9 Climate Change and Biological Invasions in South Africa

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Abstract

South Africa is a mega-diverse country situated at the southern tip of Africa flanked by two unique marine systems, one cool and one warm. Species introductions to the region have also been diverse. Given the major and growing threat to biodiversity and ecosystem functioning from biological invasions, there has been significant research on this topic. Biological invasions continue to expand and new species continue to arrive. Climate change is expected to affect invasions directly, influencing species' distributions according to individual species' tolerances and interactions with other species; and indirectly, through new introductions, and by altered pathways linked to human responses to climate change. The uncertainty relating to climate projections has narrowed considerably since the release of the Intergovernmental Panel on Climate Change Sixth Assessment Report, permitting a more focused assessment of its potential interaction with the impacts of biological invasions than was possible before. This chapter summarizes the projected changes for rainfall and temperature in the medium and long term using a middle-of-the-road socio-economic scenario based on 'downscaled' projections. Overall, projected shifts in climate, even over the long term, are less extreme than had previously been projected in national and regional assessments for South Africa, although the rate and extent of change is projected to be more extreme for southern African regions north of South Africa. Future biological invasions can be divided into: (i) expansion of existing invasions; (ii) new invasions that result from changes in the nature, volume and timing of trade and travel; and (iii) invasions that result from climate change mitigation and adaptation such as carbon sequestration projects and assisted migration. Expansion of native species, notably 'bush encroachment' in savannas, is also predicted to increase. We discuss likely patterns of change in terrestrial, freshwater and marine systems, considering first the change in current invasions and native species and then changes in pathways that are likely to affect future

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invasions in each realm. Species losses and gains are expected in all realms. On land, rising atmospheric CO_2 has likely already facilitated widespread increases in cover of indigenous tree and shrub species, and may also exacerbate invasions of alien woody plants. Managing invasions in the future will require significant efforts in pathway control. Careful balance in permitting and even facilitating range expansions, while controlling undesirable native range expansions and preventing the introduction and expansion of generalist, highly invasive alien species is paramount. Policies aimed at using indigenous species in rehabilitation and carbon sequestration projects, as well as cross-border collaboration on biosecurity and biodiversity safeguards, are critical.

Introduction

South Africa is a mega-diverse country, with both terrestrial and marine systems spanning over 1 million km^2. The nine terrestrial biomes and contrasting warm and cold currents on the east and west of the country provide for varied and diverse habitats that are home to over 65,000 described species, including 7% of the planet's birds and vascular plants, 5% of mammals, 10% of marine fish and an astonishing 25% of described octopuses and squids (Skowno *et al.*, 2019). Three biodiversity hotspots, home to global centers of endemism in multiple taxa, are recognized in South Africa, including one floral kingdom (Mittermeier *et al.*, 2004). Disturbance by grazing, browsing and wildfire are critical determinants of vegetation structure and composition in all but the forest biome (which covers a very small area). Marine biodiversity is also globally noteworthy, with an extraordinary water temperature gradient along the coast, from warm tropical waters in the east that support diverse assemblages of marine biota to cold temperate waters in the south and east that even support Pleistocene relictual polar species like the African penguin, *Spheniscus demersus*. Species introductions to the region have also been diverse (Richardson *et al.*, 2003; van Wilgen *et al.*, 2020; Table 9.1). The terrestrial invasions that have resulted are unique in that relatively few invasive animals have become widespread, while many invasive woody shrubs and trees dominate the invasive flora (as opposed to grasses and herbs in many other regions; Irlich *et al.*, 2014).

Given the obvious threat from invasive species to biodiversity and ecosystem functioning, significant research and monitoring has been done on biological invasions (van Wilgen *et al.*, 2020). One of the world's largest efforts to deal with invasions – the Working for Water program – addresses rural poverty while simultaneously removing invasive plants (van Wilgen and Wannenburgh, 2016). However, despite the introduction of new legislation in 2014, which lists 559 taxa that require compulsory control, and an estimated ZAR 1–2 billion (US$142

Table 9.1. Numbers of alien species in South Africa according to Zengeya and Wilson (2020) and van Wilgen *et al.* (2020). The totals for the number of introduced species include both established and invasive species, as well as species introduced to the offshore Prince Edward Islands. Estimates of the number of established species have only been provided for groups where recent information was available.

Organism type	Total introduced	Established
TERRESTRIAL	1737[a]	1255
Plants	913[a]	759
Vertebrates	194	30
Mammals	51	
Reptiles	49	
Birds	94	
Invertebrates	436	466
FRESHWATER	259	98
Plants	13	19
Fauna	99	77
Vertebrates	48	
Amphibians	14	2
Reptiles	7	
Fish	27	
Invertebrates	51	
MARINE	95	56
Fish	0	0
Plants	9	
Invertebrates	86	
MICROBES	114	
TOTAL	2205	1409

[a] This number does not include species currently in cultivation (estimated in the 1000s).

Table 9.2. Climate change has the potential to influence biological invasions directly by affecting both already-present alien species as well as native species, and indirectly by altering management effectiveness, current pathways and by promoting species introductions for novel reasons. These climate–invasion interactions can be negative or positive for biodiversity and ecosystem functioning.

	Negative interactions (biodiversity/ ecosystem loss)	Positive interactions (biodiversity/ ecosystem win)
Existing invasions	Competitive interactions of invasive alien species strengthened by climate change	Climate becomes less favorable for the establishment, persistence and spread of invasive alien species.
	Large stands of invasive plants block the migration of indigenous species in response to climate change.	
	Reduction in management effectiveness owing to altered climate	Improvement in effectiveness of management owing to altered climate
Native species range expansions and invasions	Native generalist species spread and become dominant across the landscape.	Communities of native species move in response to climate change and specialist species are retained.
Shifting needs, sources and destinations for goods and people	Hardy, resilient invasive species are introduced for a variety of purposes (e.g. food plants, horticulture).	Hardy, resilient locally indigenous species are prioritized for food gardening and other horticultural purposes.
	New source locations and/or destinations for invasive alien species as a result of changed trade routes and commodities	Fewer alien species are required and/ or new sources pose fewer risks than previous ones.
New reasons for introducing species (e.g. carbon sequestration, rehabilitation or managed relocations)	Planting of alien species or species outside of their natural biomes	Climate change adaptation and mitigation leads to rehabilitation of natural systems and promotes planting of locally indigenous and resilient species.

million) investment by government, invasions are expanding and novel introductions continue (van Wilgen *et al.*, 2020), indicating the extreme recalcitrance of this issue.

Climate change is expected to affect biological invasions in a number of direct and indirect ways (Irlich *et al.*, 2014), at each invasion phase (Robinson *et al.*, 2020a). These can be divided into response of existing invasive species and the arrival of new ones, which may result from native invasions (*sensu* Simberloff, 2011), new intentional introductions in response to climate change as well as new unintentional introductions as a result of changes in the nature, volume and timing of trade (Table 9.2). Direct effects alter the size and distribution of suitable climatic niches available to both native and introduced species. Related to this, climate change is expected to alter the invasibility of ecosystems, as disturbance regimes are altered, particularly through an increase in extreme events such as floods, droughts and fires (Wilson *et al.*, 2020). Another direct driver of change is the gradual rise in atmospheric CO_2 levels that impact the functioning of both plants and animals. More indirectly, effects on the physiologies and distribution of individual species will change biotic interactions in many ways, while in some areas certain functional roles may become vacant, leading to altered establishment and spread of alien species (Hellmann *et al.*, 2008). In addition, these changes may also affect our ability to manage biological invasions (Hellmann *et al.*, 2008). Further indirect effects occur through changes in the nature, intensity and location of human activity, with a particular effect on the predominant pathways of introduction. The nature of invasive species impacts, as well as our ability to control them, is also expected to change as a consequence of climate change and rising CO_2 (Hellmann *et al.*, 2008). Globally, climate change especially threatens endemic-rich ecosystems by affecting rare endemics disproportionately (Manes *et al.*, 2021).

