Chapter 11
Biological Invasions in South Africa’s Urban Ecosystems: Patterns, Processes, Impacts, and Management

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Abstract As in other parts of the world, urban ecosystems in South Africa have large numbers of alien species, many of which are invasive. Whereas invasions in South Africa’s natural systems are strongly structured by biotic and abiotic features of the region’s biomes, the imprint of these features is much less marked in urban ecosystems that exist as islands of human-dominated and highly modified habitat. Surprisingly little work has been done to document how invasive species spread in South African urban ecosystems, affect biodiversity, ecosystem services and human well-being, or to document the human perceptions of alien and invasive species, and the challenges associated with managing invasions in cities. This chapter reviews the current knowledge of patterns, processes, impacts and management of invasions in South African urban ecosystems. It highlights unique aspects of invasion dynamics in South African urban ecosystems, and identifies priorities for research, and key

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challenges for management. South African towns and cities share invasive species from all taxonomic groups with many cities around the world, showing that general features common to urban environments are key drivers of these invasions. There are, however, several unique biological invasions in some South African urban settings. The pattern of urbanisation in South Africa is also unique in that the imprint of Apartheid-era spatial planning is striking in almost all towns and cities and is aligned with stark disparities in wealth. This has resulted in a unique relationship between humans and the physical environment (e.g. very different assemblages of alien species in affluent compared to low-income areas). New ways of approaching invasive alien species management are emerging in South African towns and cities, but better facilitating mechanisms and protocols are needed for dealing with conflicts of interest.

11.1 Introduction

Urbanisation is increasing rapidly worldwide, altering ecosystem functioning and affecting the capacity of ecosystems to provide services for people (Elmqvist et al. 2015; Luederitz et al. 2015). In the face of this trend, many countries are struggling to balance the demands of economic development with the obligations to conserve biodiversity and ensure the delivery of ecosystem services (ES) to urban populations (Elmqvist et al. 2015). Perceptions regarding nature in urban areas are changing rapidly (Marris 2011; du Toit et al. 2018)—the notion of conserving nature in a pristine state (excluding humans) is shifting to the view that people are part of ecosystems and benefit from ES, and that ecosystems should be managed to ensure resilience and the sustainable delivery of ES (Mace 2014).

Urban areas are susceptible to biological invasions for several reasons. First, they are foci for the introduction (intentional and accidental) of alien species. Second, the availability of large numbers of propagules due to intensive cultivation and repeated introductions of many alien species (especially species used for ornamental horticulture, aquaculture and the pet trade) increases the likelihood of their establishment and persistence (Williamson and Fitter 1996; Pyšek 1998; Kowarik et al. 2013). Third, the complex networks of dispersal pathways and vectors in cities facilitate the rapid dissemination of propagules, both within urban settings and outwards into surrounding natural and semi-natural ecosystems (Alston and Richardson 2006; von der Lippe and Kowarik 2008; McLean et al. 2017; Padayachee et al. 2017). Fourth, altered disturbance regimes, complex physical structures, and increased resource availability associated with concentrated human activities create opportunities for the establishment, reproduction and proliferation of many alien species (Cadotte et al. 2017). Fifth, the alteration of biotic conditions, microclimatic conditions, hydrology, and soils are important mediators of the patterns and processes of biological invasions in urban ecosystems (Klotz and Kühn 2010).

Knowledge of the interplay between social and ecological systems in urban landscapes is becoming increasingly important as a growing proportion of human
populations reside in cities. The trend of rapid urbanisation in developing countries (UNFPA 2007), and the ever-increasing dependence on the provision of ES, means that growing negative impacts on these services is a rising concern for city managers (Potgieter et al. 2017). While urban ecosystems provide multiple ES for human well-being, they can also generate functions, processes and attributes that result in perceived or actual negative impacts on ES and human well-being—these are termed ecosystem disservices (EDS) (Shackleton et al. 2016; Vaz et al. 2017). Invasive animals in urban landscapes have been linked with the spread of human disease, reduction in local biodiversity, and damage to property and infrastructure (Shochat et al. 2010; Reis et al. 2008). Urban plant invasions have been implicated in human health issues, increased fire hazard, and safety and security risks (Pyšek and Richardson 2010; van Wilgen and Richardson 2012; Potgieter et al. 2018, 2019a, b).

Management of invasive species in cities differs markedly in different parts of the world. This is often closely linked to the availability of funding and the approaches for setting priorities for city planning. Some cities prioritise urban green space, while others channel limited funding earmarked for “environmental issues” to other priorities more closely aligned with socio-political imperatives (Irlich et al. 2017). City-based managers of invasive species are typically aligned to environmental or biodiversity protection mandates. This means that, although control of invasive species may be undertaken to comply with national legislation, the decisions that are made, and plans that are implemented are often aimed at alleviating pressures on, or at reversing damage to, natural ecosystems and biodiversity. Such concerns are typically highly context-specific (e.g. Potgieter et al. 2018).

Urban environments have complex land-tenure patterns, with smaller and more numerous land parcels and consequently many more landowners (e.g. privately-owned property, national and provincial government land, municipal property managed by different departments). This pattern complicates the coordination of management activities (Gaston et al. 2013). Large numbers of landowners mean a diversity of incentives, policies, and practices for managing invasive species, and a strong likelihood of conflicts of interests (Dickie et al. 2014; van Wilgen and Richardson 2014; Gaertner et al. 2016; Zengeya et al. 2017). Species that provide both ES and EDS generate conflicts around their use and management. Invasive species may provide provisioning ES (e.g. firewood), but at the expense of biodiversity, leading to conflicts over which should be prioritised (van Wilgen 2012). Indeed, management to optimise specific ES exclusively may exacerbate associated EDS, and interventions aiming at reducing EDS only may also reduce ES (Shackleton et al. 2016). Site accessibility also presents a considerable challenge in controlling alien plant invasions in the urban landscape.

Although most research on biological invasions has focussed on ecological aspects (García-Llorente et al. 2008; Hui and Richardson 2017), the ways in which social dimensions mediate responses to invasions are emerging as crucial considerations in invasion science (Kull et al. 2011, 2018; Shackleton et al. 2019b). Effective engagement with stakeholders is emerging as a crucial ingredient in invasive species management (Novoa et al. 2018; Shackleton et al. 2019a). Sustainable strategies for dealing with conflict-generating invasive species rely on
cooperation and support from all stakeholders—those who support the use of these species and those who support their control.

