

The application of selected invasion frameworks to urban ecosystems

Luke J. Potgieter¹, Marc W. Cadotte¹

¹ Department of Biological Sciences, University of Toronto-Scarborough, 1265 Military Trail, Toronto, ON, M1C 1A4, Canada

Corresponding author: Luke J. Potgieter (lukepotgieter2@gmail.com)

Academic editor: J. R. Wilson | Received 30 January 2020 | Accepted 13 July 2020 | Published 15 October 2020

Citation: Potgieter LJ, Cadotte MW (2020) The application of selected invasion frameworks to urban ecosystems. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) Frameworks used in Invasion Science. NeoBiota 62: 365–386. <https://doi.org/10.3897/neobiota.62.50661>

Abstract

Urbanization is a major driver of global change. Profound human-mediated changes to urban environments have provided increased opportunities for species to invade. The desire to understand and manage biological invasions has led to an upsurge in frameworks describing the mechanisms underpinning the invasion process and the ecological and socio-economic impacts of invading taxa. This paper assesses the applicability of three commonly used invasion frameworks to urban ecosystems. The first framework describes the mechanisms leading to invasion; the second and third frameworks assess individual species, and their associated environmental and socio-economic impacts, respectively.

In urban areas, the relative effectiveness of the barriers to invasion is diminished (to varying degrees) allowing a greater proportion of species to move through each subsequent invasion stage, i.e. “the urban effect” on invasion. Impact classification schemes inadequately circumscribe the full suite of impacts (negative and positive) associated with invasions in urban areas. We suggest ways of modifying these frameworks to improve their applicability to understanding and managing urban invasions.

Keywords

Biological invasions, framework, impacts, invasive alien plants, urban ecosystems

Introduction

Urbanization is now a major agent of change for social, economic, and ecological systems (Mumford 1961). In urban areas land transformation, climate alteration, and the addition and elimination of species from regional species’ pools have created

unprecedented ecosystems that challenge traditional approaches to management and conservation (Hobbs et al. 2009; Kowarik 2011). There are an abundance of invasion frameworks that variously describe the transport, success, impact, and management of alien species* (e.g. Davis et al. 2000; Shea and Chesson 2002; Ruiz and Carlton 2003; Catford et al. 2009; Blackburn et al. 2011; Colautti et al. 2013; Blackburn et al. 2014; Bacher et al. 2018; Cadotte et al. 2018), and which were developed to guide research into the ecology and management of invasions in non-urbanized areas. However, it is increasingly recognized that urban areas not only play a significant role in species' invasion (Rebele 1994; Shochat et al. 2010), but also that managers generally lack both a robust understanding of how urban areas influence invasions across taxa, and a conceptual and theoretical understanding of how the urban environment and species interact to shape invasions (Cadotte et al. 2017). This paper assesses how well frequently used and highly cited invasion frameworks fit urban ecosystems. We focus on plant introductions as they are ubiquitous in the urban landscape and are often actively managed. The key to assessing frameworks is to understand how urban-specific drivers like reduced competition, nutrient enrichment, pathogen/pest control, gardening/planting, importation based on human use/values, and human perception of management priorities, all shape species' persistence and spread. We assess the ability of frameworks to accommodate these urban-specific drivers and further suggest ways to alter frameworks to make them pertinent for understanding and managing invasions in urban areas.

Invasion frameworks

Basic understanding of invasion and management frameworks needs to be evaluated in urban ecosystems for several reasons. Firstly, urban areas are directly shaped by human activities that can transport and foster alien species. Secondly, the beliefs, priorities, and concerns of human populations in urban areas directly impact the creation and implementation of management policies for invasive alien species. Many frameworks exist to classify biological invasions, for example, by pathways of dispersal (Hulme et al. 2008; Wilson et al. 2009), general invasion processes (Williamson et al. 1996; Richardson et al. 2000), and impact assessment schemes (Kumschick et al. 2012; Nentwig et al. 2016). We do not aim to examine how all these frameworks apply to urban areas (though any generalized framework's applicability to urban areas should be assessed) but rather we assess three commonly used frameworks that evaluate and explain the invasion process and associated impacts.

We selected three invasion frameworks: the Unified Framework for Biological Invasions (Blackburn et al. 2011), the Environmental Impact Classification of Alien

* A note about terminology. There are a variety of terms used to identify and describe imported species, some of which are less emotive than others (Colautti and MacIsaac 2004), but to better align with frameworks, we will use 'alien' to describe species introduced into new regions due to human activities. We recognize that native species can become invasive, but for this paper, 'invasive' refers only to alien species. Invasive alien plants refer to alien plant taxa which are invasive.