Overview of Projected Climate Change and Related Terrestrial and Freshwater Changes

The uncertainty relating to climate projections has lessened considerably since the release of the Sixth Assessment Report of the United Nations Intergovernmental Panel on Climate Change (IPCC AR6) where the estimated range of climate sensitivity to greenhouse gas increase was narrowed by about 50% (IPCC, 2021). Regional modeling of climate in southern Africa has advanced, narrowing the uncertainty in projected temperature and rainfall regimes this century. Finally, increasing urgency in international negotiations may precipitate more effective efforts to reduce emissions, greatly reducing the likelihood of higher-level emissions scenarios. A narrower range of likely climate futures can thus be anticipated for South Africa than has been the case previously.

Mean projected changes for rainfall and temperature are described here based on a mixed development, middle-of-the-road socio-economic scenario that is matched with a 4.5 W/m^2 greenhouse gas forcing by 2050 (Fig. 9.1). The much more extreme 8.5 W/m^2 scenario is considered unlikely. We present summaries sourced from the IPCC AR6 interactive Atlas, based on 'downscaled' projections developed by Cordex (Teichmann *et al.*, 2021), against a baseline condition that averages 1981–2010. Projections are to 2041–2060 (medium term) and 2081–2100 (long term). Mean differences for 21 of the independent climate models involved in CMIP6 (see Eyring *et al.*, 2016) are presented for the four variables highlighted here, namely mean annual rainfall, minimum and maximum annual surface air temperature, and the number of days where maximum air temperature exceeded 35°C annually. Overall, even long-term projected shifts in climate are somewhat less extreme than previous national and regional assessments for South Africa, but for southern African regions north of the country's border, the rate and extent of change is projected to be more extreme. Rainfall is projected to decline by up to 14% by 2050 along the western escarpment running from the Cape Fold Belt in the south to central Namibia and by up to 10% in the inland Kalahari, with some further reductions in this region and associated coastal regions by 2100, particularly in southern coastal Namibia and southwards into the Richtersveld massif of the Northern Cape province (northwest of South Africa). Aridification of up to 12% is projected to occur mainly between 2050 and 2100 in an inland region stretching from eastern Botswana and southern and eastern Zimbabwe to northeastern South Africa (Lowveld to Highveld transition zone). Relatively little annual rainfall change is projected elsewhere, with some rainfall increases of less than 5% projected in central inland South Africa, northeastern Namibia, northern Zimbabwe and eastern Mozambique. Eastern coastal regions are thus projected to get up to 5% wetter, and western coastal regions up 10% drier (mean annual rainfall). Annual minimum and maximum temperatures increase by up to 2°C by 2050, with their maximum centered on western Botswana, while coastal regions warm by about 1.3°C; by 2100 these increases are up to 2.6°C for the interior and grading to 2°C in the area's coastal regions (Fig. 9.1). By 2050, maximum annual temperatures increase by at least 2°C more over a larger region of central to western southern Africa than is the case for minimum annual temperatures. This faster increase on maximum temperature is reflected in substantive changes in the number of days with maxima exceeding 35°C, by more than 40 days in the northwest of South Africa, Botswana, Namibia and Mozambique by 2050, and more than 50 days by 2100 in a similar set of areas (Fig. 9.1).

Overall, the combination of rainfall and temperature changes will introduce more challenging conditions for plant productivity and ecosystem functioning in the western and interior northern parts of southern Africa, which may be somewhat offset by some rainfall increases in eastern regions. These warmer conditions are increasingly implicated in significantly adversely affecting the ecological success

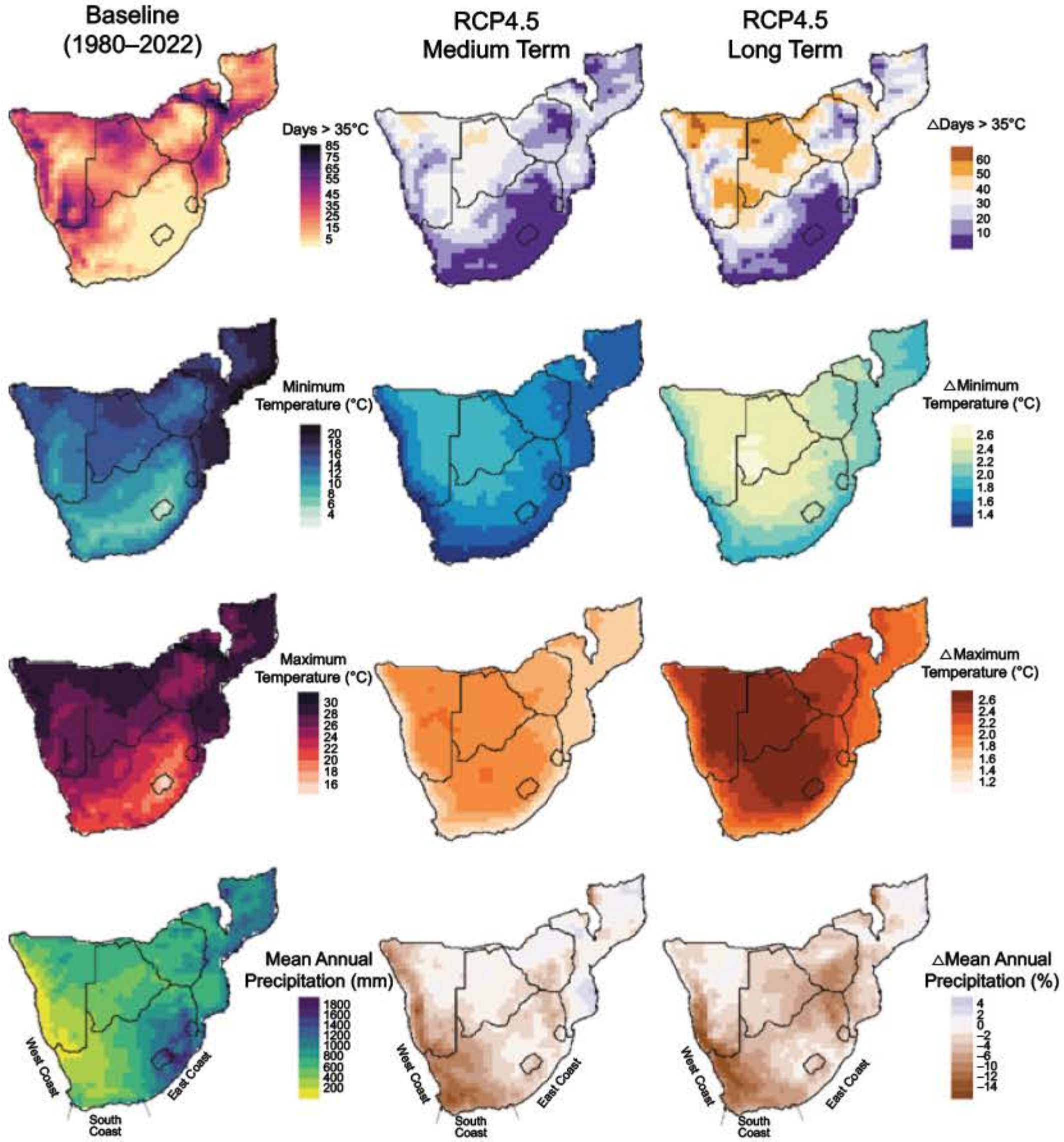

Fig. 9.1. Baseline climate conditions (left panel) and predicted change from this baseline in the southern African climate in the medium term (2041–2060; middle panel) and the long term (2081–2100; right panel) under Representative Concentration Pathway (RCP) 4.5 for days above 35°C, mean annual minimum and maximum temperature and total annual precipitation.

of many endemic and native bird species of the arid grasslands and savannas of southern Africa (van de Ven *et al.*, 2019), and unique, endemic succulent plant species are suspected to be vulnerable to these combined warmer and drier conditions (Young *et al.*, 2016).

Although it is obvious that climate changes can result in changed hydrological responses (Kundzewicz *et al.*, 2002; Kusangaya *et al.*, 2014), most assessments of these impacts have been at course scales, masking the complex hydrological interactions that take place within catchments (Schulze, 2000). Documented streamflow responses to climate change reported to date have therefore varied (Kusangaya *et al.*, 2014). In addition, land use and land cover, inter-basin water transfers, water abstractions, and presence of dams and weirs also have significant effects on hydrological responses, often making climate change trends impossible to detect (Warburton and Schulze, 2005; Kusangaya *et al.*, 2014). Hydrological responses to climate change in southern Africa have mostly been studied with rainfall-runoff hydrological models that generally predict reduced runoff.

