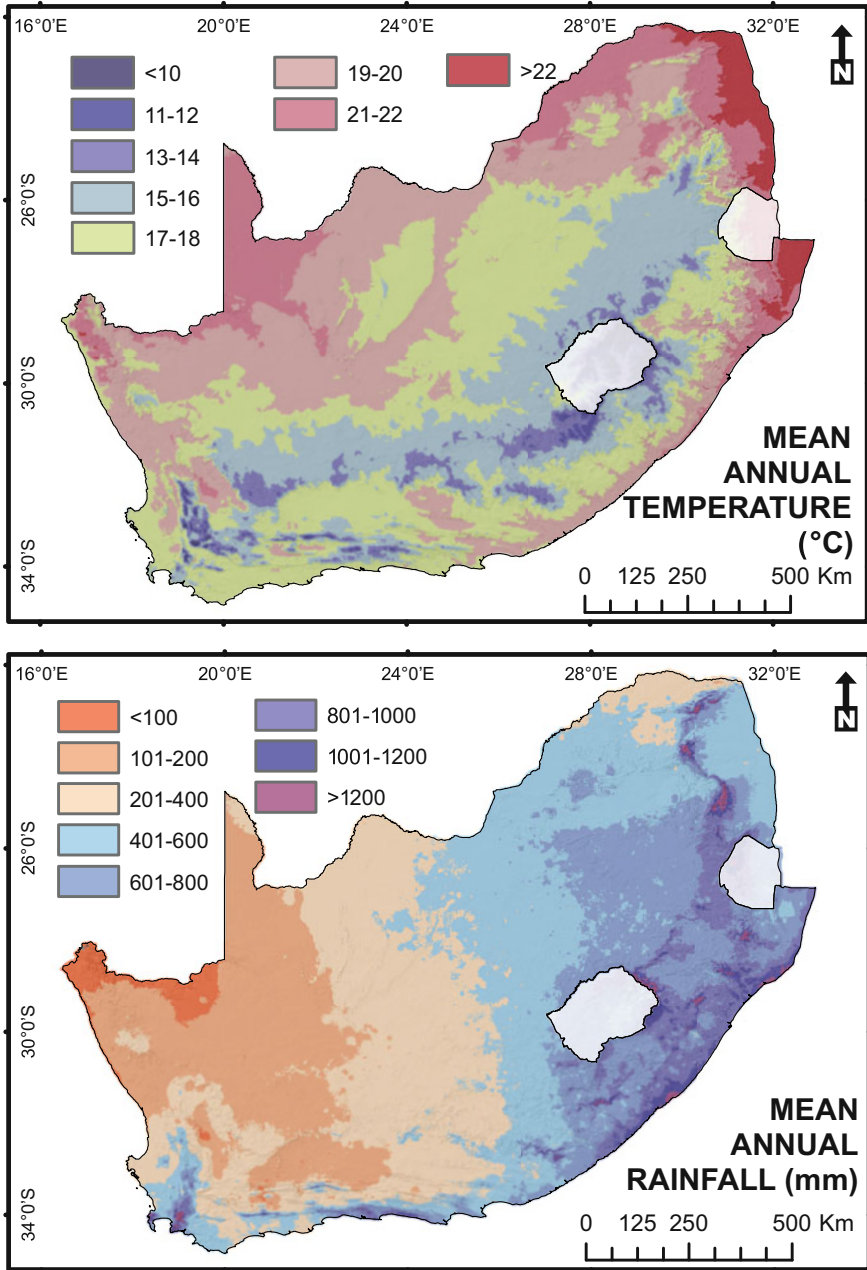
Fig. 13.1 (continued) MEAN ANNUAL TEMPERATURE: South Africa's mean annual temperatures range from <10 °C along the escarpment to over 22 °C in the far north-east. The effects of diurnal, monthly and seasonal patterns of maximum and minimum temperatures are smoothed in this statistic, as described by Schulze and Maharaj (2007a). MEAN ANNUAL RAINFALL: A clear east-to-west rainfall gradient is visible across South Africa with <100 mm falling in the north-west and over 1200 mm in the east (Schulze and Lynch 2007).
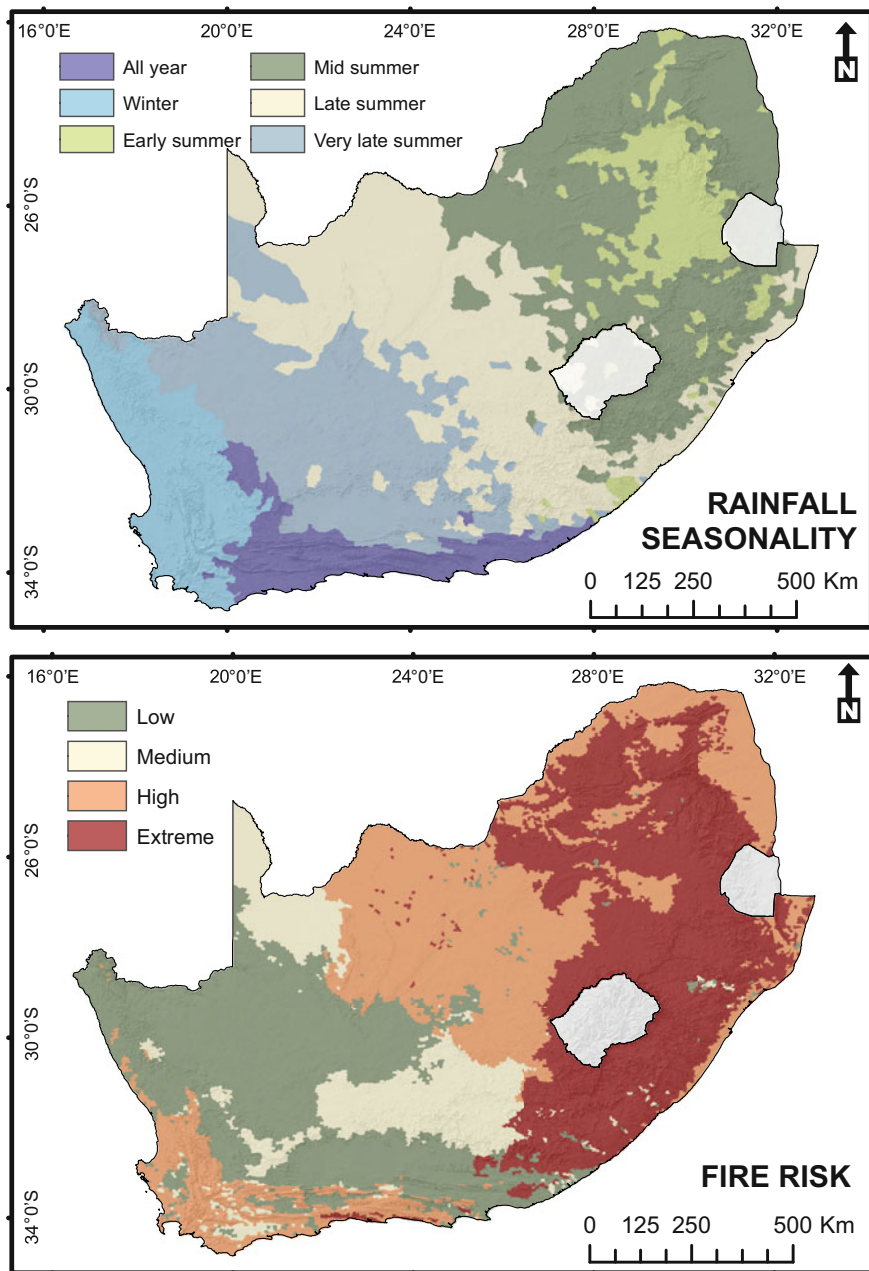
Fig. 13.1 (continued) RAINFALL SEASONALITY: The season in which rainfall predominantly falls is described by Schulze and Maharaj (2007b) as year round, winter, early-summer, mid-summer, late-summer, and very-late-summer. FIRE RISK: In developing a framework for the implementation of a National Veld and Forest Fire Act and providing a protocol for veldfire risk assessment for the National Disaster Management Framework, (Forsyth et al. 2010) quantified the level of risk for different fire scenarios across South Africa. A visual comparison of South Africa's mean annual rainfall and fire risk shows how increased rainfall leads to increased biomass resulting in more frequent fires