Taxa scheme (EICAT, Blackburn et al. 2014; modified by Hawkins et al. 2015); and the closely-related Socio-Economic Impact Classification of Alien Taxa (SEICAT, Bacher et al. 2018). The first framework provides a terminology and categorization for alien species’ populations at different points in the invasion process. The second and third frameworks assess individual species and their associated environmental and socio-economic impacts, respectively. We selected these frameworks as they are among the most widely adopted (Wilson et al. 2020). For example, the Unified Framework for Biological Invasions proposed by Blackburn and colleagues (2011) has been proposed for use in international biodiversity standards (i.e. Darwin Core, Groom et al. 2019). EICAT is receiving increasing international support and has recently been adopted by the International Union for the Conservation of Nature (IUCN) (IUCN 2020). Here, we assess how these apply to urban areas and whether additional considerations are required.

The frequently employed and commonly cited Unified Framework for Biological Invasions proposed by Blackburn et al. (2011) combines previous stage-based and barrier models into a single conceptual framework, employing an effective terminology to describe the underlying elements and processes involved in invasions (see Fig. 1). They divide the invasion process into a series of stages, and for a species or population to move onto the next stage, it must overcome a series of barriers, e.g. geographical (transport), survival (establishment), and dispersal (spread). This framework not only focusses attention on these discrete stages, but also on the bottlenecks where policy and management actions can reduce invasions.

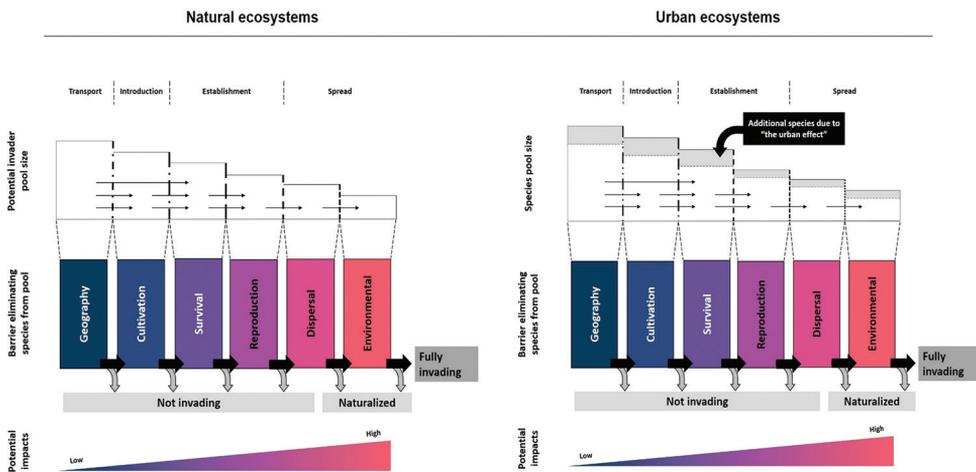


Figure 1. The unified framework for biological invasions by Blackburn et al. (2011) on the left showing how alien species must pass through a series of barriers to establish and invade a new area. At each stage, the pool of species passing through decreases. However, in urban ecosystems, the invasion barriers are changed, resulting in different species crossing each barrier and, in general, more species moving through each of the invasion stages, i.e. the “urban effect” on invasion. The magnitude of an alien species’ impact is likely to increase along the invasion framework (introduction – naturalization – invasion continuum) in both natural and urban ecosystems. However, in urban areas, this impact will manifest in different ways (e.g. greater socio-economic impact).

The EICAT scheme classifies alien taxa in terms of the magnitude of their impacts on the environment. It relies on published evidence of impacts via an exhaustive literature search to identify all published literature on the impacts of each alien taxon under assessment. Each impact record for an alien taxon is classified into one of five sequential categories in ascending order of impact, from “Minimal Concern” to “Massive” depending on the level of biological organization (individual, population, community or ecosystem) impacted. This includes the mechanisms (and magnitude) of impact for each taxon, a confidence score for each record, and additional information including the spatial location at which the impact is realized, and which native species are impacted.

Based on the capability approach from welfare economics, the SEICAT scheme presents a system for ranking and comparing the negative impacts of alien taxa on human well-being. The process also relies on published evidence to classify alien taxa based on changes in human activities that result from their impacts. By focusing on changes in people’s activities, SEICAT captures impacts of introduced species on human well-being that systems based on monetary values cannot. The scheme defines eight categories into which alien taxa can be classified according to the magnitude of changes in people’s realized activities. This classification is analogous to the EICAT and IUCN Red List schemes (Mace et al. 2008).