The interplay of droughts and storms can interact with environmental pollutants to have noxious effects. For example, storms following drought may flush sewage and agricultural chemicals and nutrients into freshwater systems. Increased nutrient loading, in turn, and in combination with warmer water, reduces dissolved oxygen concentrations, promoting algal growth and greater turbidity (Matthews and Bernard, 2015). These interactions can promote the growth and spread of invasive species.

Expected Changes in the Ocean

Oceans cover roughly two-thirds of the Earth's surface and act as a sink for atmospheric heat and CO_2. More than 90% of excess human-generated heat produced in the past 50 years and half of anthropogenic emissions since the Industrial Revolution have been absorbed by the ocean (Mikaloff Fletcher *et al*., 2006; IPCC, 2019). While this has reduced the rate of climate change at a global scale (Rhein *et al*., 2013), it has resulted in remarkable changes in oceanographic processes as well as species' habitats (Johnson *et al*., 2011). Despite the geographic scale of these changes, our understanding of their severity and consequences for marine organisms lags behind that of terrestrial systems (Hoegh-Guldberg and Bruno, 2010).

The South African marine environment is complex and diverse. The east and south coasts are tropical to warm, and are influenced by the Agulhas current. In contrast, the cool temperate west coast is typified by upwelling and the cold Benguela current. Because of this complexity, the impacts of climate change are diverse and region-specific (Kelly *et al*., 2019; Fig. 9.1; Table 9.3). Following global trends, the Agulhas current has warmed over the past 50 years, with a decadal increase of 0.7°C since 1980 (Rouault *et al*., 2009). Interestingly, this region is the most thermally stable with respect to extreme events, and experiences fewer heatwaves or cold spells than the rest of the coast (Schlegel *et al*., 2017). Along with the greatest warming, the east coast has also been most influenced by sea-level rise with an annual increase of 2.74 mm over recent decades (Mather *et al*., 2009). Ocean acidification occurs with uptake of atmospheric CO_2, changing ocean carbonate chemistry. While baseline data on the pH of coastal waters is sparse for the South African coast, available data suggest that pH remains above 8 in the northern region of the east coast (Hayman, 2015). The west coast, however, has recorded pH levels below 7.5 at multiple coastal sites (T.B. Robinson, unpublished results). Notably, these levels fall below the global predictions for ocean pH by the year 2100 (IPCC, 2019). These low pH levels likely reflect regional-scale amplification of acidification owing to the upwelling of cold organically rich waters. In contrast to warming on the east coast, the west coast has experienced regional cooling as a result of intensification of wind-driven upwelling of cold water (Lamont *et al*., 2018), but marginally less sea-level rise than the east coast, with an annual rise of 1.87

Table 9.3. Environmental status and trends along the west, south and east coasts of South Africa in recent decades.

	West coast	South coast	East coast
Temperature (Lamont *et al*., 2018)	Cooling	Cooling	Warming
Vulnerability to extreme thermal events (heatwaves/cold spells) (Schlegel *et al*., 2017)	Moderately vulnerable	Most vulnerable	Least vulnerable and most thermally stable
Sea-level rise (Mather *et al*., 2009)	1.87 mm/year	1.84 mm/year	2.74 mm/year
pH (Kelly *et al*., 2019)	Often below 7.5	Unknown but likely reduced in upwelling cells	Above 8

mm (Mather *et al.*, 2009). The south coast has experienced environmental changes similar to both the east and west coasts. Temperatures in this region have cooled, a pattern driven by intensified southeasterly and easterly winds and associated upwelling (Rouault *et al.*, 2010). Notably, while the same number of extreme temperature events occur in this region as in the rest of the coast, the intensity and duration of them are more severe (Schlegel *et al.*, 2017). As with the rest of the coast, sea-level rise has been noted in this region at a similar rate to the west coast (i.e. 1.84 mm/year; Mather *et al.*, 2009). No information is available on coastal pH along the south coast. However, knowledge on the west coast and other temperate regions (e.g. Leinweber and Gruber, 2013) suggests that reduced pH occurs where upwelling is prevalent.

Terrestrial Invasions

Most terrestrial alien species in South Africa, particularly plants, were intentionally introduced, for diverse uses, including agriculture and forestry, and medicinal and ornamental purposes (Richardson *et al.*, 2003, 2020; Visser *et al.*, 2017; Williams *et al.*, 2021). Vertebrates were introduced for hunting, aesthetic purposes and as pets (van Rensburg *et al.*, 2011; Measey *et al.*, 2020a). Although the exact introduction pathway for many terrestrial alien invertebrates is unknown, over 100 species have been introduced for biological control of plants, and many others were accidentally introduced as contaminants on imported plants (e.g. pests of crop or ornamental species, Saccaggi *et al.*, 2022), animals and products, or as stowaways (Janion-Scheepers and Griffiths, 2020; Zengeya and Wilson, 2020). Changes in socio-economic factors have caused South Africa's introduction pathways to change over time (Richardson *et al.*, 2003; Faulkner *et al.*, 2020). However, new species continue to be introduced through the ornamental plant trade, for medicinal use, and in the pet trade (Middleton, 2015; Nelufule *et al.*, 2020; Williams *et al.*, 2021). Trade in ornamentals and pets is likely to be exacerbated by the growing online trade (Humair *et al.*, 2015; Nelufule *et al.*, 2020). Owing to increasing transport and trade, and improved regulation of intentional introductions, accidental introductions are also likely to increase in importance (Faulkner *et al.*, 2020; Measey *et al.*, 2020a). The dispersal of alien species into South Africa from other African countries where they have been introduced is also a growing concern (Faulkner *et al.*, 2017a; Zengeya and Wilson, 2020), although South Africa is more likely to act as the bridgehead for northward introductions to the continent (Measey *et al.*, 2020b).

Estimates of the extent of terrestrial invasions in South Africa are outdated, though there are many plant species and a few bird species (the two groups for which consistent data exist) that are widespread, spanning at least a-quarter of South Africa (van Wilgen *et al.*, 2019). Invasive species richness is highest in the east of South Africa in the savanna and grassland biomes, as well as the Indian Ocean coastal belt. The extent of invasions is, however, estimated to be greater in the fynbos-dominated Western Cape province. One of the major impacts of terrestrial plant invasions is a reduction in freshwater runoff estimated at between 1450 and 2450 million m^3 annually (van Wilgen *et al.*, 2019). While reductions in rangeland productivity and biodiversity intactness owing to biological invasions are currently estimated to be low, impacts are expected to grow substantially, in particular if invasive species are not managed and are allowed to reach their full potential ranges. Alien species have been implicated in threats to a large number of species, although very few definitive studies quantifying such impact or its mechanisms have been conducted (Zengeya *et al.*, 2020).

Animals

South Africa has a range of terrestrial extralimital and alien invasive vertebrates (see van Rensburg *et al.*, 2011; Measey *et al.*, 2020a). Of these, the majority is associated with urban and agricultural contexts and so is likely to respond to anthropogenic changes in land use with climate change. In particular, rising poverty predicted in many areas through climate change is likely to increase the impacts of mice (*Mus musculus*), rats (*Rattus rattus*, *R. norvegicus* and *R. tanezumi*), pigeons (*Columba livia*) and house crows (*Corvus splendens*), all of which benefit from expanding informal housing areas (Taylor *et al.*, 2008; Measey *et al.*, 2020a), which in turn may increase their potential to spread disease (van Rensburg *et al.*, 2011; van Helden *et al.*, 2020) and their co-invasive parasites (Julius *et al.*, 2018a, b).

The southwestern corner of South Africa has been a historic introduction point for many of these aliens, which, although currently established and spreading now, may not perpetuate with the ongoing drying and warming experienced in this region (e.g. *Fringilla coelebs*, chaffinch; *Alectoris chukar*, chukar partridge (restricted to Robben Island); *Oryctolagus cuniculus*, European rabbit). Terrestrial vertebrate aliens that are water-limited will become more dependent on sources of deliberate or commensal supplementation (e.g. *Sus scrofa*, domestic pig; *Pavo cristatus*, common peafowl). Mallards (*Anas platyrhynchos*) are currently expanding within metropolitan regions of South Africa, but a changing climate may increase their propensity to migrate across large expanses in southern Africa, thereby exacerbating their hybridization impact on native yellow-billed ducks (*A. undulata*; see Stephens *et al.*, 2019).