Two major river systems, the Limpopo and the Orange, both forming part of South Africa's northern border, contain more than 85% of South Africa's freshwater. Most other catchments are relatively small, and there are no large lakes. South Africa has a 2798 km long coastline, with estuaries making up a small but important component of South Africa's ecosystems [with a total of 465 estuaries, including the largest estuary in Africa, the St Lucia estuary in iSimangaliso Wetland Park in northern KwaZulu-Natal (Allanson and Baird 1999)]. South Africa has a significant marine exclusive economic zone (not including the sub-Antarctic islands) of just over 1 million km^2, a large proportion of which is on the continental shelf. There are two main oceanic currents, the warm Agulhas current that runs from the north-east to the south-west, and the cold nutrient-rich Benguela current that runs northward along South Africa's west coast. In this chapter we discuss flooding, but the impact of environmental factors on freshwater and marine invasions is discussed elsewhere (Robinson et al. 2020, Chap. 9; Weyl et al. 2020, Chap. 6). Urban ecosystems (and the particular climatic conditions they represent) are also discussed elsewhere (Potgieter et al. 2020, Chap. 11).

The key environmental features of South Africa are summarised in Fig. 13.1. The influence of these conditions on establishment, spread, and the impact of invasives is summarised in Table 13.1, and discussed in more detail using case-studies in the sections that follow.

13.2   Geomorphology

South Africa has a fascinating range of landscapes, and, as a result, a complex array of potential biogeographical barriers. There is substantial variation in elevation—43% of the country is under 1000 m asl; 55% 1000–2000 m asl; and while only 2% is over 2000 m asl, the maximum is 3450 m asl. Elevation in itself is unlikely to have a significant effect on invasions, though due to correlations with remoteness, pathways of introduction, and the impact of road development, the study of elevational patterns of invasions and how these change over time has been (and should continue to be) a valuable topic of applied research in South Africa (e.g. Kalwij et al. 2015). Relief is sharp in many parts of the country, with "topographic roughness" an important correlate of naturalised plant species richness (Richardson et al. 2005).

In comparison to the diversity of landscapes, there is relatively little seismic activity, no volcanoes, and few earthquakes. As in other countries, over-grazing, fires, and injudicious control of bush-thickening vegetation can result in landslides, but relative to other countries, landslides are not a major source of disturbance. The extraction of water through boreholes, the collapse of old mines, and the possibility of fracking, could lead to an increase in the frequency of disturbances (e.g. sinkholes), but it seems unlikely that these will provide major opportunities for invasions.

There are substantial opportunities to investigate the interaction between geo-morphology and invasions. Some areas, e.g. mountain tops, are much less invaded, and an evaluation of which elements of the South Africa landscape are currently more invaded and an assessment of the potential for future invasions would be very useful.

13.3   Soils

Soil properties such as pH, texture, redox potential, and nutrient status have myriad effects on the flora and fauna, but our understanding of how they influence invasions is still rudimentary. In general, however, invasibility might be expected to be correlated with the degree of disturbance (e.g. human-mediated physical or chemical disturbance). This is because each soil type has a unique array of chemo-physical properties, and through evolutionary time the native flora and fauna would have developed specific adaptations to deal with these. For example, alien grass species are known to thrive in the Fynbos Biome on old agricultural lands that have in the past been fertilised (Milton 2004). The native fynbos plants did not in general evolve on nutrient-rich soils and this places them at a disadvantage in such environments (Cramer et al. 2014). Similar issues certainly affect the distribution of some alien animal species, such as earthworms (Janion-Scheepers and Griffiths 2020, Chap. 7; Janion-Scheepers et al. 2016).