Cities are “surrogates for global change” (Lahr et al. 2018) and we need to further our understanding of invasion in urban areas. Although urban ecosystems are hotspots for biological invasions, invasion science has given scant attention to exploring the invasion dynamics and the challenges facing managers in towns and cities, particularly in developing countries (Gaertner et al. 2017a). This is also the case in South Africa which has a long history of managing biological invasions in natural and semi-natural ecosystems (Macdonald et al. 1986a; van Wilgen 2020, Chap. 2). This chapter reviews the emerging knowledge of patterns and processes, impacts, perceptions and management of biological invasions in urban ecosystems in South Africa.

11.2 Patterns and Processes

Urban ecosystems are those where humans live at high densities and where the built infrastructure covers a large proportion of the land surface (Pickett et al. 2001). Following the South African settlement typology (van Huyssteen et al. 2015), this chapter focuses primarily on towns and cities, but examples are also drawn from smaller human settlements such as staff and tourist villages in protected areas (Foxcroft et al. 2008) and military bases surrounded by natural vegetation (e.g. Milton et al. 2007).

Alien species are abundant in all cities, but the understanding of invasion dynamics (i.e. the factors that mediate the introduction, establishment, proliferation and spread of alien species) in urban ecosystems is generally poor worldwide (Gaertner et al. 2017b). In South Africa, knowledge of the patterns and processes of invasions in urban settings is poor despite a long history of alien species introductions into urban centres across the country. Urban areas throughout South Africa, like those worldwide, share certain features that facilitate the proliferation of some alien species. These attributes exist irrespective of the biome in which the town or city occurs. While there is some “overflow” of natural-area invaders into urban settings (e.g. Australian wattles in Cape Town; Chromolaena odorata, Trifid Weed, in Durban), urban areas in South Africa share a similar set of invasive species from all taxonomic groups with many cities around the world, e.g. Ailanthus altissima (Tree of Heaven), Rattus rattus (Black Rat). For these species, general features common to urban environments, rather than biome-specific factors, are the dominant drivers of invasions. However, South Africa’s unique history has had a major imprint on the composition of alien species pools in urban areas, the ways in which alien and invasive species are perceived, their impact on ES and human well-being, and on approaches to management.

A wave of alien species introductions followed the colonisation of South Africa by Europeans from the mid-seventeenth century (van Wilgen et al. 2020, Chap. 1). From this time, distinct phases of introductions driven by the needs and activities of
humans occurred, often leading to notable invasion episodes (Richardson et al. 2003). The last third of the twentieth century saw substantial social transformations in South Africa, leading to significant changes in human demographics, micro- and macro-economic climates, and in the country’s role in the global economy. These factors all continue to influence the relationship between South African societies and alien species and consequently the vectors and pathways for alien taxa (Richardson et al. 2003; Le Maitre et al. 2004). Below we discuss key drivers of invasions of alien plant and vertebrate species in urban areas of South Africa.

11.2.1 Plants

The history of plant introductions has been crucial for driving invasions of alien plants in many South African cities, and demonstrates in part why invasions in cities are very different to those in natural or semi-natural areas (where most alien plants were introduced for purposes other than ornamental horticulture) (Fig. 11.1).

While there are similarities in the process between urban and rural or natural invasions (e.g. lag phase), the dynamics and characteristics of the receiving environments differ. The high heterogeneity of the urban landscape, altered disturbance regimes, and increased resource availability associated with concentrated human activities provide opportunities for the establishment, reproduction and proliferation of many alien plant species even in marginal sites (Figs. 11.1a and 11.2a). The horticultural industry has been a particularly important pathway for the introduction of alien plants to South Africa, and the escape of ornamental plants from cultivation and gardens has resulted in some of the most extensive biological invasions in the country (Figs. 11.1b and 11.2b, c; Richardson et al. 2003; Foxcroft et al. 2008; Geerts et al. 2013, 2017; Holmes et al. 2018).

Invasibility is strongly influenced by propagule pressure—massive propagule pressure (many large trees) ensures that even suboptimal microsites are invaded (overcoming abiotic barriers and biotic resistance) (Rejmánek et al. 2005). Donaldson et al. (2014) show that the number of trees introduced into urban areas was the most important parameter influencing abundance and extent of invasive Australian Acacia populations. A survey along the Eerste River in Stellenbosch found that areas along the river bordered by urban land had the highest numbers of alien plant species (Fig. 11.2d; Meek et al. 2010). Another notable example is the invasion of Metrosideros excelsa (New Zealand Christmas Tree) in Betty’s Bay, Western Cape—where relatively large areas of natural vegetation within the town’s border are dotted with ‘islands’ of human habitation in the form of single residences (Figs. 11.1c and 11.2e). In the late 1960s, horticulturists recommended the planting of M. excelsa as a “safe” replacement hedge plant for the highly invasive Leptospermum laeavigatum (Australian Myrtle). Today, M. excelsa is a serious invader in and around several coastal towns in the Western Cape (Richardson and Rejmánek 1998).