Our understanding of South Africa's introduction pathways has increased through directed research in the past decade. However, owing to the complexity of the systems involved and the potential impact of unpredictable events on these systems (e.g. the dramatic impact of the COVID-19 pandemic on global air traffic (Suau-Sanchez *et al.*, 2020) and the rise of Chinese trading (Measey *et al.*, 2019), it is challenging to predict how climate change could alter these pathways (see 'Pathways under climate change').

The role of physiological traits

Terrestrial invertebrates, as ectotherms, rely on the external environment to control their body temperature for dispersal, reproduction and feeding. Climate change impacts these behaviors through warming and freezing events, which can impact invasive alien terrestrial invertebrates in different ways. For this reason, knowledge of the physiological traits and how these differ between native and invasive species can provide insight into more accurate risk assessments and aid in the detection and management of invertebrate introductions (Kumschick *et al.*, 2016). This is especially relevant with the prediction of an increase in extreme events (Fig. 9.1).

Invasive Collembola (springtails), thought to have been introduced with fodder several decades ago, can tolerate warmer, drier conditions than can native species. Observations through climate manipulation experiments and lab-based desiccation experiments have shown that invasive species have an advantage over their native counterparts (Marion Island; McGeoch *et al.*, 2006; Chown *et al.*, 2007). Other work from Marion Island, a sub-Antarctic territory belonging to South Africa, has highlighted desiccation intolerance as a limiting factor in preventing invasion at higher altitudes in the invasive slug *Doroceras panormitanum* (Lee *et al.*, 2009) and parasitoid wasp *Aphidius matriciae* (Lee and Chown, 2016).

Climate change response studies are often focused on critical thermal maxima (CT_{max}), which is the highest temperature at which an organism can function. Generally, invasive species can tolerate a broader range of environmental conditions and have greater phenotypic plasticity than native species (Janion-Scheepers *et al.*, 2018). The mechanisms underlying these patterns are not fully understood. Studies across life stages are encouraged to shed light on the response of different traits, for example, such as on the performance of the invasive ladybird *Harmonia axyridis* (Shinner *et al.*, 2020). Observed inter- and intra-species variation in thermal tolerances can impact species assemblages (Janion *et al.*, 2010) and even whole communities (Franken *et al.*, 2018), although the impact on ecosystem functioning is largely unknown. The impact of climate change on the critical thermal minima (CT_{min}) is often neglected. Increased freezing events could take place either owing to lower snowfall, which acts as a buffer, or to increased cloudless nights. Such extreme low-temperature events can impact the relative abundances of indigenous and invasive species differently (Janion *et al.*, 2009). Freeze events may also prevent or reduce the distribution of invasive pest species such as the fall armyworm (Zhang *et al.*, 2021), making any declines in these events significant.

One particular concern is the potential interaction of climate change and pests of crop plants, which could impact food security. Physiological limits of agricultural pest species (in most cases invasive alien species) have been well documented. However, the responses of insect pest species to climate warming are often complex and cannot be generalized (Lehmann *et al.*, 2020). Phenotypic plasticity and local adaptation play an important role in the invasiveness of species (Nyamukondiwa *et al.*, 2013; Weldon *et al.*, 2018). More work is needed to investigate baseline physiological traits, such as thermal tolerances and desiccation tolerance, of invasive terrestrial invertebrates in South Africa. When coupled with monitoring of conditions and detection rates, this information can aid in the early detection or even prevention of invasive and pest species (Karsten *et al.*, 2016; Saccaggi *et al.*, 2016), which are predicted to increase with climate change (Bebber *et al.*, 2013; Pecl *et al.*, 2017). Metabolic rate measurements may also shed light on newly emerging pest species, as shown recently for the native sugarcane pest, *Cacosceles newmannii* (Smit *et al.*, 2021). Other synergistic effects between climate change and global change drivers also need to be investigated. For example, pesticide resistance may also be impacted by seasonality and overwintering sites (Ma *et al.*, 2021).

Impacts on management effectiveness of biological control

Changes in climate are likely to influence the effectiveness of biological control. Mismatches between biological control agents and their hosts are often due to low temperature tolerances (Harms *et al.*, 2021). Prior knowledge of species' thermal tolerances can aid in the acclimation of biocontrol agents prior to release events to aid in regional survival (Griffith *et al.*, 2019). Knowledge of plant responses to climate change also need to be considered. For example, elevated CO_2 concentrations may reduce insect feeding and thus the efficacy of biological control agents for invasive aquatic weeds (Baso *et al.*, 2021). In addition, the thermal landscape created by invasive alien plants can negatively impact ectotherm species richness, abundance and communities (Garcia and Clusella-Trullas, 2019). Highly heterogeneous landscapes have more microclimates available to ectotherms, while homogeneous landscapes reduce the availability of suitable microclimates and may therefore increase competition (Sartorius *et al.*, 2002).

Plants

Thousands of alien plant species have been introduced to South Africa, where biomes are largely shaped by disturbance drivers (grazing, browsing and wildfire). Disturbance-controlled biomes tend to be 'open' and rich in light availability, seldom achieving their theoretical maximum plant cover and leaf area index (Bond, 2019). This feature allows high water yield rates that benefit humans. Reviewing the estimates that have been made to date, Richardson *et al.* (2020) suggest that at least 10,000 alien plant species are present in the country, including around 2000 tree species. At least 759 alien plant taxa are known be naturalized or invasive (Table 9.1). Many species have invaded large areas, but a large number (even those that are currently widespread invaders) have substantial potential to spread further (Rouget *et al.*, 2004).

A macro-ecological analysis of the distribution of naturalized and invasive alien plants in South Africa revealed four 'alien plant species assemblage zones': fynbos-specific invaders, grassland-specific invaders, moist-subtropical invaders and semi-arid invaders (Richardson *et al.*, 2020). This shows that biogeographical patterns of alien plants are driven by the same environmental conditions and biotic interactions shaping South Africa's terrestrial biomes and their biotas (Richardson *et al.*, 2004; Rouget *et al.*, 2015). This implies that ecological factors have generated biogeographical patterns over a few centuries that map closely onto patterns generated through colonization, extinction and speciation events over millennia.

However, reviewing the influence of geomorphology, soils, climate and fire in shaping the country's invasive biota in conjunction with inter-specific interactions and interactions with land use and other drivers reveals a complex interplay of biotic and abiotic factors (Le Roux *et al.*, 2020; Wilson *et al.*, 2020). Increasing disturbance under climate change, and the expected loss of biodiversity and compromised ecosystem functioning, could reduce the number of biotic interactions. Whether such changes would facilitate invasions through reduced competition or whether loss of mutualisms would retard invasions remains uncertain, although an increase in pioneer and weedy species is likely.

Trees and shrubs are especially prominent in South Africa's invasive flora; indeed, South Africa has been termed the 'world capital of tree invasions' (Richardson *et al.*, 2020). The following paragraphs discuss the roles of key drivers, and interactions, in initiating, sustaining, favoring, and potentially managing tree and shrub invasions. These examples highlight the pivotal role of several drivers, the radical changes that occur when these drivers change, and the inherent complexity in predicting how changes could affect invasions and the implications for management.