Given the above principles, the effects of soils on invasions should be analysed on a case-by-case basis. However, it might be possible to generalise for alien trees invading Fynbos and Grassland. In particular the shift from a relatively short plant form (shrubs or grasses) to a tall plant form (trees) can be explained in part by the Catabolic Theory (Milewski and Mills 2010; Mills et al. 2016, 2017). The theory has three main premises: first the availability of catabolic versus anabolic nutrients has marked effects on vegetation structure; second that short plants (e.g. shrubs and grasses) are more competitive than tree seedlings where demand for catabolic nutrients is met by supply; and third that demand for catabolic nutrients is dependent on the rate of photosynthate production (Milewski and Mills 2015; Mills et al. 2013a, b, 2016).

The presence or absence of alien trees in fynbos and encroaching native trees in grassland environments of South Africa have been linked to a wide range of nutrients, soil properties, and soil treatments, including pH, acid saturation, Mg, Ca, Mn, Cu, Zn, B, P, and N-fertilisation (Mills and Allen 2018; Mills et al. 2017). Unpublished data collected from 25 diverse sites across South African Fynbos, Grassland and Savanna sites have shown that soils in sub-sites relatively poor in boron or relatively rich in phosphorus tend to be less wooded than adjacent sub-sites. Boron is of particular interest with regards to tree invasions because the physiological demand for boron per unit photosynthate produced from short, monocotyledonous plants such as grasses is considerably less than for dicotyledonous trees. Indeed, it is the only nutrient that has this distinct difference in demand between grasses and

trees. In the context of the Catabolic Theory, poverty of boron will reduce anabolism, reducing the demand for catabolic nutrients, preventing plants from building up a surplus of photosynthates, and thereby favouring short herbaceous plants over tall woody plants. By contrast, phosphorus is predominantly catabolic as it is needed for producing adenosine triphosphate (the molecule that stores the energy released from the breakdown of carbohydrates and so the ultimate endpoint of catabolism in plants). A deficiency of phosphorus, like deficiencies of copper and zinc, results in accumulation of carbohydrates in plant tissues (Broadley et al. 2012; Graham 1980). Further research is needed to establish whether soil amendments that bind boron or increase phosphorus availability can constrain the establishment of alien tree seedlings.

Tree invasions can also be explained by increases in carbon dioxide levels. As carbon is a limiting anabolic element (as per The Catabolic Theory), increases in carbon in the soil boosts anabolism relative to catabolism, resulting in a surplus of carbohydrates. Thus, greater carbon dioxide levels shift the competitive balance towards carbohydrate-rich plants such as trees.

The impact of edaphic factors on invasions is still, however, an area ripe for more research. There have been a few fairly limited autecological studies [e.g. granite specialists such as Sweet Hakea (*Hakea drupacea*) occur on granite; and the invasive New Zealand Christmas Tree (*Metrosideros excelsa*) in the Western Cape requires moist organic-rich substrates for germination and establishment, allowing fine-scale habitat suitability to be accurately predicted based on native species with similar edaphic preferences (Rejmánek et al. 2005)]. There is, however, also on-going broader-scale research in the Fynbos Biome. Although fynbos soils are very poor in key nutrients, similarly nutrient-poor soils elsewhere in the world, e.g. Western Australia, support forest vegetation. The paucity of trees in fynbos has been attributed to nutrient and/or water limitations. However, the success of alien trees such as acacias and pines dispels the myth of such resources as a major barrier to tree growth in the fynbos (Richardson and Cowling 1992). Moreover, the interaction between nitrogen-fixing alien *Acacia* species and the nitrogen-poor soils has resulted in dramatic ecosystem-level impacts and regime shifts (Gaertner et al. 2014; Holmes et al. 2020, Chap. 23). Again, this emphasises the importance of considering biotic-abiotic interactions in mediating invasions and their impacts, e.g. the fynbos is highly susceptible to soil-altering invaders. Another result of the fact that many of the landscapes, particularly in the greater Cape Floristic Region, can be characterised as OCBILs i.e. "old, climatically buffered, infertile landscapes" (Hopper 2009), is that the edaphic fauna is composed of many ancient lineages. Such lineages show little biotic resistance to invasion, although this has not been well studied (Janion-Scheepers et al. 2016).

13.4 Climate

South Africa has hot summers, which, combined with aridity, produces significant water stress. Moreover, rainfall seasonality changes dramatically across the country (Fig. 13.1) influencing runoff and evapotranspiration (Schulze and Maharaj 2007b). The majority of the country receives summer rains from the Intertropical Convergence Zone to the east. However, along the west and southwest coast winter rainfall comes from westerly winds over the cold Benguela current (Chase and Meadows 2007; van Wilgen et al. 2020a, Chap. 1). Between these areas, rainfall is intermittent throughout the year. This variation in rainfall seasonality creates distinct phenology among native flora and fauna, and often demarcates the distribution of species (Colville et al. 2014), or maps onto genetic disjunctions within species (Tolley et al. 2014). But such limitations can be alleviated by human-made irrigation schemes or dams [for a discussion of interbasin water transfer (IWT) schemes in South Africa see Box 12.2 in Faulkner et al. (2020), Chap. 12; and Muller (1999)]. Anthropogenic changes in seasonal water availability has resulted in the range expansion of a variety of native species (Okes et al. 2008), and facilitated invasions (Davies et al. 2013; De Villiers et al. 2016; Measey et al. 2020, Chap. 5; Moodley et al. 2014).

The incidence of frost also varies significantly across the country. The low-lying coastal areas tend to be frost-free, but the high-elevation central plateau experiences frost in most years. While frost incidence has severely limited the presence of native trees on the Highveld, many alien trees are frost-hardy and able to invade treeless ecosystems. Moreover, frost damage ("frost heave") in otherwise dense and impenetrable grass swards in the Cathedral Peak area of the Drakensberg has been implicated in creating opportunities for the establishment of Patula Pine (*Pinus patula*) seedlings (Richardson and Bond 1991).