The influence of propagule pressure on invasibility is also evident in smaller settlements. While large cities are usually the first sites of introduction, small human
Fig. 11.1  Schematic representation of the role of introduction history in mediating alien plant invasions along the urban-wildland gradient (graphical depiction inspired by Donaldson et al. 2014). The escape of ornamental plants from cultivation and gardens has resulted in some of the most extensive biological invasions in South Africa. (a) The heterogeneity of the urban landscape provides artificially modified, highly disturbed micro-habitats (e.g. vacant lots) which allow establishment of invasive species even in marginal sites, especially when propagule pressure is high; (b) Ornamental trees cultivated in suburban gardens spread beyond the confines of the garden into the surrounding natural vegetation; (c) Relatively large areas of natural vegetation within the boundaries of towns may be dotted with ‘islands’ of human habitation in the form of single residences, which can serve as individual launching sites for the spread of alien ornamental plants into surrounding natural areas; (d) Small human settlements are more numerous than large cities or towns and are more likely to act as launching sites for plant invasions into natural areas as they share proportionally greater boundaries with their surroundings.
Fig. 11.2 Examples of alien plant species invading urban areas in South Africa. (a) *Acacia saligna* (Port Jackson Willow) and *Leptospermum laevigatum* (Australian Myrtle) invading a vacant plot in Fisherhaven, Western Cape (Photograph courtesy of DM Richardson); (b) *Ailanthus altissima* (Tree of Heaven) spreading from an ornamental planting in Stellenbosch, Western Cape (Photograph courtesy of DM Richardson); (c) *Anredera cordifolia* (Madeira vine) causing infrastructural damage in Wilderness, Western Cape (Photograph courtesy of N Cole); (d) *Sesbania punicea* (Red Sesbania) spreading along the Eerste River, Stellenbosch, Western Cape (Photograph courtesy of DM Richardson); (e) *Metrosideros excelsa* (New Zealand Christmas Tree) invading fynbos vegetation in the coastal town of Betty’s Bay, Western Cape from trees planted around houses (seen in the background) (Photograph courtesy of DM Richardson); (f) *Myrtillocactus geometrizans* (Bilberry Cactus) spreading into natural karoo vegetation from a 40-year-old cactus garden near the town of Prince Albert, Western Cape (Photograph courtesy of SJ Milton)
settlements are more numerous and are more likely to act as launching sites for plant invasions into natural areas as they share proportionally greater boundaries with their surroundings (Fig. 11.1d; Foxcroft et al. 2008; McLean et al. 2017). For example, a survey inside a military base near Kimberley in the Northern Cape showed that alien fleshy-fruited trees cultivated mostly as ornamentals, for shade, or to provide fruit, spread beyond the confines of the base into the surrounding savanna (Milton et al. 2007). Dean and Milton (2019) describe the invasion of *Myrtillocactus geometrizans* (Bilberry Cactus) into natural vegetation near the town of Prince Albert, Western Cape, from a 40-year-old cactus garden in the town (Fig. 11.2f). Cilliers et al. (2008) found that the cover of alien species increases with increasing proximity to the edge of native grassland patches surrounded by urban and rural landscapes in South Africa and Australia. Such examples provide evidence of a key process driving many urban plant invasions.

During the Dutch and British colonial periods (1652–1871), most alien plant species were introduced for timber production (forestry), fuelwood, shade and dune reclamation (Richardson et al. 2003). Such introductions have left a major imprint on plant invasions in natural and semi-natural ecosystems (Richardson et al. 2020, Chap. 3). However, by the twentieth century there was an increasing emphasis on amenity plantings in gardens and urban open spaces (Richardson et al. 2003). This trend increased exponentially, and there has been an explosion of large and small organisations (e.g. online traders) specialising in the dissemination of plants (usually in the form of seeds or bulbs) worldwide in the last decade (e.g. Humair et al. 2015).

Despite a recent upsurge in the popularity of wild, drought-tolerant gardens comprising mainly native plants, alien plants remain conspicuous features in all South African cities. Early European settlers wanted to reconstruct the gardens of Europe and these introductions were, in many cases, assimilated into local culture, which perpetuated their further use (e.g. Davoren et al. 2016). Examples include oaks (*Quercus* species) in Stellenbosch (nicknamed Eikestad in Afrikaans, i.e. “Oak City”), and *Jacaranda mimosifolia* in Pretoria (“Jacaranda City”). At least 25 alien tree species are protected as “Champion Trees of South Africa” under the National Forests Act of 1998. Many of these occur in urban settings—68% of species listed as “champion trees” are alien and 25% are currently listed as invasive. Updated information from the South African Plant Invaders Atlas (SAPIA, accessed 12 December 2018) shows that 18% of invasive alien plant taxa recorded for South Africa occur in urban open spaces or around human habitation (Henderson and Wilson 2017). The proportion of “urban invaders” in South Africa’s invasive flora is, however, much greater than this, as 76% of taxa listed in Henderson’s (2001) book on “Alien weeds and invasive plants” are ornamental plants that are grown in urban areas, and because Henderson’s book focusses largely on natural-area invaders.

Life-history traits such as flower and fruit size and shape, growth rates, and the capacity to flourish under harsh environmental conditions have driven the importation of many alien plants into urban areas of South Africa. As a result, large showy flowers, colourful fruits, the capacity for rapid growth and the ability to survive without irrigation are features of many widely planted alien plants in South Africa. Waves of interest in new types of alien trees with particular features have occurred in
recent times. Such traits are also associated with reproductive success and efficient dispersal and allow species to establish and spread into new environments (Aronson et al. 2007; Moodley et al. 2013). For example, following a lag phase of several decades, several paperbark (Melaleuca spp.) species (introduced for ornamental purposes) are now emerging as invasive (Jacobs et al. 2017). This trend in human preference for particular plant traits has led to an increase in the proportion of invasive alien trees and shrubs in many urban areas due to the spread of species introduced for ornamentation (Potgieter et al. 2017). Indeed, some invasive plant species are still available in nurseries around the country (Cronin et al. 2017).

Many alien plant species also hybridise with other alien and native congeners introduced by horticulturists. This process can compromise the genetic integrity of native taxa and/or enhance the invasive ability of their hybrid offspring (Williamson and Fitter 1996). An example in South Africa is the genus Celtis, where the introduced C. sinensis (Chinese Hackberry) hybridises with the native C. africana (White Stinkwood; Siebert et al. 2018). Invasive populations of Celtis species in South Africa are almost certainly hybrids (Milton et al. 2007). Problems with identification have exacerbated invasions in some cases. For example, C. sinensis is often incorrectly identified, labelled, sold and disseminated as the native C. africana (Siebert et al. 2018).

11.2.2 Vertebrates

Aside from domestic pets and agricultural livestock, most alien terrestrial vertebrates in South Africa were introduced as novelties for private collections, for game viewing, or for hunting (Richardson et al. 2003; van Rensburg et al. 2011; Measey et al. 2020, Chap. 5). Trading in animals between landowners provides opportunities for invasion, or for genetic contamination of native species through hybridisation (Spear and Chown 2009a, b). Most alien bird taxa that arrived in South Africa (apart from those intentionally introduced by C.J. Rhodes between 1853 and 1902, and the House Crow Corvus splendens), appear to have been imported for aviaries.