Fire as a driver of tree and shrub invasions

Fire plays a fundamental role in the invasion ecology of *Acacia*, *Hakea* and *Pinus* species in the fynbos biome (Richardson *et al.*, 1997). In the absence of alien trees and under naturally occurring fire regimes, native fynbos shrub species follow a cyclical replacement sequence. Different fire regimes favor different native species, depending on frequency, intensity and season, resulting in compositional fluctuation at the decadal scale, but constant communities over longer timescales. This cyclical replacement sequence also drives evolution and speciation in these shrublands (Cowling and Gxaba, 1990). However, invasion by acacias, hakeas and pines rapidly disrupts the cyclical sequence, shifting the system to a species-poor woodland/forest system dominated by the aliens. Unlike the situation in the absence of alien trees, the alien-dominated ecosystem is locked in this state, and fire does not destabilize it. Such regime shifts are evident over vast areas of the fynbos biome. The only way to return to the pre-invasion state is through very expensive manual clearing of the alien species (Richardson and Cowling, 1992). Fire is the overriding driver of the invasion dynamics of fire-adapted woody plants in fynbos; it stimulates seed release from serotinous cones (hakeas and pines), triggers germination of soil-stored seeds (acacias), prepares an ash bed for seed germination and seedling growth, and removes competing vegetation. Theoretically, management can utilize fire by synchronizing mechanical clearing operations with fires so that fires occur after felled trees and shrubs have released their seeds, and seeds have germinated (for hakeas and pines). Fire then kills seedlings of hakeas and pines and stimulates germination of acacia seeds, which can then, again theoretically, be dealt with through follow-up operations involving herbicide application and hand-pulling of seedlings (van Wilgen *et al.*, 1992). However, synchronization of control operations with fires is becoming increasingly difficult; in many areas unplanned fires either nullify gains achieved by management, or they promote further densification, population growth and spread (van Rensburg *et al.*, 2017). The introduction of fires to parts of the fynbos biome where fires have been excluded has triggered the initiation of invasions of fire-adapted alien species (e.g. Geerts *et al.*, 2013).

In recent decades, fires in most parts of the fynbos biome have been unplanned (as opposed to prescribed burns) and are occurring more frequently owing to increased ignition events attributable to human activities (van Wilgen *et al.*, 2010). This trend is likely to spread throughout the fynbos biome as human populations increase. A trend toward more frequent large fires owing to more frequent 'fire weather' is already apparent (Southey *et al.*, 2009), and is likely to be further facilitated by climate change (Wilson *et al.*, 2010). Invasions literally add fuel to these trends, increasing fuel loads and, in so doing, fire intensity (Kraaij *et al.*, 2018), leading to soil damage and excessive erosion (van Wilgen and Scott, 2001). Warmer growing-season conditions favoring increasing cover of both native and alien grasses will exacerbate this trend by increasing the rate of fuel build-up between fires. The increased frequency and size of fires in fynbos is set to trigger regime shifts whereby invasive grasses, acacias, hakeas and pines become increasingly widespread and dominant and create feedback loops that ensure further invasions; increasing frequency of wildfire especially compromises slow-maturing native species (Altwegg *et al.*, 2015). More frequent fires also expose endemic and native flora to post-fire droughts that adversely affect reseeding Proteaceae species (Slingsby *et al.*, 2017). Incursion of fire into fire-sensitive vegetation types that have until now been protected from fire would facilitate new invasions, leading to potentially widespread impacts especially in azonal wetter sites important for hydrological functioning.

Beyond the fynbos, invasion by alien grasses may introduce fire to otherwise fire-free biomes (Rahlao *et al.*, 2009). Fire is also an important management tool for dealing with the growing problem of bush encroachment and with certain savanna and grassland invasions (Lohmann *et al.*, 2014). In mesic savannas, *Lantana camara* and *Chromolaena odorata* outcompete flammable grass species and reduce fire activity. Fire has been used as a management tool for *Chromolaena* in Hluhluwe iMfolozi Park (te Beest *et al.*, 2012). In addition, in savannas, *Chromolaena* stems create fuel ladders, allowing fire to transition from surface to canopy fires, killing native trees. In the mesic savannas, a reduction in fire is exacerbating bush encroachment. This is driven and compounded by the advantages of higher atmospheric CO_2 on the growth and recovery rates of C3 woody plants with the ability to shade out competitors, leading to a competitive advantage over short, herbaceous C4 grasses (Bond and Midgley, 2012).

Tree invasions in arid areas

Most of South Africa's terrestrial area is classed as arid or semi-arid (Wilson *et al.*, 2020). Several *Prosopis* species and their hybrids (mesquite) have invaded large areas of the arid interior, particularly along seasonal river courses, and the extent of invasions is increasing rapidly (Shackleton *et al.*, 2017). Richardson *et al.* (2000) reviewed the factors that are known to have led to increases or decreases in the range and abundance of mesquite. Key factors that triggered new mesquite invasions or stimulated further spread included hybridization (made possible by the introduction of additional species), increased rainfall or extreme rainfall events and flash floods, high temperatures, irrigation, increased opportunities for dispersal owing to the increased abundance and human-assisted movements of several species of livestock, and reduction of herbaceous vegetation cover owing to grazing. The interaction of these factors helps to explain recent changes in mesquite invasions in the region and provides clues on likely trajectories of mesquite invasions in the face of climate change. Another factor promoting mesquite success may be the beneficial effects of rising CO_2 on the species' growth rate.

Another widespread invader of semi-arid parts of South Africa is the Peruvian peppertree *Schinus molle*. The species' range is predicted to shrink in South Africa (Richardson *et al.*, 2010). However, fundamentally different responses were predicted in different biomes. For example, where the species is already highly invasive the large propagule pressure could facilitate persistence and perhaps even drive further expansion, even if climate conditions become marginal. Elsewhere, the changing dynamics of rivers (which create microsites for establishment and facilitate dispersal) and fire regimes are likely to shape invasion dynamics in ways that cannot be accommodated in standard species distribution models (Richardson *et al.*, 2010).

The relative proportion of C3 and C4 grass photosynthetic types appears sensitive to shifts in rainfall seasonality (Schulze *et al.*, 1996), and contemporary remote-sensing studies demonstrate how climate variability sensitively controls grass frequency in the Nama Karoo–grassland biome interface (Hoare and Frost, 2004). So-called greening trends in semi-arid and arid grassland ecosystems have been observed globally (Cook and Pau, 2013) and have been attributed to rainfall variability, growing-season length (especially at high latitudes) and CO_2 fertilization. A key mechanism behind this effect in arid systems seems to operate through increasing soil water, revealed by analysis of multiple studies of elevated CO_2, showing a 17% increase in soil water in drylands vs. only 9% in non-dryland sites (Lu *et al.*, 2016). Thus, warming trends and changing soil moisture may enhance the success of grassy plant forms in arid regions, consequently increasing the risk of wildfire (du Toit *et al.*, 2015).

Pathways under climate change

Climate change is expected to alter pathways through two major mechanisms. First, climatic events can impact directly on invasion pathways. For example, the predicted increase in the frequency of extreme climatic events could alter dispersal opportunities (Robinson *et al.*, 2020a). Cyclonic winds have transported alien plants to South Africa from neighboring countries where they had previously been introduced (Wilson *et al.*, 2020). An increase in the frequency of such events (Engelbrecht *et al.*, 2019) could lead to increased opportunities for alien species in neighboring countries to disperse into South Africa and/or facilitate spread within South Africa (Wilson *et al.*, 2020). Natural southerly dispersal of invasive species already present in countries to the north of South Africa can also be expected given the more dramatic predictions of change in these areas (Fig. 9.1). Similarly, rivers act as an important invasion pathway. Many South African rivers are fringed with dense stands of alien trees. The composition of alien species along rivers is determined by hydrological regimes (e.g. Foxcroft *et al.*, 2008) and land use in catchments (Meek *et al.*, 2010). Rapidly changing hydrological regimes, increased urbanization and disturbances in riparian ecosystems are likely to enhance the opportunities for dispersal and proliferation of alien woody plants along rivers.

A second mechanism for changing pathways relates to altered trade routes, traded items and locations of diverse socio-economic activities. The predicted changes to South Africa's climate will impact the types of terrestrial organisms that can survive and be used for various purposes, including agriculture and forestry, which are unlikely to continue in the same way or the same places (e.g. Lötter *et al.*, 2019). Adaptation strategies could lead to a new wave of intentional introductions as new species are targeted to fulfill various purposes (e.g. Scholes, 2003; Tibesigwa *et al.*, 2017). For example, new plant species and varieties adapted to South Africa's new conditions could be targeted for ornamental purposes (van Kleunen *et al.*, 2018). Indeed, droughts and related water restrictions in Cape Town have already led gardeners to preferentially select plants that are heat-tolerant and that survive without frequent watering (Goodness, 2018). Some native plants meet these requirements (Goodness, 2018), but alien species that are more likely to naturalize than the types of species previously introduced for this purpose could be imported (Donaldson *et al.*, 2014). While the introduction of alien species is regulated, including a risk analysis (Kumschick *et al.*, 2020), alien species are still brought in illegally. Ornamental plants in South Africa are also often grown beyond their climatic limits (Donaldson *et al.*, 2014), but climate change could create more opportunities for warm-adapted species to naturalize (Dullinger *et al.*, 2017; van Kleunen *et al.*, 2018). Climate change is also likely to change the efficacy of biological control agents (Sun *et al.*, 2020). Therefore, new agents may be required, not only to control new invaders but also to replace agents whose efficacy has declined (although for some agents reintroductions may be possible; Allen *et al.*, 2014).