Insect establishment and spread is similarly known to be affected by abiotic conditions. For example, Zimmermann and Moran (1991) argued that rain, hail, and heavy wind (together with predation of eggs by native ants) provided a substantial barrier to the establishment of the biological control agent Cactus Moth (*Cactoblastis cactorum*); and Singh and Olckers (2017) argued that temperature and humidity limited the spread of the biological control agent *Anthonomus santacruzi* that was introduced to control Bugweed (*Solanum mauritianum*).

13.4.1 Species Distribution Models

The marked gradients in temperature, mean annual precipitation, rainfall seasonality, and frost (Fig. 13.1) mean that South Africa is arguably well suited to using species distribution models to predict invasions (Rouget et al. 2004). Species distribution models, which attempt to quantify the environmental niche suitable for a species, have been used to predict the potential distribution of several major plant invaders

Table 13.1 How environmental conditions of South Africa influence biological invasions, and how invasions can influence them. These issues are discussed (and referenced) in more detail in the text. See Fig. 13.1 for relevant maps

Factor	Geographic distribution	Influence on establishment	Influence on spread	Influence on impact
Geomorphology	Low coastal areas, but rising (in some cases sharply) to a large inland plateau. There are several substantial mountain ranges, with two main systems—the Drakensberg, and the Cape Fold Belt.	Elevation itself is unlikely to be a barrier to establishment, though many of the mountain tops are rarely visited so generally subjected to lower colonisation pressures.	The mountains are substantial barriers to natural dispersal and significant sources of native species biogeographical variation. However, a network of paved mountain passes has increased the potential for spread both through mountain systems and up them. Species often spread extensively from mountain tops down.	Areas with high levels of relief greatly complicate management efforts.
Soils	South Africa is generally geologically old with no recent volcanic activity or glaciation. Consequently, soils tend to be nutrient-poor, but there is a substantial mosaic. Agricultural and other activities have profoundly altered soil properties, and the legacy effects of such disturbances on native soil biodiversity and soil chemistry are still poorly understood.	The impact of soils on establishment success of alien species is likely to be context-dependent. Few alien species are known to be soil specialists, but such relationships have not been studied in detail.	The movement of soils around the country by humans (deliberately and accidentally) has an important but as yet unquantified role in the dispersal of alien and native species. Little is known about the role of soils in mediating spread.	Addition of nutrients (e.g. through legume invasions) can radically alter soils. The resulting physical changes to the ecosystems present a major challenge to restoration.

(continued)

Table 13.1 (continued)

Factor	Geographic distribution	Influence on establishment	Influence on spread	Influence on impact
Climate	Mean annual precipitation varies profoundly across the country, with rainfall seasonality changing from south-west to north-east. Temperatures co-vary along the altitudinal and latitudinal gradients, with most of South Africa colder than its northern neighbours.	The seasonal variation in water availability limits the establishment of some species in some parts of the country, although urban areas, irrigation, and other human modifications can facilitate spread to areas otherwise climatically unsuitable. Low temperatures are a significant barrier to spread from tropical Africa.	Strong (often gale-force) winds are a feature of many parts of the Fynbos Biome and have likely substantially increased the rates of spread of alien tree species (pines and hakeas in particular).	The interaction between climate change and invasions is complex, but there are likely to be a few general trends: more of South Africa will become suitable for tropical species; temperate invaders will increasingly be pushed out; and invasive species will reduce the opportunities for native species to shift in range.
Floods and droughts	All regions of South Africa periodically experience floods and droughts of varying intensity. Global climate change is increasing the frequency and intensity of these.	Floods create disturbance which opens habitat for invasions. There is an increase in resources and additional nutrients released in the system. Periods of inundation following floods provide for stochastic recruitment events. Droughts induce high levels of environmental stress, potentially reducing biotic resistance. Droughts therefore can create invasion windows if alien species can establish more quickly than native species can recover.	Floods play a major role in the wide-scale distribution of propagules. Species already present can be more widely distributed, and new species can be brought into an area. During a drought, resistant alien species that produce seeds might be favoured by animal dispersers (e.g. birds) over native species. Indirectly, many species are selected for drought-resistant traits, and are widely spread for agriculture and other uses. Injudicious disaster relief can introduce new invasive species that undermine the long-term environmental sustainability of affected regions.	The relatively small catchments and often low levels of water mean that alien species that alter hydrological features of catchments (in particular those that tap into ground water) can have profound impacts, worsening the effects of droughts. By changing stream dynamics, and in some cases blocking river flow, invasive plants can also significantly worsen the consequences of floods. Flood and drought events, especially extreme events, add complexity to understanding species traits and ecosystem properties driving invasions.

Fire	Many of the biomes in South Africa (the Fynbos, Savanna, and Grassland Biomes in particular) are fire-adapted and have evolved to cope with burning (Table 13.2)	Large areas of the country are not suitable for fire-sensitive species, and so there are a suite of species that, while prominent along road-sides, do not spread into natural ecosystems.	Some species actively disperse as a result of fire (e.g. serotinous pines and hakeas). In addition, the post-fire environment provides an opportunity for species to invade new areas.	In the fynbos, invasion of low shrublands by alien trees can increase the intensity of fires, damaging soils and threatening biodiversity, personal property, and human lives.
Land use	Most of the natural environment (~70%) is used either for livestock production or wildlife ranching, although crop cultivation (dryland and irrigated) also occurs over a significant part (~11–13%) of the country. The remaining area is used for a wide range of other purposes such as nature conservation, forest plantations, mines, roads, and urban settlements. Grazing is country-wide with intensity linked to aridity, and it is higher in communally owned areas.	Cultivation and urbanisation, by buffering adverse conditions, can increase the ability of populations to establish, although disturbance caused by cultivation and urbanisation might also limit invasions. Grazing pressures have seen a shift to unpalatable species (some of which might be alien).	The availability of water islands has allowed the spread of species through otherwise hostile dry regions, and also allowed for the expansion of several native species including the Hadeda Ibis (*Bostrychia hagedash*), and the Painted Reed Frog (*Hyperolius marmoratus*). Roads and railways act as important conduits for invasive spread. Livestock can disperse alien species both as a result of stock movements and by moving around paddocks and encampments.	Invasive species (*Prosopis* species in particular) have, in some cases, prevented access to grazing areas or rivers, and through direct damage reduced the land available for pastoralism. Grazing can self-select to reduce grazing (i.e. a non-virtuous cycle).