Invasibility of urban ecosystems

Urban environments result in novel ecological patterns and processes, and dynamics (Faeth et al. 2005; Wilby and Perry 2006; Pickett et al. 2008; Ricotta et al. 2009; Williams et al. 2009; Kowarik 2011; Alberti 2015), which can benefit taxa that are generalist, fast-growing, rapid at reproducing, and resilient to stress and disturbance (Cadotte et al. 2017). The pool of species in any city will be a filtered subset of the regional pool of native species along with other species from the global species’ pool, introduced directly through human activities (Aronson et al. 2016). These introductions can be intentional or accidental. Alien species are more likely to benefit from, or at least be less impacted by, urbanization compared to native species simply because they represent a non-random subset of species with appropriate behavioural or life-history traits and strategies (Ariori 2014). Human activities associated with urbanization present improved invasion opportunities for alien plant species by, for example, removing the negative effects of competition or control from enemies (Faeth et al. 2005; Alberti 2015). This, coupled with the novel environmental conditions in cities (e.g. novel habitats, high spatial heterogeneity, increased resource availability, high disturbance levels, and altered climatic conditions), provides opportunities for alien species with appropriate life-history attributes to flourish. Additionally, cities are highly interconnected through transport routes and trade activities. Culture, language, shared history, industrial products and transcontinental trade agreements could be as important for directed

movement between cities as geographical distance (di Castri 1990; Maluck and Donner 2015; Khanna 2016), thus explaining the movement of alien plants (Chapman et al. 2017). As a result, cities are often the first entry point for new alien species (Pyšek et al. 2010). High levels of propagule pressure (e.g. through repeated introductions of alien plant species for the horticultural trade) also increases the likelihood of successful establishment.

Through sustained human facilitation in cities, intensive cultivation and repeated introductions of many alien species, biotic and abiotic manipulation, humanity's preference for traits associated with high reproductivity (e.g. large showy flowers, colourful fruits), greater number and diversity of pathways and vectors that can facilitate the movement of alien plants, and increased levels of human-mediated habitat disturbance, collectively increase the likelihood of establishment and spread of alien plant species in urban areas.

Applying invasion frameworks to urban systems

Introduced alien species must pass through a series of barriers before naturalizing in their new environment (Blackburn et al. 2011; Fig. 1). Specifically, urban areas reduce the effectiveness of barriers thereby increasing the number of species that could potentially establish and increase the range of dispersal compared to neighbouring natural areas (Table 1). The Unified Framework will only classify an alien species' population as invasive in an urban setting if the invasion is one among several other invasion foci. The previous invasion stage categories explicitly require alien populations to be self-sustaining outside of captivity or cultivation, termed "in the wild". This is not always applicable in urban contexts and highlights an important shortcoming of the framework. During the invasion process, species will cause a range of ecological and socio-economic impacts (either negative and/or positive), and in urban areas these impacts can be more complex and felt more acutely. Box 1 provides a case study of a successful urban invader and describes the mechanisms facilitating the invasion process. Below we discuss how the barriers to invasion defined by Blackburn et al. (2011), as well as two impact classification schemes (EICAT and SEICAT), differ in urban systems.

Unified Framework for Biological Invasions

Urban areas as hotspots of globalization provide significant opportunities for alien species' introduction

Human activities are progressively weakening biogeographical barriers to dispersal (di Castri 1990; Helmus et al. 2014), resulting in the establishment and spread

Box 1. The vine that strangled a city.

The perennial herbaceous vine *Vincetoxicum rossicum* (Kleopow) Barbar. (Asclepiadaceae; syn. *Cynanchum rossicum*), also known as dog-strangling vine, is a prolific invader in the city of Toronto, Canada. Below we describe how *V. rossicum* overcame the barriers to invasion defined by Blackburn et al. (2011) to become one of the most impactful invaders in the city.

Geographic barrier

Vincetoxicum rossicum was directly imported into the city of Toronto in the late 1800s from the Ukraine and planted as an ornamental and for erosion stabilization in several locations in the city (Kricsfalusy and Miller 2008).

Captivity barrier

There was a significant lag period before *V. rossicum* became a species of concern, but by the 1980s, it had become widespread and abundant in Toronto, especially in urban woodlots and meadows. Its ornamental use, likely facilitated by the nursery trade, provided opportunities for its escape from captivity (Kricsfalusy and Miller 2008).

Survival barrier

Gardeners allowed *V. rossicum* to escape its natural enemies, resulting in much improved fitness. It demonstrates wide environmental tolerance to variations in light intensity and soil moisture (DiTommaso et al. 2005; Douglass et al. 2009).