Efforts aimed at climate change adaptation and mitigation could also facilitate new intentional introductions (Pyke *et al.*, 2008), for example through expanded production of biofuel crops and carbon sequestration projects (Blanchard *et al.*, 2011). Indeed, exploration of plant species for use as biofuels has led to the importation of unspecified bamboo species (Canavan *et al.*, 2019). Unfortunately, the characteristics that make plants suitable for these purposes also make them good invaders, and many well-known invasive species are used for biofuel and carbon sequestration (Pyke *et al.*, 2008; Irlich *et al.*, 2014). Managed relocations (*sensu* Richardson *et al.*, 2009) are also likely to become more prominent. While most managed relocations will involve native species (Irlich *et al.*, 2014), complications such as hybridization and competition can be expected (Measey *et al.*, 2017; Stephens *et al.*, 2019), so an era of complicated ethical debates and trade-offs between biodiversity, wilderness and neo-native environments is anticipated. Climate change is also expected to have a large, negative impact on South Africa's agricultural production (Lötter *et al.*, 2019), and alternative food sources may be developed to mitigate the impact on food security. Globally, insects are increasingly being seen as an alternative, sustainable protein source (van Huis and Oonincx, 2017); however, many of the farmed insects are invasive species, and escapes have been recorded (Bang and Courchamp, 2021). Facilities in South Africa to mass-rear insects for various purposes (Woods, 2017) have not, to the best of our knowledge, led to biological invasions. However, if the industry grows, opportunities for invasion increase (Bang and Courchamp, 2021).

Climate change could also alter the unintentional pathways of introduction. The volume and type of imported goods as well as their production source and transit routes are

Fig. 9.2. The potential impact that the melting of the Arctic sea ice and the opening of trans-Arctic shipping routes could have on South Africa's introduction pathways. (Based on Smith and Stephenson, 2013; Miller and Ruiz, 2014; Stephens, 2016; Faulkner *et al.*, 2017b; Sardain *et al.*, 2019; Faulkner *et al.*, 2020.)

likely to shift as the climate changes (Calzadilla *et al.*, 2014), potentially exposing South Africa to new pools of species and altering propagule pressure for the types of organisms that are transported as contaminants on imported goods (Seebens *et al.*, 2018). For example, food imports could increase in an effort to mitigate impacts on food security (Juana *et al.*, 2012; Engelbrecht *et al.*, 2019). Terrestrial organisms are also often introduced as stowaways on transport vessels or contaminants of goods (Chapman *et al.*, 2017; Faulkner *et al.*, 2020), and so changes to global transport networks driven either directly or indirectly by climate change (Fig. 9.2) will also impact accidental introductions. It is difficult to predict these changes locally, but new sources of alien species or increased traffic to South Africa are likely to increase the rate of unintentional introductions. Additionally, if transit times to South Africa and the environmental variability experienced in transit are reduced, the probability of introducing accidental stowaways alive increases (Hellmann *et al.*, 2008).

Climate change is expected to cause the migration of millions of people globally (Hoffmann *et al.*, 2020). Groups of people that have previously migrated into South Africa have brought with them new alien species (e.g. medicinal plants; Williams *et al.*, 2021). However, migrations driven by environmental factors tend to occur within countries, and so climate change is more likely to cause a redistribution of people within South Africa (Mastrorillo *et al.*, 2016; Ngepah *et al.*, 2019). Nonetheless, globally, there has been concern around the potential for climate change refugees (Berchin *et al.*, 2017) and the dramatic changes expected for countries north of South Africa (Fig. 9.1) may well result in major threats to livelihood, resulting in cross-boundary migrations.

Freshwater Invasions

Many alien freshwater species have been intentionally introduced to South Africa – fish for recreational angling or aquaculture (Weyl *et al.*, 2020), and plants for ornamental purposes, or as part of the aquarium trade, with subsequent escape (Hill *et al.*, 2020). Some freshwater fish and invertebrates were also released for biological control, and a few were imported for the pet trade (Weyl *et al.*, 2020). Information on introduction pathways is scarce for freshwater invertebrates, but many were likely introduced as contaminants of intentional freshwater plant and animal introductions (Weyl *et al.*, 2020). Interestingly, not all freshwater invasion pathways have been noted in South Africa. For example, South Africa has no navigable rivers and therefore ballast water is not a freshwater concern (Mitchell, 2014). Similarly, none of South Africa's inter-basin water schemes connects South African river basins to river basins in other countries (Faulkner *et al.*, 2020), precluding built infrastructure. Owing to the wide variety of fish already available for recreational angling, new fish introductions for this purpose are unlikely (Faulkner *et al.*, 2020; Weyl *et al.*, 2020). However, aquaculture is currently being promoted as a source of food and, consequently, aquaculture production has increased (van Deventer *et al.*, 2019).

Understanding of effects of climate change on the freshwater fauna of South Africa is relatively patchy owing to the many distinct freshwater ecoregions of the country combined with a lack of comprehensive information on the ecology of native freshwater species. While areas of high endemic biodiversity, such as the Cape Fold Ecoregion, have been prioritized for assessment in response to climate change, results cannot be extrapolated (Dallas *et al.*, 2020). As a result, invasion history and eco-evolutionary context can be a useful tool in inferring possible trends of biotic interactions and population dynamics in response to thermal change. Owing to aquatic species being ectothermic, they are inherently affected by thermal change whereupon metabolism increases with temperature resulting in a hump-shaped feeding relationship (Uiterwaal and DeLong, 2020). This effect is enhanced in habitats where dispersal and refugia are limited as a result of fragmentation or riparian degradation.

Animals

The ecologically damaging brown trout (*Salmo trutta*) is listed as being highly vulnerable to climate change, meaning that in the future, populations may dwindle and impacts subsequently decline as a result of warming in headwater streams (Shelton *et al.*, 2018; Dallas *et al.*, 2020). While this seems positive for native biodiversity, it is likely that warm-adapted species such as black bass (*Micropterus* spp.) or Mozambique tilapia (*Oreochromis mossambicus*) from the lower reaches of river systems will invade the empty niche in the now-warmer waters and increase in abundance (Mofu *et al.*, 2019). Rising temperatures would then support the proliferation of black bass populations across the country showing a potential for huge invasion debt given the shift toward optimal climatic variables and a predicted increase in dam creation in response to water shortages (Khosa *et al.*, 2019).

Changes to water flow regimes can both facilitate and impede alien species dispersal. Extreme flood events may wash propagules from upstream populations downstream; for example, flash-flood events in Mpumalanga have been associated with spread of invasive crayfish (*Cherax quadricarinatus*) from farm dams into the Komati river. In the same instance, prevailing drought and drying of streams may negatively affect invasive alien species by increasing patchiness and decreasing opportunities to invade upstream. For example, in Addo Elephant National Park, stream-drying regimes have prevented the upstream spread of largemouth bass into refugia pools inhabited by the endangered forest redfin, *Pseudobarbus afer* (Ellender *et al.*, 2018).

Largemouth bass (*Micropterus salmoides*) and Florida bass (*Micropterus floridanus*) were introduced specifically to develop a recreational sport fishery across the country. They are morphologically indistinguishable but genetically distinct. Florida bass can tolerate warmer water than largemouth bass (Barthel *et al.*, 2010). They grow to larger sizes and are more aggressive than largemouth bass. Both species are ecologically damaging and responsible for the extirpations of a variety of redfin minnow species (Kimberg *et al.*, 2014; Ellender *et al.*, 2018). Increasing temperatures, enhance the predatory capacity of Florida bass by decreasing the time taken to process prey items, having a higher maximum feeding rate than largemouth bass at higher temperatures suggesting that the damage from this species will be enhanced and may outcompete native predators (Khosa *et al.*, 2019; Luger *et al.*, 2020). Introgression between the two species is very common but it is not known whether hybrid individuals carry the same physiological traits. Furthermore, black bass are visual and olfactory predators that benefit from clear-water conditions to pursue and consume prey (Luger *et al.*, 2020). As unseasonal wildfires become more common, especially in areas with high abundances of invasive riparian trees, this causes ash runoff, which temporarily increases water turbidity and may negatively affect black-bass foraging. However, the response of native species to this type of perturbation is unknown and the unpredictable interaction effects of multiple stressors may not result in a relief of pressures.