(Higgins et al. 1999; Robertson et al. 2001; Rouget et al. 2004; Trethowan et al. 2011; Walker et al. 2017), and a wide range of other taxa including alien amphibians (Davies et al. 2019), crayfish (Nunes et al. 2017), fish (Lubcker et al. 2014; Zengeya et al. 2013), and fruit flies (De Meyer et al. 2010). Such models have also been used to predict future potential invaders, e.g. to assist in the development of a watch list of species (Faulkner et al. 2014), and to inform surveillance efforts (Faulkner et al. 2017).

Importantly, however, the broad-scale environmental variables typically used as input to species distribution models permit only broad-scale predictions. Human-mediated changes, for instance to water stress (e.g. through irrigation) are difficult to capture in such models. There has been more success in integrating the role of human-caused disturbances by using integrative variables like the "human footprint" ("Global Human Influence Index") metric or other proxies of human influence such as road density or human population density (e.g. Donaldson et al. 2014; Richardson et al. 2005; Thuiller et al. 2006).

To date, most of the distribution modelling has relied on correlative approaches but an increasing use of mechanistic models is likely to both improve the predictions and help identify testable hypotheses that can provide insights for management (Kearney and Porter 2009). Studies have also investigated issues associated with predicting potential distributions, in some cases highlighting important invasion dynamics (Le Maitre et al. 2008; Wilson et al. 2007). For example, the distribution of Port Jackson Willow (*Acacia saligna*) in South Africa does not match its climatic envelope in Western Australia due to introductions originating from an admixed novel genetic entity (Thompson et al. 2011). Understanding sub-specific variation in potential distributions is increasingly recognised as an important consideration in species distributions modelling for invasions (Smith et al. 2019).

13.5 Extreme Climatic Events and Large Infrequent Disturbances

Extreme climatic events (Easterling et al. 2000) and large infrequent disturbances (Turner and Dale 1998) can have profound and long-lasting impacts on the function of ecosystems (Parsons et al. 2006), including on where alien species establish, spread, and invade. Globally, disturbances such as floods and droughts are predicted to increase in severity and frequency due to the effects of global climate change (Lesnikowski et al. 2015). In South Africa, while there is considerable variability in precipitation spatially and temporally (Rouault and Richard 2003), this inter-annual variability has increased over the last ~50 years (Fauchereau et al. 2003). Droughts are likely to become more intense and widespread, and trends show the probability of extreme rainfall increasing (van Wilgen et al. 2020b, Chap. 29). Such changes in climatic conditions are expected to influence invasions (Chown 2010), although the implications and mechanisms are not well understood (Diez et al. 2012).

Major tropical storms or tsunamis are not common in South Africa, nor are there major snowstorms. However, global climate change is expected to lead to a greater frequency of cyclones that affect the east of the country, and these might lead to dramatic increases in the extent of some invasive species. For example, McConnachie et al. (2011) noted that Parthenium Weed (*Parthenium hysterophorus*) "*...reportedly became common and invasive after Cyclone Demoina caused extensive flooding along the east coast of southern Africa in 1984*". Further occurrences such as the March–April 2019 Cyclones Idai and Kenneth, and subsequent flooding events in eastern Mozambique, will probably have similar impacts on the spread of invasive species in this area. In the next sections we discuss how floods and droughts (which are common in the region) have major impacts on a wide range of biological invasions.

13.5.1 Floods

Alien species can often take advantage of flood-induced disturbance, particularly if they tolerate wider environmental conditions (Dukes and Mooney 1999), and/or exhibit traits that facilitate rapid resource acquisition, growth, and colonisation (Pyšek and Richardson 2007). By contrast, large infrequent floods can also act to remove invasions. For example, the flood in the Sabie River in Kruger National Park in 2000 [which had an estimated return interval of 90–200 years depending on the position in the catchment (Smithers et al. 2001)] removed all vegetation and restructured the physical template (Parsons et al. 2006). By 2004 few alien species had re-established—only 19 of 119 herbaceous species and nine of 136 woody species (Foxcroft et al. 2008)—and their abundance was low—6% of all herbaceous species and 3% of all woody species. This state was not stable, however, and a survey of the same sites in 2015 revealed that the number of alien species present had increased (to 40), herbaceous alien species had densified (to 70–80% of the total density), although woody species remained at very low densities (TE Sibiya, unpublished data).

Recruitment of native species in arid regions is frequently linked to rare rainfall events, and it is likely that alien species use the same strategy. Milton and Dean (2010) reported that seedlings of Pink Tamarisk (*Tamarix ramosissima*) occasionally recruited in large numbers following floods in dry riverbeds and dams. *Prosopis* species (Mesquite) in the Karoo appeared to spread substantially following large floods in 1970s and 1980s (Harding and Bate 1991), with a fourfold increase between 1974 and 1991 during above-average rainfall years (Hoffman et al. 1995). Floods disperse Giant Reed (*Arundo donax*) rhizomes, which take advantage and establish in bare disturbed rivers, from where it rapidly invades (Guthrie 2007).