Reproduction barrier

Seeds of *V. rossicum* are often polyembryonic, giving rise to two, three and (rarely) four seedlings (Ladd and Cappuccino 2005). Unpalatable to herbivores and occupying ample, low-competition habitat resulting from urban disturbances, *V. rossicum* has extremely high fecundity in Toronto.

Dispersal barrier

Vincetoxicum rossicum possesses feathery pappus-covered seeds that are easily carried by wind, and with cars and trains creating air currents, seeds can travel long distances along linear corridors (Ladd and Cappuccino 2005).

Environmental barrier

Vincetoxicum rossicum successfully establishes and survives across a range of disturbance regimes, and improved growth has been shown in more disturbed habitats (Averill et al. 2010). In its native range, this vine largely grows in forest understories, but in Toronto it grows across several habitat types including gardens, lawns, hedgerows, forest understories, and fully open meadows.

Box I. Continued.**Impacts**

Having successfully overcome these barriers, *V. rossicum* negatively impacts native biodiversity – it reduces the diversity of plant and other trophic levels by excluding species with certain traits (DiTommaso et al. 2005; Ernst and Cappuccino 2005; Sodhi et al. 2019; Livingstone et al. 2020). It produces chemicals (Douglass et al. 2009) which can inhibit growth of other plants (allelopathy), alter soil biota, and make foliage unpalatable to native herbivores. It is considered the most impactful and difficult-to-manage plant invader in the city.



Figure B1. An urban site in Toronto, Canada, where the invasive *Vincetoxicum rossicum* forms a monoculture in open and understory habitats (photo credit: LJ Potgieter).

of an increasing number of alien plant species (Ricotta et al. 2014), especially as increasing globalization of trade connects more places with greater movement frequency (Hulme 2009). New international air, land, and sea trade links open novel pathways for the spread of alien species. As hubs of human activity, urban areas are often the first entry point for newly introduced alien species (Pyšek et al. 2010), and so result in a greater proportion of alien species (relative to native species) in urban than in rural or natural areas (Rebele 1994).

Table 1. The barriers to invasion proposed by Blackburn and colleagues (2011) in the context of urban areas, and the underlying mechanisms driving invasion in urban areas. *Indicates potential mechanisms strengthening the barriers to successful establishment of alien plants in urban areas.

Barriers to invasion	Urban effect on barriers	Facilitating mechanisms	References
Geographic	Significant opportunities for alien species introduction	<ul style="list-style-type: none"> Urban areas are often the first entry point for newly introduced alien species. Cities serve as transportation and trade hubs, and are highly interconnected, thus increasing the movement of species globally. 	Pyšek et al. (2010)
Captivity or cultivation	Significant opportunities to escape captivity / not relevant	<ul style="list-style-type: none"> Horticultural activities result in a major pathway for the repeated importation of many alien plants into urban areas (e.g. gardens which serve as regular sources of alien plant propagules). Small urban settlements act as launching sites for plant invasions into natural areas. Alien species introduced unintentionally by humans directly into the new environment. 	Dehnen-Schmutz et al. (2007); Bigirimana et al. (2012); McLean et al. (2017); Padayachee et al. (2019)
Survival	Significant potential for survival opportunities, unlike neighbouring, less disturbed areas	<ul style="list-style-type: none"> Humans manipulate abiotic and biotic conditions to improve the survivorship of alien plant species. For example, reducing competition, increasing nutrient and water input, and altering soil pH. Urban heat island effect can provide suitable conditions for more heat-tolerant alien plants. Selective breeding and dissemination of 'urban suitable' genotypes. Intra- and inter-specific hybridization can create novel, potentially invasive genotypes. *Repeated introductions of the same species at a location (propagule pressure) can increase the likelihood of successful establishment. 	Gilbert (1989); Ellstrand and Schierenbeck (2000); Kowarik (2005); Kowarik (2011)
Reproduction	Potential opportunities for reproductive success for <i>some</i> alien plants	<ul style="list-style-type: none"> Habitat fragmentation selects for species with high seed production. Selective breeding or intraspecific hybridization of cultivars can increase reproductive success. Longer growing season and earlier flowering and seeding for alien plants in response to urban climates. Cultivar selection for desirable traits can inadvertently result in greater fecundity. *Habitat fragmentation reduces the size and increases the isolation of urban plant populations, increasing extinction risk and reducing pollination. 	Cunningham (2000); Kitajima et al. (2006); Culley and Hardimann (2008); Huebner et al. (2012); Dubois and Cheptou (2017)
Dispersal	Potential for dispersal opportunities unlike neighbouring less disturbed areas	<ul style="list-style-type: none"> Alien plants which possess traits conducive to effective dispersal through prominent urban dispersal pathways are more likely to proliferate, such as wind dispersal by vehicle traffic. *Many alien plants do not possess the appropriate suite of traits required for efficient dispersal in urban areas. *Increased propagule pressure can enable alien species to overcome urban dispersal barriers despite poor dispersal abilities. 	Aronson et al. (2007); von der Lippe and Kowarik (2007)
Environmental	Environmental conditions provide potential opportunities for alien plant spread	<ul style="list-style-type: none"> High level of heterogeneity and disturbance results in frequent colonization opportunities for alien plants. *Habitat fragmentation can limit the spread from established alien plant populations. *High levels of disturbance can also act as a barrier to the establishment of some plant species. 	Kowarik (1995); Donaldson et al. (2014)