Few alien mammals have been intentionally introduced into urban South Africa. The Grey Squirrel (Sciurus carolinensis) which was introduced to the Cape Peninsula by C.J. Rhodes as part of his programme to “improve” the amenities at the Cape (Brooke et al. 1986; Picker and Griffiths 2017). This species has persisted in urban environments and spread in areas where alien pines and oaks occur, but cannot colonise widely separated patches of these trees, except with assistance of humans (Smithers 1983). The Black Rat (Rattus rattus) was probably introduced accidentally by Arab traders moving down the east coast, with subsequent additional undocumented arrivals (Brooke et al. 1986). The Brown Rat (R. norvegicus) and the House Mouse (Mus musculus) arrived as stowaways on ships from Europe, while the Asian House Rat (Rattus tanezumi) from South-East Asia was first recorded in South Africa in 2005 (Bastos et al. 2011). Some naturalised populations of alien mammals originated from escapees from zoological collections (e.g. Himalayan
Urbanisation in Johannesburg and the Gauteng metropolis has transformed large tracts of grassland to urban woodland over the past 150 years. This has resulted in a positive relationship between the number of invasive species, the proportion of transformed land and the land-use heterogeneity index, as well as a shift in local species composition (Symes et al. 2017). For example, the distribution and population densities of the Common Myna (*Sturnus tristis*), independently introduced to South Africa on at least two occasions since the late nineteenth century, are closely tied to that of people and are associated with highly transformed land (Peacock et al. 2007).

Urbanisation has also contributed to major range expansions of several native South African species. For example, the Haded Ibis (*Bostrychia hagedash*) and Speckled Pigeon (*Columba guinea*) are now common in nearly all South African cities (Duckworth et al. 2012). Hadedas rely on (many alien) trees in which to nest, and irrigated lawns (mainly alien grass species) for foraging (Macdonald et al. 1986b). Similarly, Guttural Toads (*Sclerophrys gutturalis*) translocated from their native range in Durban to a peri-urban area of Cape Town have become established (Telford et al. 2019), as this area of the city has low-density, high-income housing with frequent water features in which the animals could breed (Measey et al. 2017). Although movement from the summer rainfall area of South Africa into the winter rainfall zone would normally result in failure to establish (Vimercati et al. 2018), the availability of garden ponds meant that this species expanded rapidly over 15 years to cover much of the suburb (~5 km² Measey et al. 2017; Vimercati et al. 2017a). Moreover, attempts to control the population were severely hampered by restricted access to the properties of multiple private landowners, enabling the spread to continue (Vimercati et al. 2017b).

The desire to have gardens with trees, lawns and ponds has facilitated many of the invasions of alien vertebrates in urban areas of South Africa. The desire to emulate a European garden is normally only enacted in the most affluent suburbs. Invasions in these areas are clearly mediated by factors such as changes in gardening practices or the densification of human settlements which alters the extent of suitable habitat and the effectiveness of dispersal corridors (Moodley et al. 2014). Rivers are key dispersal conduits for alien plant dispersal in South African towns and cities (e.g. Kaplan et al. 2012).

### 11.3 Positive and Negative Effects of Invasive Alien Species in Urban Areas

In some instances, the introduction of alien species results in a novel set of ecosystem services (ES) and ecosystem disservices (EDS) for urban residents. For example, many alien trees were introduced into towns and cities situated within the Fynbos
Biome (a region with few native tree species) to provide ES which could not be provided by the native flora. However, many introduced tree taxa such as Australian acacias, hakeas and pines became invasive, threatening the delivery of ES (van Wilgen et al. 2008; van Wilgen and Richardson 2012; Le Maitre et al. 2020, Chap. 15; Zengeya et al. 2020, Chap. 17) and creating a novel suite of EDS such as increased safety and security risks (Potgieter et al. 2018, 2019b; Supplementary Appendix 11.1).

11.3.1 Ecosystem Services

Plants  South Africa presents a unique case study in that some urban centres are located within areas that are depauperate in native trees (e.g. Cape Town situated within the CFR and Johannesburg on the Highveld) (Rundel et al. 2014). The introduction of alien species to these urban centres (and subsequent proliferation into surrounding natural areas) provided a novel suite of ES and as a result, urban residents have forged new relationships with such species (Box 11.1).

Box 11.1 Key Ecosystem Services Provided by Invasive Plants in Urban South Africa

Provisioning services: Shackleton et al. (2017) show that harvesting of native and alien plant species (e.g. providing foods, medicines, and materials) is a widespread practice in urban, suburban and peri-urban landscapes globally. Many invasive alien trees are an important source of firewood for urban residents in South Africa, particularly in low-income areas (figure below). For example, in Cape Town, there are relatively few widespread native tree species available as a source of firewood, and many residents utilise invasive alien shrubs and trees for these purposes, including *Acacia cyclops* (Rooikrans), *A. mearnsii* (Black Wattle), *A. saligna* (Port Jackson Willow), *Eucalyptus* species (eucalypts) and *Pinus* species (pines) (Gaertner et al. 2016; Potgieter et al. 2018).

(continued)
Acacia mearnsii (Black wattle) sold as firewood in Cape Town, Western Cape, South Africa. Photograph courtesy of Woodgurus

**Cultural services:** Many of the alien species introduced by European settlers (particularly alien trees) now have strong cultural and historical links to South African heritage. While many of the species have become naturalised or invasive around the country, some exceptional individuals are protected under the National Forests Act of 1998 and still provide key ecosystem services (ES). While the horticultural trade is a major introduction pathway for alien plant species around the world (Dehnen-Schmutz et al. 2007), alien trees and shrubs (many of which have subsequently spread into surrounding natural areas) have provided a novel suite of ES in urban areas in South Africa. Many invasive alien tree species are highly valued by urban residents for their aesthetic appeal. For example, species as *Acacia elata* (Pepper Tree Wattle) and *Ailanthus altissima* (Tree of Heaven) are popular ornamental subjects in many residential gardens across South Africa (first figure below; Donaldson et al. 2014; Walker et al. 2017). Invasive aquatic plants such as *Eichhornia crassipes* (Water Hyacinth) and *Nymphaea mexicana* (Mexican Water Lily) are also highly valued for their visual amenity. Plantations of invasive alien trees from the genus *Eucalyptus* (e.g. *E. camaldulensis, E. diversicolor* and *E. gomphocephala*) close to urban areas also have considerable appeal to hikers, cyclists and tree enthusiasts (Gaertner et al. 2016). Some alien and invasive plant taxa provide roosting and breeding sites for rare raptors (supporting services—second figure below) and serve as important tourist attractions. Urban areas comprise a diversity of cultures and the long history
Box 11.1 (continued)
of alien plant introductions (and invasions) in many urban areas around South Africa has resulted in unique cultural attachments. For example, in some areas of Cape Town, stands of invasive *A. saligna* serve as important sites for Xhosa initiation rituals (C. Rhoda 2017, pers. comm.).