A large amount of research in South Africa has focussed on the impacts of plant invasions on ecosystem services [e.g. on surface water loss (Le Maitre et al. 2000) and on the risk of flood damage (Le Maitre et al. 2014)]. The role that floods play in the invasion process, however, requires further attention. As argued by Richardson

et al. (1997), "*Features of the riparian environment that promote invasions include the easier access to moisture (which reduces any drought stresses imposed by prevailing features that delimit the biomes), and periodic disturbances in the form of floods that disperse seeds, prepare them for germination, provide seed beds, and remove competing plants*". Invasive woody trees like Weeping Willow (*Salix babylonica*) and Red Sesbania (*Sesbania punicea*) can form dense stands, obstruct flow, alter watercourses, and convert well-defined rivers into diffuse systems of shallow streamlets and trickles. An important finding of Galatowitsch and Richardson (2005), working on the Eerste River in the Western Cape, was that "*seed regeneration of indigenous trees in these headwater rivers is not disturbance-triggered.*" This is in contrast to the major invaders of such rivers, for which germination is typically very clearly disturbance-related. With major alterations of the flow regimes in such rivers (Meek et al. 2010), flooding is more common, which provides abundant opportunities for regeneration of the invasive species. These processes, and the impacts caused, can be exacerbated by violent thunder-storms that typify some parts of South Africa (e.g. much of the Grassland Biome).

13.5.2 Droughts

Droughts induce extreme stress conditions that can reduce the biotic resistance of a community over time. If alien species survive longer, and respond quicker once a drought lifts, they will have significant opportunities post-drought (Diez et al. 2012). *Prosopis* species were introduced to South Africa in the late 1880s, and widely distributed as they provide fodder and shade when water is scarce. It is now estimated that invasive *Prosopis* populations cover 1.8 million ha in South Africa (Shackleton et al. 2015). Similarly, the Peruvian Pepper Tree (*Schinus molle*) was selected for its drought tolerance and widely planted along roadsides in arid areas over the past 60 years (Iponga et al. 2008). It out-competes native species and is increasing in abundance (Iponga et al. 2009). Cactaceae species, in particular Mission Prickly Pear (*Opuntia ficus-indica*), were widely planted in some arid regions for a variety of benefits, and have invaded at least 900,000 ha, displacing natural vegetation (Annecke and Moran 1978). Although the importance of drought in facilitating these invasions is not clear, their competitive ability under drought conditions clearly played a role in their ability to establish, persist, and dominate.

13.6   Fire

A combination of periods of hot, dry weather, flammable vegetation, and abundant sources of ignition means that fires are a regular feature of many (but not all) of the terrestrial landscapes in South Africa (see Table 13.2 for examples; van Wilgen and Scholes 1997). Specifically the Fynbos, Grassland and Savanna Biomes have

Table 13.2 Fire regimes in fire-prone biomes in South Africa, with examples of how fires can select for particular plant invasions

Biome	Fire regime	Examples of invasive taxa Whose spread is promoted by fire	That are resistant to fire	That are excluded by fire
Fynbos	Regular fires, typically at intervals between 8 and 15 years, mainly in the dry summer (in the west) or in all months (in the east) (Kraaij and van Wilgen 2014). Fire intensities of up to 21,000 kW m^{-1} measured in experimental fires; intensities in wildfires can be considerably higher (van Wilgen et al. 1985).	Some *Hakea* and *Pinus* and other serotinous trees and shrubs; *Acacia, Paraserianthes* and other taxa that survive by means of soil-stored seed banks that are stimulated to germinate by fire.	*Eucalyptus* and *Populus* trees, and other taxa with the ability to re-sprout after fires.	*Pittosporum undulatum, Solanum mauritianum* and other species that invade forests and lack adaptive traits to survive fires.
Grassland	Regular fires at intervals of 2–5 years in the dry winter months. Fires are more frequent in areas with higher and more regular rainfall, while at more arid sites, there is a large inter-annual variation in rainfall, and fires are less frequent. Fire intensities have not been quantified, but presumably are similar to savanna.	*Chromolaena odorata, Lantana camara, Parthenium hysterophorus,* and other herbaceous taxa are pre-adapted to frequent fires. Whether or not fire promotes invasion has not been investigated in the Grasslands or Savanna Biomes.		*Pinus patula* and other large woody plant invaders can be prevented from reaching maturity between fires. Cactaceae and other taxa that are pre-adapted to arid climates where fires are absent are also excluded.

(continued)

Table 13.2 (continued)

| Biome | Fire regime | Examples of invasive taxa | | |
		Whose spread is promoted by fire	That are resistant to fire	That are excluded by fire
Savanna	Regular fires at intervals of 2–5 years in the dry winter months. Fires are more frequent in areas with higher and more regular rainfall, while at more arid sites there is a large inter-annual variation in rainfall, and fires are less frequent (van Wilgen et al. 2004). Fire intensities of up to 21,000 kW m^{-1} measured in experimental fires; intensities in wildfires can be considerably higher (Govender et al. 2006).			High-intensity fires can be used to retard invasion by *Chromolaena odorata* (te Beest et al. 2012).

evolved with fire; fires are either absent or very infrequent due to a lack of fuel in the Nama Karoo, Succulent Karoo, Desert Biomes, and arid parts of the Savanna Biome; and in the Forest and Albany Thicket Biomes fires are largely excluded due to the non-flammable vegetation (van Wilgen et al. 1990).

Fires can either promote or retard invasions, depending on the ability of individual species to respond to fires. There are four broad types of responses of plants to fire.

1. Serotiny

Serotiny has evolved specifically as a mechanism for plant populations to persist in regions characterised by frequent fires (Lamont et al. 1991). Several major invasive plant species in South Africa (e.g. *Hakea* and *Pinus* species) accumulate seed banks in serotinous cones or follicles over several flowering seasons. These plants are typically killed by fires and spread over considerable distances by means of winged seeds that germinate in the post-fire environment. Spread and densification is therefore facilitated by fires which occur at intervals that allow the plants to mature and accumulate large seed banks during inter-fire periods (Richardson et al. 1987). Without such fires, invasions are either very slow or do not happen (e.g., Geerts et al. 2013b).

2. Soil-Stored Seed Banks

Trees and shrubs in the genera *Acacia* and *Paraserianthes* have soil-stored seed banks whose germination is stimulated by fire (Richardson and Kluge 2008). The hard-coated seeds are shed each year and accumulate in the soil. The heat from fires stimulates mass germination, so that stands of these invasive plants become denser after each fire.