Two invasive crayfish (*C. quadricarinatus* and *Procambarus clarkii*) have established populations in the Inkomati Basin and the Ndumo Game Reserve, and a dam in the Free State, respectively (Madzivanzira *et al.*, 2021b). Increasing temperatures have differential effects on the biotic interactions of these two species in comparison with a native analogue (potamonautid crab; *Potamonautes perlatus*). At 19°C, *P. clarkii* consumes less fish prey than the native crab and *C. quadricarinatus* impacts were negligible. However, when temperatures increased to 28°C, *P. perlatus* decreased consumption, *P. clarkii* increased in predatory capacity and *C. quadricarinatus* did not experience a thermally induced change in feeding (Madzivanzira *et al.*, 2021a). Thereby, *C. quadricarinatus* has the capability to consistently exert deleterious effects on native biodiversity and *P. clarkii* is likely to benefit from the predicted climatic change.

Plants

As with fish, freshwater plant species lack context-specific impact assessments in South Africa. Freshwater macrophytes, in particular floating species that form dense mats, cause a variety of impacts on water quality and biotic communities by blocking light to submerged plants, which depletes oxygen in the water column (Midgley *et al.*, 2006; Coetzee *et al.*, 2014). This has negative knock-on effects across the entire biotic community, as the phytoplankton is outcompeted, which reduces both food and oxygen for benthic invertebrates and consequently drives fish and bird species decline (Hill, 2003). With increasing temperatures these effects are likely to be exacerbated in the future owing to the negative relationship between temperature and dissolved oxygen. Invasive freshwater plants are highly likely to alter sedimentation rates, especially within wetland environments, which will affect hydrological dynamics and water provisioning in these systems (Hill *et al.*, 2020).

Uncontrolled mats and macrophyte stands can block access for water sports and clog pumps, and cause numerous economic and social impacts. Especially concerning is the damage and maintenance costs incurred to machinery related to water supplies under increasing drought conditions (Hill *et al.*, 2020). Invasion success is linked to eutrophication, which is expected to increase under climate change. Unless this is addressed, these impacts will be exacerbated in the future (Matthews and Bernard, 2015). Furthermore, many species have rapid asexual reproduction, which enhances spread. The latter may also be accelerated by invasion meltdown dynamics where shredder species such as freshwater crayfish, or herbivorous fishes, increase fragmentation rate (Thouvenot *et al.*, 2017).

Under current climatic conditions, 38% of South Africa's dams are suitable for invasion and establishment by at least one of the 'bad five' most invasive freshwater plants: water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*), parrot's feather (*Myriophyllum aquaticum*), Kariba weed (*Salvinia molesta*) and red water fern (*Azolla filiculoides*). Under predicted change, *M. aquaticum* and *P. stratiotes* are expected to contract their current range by around 9–10%, whereas *E. crassipes* and *A. filliculoides* are unlikely to see much change, with the latter under good biological control (McConnachie *et al.*, 2003). *Salvinia molesta* is, however, expected to experience an increase of 10% in suitable climatic range and should be prioritized for management interventions (Hoveka *et al.*, 2016). Although, in this case, water-specific variables were not incorporated into the models and therefore may be affected by regional and localized microclimate trends. Potential interactions between invasive freshwater plants and diseases of human relevance such as malaria, or bilharzia, will need to be managed as the distribution of malaria areas and climatic niche of schistosomiasis snail vectors is predicted to shift in response to climate change.

Pathways under climate change

South Africa is a water-scarce country, and climate change is likely to exacerbate this problem (Cullis and Phillips, 2019; Engelbrecht *et al.*, 2019). Potential adaptations include increasing the number of dams and the development of water-transfer schemes across countries in southern Africa (Engelbrecht *et al.*, 2019). The building of dams could create new sites for recreational activities and therefore increased exchange of species between waterbodies on fishing gear and other equipment (Rahel and Olden, 2008; Irlich *et al.*, 2014). Successful invasive freshwater plants typically benefit from disturbances such as reduced water flows owing to abstraction and fragmentation (Hill *et al.*, 2020). Inter-basin transfers have already been implicated in invasions (Richardson *et al.*, 2003), but if new schemes connect South Africa's river basins to the river basins of other countries, then these schemes will create major new invasion corridors (Rahel and Olden, 2008; Irlich *et al.*, 2014).

Another potential climate change adaptation is improvement of food security through aquaculture. With current industries reliant on alien species, an increase in propagule pressure of these species or new introductions may be expected. Some socio-economically important aliens such as carp (*Cyprinus carpio*) and sharptooth catfish (*Clarias gariepinus*) may benefit from by climate change, while other fisheries that rely on temperate and cool-water climates may not. Rainbow trout (*Oncorhynchus mykiss*) is currently the most important species for freshwater aquaculture, in terms of annual production, but as this is a cool-adapted species, the climate is likely to become less suitable for it (van Deventer *et al.*, 2019). This will have impacts on the socio-economic resilience of both informal subsistence fisheries as well as aquaculture production. On the other hand, this shortfall could be overcome by increasing production of other species. The highly socio-economically valuable trophy bass fisheries and associated revenue streams will benefit from warming waters and increased reservoir habitats (Khosa *et al.*, 2019). In both cases, movement of aquaculture hubs will result in new opportunities for escapees and changes in abundance and distribution patterns.

Climate change could also create more opportunities for freshwater alien species to escape from captivity and, for some of these organisms, will increase the suitability of the environment and, therefore, their chances of establishing. For example, the predicted increase in the frequency of flooding events (Le Maitre *et al.*, 2019) could create more opportunities for freshwater species kept in aquaculture facilities and ponds to escape into natural systems (Rahel and Olden, 2008; Robinson *et al.*, 2020a; also see Raj *et al.*, 2021). Likewise, flash flooding can rapidly disperse propagules throughout a system. Floating plants and aquatic invertebrates in particular will benefit from these dynamics as they are more mobile and often have traits to prevent desiccation (Hussner *et al.*, 2021). Eutrophication as a result of farming runoff, and indeed even *in situ* aquaculture pollution, may then enhance freshwater plant invasions, which benefit from the excess in nutrients while experiencing temperatures closer to their thermal optima.

Increased water temperature of freshwater bodies (Snaddon *et al.*, 2019) could provide more suitable environments for the establishment of the warm-adapted freshwater organisms that tend to be sold in the ornamental plant, pet and aquarium trades (Hellmann *et al.*, 2008; Rahel and Olden, 2008; Della Venezia *et al.*, 2018). The new introductions and escapes of alien freshwater organisms that climate change facilitates could also lead to further accidental introductions as contaminants (such as *Craspedacusta sowerbii*) or parasites of these organisms are introduced alongside them.

Marine Invasions

The vast majority of marine alien organisms in South Africa were introduced accidentally through shipping, either through the release of ballast water by visiting ships or through biofouling (Robinson *et al.*, 2020b). A few marine species have been introduced intentionally for mariculture, and with them contaminant alien organisms. None has been introduced through the pet trade, despite this trade facilitating marine introductions in other countries (Robinson *et al.*, 2020b). At an international scale, ballast water introductions are being addressed by the Ballast Water Management Convention, which entered into force in 2017. Therefore, fewer species should be introduced by ballast water, but biofouling introductions will continue (Faulkner *et al.*, 2020; Robinson *et al.*, 2020b). In future, marine species are also likely to be introduced for mariculture, which is currently being promoted in South Africa, and the pet trade is also a concern (van der Bank *et al.*, 2019; Robinson *et al.*, 2020b). These introductions could also facilitate further accidental introductions as contaminant organisms could be introduced alongside these target species. As the South African government aims to make South Africa a premier destination for the maintenance of oil and gas infrastructure, marine alien species could be accidentally introduced through this pathway in future (Robinson *et al.*, 2020b).