*Ailanthus altissima* (Tree of heaven) planted for ornamental purpose in a residential complex in Stellenbosch, Western Cape, South Africa. Photograph courtesy of Ulrike Irlich

(continued)
Box 11.1 (continued)

Stephanoaetus coronatus (Crowned Eagle) perched in a Eucalyptus tree in Pietermaritzburg, KwaZulu Natal, South Africa. Photograph courtesy of A Froneman

Regulating services: The introduction of alien trees into urban centres around South Africa provided shade for urban residents (figure below). Many plantations, especially stands of Pinus radiata (Monterey Pine) in Cape Town, are heavily utilised by urban residents for recreation (picnicking, cycling, walking), mainly because of the shade they provide (Potgieter et al. 2019a). Acacia elata is valued as a shade and amenity tree, especially on golf courses (Donaldson et al. 2014), while other alien trees such as E. gomphocephala (Tuart) are important for providing shade in informal settlements and townships (Gaertner et al. 2016). (continued)
Box 11.1 (continued)

Eucalyptus sp. providing shade for a street vendor in Cape Town, Western Cape, South Africa. Photograph courtesy of LJ Potgieter

Supporting services: Invasive plants can also provide important habitat for other species. For example, invasive *Eucalyptus* trees are used extensively as roosting sites by the vulnerable *Falco naumannii* (Lesser Kestrel) and *Falco amurensis* (Amur Falcon) (Bouwman et al. 2012) and as breeding sites by *Haliaeetus vocifer* (African Fish Eagle) (Cilliers and Siebert 2012) and *Stephanoaetus coronatus* (Crowned Eagle) (McPherson et al. 2016).

Vertebrates  Most people in South Africa’s urban environments are unaware that many of the dominant species in their cities are alien (Novoa et al. 2017). Many people enjoy interacting with alien species that have become accustomed to receiving food from city residents. For example, Mallards (*Anas platyrhinchos*) are fed bread by city residents, and squirrels are provided with nuts and kitchen scraps. Human attachment to cats has ensured their persistence, as they centre their home range movements around supplemental resources such as food (e.g. in the town of Pietermaritzburg; Pillay et al. 2018). The use of amphibians as educational aids also
led to the facilitated movement of Guttural Toads outside of their invaded range in Cape Town (Measey et al. 2017). Many people still value these animals for the original ornamental attributes for which they were introduced, and this has led to several conflict situations with control.

11.3.2 Ecosystem Disservices (EDS)

**Plants** Since alien plant species make up a large proportion of urban floras (e.g. Pyšek 1998; Kühn and Klotz 2006), it is important to weigh the detrimental effects of alien plant species against the ways they enhance local diversity and maintain important functions (Elmqvist et al. 2008). Arguments for and against managing invasive species in urban areas increasingly hinge on their contributions to the delivery of ES and EDS (Potgieter et al. 2017, 2018; Vaz et al. 2017). Many alien species that were introduced specifically to supply, augment or restore ES have spread beyond sites of original containment, captivity or plantings to become invasive. Some of these invasive alien plant species can alter ecosystem functions, reduce native biodiversity, and have a negative impact on ES (Box 11.2; Pejchar and Mooney 2009; Shackleton et al. 2016). Negative impacts include financial costs (e.g. costs of pruning, repairing damage to urban infrastructure), social nuisances (e.g. allergenic pollen, safety hazards from falling trees) and environmental costs (e.g. alteration of nutrient cycles, displacement of native species), which impact negatively on human well-being (Escobedo et al. 2011; Roy et al. 2012; Potgieter et al. 2017; Vaz et al. 2017).

**Box 11.2 Key Ecosystem Disservices Provided by Invasive Plants in Urban South Africa**

*Biodiversity:* The effects of urbanisation on biodiversity are particularly serious in South Africa because many urban centres occur in or around areas with high levels of species richness and endemism. For example, in Cape Town the impact of invasive species on the rich biodiversity is of major concern (Holmes et al. 2012). The city is located within the Cape Floristic Region (CFR), a global centre of plant endemism (Cowling et al. 1996). The city (2445 km² in extent) surrounds the Table Mountain National Park (221 km²), 17 smaller nature reserves, and 500 biodiversity network sites that together cover 270 km². Invasive tree species such as pines (*Pinus* species) grown in plantations, and Australian wattles (e.g. *Acacia saligna*) planted mainly along the coast for dune stabilisation, have spread widely into natural vegetation (figure below) where these species outcompete and replace natural vegetation leading to homogenisation and a decrease in native biodiversity (Rebelo et al. 2011). For example, *P. radiata* that occurs in commercial plantations in and around Cape Town is highly invasive (Richardson and Brown 1986) and poses
Box 11.2 (continued)
a substantial threat to the biodiversity of TMNP (Richardson et al. 1996). *Acacia saligna* also reduces avian species richness in urban and peri-urban areas of Cape Town (Dures and Cumming 2010).

*Pittosporum undulatum* (Australian Cheesewood) and *Pinus* sp. spreading into natural vegetation in Cape Town, Western Cape, South Africa. Photograph courtesy LJ Potgieter

Fire: Fire is an important natural process in many parts of South Africa, especially in the Fynbos, Grassland and Savanna Biomes, which are all fire-adapted and fire-dependent (van Wilgen 2009). However, accidental (and often intentional) fires started by people have led to more frequent and uncontrolled fires, which threaten property and the safety of people (van Wilgen and Scott 2001). The increase in biomass resulting from alien plant invasions (particularly woody alien plant taxa such as eucalypts, pines and wattles, but also tall grass species, notably *Arundo donax*) close to urban infrastructure represents a substantial fire risk (figure below; van Wilgen et al. 2012), threatening property and the safety of people (van Wilgen and Scott 2001), while also providing opportunities for those engaged in criminal activity (Supplementary Appendix 11.2). Other areas such as vacant properties, public open spaces and riparian areas have also become invaded to the degree that they pose a fire risk to infrastructure.