3. Resprouting

Species pre-adapted to survive fires by means of re-sprouting do so either from underground rootstocks or from epicormic buds at the base of the stem or below the bark in the canopy (e.g. *Eucalyptus* and *Populus* species, and some alien perennial grass species). In cases where species resprout vigorously after a fire, the lack of competition in the post fire environment can mean that regular fires enhance invasion [e.g. Kudzu Vine (*Pueraria montana*) (Geerts et al. 2016)].

4. Fire Sensitive Species

Alien plant species native to areas where fires do not occur are unlikely to possess mechanisms to persist in fire-prone areas. Examples include plant species that invade forests [Sweet Pittosporum (*Pittosporum undulatum*), *Bugweed (Solanum mauritianum)*] or very arid areas that seldom experience fire (Cactaceae). An intolerance to natural fire regimes has been cited as a main reason why some alien plants are limited to disturbed road-sides and do not invade natural ecosystems (Geerts et al. 2013a; Holmes et al. 2018). Native forest trees that are embedded in fire-prone fynbos vegetation are fire-sensitive, but native forest patches are able to persist because of differences in their fuel properties that exclude fires (van Wilgen et al. 1990). The seeds of native forest trees can germinate on recently-burnt fynbos

sites, but do not establish or persist, as they require enhanced nutrients and moisture, as well as long fire-free intervals (Manders and Richardson 1992).

5. The Influence of Fire Regimes

The effect of fires on invasions also depends on fire frequency. Invasive alien trees and shrubs, such as *Pinus* and *Hakea* species, invade the treeless fynbos because they are pre-adapted to fire-prone ecosystems, and can establish and reach reproductive maturity between fires. The frequency and intensity of fires in Africa has also been postulated as the main reason why African grasses are widespread invaders elsewhere in the world, but alien grasses are relatively unsuccessful in Africa (Visser et al. 2016). Higher-rainfall Grassland and Savanna Biomes can burn every second year, killing most serotinous species before they reach reproductive age, thus preventing invasions [Table 13.2, though cf. species such as Pompom Weed (*Campuloclinium macrocephalum*) and American Bramble (*Rubus cuneifolius*) that are tolerant of frequent fires and thus able to invade]. Fynbos, on the other hand, usually burns at intervals of 10 years or more (Kraaij and van Wilgen 2014) which allows serotinous plants to mature and invade. The short fire cycles explain why *Pinus patula* is not as aggressively invasive in the Grassland Biome (despite widespread plantations) as other *Pinus* species in the Fynbos. Importantly, however, invasive species can also alter fire frequencies to their advantage, e.g. frequent fires can prevent resprouting or reseeding species such as Australian wattles (*Acacia* species), but once such invasive species become dominant, they shade out grasses, remove the primary fuel for fires, and alter fire frequency in a way that gives them a competitive advantage (Gaertner et al. 2014).

Of course, fire does not act alone in promoting invasions, and there are strong interactions between herbivory, fire, and invasion. Over-grazing removes fuel before the vegetation can burn, leading to the removal of fire from the dynamics of the ecosystem and allowing some invasive plants to colonise areas disturbed by over-grazing (O'Connor and van Wilgen 2020, Chap. 13). In the Fynbos, the interaction between fire and wind has been crucial in shaping the invasion window for alien trees and shrubs such as hakeas and pines (Richardson and Brown 1986).

13.7   Interactions Between Land Use and Other Drivers

Land use reflects the socioeconomic function of land (Martinez and Mollicone 2012) and refers to the multitude of ways in which people utilise, manipulate, manage, or unintentionally modify the environment, usually to obtain a product that can be consumed, traded or sold. Abiotic factors, such as climate, geomorphology and soils, play a key role in determining the nature and intensity of land use as well as the influence that land use has on invasives. In South Africa, most of the environment (~70%) is used either for livestock production or wildlife ranching (Meissner et al. 2013) although crop cultivation (dryland and irrigated) also occurs over a significant part (~11–13%) of the country (Schoeman et al. 2013). The remaining area is used

for a wide range of other purposes such as nature conservation, forest plantations, mines, roads, and urban settlements (Fairbanks et al. 2000).

The impact of land use on invasions is context-dependent and changes across spatial and temporal scales depending on regional climatic, habitat, and local disturbance factors (Cabra-Rivas et al. 2016; Gonzalez-Moreno et al. 2014; Walker et al. 2017). At large spatial scales environmental factors, especially climate, seem most important (Terzano et al. 2018), while at landscape or habitat scales, local land-use practices also influence the establishment and spread of alien species (Thuiller et al. 2006). Examining plant invasions in South Africa, Rouget and Richardson (2003) found that there is a stronger response to environmental factors at large spatial scales. Exploring this in more detail for invasive tree species that are also commercially important crops in South Africa, Rouget et al. (2002) found that the distribution of invasive stands was largely explained by climatic factors, even when key factors that are known to drive invasions at the landscape scale, such as propagule pressure from plantations and landuse, were included in models. In a study at the landscape scale, Rouget et al. (2001) found soil pH to be the most important variable for explaining invasive pine distribution in a highly fragmented semi-arid shrubland. Similarly, Goodall et al. (2011) showed that the presence of the herbaceous Pompom Weed in the grasslands of Gauteng Province is affected by environmental factors such as rainfall, topography, and soil texture at large spatial scales. However, at a more local level, historical contingencies, and specific land use practices, were more important in determining where plants are found. In their study, degraded rangelands, fallow fields, and drained wetlands exhibited a greater dominance of Pompom Weed than did rangelands that were covered by a healthy grass sward. Well-managed rangelands in relatively good condition, therefore, were better able to resist invasion by Pompom Weed than overgrazed, frequently-burned rangelands in poor condition.