While the implications of climate change for marine alien species along the South African coast have received little attention, insights can be drawn based on the regional impacts of climate change. For example, the warming being experienced along the east coast (Rouault *et al.*, 2009) is likely to make this region vulnerable to invasions by tropical species. Alien species that are currently restricted to the warmest part of this coast near the Mozambique border (e.g. the filamentous green algae *Cladophora prolifera*; Mead *et al.*, 2011) could spread further south and increase their distribution as the region warms.

In a similar fashion, cooling along the south coast (Rouault *et al.*, 2010) could see the spread of alien species that are presently restricted to the cool temperate west coast (e.g. the ascidian *Ascidiella aspersa*). Such spread has been observed for native cold-water species (e.g. the kelp *Ecklonia maxima* (Bolton *et al.*, 2012) as well as alien taxa (e.g. the Pacific barnacle *Balanus glandula* (Robinson *et al.*, 2015) and the bisexual mussel *Semimytilus patagonicus* (Ma *et al.*, 2020)). The implications of extreme thermal events along the south coast remain unknown for both alien and native taxa. However, as this region is cooling it is likely that cold spells could facilitate cold-water invasions from the west coast. In contrast, heatwaves could favor subtropical species, especially in the region of transition between the south and east coasts. Recent work has highlighted that extreme thermal events can select for genotypes best able to survive these challenging conditions (Coleman *et al.*, 2020). While there is currently no basis for predicting if this would favor alien or native species, it could play a pivotal role in determining which taxa may come to dominate under these variable conditions.

The regional cooling noted on the west coast (Lamont *et al.*, 2018) contrasts with the predictions of warming in most other areas (IPCC, 2019). As such, in the absence of local research it is very difficult to predict how particular species may respond to future predicted conditions. What is clear is that the region will remain vulnerable to invasions from other cool temperate systems. This is particularly worrisome when dominant vectors like shipping link the west coast to climatically similar source regions. Such climatic matching has already been implicated in the successful introduction of three Chilean species to Saldanha Bay on the west coast since 2009 (Peters and Robinson, 2018). Considering the low ocean pH already noted on the west coast (T.B. Robinson, 2021, unpublished results), acidification is likely to be an important determinant of invasion success. Notably, the invasive mussels *Mytilus galloprovincialis* and *S. patagonicus* both experience increased shell dissolution under reduced pH conditions (Emanuel *et al.*, 2020), but what this means for their competitive advantage over native mussels (Sadchatheeswaran *et al.*, 2018) remains unknown.

An important aspect of climate change in marine systems is the increase in frequency and intensity of storms (Scavia *et al.*, 2002). As storms are a source of disturbance, they can facilitate invasions through the removal of native taxa and the clearing of open space (Altman and Whitlatch, 2007). Although the timing of storms along the South African coast is seasonal with the west and south coasts experiencing winter storms and the east coast prone to summer storms, the facilitation of invasions owing to these events could manifest in all regions but the implications thereof will be dependent on the species present.

Pathways under climate change

Accidental marine introductions facilitated by shipping will be greatly impacted by any changes to the global shipping network caused by climate change. However, these changes and their local impact are difficult to predict and are driven by changes to the regions that are connected (Fig. 9.2). Increased ship traffic, as predicted by Sardain *et al.* (2019), would increase propagule pressure of many species, particularly if transit times and the environmental variability experienced along routes to South Africa are reduced (Hellmann *et al.*, 2008). Interestingly, shipping traffic from Asia currently poses the greatest marine invasion threat to South Africa (Faulkner *et al.*, 2020), and is likely to continue to do so under climate change (Sardain *et al.*, 2019).

Climate change mitigation and adaptation could impact introductions of marine alien species to South Africa. Although it has been predicted that future accidental introductions of marine species could be facilitated by oil and gas infrastructure (Robinson *et al.*, 2020b), efforts to mitigate climate change by using alternative energy sources may reduce the number of accidental introductions facilitated by such infrastructure. However, adaptations for food security could lead to further pressure to increase production of alien mariculture species. Alien species currently farmed in South Africa include the bivalves *Mytilus galloprovincialis* and *Crassostrea gigas* and the shrimp *Litopenaeus vannamei* (Majiedt *et al.*, 2019). However, predictions of lower pH in future will have significant implications for mariculture, particularly the production of organisms, like bivalves, that have carbonate-based shells (Kelly *et al.*, 2019). If mariculture operations are increasingly performed in facilities that are not connected to the sea, propagule pressure of farmed alien species could decrease.

Changes to the sites where activities such as fishing or mariculture occur, as well as the redistribution of people owing to human migration (Kelly *et al.*, 2019; Ngepah *et al.*, 2019), could also alter the locations where marine intentional and accidental introductions occur. Climate change will improve the suitability of some of these sites for alien species, while other sites will become less suitable (Swart and Robinson, 2019). For example, increasing sea surface temperatures on the east coast of South Africa could provide more suitable environments for the establishment of marine species in the pet trade, which tend to be tropical. Therefore, if these species are irresponsibly released or escape, their chances of establishing in South Africa may increase under climate change (Hellmann *et al.*, 2008).

Implications for Policy

Climate change and biological invasions do not act in isolation. They both influence and are influenced by local, regional and global trends in energy and resource use, land use and related pollution. Of particular concern is the existence of tipping points beyond which ecosystems cannot recover. In the South African context, desertification (Bell *et al.*, 2021; Spinoni *et al.*, 2021), eutrophication of water resources (linked to land use and use of pesticides in conjunction with rising temperatures; e.g. Dabrowski *et al.*, 2014) and loss of forage area related to bush encroachment (Lohmann *et al.*, 2014) are of particular concern in terrestrial and freshwater systems. While mostly small in scale, regime shifts have already been detected in marine, terrestrial and freshwater environments. Examples include expansion of kelp forests and related marine community shifts (Blamey *et al.*, 2015), fire-driven fynbos-forest dynamics (MacPherson *et al.*, 2019), conversion of species-rich fynbos shrublands to species-poor woodlands of invasive trees and shrubs (Gaertner *et al.*, 2014), bush encroachment and grassland and savanna or woodland switches (Midgley and Bond, 2015), and changes in vertebrate and invertebrate assemblages related to the presence or removal of alien fish (Weyl *et al.*, 2014). While biomes are driven by complex abiotic and biotic interactions, interacting global change drivers can be expected to accelerate the occurrence of tipping points and regime shifts. A recent joint assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the IPCC (Pörtner *et al.*, 2021) has highlighted that biodiversity loss and climate change cannot be tackled separately. Systemic and holistic change in human behavior and land use is clearly required to deal with a suite of global change drivers and pressures simultaneously (Leclère *et al.*, 2020). Management of invasive species is one of the key areas where current biodiversity impacts can be reduced, while at the same time there is significant opportunity for policy to minimize future impacts.

While some pathways of introduction of invasive alien species are difficult to control when food security and livelihoods are at stake, there is significant scope for policy intervention to minimize harmful introductions and steer alien species and climate change interactions in a more positive direction (Table 9.2). One major focus should be the control of carbon sequestration projects such that ecosystem rehabilitation using native species adapted to the relevant biome is strongly promoted (Bond, 2019). Global meta-analysis of species' climate responses to date shows significant adverse effects of climate change on native species, particularly endemics (including many from South Africa), while in many instances, invasive species stand to benefit (Manes *et al.*, 2021). Connected functioning ecosystems will be key to retaining biodiversity. Stewardship agreements and other conservation planning tools can be used to facilitate response of native species to climate change (Keeley *et al.*, 2019) in ways which allow specialist species to adapt and which prevent invasion by generalist species (e.g. Marvier *et al.*, 2004) from causing significant biodiversity loss. Cross-border collaboration will also be essential, since climate change impacts are predicted to be far more extreme in countries north of South Africa. Finally, pathway control will remain paramount to ensure that new food sources (including those from aquaculture and mariculture) are adequately screened (Bates *et al.*, 2013); where appropriate, measures must be taken to minimize the introduction of stowaway species with such introductions (e.g. Heather and Hallman, 2008). Current legal frameworks are poorly prepared, globally, for redistribution of species and land productivity expected under climate change (Titley *et al.*, 2021). Increasing flexibility in governance tools will be required to balance biodiversity and human livelihoods into the future (Pecl *et al.*, 2017).

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