(continued)
Box 11.2 (continued)

A wildfire that was exacerbated by invasive vegetation threatening infrastructure in Glencairn, Western Cape, South Africa. Photograph courtesy of the Cape Argus Newspaper from 2000

**Water**: The sustainable provision of water is a major challenge in many parts of South Africa. Many natural surface water options have been depleted and the continued spread of invasive plants in catchments that supply urban areas with water is adding further strain to the dwindling resource (figure below). Stands of invasive trees use significantly more water than the low-statured native vegetation, thereby decreasing surface run-off and ultimately water supply and security to towns and cities (Le Maitre et al. 2015). For example, *E. camaldulensis* (River Red Gum) is a highly invasive species which has invaded riparian zones, significantly reducing surface water run-off (Forsyth et al. 2004; Gaertner et al. 2016). These effects are exacerbated by the periodic drought in many cities (particularly in the Western Cape). Many aquatic invasive species such as *Eichhornia crassipes* also block waterways and affect water quality (Richardson and van Wilgen 2004).

(continued)
Vertebrates  Invasive vertebrates exhibit a wide range of impacts (ecological, economic and health) worldwide (Vilà et al. 2010), but few South African studies have assessed these impacts in an urban context. Among the most important impacts of rats in South African urban areas are those of zoonotic diseases, including leptospirosis, plague (caused by the bacillus *Yersinia pestis* transmitted from rats to humans by fleas), and toxoplasmosis in humans (Taylor et al. 2008). They also carry several co-invasive parasites (Julius et al. 2018). It has also been suggested that zoonotic disease prevalence may increase due to the compromised immune systems of HIV/AIDS patients in South African urban areas (van Rensburg et al. 2011).

The impacts of birds in urban South Africa are various, reflecting the diverse impacts recorded for avifauna globally (Evans et al. 2016). For example, Mallards (*Anas platyrhynchos*), introduced for game hunting but increasingly popular as an ornamental species, hybridise with the native Yellow-Billed Duck (*Anas undulata*) (Stephens et al. in press). The House Crow (*Corvus splendens*) arrived in the harbours of Durban and Cape Town by hitching rides on small vessels (see Supplementary Appendix 11.2). They are a serious pest in many cities around the world where they live in close association with humans. This species is noisy and threatens public health, agriculture, urban wildlife, and aircraft electrical installations (Berruti and Nichols 1991). It been identified as the carrier of human enteric disease
organisms (Enterobacteriaceae) such as *Salmonella* species, *Shigella* serotypes, *Proteus* species, *Vibrioaceae* species, *Pseudomonas* species, *Escherichia coli*, *Campylobacter* species, and Newcastle disease (Sulochana et al. 1981; Ryall and Reid 1987; al-Sallami 1991). These diseases are likely due to the tendency of populations to frequent areas where waste foods and faeces are dumped. It is also a known faecal contaminator of human environments and water resources. The crows may also hold potential for spreading bird flu viruses.

Cats have devastating effects on native biodiversity worldwide (Hagen and Kumschick 2018), and South Africa’s feral and domestic cats appear to be no different. Cats on the urban edge have been shown to have a significant impact on adjoining biodiverse areas in the Table Mountain National Park (George 2010; Morling 2014).

The negative impacts of invasive alien fish in the context of urban rivers and water bodies in South Africa remains poorly understood. Kruger et al. (2015) reported a negative effect of the invasive predatory Mosquitofish (*Gambusia affinis*) on native amphibian community assemblages and abundance in Potchefstroom.

**Pests and pathogens** Internationally, trees in urban environments play an important role in preserving biodiversity and supplying ES in urban areas, and as the world becomes more globalised, urban forests will provide increasingly valuable benefits. However, trees in urban environments are particularly vulnerable to pest and pathogen invasions. Most tree damaging insect pests and pathogens (hereafter referred to as pests) arrive as accidental introductions, a by-product of increasing trade and globalisation (Santini et al. 2013; Meurisse et al. 2018). Urban areas are hubs for international trade and frequently serve as the first point of entry for alien forest pests (Paap et al. 2017). Besides being subjected to high propagule pressure, urban trees experience stressful conditions resulting from anthropogenic disturbances, increasing their susceptibility to pest attack (Paap et al. 2017). Once established in urban environments, introduced pests can spread into natural or planted forests often resulting in permanent damage, and efforts at controlling such invasions can become costly.

Considering the vulnerability of urban trees to invasive pests, there have been moves globally to focus surveillance on urban trees for early detection of new pest invasions. Most pests are not problematic in their natural range, which means that many damaging invasive pests were unknown to science before they arrived and established in a new environment. Such pests were therefore not on watch lists and could not have been regulated against. ‘Sentinel plantings’, that is, plants established outside their natural range, are increasingly being used to identify new host-pest associations, predict future tree health threats and fill gaps in pest risk analyses (Eschen et al. 2018; Poland and Rassati 2018). The range of impacts caused by damaging invasive pests on tree health in South Africa are highlighted by the following case studies.

Some invasive alien pests in South Africa may only be problematic on alien tree hosts with no risk to agriculture, planted forests or the natural environment. The Sycamore Lace Bug (*Corythucha ciliata*), a highly invasive tingid native to eastern parts of North America and Canada, is a recent invader in South Africa (Picker and
Griffiths 2015). To date it has only been identified from London Plane trees (*Platanus × acerifolia*) in the Western Cape. These bugs are sap suckers and form dense colonies on the underside of leaves with damage becoming apparent in late summer. These leaves may be excised earlier than normal, and where severe damage occurs over several consecutive years in the presence of additional stress factors, tree death may result (Barnard and Dixon 1983).

Other invasive alien pests may initially establish on ornamental species but as populations build and spread, present a threat to native plants. For example, the Cycad Aulacaspis Scale (CAS), *Aulacaspis yasumatsui*, an insect native to Southeast Asia, is an important pest of cycads. This pest has spread globally through the trade of cycads and is now a major threat to ornamental and native cycads in many countries. The International Union for Conservation of Nature, Species Survival Commission-Cycad Specialist Group refer to CAS as the single most important threat to natural cycad populations globally and it is listed as a prohibited species in South Africa’s National Environmental Management: Biodiversity Act (Act No. 10 of 2004) (NEM:BA) Alien & Invasive Species Regulations. In 2015, CAS was identified from the alien *Cycas thouarsii* (Madagascar Cycad) in the Durban Botanic Gardens (Nesamari et al. 2015). Further surveys identified the pest present in three South African provinces on cultivated *Cycas* as well as native *Encephalartos* species. Infested *Cycas* were also found in two commercial nurseries, demonstrating the high risk of spread of this pest through the nursery trade.