In rangelands, herbivory on both native and alien species affects the abundance and rate of spread of invasive species. Steinschen et al. (1996) found that heavy grazing in Namaqualand's rangelands promoted the spread of annual alien grasses such as Japanese Brome (*Bromus pectinatus*). Continuous, heavy grazing removes the competitive dominance of perennial shrubs, which, in turn, promotes the spread of annual grasses, with concomitant negative impacts for sheep production in the affected region. However, local environmental conditions also influence specific outcomes and biotic interactions are mediated in complex ways by abiotic factors such as climate and soil. For example, a field experiment in the arid savanna of the Northern Cape involving the manipulation of seedlings of the naturalised Peruvian Peppertree (*Schinus molle*) showed that browsing reduced the establishment, growth and survival of seedlings (Iponga et al. 2009). The precise outcome was strongly influenced by soil type (greater success in fertile versus low nutrient status soils) and microsite (greater survival under large native tree canopies than in the open).

The land use type (e.g. livestock production, arable lands) and the intensity of land use do not always affect the establishment and rate of spread of invasive species in intuitive ways. For example, Schor et al. (2015) showed how disturbance influences the spread of the invasive Bugweed in KwaZulu-Natal. They suggest that

intense land use (e.g. overgrazing) leads to reduced frugivore abundance, which, in turn, means that fewer fruit of the invasive Bugweed are eaten and dispersed by animals and, by inference, reduced rates of spread. However, increased land use intensity can also lead to an increase in the abundance of particular alien species such as Australian Pest Pear (*Opuntia stricta* var. *stricta*) (Strum et al. 2015).

In protected areas the number of settlements and cultivated fields as well as the intensity of grazing are generally far lower. Opportunities for long-distance dispersal via road corridors are also significantly curtailed since the road network is less extensive and used less. The boundaries of protected areas can, therefore, provide an effective filter to the spread of invasive species which generally decline in abundance inside the reserve. In their study of the Kruger National Park, for example, Foxcroft et al. (2011) concluded that the park boundary provided an effective barrier to invasions since the records of invasive plant species declined rapidly beyond 1.5 km inside the park.

Proximity to highly-disturbed environments has an important influence on the cover and richness of alien plants. In general, urban areas act both as points of introduction and as bridge-heads for alien species (Gaertner et al. 2017; Potgieter et al. 2020, Chap. 11). This is evident both at regional scales and at landscape scales (Donaldson et al. 2014; Milton et al. 2007). Small towns in particular contain a high diversity of alien plants and opportunities for spread into neighbouring natural ecosystems (McLean et al. 2017, 2018). Roads and railways can also both facilitate the spread of alien plants in South Africa and, by providing disturbance, provide sites for establishment [cf. Faulkner et al. (2020, Chap. 12); though see also Kalwij et al. (2008)]. For example, the distribution of the invasive Fountain Grass (*Pennisetum setaceum*) closely tracks the road-network and associated disturbances (Rahlao et al. 2010), while *Schinus molle* was often planted as a road-side shade tree, creating foci for invasions (Richardson et al. 2010). Other human modifications of the environment, e.g. fencing and the construction of telegraph poles, will presumably have had a similar range of impacts on invasions and their spread. The development of highly disturbed agricultural fields poses a particular problem for the spread of invasive aliens (van Rensburg et al. 2018), which is perhaps greatest for riparian zones. Meek et al. (2010) surveyed the vegetation of a river corridor passing through different types of land use in the fynbos. They showed that alien plants were significantly more abundant at sites adjacent to agricultural fields and urban areas as compared with natural areas or grazing lands.

Perhaps the best example of how land use disturbance facilitates the spread of invasive species is the role that plantation forestry has played in the expansion of alien conifers in South Africa. Van Wilgen and Richardson (2012) estimated that the extent of invasive conifer stands, mostly pines, is more than four times greater than the extent of formal forestry plantations (0.66 vs. 2.9 million ha), but that formal plantations continue to provide propagules for invasive conifers to expand their range into natural environments across South Africa.

The type and intensity of land use and how it has been practised over time are, therefore, useful predictors of the distribution of alien species. For management purposes, the influence of particular land use practices on the abundance and rate of

spread of invasive species provides practical insights. These include insights into how alien species are introduced [e.g. as ornamentals introduced in small numbers to multiple foci (towns) or as forestry species introduced in large numbers to a few locations (Donaldson et al. 2014)]; and insights into how they are spread around [e.g. through road maintenance equipment (Geerts et al. 2016; Kaplan et al. 2014)]. Understanding such mechanisms can be used to prioritise surveillance and control measures (Wilson et al. 2017). However, despite there being widespread recognition that the human footprint is a key determinant of the success of alien species (Thuiller et al. 2006), very few details of how land use affects alien species distributions in South Africa are known.

13.8   Conclusion

Various hypotheses in invasion science are related primarily to environmental factors—habitat filtering; environmental heterogeneity; increased resource acquisition; disturbance; dynamic equilibrium model; opportunity window; and resource-enemy release (Catford et al. 2009; Jeschke and Heger 2018). Many of these hypotheses are underpinned by the notion that abiotic factors can both promote and limit invasions, and that there is a "sweet-spot". For example, Buckley et al. (2007) argued that at an intermediate level of disturbance there is a "weed-shaped hole" when there is sufficient disruption of native communities to create opportunities for alien plant species without conditions being so adverse as to prevent establishment at all.

In light of this, it is not surprising that the probability of invasions in South Africa is profoundly influenced by environmental factors in often complex ways. In general, climate is most influential at a broad-scale; microsite conditions at a local scale; and the influence of humans operates across scales by determining where alien species are introduced and where they can establish and spread. Nonetheless, most invasions are context-specific. In consequence: (1) rules of thumb often do not have the discriminatory power needed to reliably inform management and policy; and so (2) there is still much to be gained from autecological studies [e.g. see Richardson et al. (2000) for a discussion of the interacting factors that determine the distribution of *Prosopis* spp. invasions in South Africa]. Will it inevitably always be this way? Possibly, but it certainly seems that the interaction between invasions and environmental factors is likely to become more complicated as it plays out in the context of other global change drivers.

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