A second case is exemplified by the fungal root rot agent *Armillaria mellea*. First detected in Cape Town in 1996, there is evidence that it was introduced during the establishment of Company Gardens by early Dutch settlers in the mid-1600s (Coetze et al. 2001). Some years later *A. mellea* was identified in Kirstenbosch National Botanical Gardens (Coetze et al. 2003), and more recently has spread further and is causing root rot of woody plants and trees in natural ecosystems around Cape Town. Most significantly it has now invaded the ecologically important natural environment of Table Mountain National Park, where it is threatening several rare and endangered woody plant species (Coetze et al. 2018).

Pests of economically important crop trees and plantation forests are well documented in comparison to tree pests occurring in urban or natural environments, an area that has been suggested as under-represented in invasion biology in South Africa (Wood 2017). The recent discovery of the highly damaging invasive Polyphagous Shot Hole Borer (*Euwallacea fornicatus*), however, has brought to light the extensive economic, ecological and social impacts that urban areas face with the arrival and establishment of a ‘worst-case scenario’ pest (Box 11.3).
Box 11.3 The Polyphagous Shot Hole Borer and *Fusarium* Dieback in South Africa

(a) Female Polyphagous Shot Hole Borer (*Euwallacea fornicatus*); (b) a stump of infested Chinese maple (*Acer buergerianum*) with extensive beetle galleries. Photographs courtesy of (a) Samantha Bush and (b) ZW de Beer

The Polyphagous Shot Hole Borer (PSHB), *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae; part (a) figure above) is probably the most damaging invasive alien pest to arrive and establish in South Africa’s urban environments. It was first detected in the KwaZulu-Natal National Botanical Gardens in Pietermaritzburg in 2017 (Paap et al. 2018). An ambrosia beetle native to Southeast Asia, PSHB has a symbiotic relationship with three fungal species, including the pathogen *Fusarium euwallaceae*. In susceptible host trees this leads to *Fusarium* dieback, a disease causing branch dieback and in some species, tree death. Soon after its detection in Pietermaritzburg it became evident that the beetle was already well established in the country, predominantly in urban areas, including Durban, George, Knysna, Somerset West, Nelspruit and Johannesburg. There is no direct evidence for the means of introduction of PSHB from Asia to South Africa, but non-compliant wood packaging material and dunnage are widely recognised as important pathways for the introduction of alien insect pests. PSHB was probably present for several years prior to its detection, during which time populations built up and spread. This pest is now causing the deaths of thousands of trees in urban environments and threatens millions of trees across the country.

At least 80 tree species, 35 of them native, are known to be attacked in South Africa (Z.W. de Beer unpublished data). While the outcome of PSHB attack is not yet known for each tree species, it seems that many reproductive hosts (those on which the beetle can breed) ultimately succumb. High levels of beetle tunnelling activity also weaken trees (part (b) figure above), causing branches to fall. To date, 20 tree species including maples (*Acer* species),
Box 11.3 (continued)

Liquidambar (*Liquidambar styraciflua*), Plane Trees (*Platanus* species), oaks (*Quercus* species), willows (native and alien *Salix* species), native coral trees (*Erythrina* species) and bushwillows (*Combretum* species) have been found to be susceptible reproductive hosts and stand to be lost from the urban landscape. Besides its impact in the urban environment, PSHB poses a threat to many economically important tree crops including Pecan Nut (*Carya illinoinensis*) and Avocado (*Persea americana*), plantations of Australian *Acacia* species, and to natural ecosystems.

The full extent of PSHB impact on the South African urban environment will only be ascertained over time. Municipalities already face the costly removal of many heavily infested street trees. This loss will have a profound impact on urban biodiversity and ecosystem services and result in reduced amelioration of the urban heat-island effect. Besides the financial burden of tree removal there are losses associated with reduced residential property values, and in the longer-term municipalities will also bear the cost of tree replanting.

South African municipalities have never had to deal with a tree-killing pest of this magnitude before (unlike cities in North America, Europe, and Australasia). With limited resources available, a coordinated and strategic response has been slow to emerge. Without prioritisation of removal of reproductive host trees and disposal at designated dumping sites (by chipping and composting or solarisation), the unintentional dispersal of PSHB (potentially over great distances) through the movement of infested wood sold as firewood is inevitable. Therefore, the situation requires a consolidated strategy and action plan, with input from research, engagement with stakeholders, and guidance from national government departments with a strong focus on effective communication and awareness campaigns.

11.4 Management

The Alien and Invasive Species regulations promulgated under the NEM:BA places a ‘Duty of Care’ on all landowners, whether private or public, to control invasive species on their land. This legislation requires all ‘Organs of State’ at all spheres of government (from national through to local government) to compile invasive species monitoring, control and eradication plans for land under their control. However, such “organs of state” face multiple challenges which makes compliance with the NEM:BA regulations difficult (Irlich et al. 2017).

Urban ecosystems present a new set of challenges relating to the understanding and management of biological invasions, and there is an urgent need for greater exploration of invasion processes and impacts in urban areas (Gaertner et al. 2017a, b; Irlich et al. 2017). Arguments for and against managing invasive species in urban
areas increasingly hinge on the contributions of invasive species to deliver ES and EDS (Potgieter et al. 2017; Vaz et al. 2017). Decisions must be made on whether to manage to enhance ES provision, or to minimise EDS. Such decisions are largely context-specific, and managers need to consider the knock-on effects when reducing EDS or enhancing specific ES, as other ES may be indirectly disrupted, or novel EDS created. Decisions need to be transparent and must consider opinions of a wide range of stakeholders including the public and those involved in urban land-use and ecosystem management decisions (Novoa et al. 2018). Furthermore, a variety of approaches (e.g. citizen science, remote sensing, and active surveillance) are needed to determine the distribution patterns of native and alien species (as influenced by environmental factors) and to assist in quantifying the impact of invasive species at broad scales based on responses on a finer scale (Odindi et al. 2016; Mavimbela et al. 2018).

11.4.1 Conflicts of Interest

Invasive species that provide both ES and EDS often generate conflicts around their use and management. Aesthetic and recreational opportunities provided by invasive alien tree species are highly valued in urban areas through their provision of shade, and plantings for green spaces, street plantings or gardens around urban centres (Dickie et al. 2014). For example, attempts to regulate and remove planted individuals of *Jacaranda mimosifolia* in Pretoria (planted in gardens and along streets for aesthetic purposes) to eliminate seed sources driving invasion of savanna areas, resulted in massive public resistance (Dickie et al. 2014).

Conflicts of interest are most obvious in urban areas with a steep urban-rural gradient, as epitomised by Cape Town (Alston and Richardson 2006; Dickie et al. 2014). For example, *Eucalyptus* and *Pinus* species, historically grown in plantations along the urban edge of Cape Town, are utilised for recreation by the city’s residents, many of whom regard the trees as attractive and ecologically beneficial (van Wilgen and Richardson 2012). As a result, control programs have been controversial.

Managing invasive animals is often controversial and residents frequently challenge the ethics of killing or removing animals, highlighting the perceived cruelty of these operations. For example, a decision to control Mallards (*Anas platyrhynchos*) due to their impacts on native waterfowl was met with substantial public resistance (Gaertner et al. 2016). Management efforts were effectively halted because the arguments for the campaign (genetic contamination of a single native species) were less convincing to the public than arguments for the widespread ecological impacts of more damaging invasive species (Gaertner et al. 2017a).

There is increasing recognition of the importance of engaging stakeholders affected by alien species or by their management (Novoa et al. 2018). Consideration of stakeholder views and the social consequences of management actions are needed to supplement traditional management approaches (Gaertner et al. 2016). Novoa et al. (2018) developed a step-by-step approach to engaging stakeholders in the management of alien species, and Gaertner et al. (2017a) developed a framework which groups species into three management approaches (control priority, active...
engagement, and tolerance) depending on their real or perceived benefits and their potential to generate negative impacts. Such approaches need to be implemented to ensure that all relevant ecological and socio-economic dimensions influencing invasive species management are addressed. Communication, education and use of citizen science platforms should also be used to highlight and document the danger of invasive species. Alternative, less harmful species could be proposed and substituted for conflict or desirable invasive species.

Many urban centres around the country have recently grown to engulf natural areas and surround existing conservation areas. Management of the latter (for biodiversity conservation) may be compromised owing to social preferences for invasive plants. Therefore, the management of conflict species in conservation areas in and around urban areas may require different approaches compared to modified sites in urban areas.

11.4.2 Socio-ecological Challenges

South Africa’s people are becoming increasingly urbanised (Anderson and O’Farrell 2012). The spatial arrangement of many urban centres around South Africa is racially defined and aligned with significant wealth disparities (Swilling 2010). Informal settlements (inhabited mostly by poorer communities) and townships established during the previous century and enforced through apartheid planning, are mostly located on the outskirts of cities. Major socio-economic challenges include the provision of education, housing, nutrition and healthcare, and transport infrastructure (Goodness and Anderson 2013). Pressure to address development issues of unemployment, poverty, and the formal housing shortfall, all place significant demands on remaining patches of natural habitat, which are highly sought after for conversion to housing or industrial development (Goodness and Anderson 2013).

Lower income areas such as informal settlements have smaller areas of public green space (McConnachie and Shackleton 2010). These areas have fewer resources than more affluent areas and rely heavily on ES provided by the natural resources of the immediate environment (including those provided by invasive plants). However, careful evaluation of the demands of the communities is required as there are likely to be divergent viewpoints and competing objectives. Managing to reduce EDS in the surrounding areas requires rigorous social assessments to avoid potential conflicts of interest. For example, clearing invasive alien trees close to informal settlements affects the livelihoods of residents who may rely on these species for firewood or construction material.

The increase in biomass resulting from alien plant invasions close to urban infrastructure increases the risk of severe fires. Fire management in and around urban areas is challenging because conflicts often arise due to the need for prescribed burning to achieve ecological goals, the need to ensure the safety of humans and infrastructure by reducing fire risk at the urban edge, and the need to maintain low-stature vegetation to reduce the risk of crime. Public safety becomes the primary goal and not biodiversity conservation (van Wilgen and Richardson 2012; Kraaij et al.
This requires integration of both ecological and societal aspects in the development of an adaptive fire management plan. The challenge is to manage these sites in such a way to restore biodiversity and ES provision, while improving public safety.

11.5 The Way Forward

New ways of approaching invasive species management in South African towns and cities are emerging and are being driven by: (1) special problems, innovations and recent projects in several cities (notably Cape Town and Durban); (2) national legislation on alien and invasive species (which was implemented largely to deal with invasions of natural ecosystems); (3) changes worldwide in approaches to urban planning and human perceptions of biodiversity in human-dominated ecosystems (including attempts to adapt these systems to deal with climate change).

For management of invasive species to be effective in South African urban ecosystems, more research and better facilitating mechanisms are required, and protocols for dealing more effectively with conflicts of interest must be developed. Some key issues that require further research are listed below.

- Regional management strategies must incorporate plans for dealing with invasions in all categories of landscapes across the urban-wildland gradient (“the whole landscape” sensu Hobbs et al. 2014). This is important because urban areas act as launch pads for invasions into wildlands, and wildland invaders are increasingly causing problems at the urban-wildland interface.
- Objective frameworks are needed for assessing impacts (positive and negative) of invasive species in urban areas in South Africa. Such frameworks could provide the foundation for the objective assessment of the capacity of native and alien species to provide benefits (ES) and negative impacts (EDS) in South African towns and cities. Such information is increasingly important as urban planners are giving more attention to adaptation of cities to climate change; impact assessment schemes (e.g. EICAT (Blackburn et al. 2014) and SEICAT (Bacher et al. 2018); Kumschick et al. (2020), Chap. 20) provide a good starting point but need to be adapted for South African urban settings.
- National legislation on alien and invasive species requires urban managers to prepare ‘invasive species monitoring, control and eradication plans’ for invasive species. Protocols for preparing effective plans are lacking. Guidelines are needed for: compiling inventories of alien species in urban areas; developing effective and realistic strategies of intervention for different types of invasive species, including the development and application of tools for prioritising actions; and approaches for engaging with stakeholders.

South Africa is an excellent study system for developing a typology, lexicon and set of associated concepts, theories and approaches for dealing with biological invasions in different categories of human-dominated ecosystems (ranging from small human settlements embedded in large natural ecosystems to megacities and metropoles). To determine the magnitude of economic and ecosystem impacts of alien species
invasions in cities around the world, a Global Urban Biological Invasion Consortium (GUBIC) has been established. Comprising more than 70 collaborators from at least 40 cities in 21 countries, GUBIC facilitates global communication and provides a platform to synthesis and share data and develop management and policy frameworks.

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**Electronic Supplementary Material**

The online version of this chapter contains supplementary material, which is available to authorised users: Supplementary Appendices 11.1 and 11.2 (https://doi.org/10.5281/zenodo.3562067).

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