Urban areas have more alien taxa in captivity and cultivation, and so greater propagule pressure.

Invasibility is strongly influenced by propagule pressure (Colautti et al. 2006). In addition to neighbourhood propagule pressure that originates with propagules dispersing from naturalized populations within invaded habitats (spread stage) (Davis et al. 2016), urban areas are exposed to large numbers of alien plant propagules through repeated local introductions and high numbers of propagules in each introduction (e.g. gardens serve as regular sources of plant propagules). This increases the likelihood of their establishment and persistence even in suboptimal microsites (overcoming abiotic barriers and biotic

resistance) (Rejmánek et al. 2005; Kowarik et al. 2013). The horticultural industry has been a particularly important pathway around the world (Dehnen-Schmutz et al. 2007), and the escape of ornamental plants from cultivation in gardens has resulted in some of the most extensive biological invasions (Bigirimana et al. 2018; Holmes et al. 2018).

The effect of propagule pressure on invasibility is also apparent in smaller urban settlements which can act as launching sites for plant invasions into rural (Cilliers et al. 2008) and natural areas (McLean et al. 2017) as they can be more numerous in the landscape and share proportionally greater boundaries with their surroundings compared to large cities. Life-history traits such as flower size, fruit size, and growth rates have driven the importation of many alien plants into urban areas (Aronson et al. 2007). These traits are usually associated with reproductive success and allow species to establish and spread into new environments (Moodley et al. 2013).

The captivity and cultivation barrier might also be skipped entirely by alien species which are introduced unintentionally by humans (e.g. as a contaminant (stowaway) of a commodity) (Blackburn et al. 2011). Owing to an increased number and variety of entry methods, urban areas experience multiple accidental introductions (Padayachee et al. 2019).

Human intervention improves the survivorship of alien species

Inherent features of the urban landscape could serve to select for species that are able to persist under more stressful conditions or rapidly take advantage of the resource-rich conditions. For example, higher temperatures associated with urban areas (i.e. urban heat island effect) might select for the establishment of alien plants preadapted to warmer conditions than the natural environment provides (Sukopp 2004). An introduced population can fail to establish because individuals in the population either fail to survive or survive but fail to reproduce (Blackburn et al. 2011). However, human intervention can improve the survivorship of alien species by, for example, reducing competition by purposefully removing undesirable individuals (lowering biotic resistance), increasing nutrient and water input, or altering soil pH (Gilbert 1989). The net result is that a wide range of species experience positive fitness in urban areas that would otherwise be unable to complete their life cycles and successfully reproduce.

Below the species' level, genotypes proving successful in urban areas are selectively bred (e.g. for flowering, architecture, foliage and for disease-resistance traits) and are widely disseminated through plant exchanges and the horticultural trade (regulated and unregulated) (Kowarik 2005; Sæbø et al. 2005; Dehnen-Schmutz et al. 2007), the fertile taxa of which have the opportunity to naturalize. Intraspecific hybridization and selection can also act to create novel, potentially successful genotypes (Ellstrand and Schierenbeck 2000) adapted to the selection pressures of the urban environment.

While the survival barrier in urban areas might be high for some species, the failure of individuals or populations to survive is not just a consequence of the environment, for subsequent human-mediated introductions of the same species at that location could succeed (Blackburn et al. 2011). Thus, propagule pressure can reduce the effectiveness of the survival barrier.

Urbanization can enhance reproductive success of *some* alien plants

Urban habitats are highly fragmented, thus reducing the size and increasing the isolation of urban plant populations, resulting in a decline in pollinator services and ultimately lowering reproductive success of plants (Dubois and Cheptou 2017). However, the process of habitat fragmentation generally selects for species with high seed production (Cunningham 2000), seed banking capabilities, high dispersal capacity, and independence from mutualisms, such as specific pollinators and specialized mycorrhizae (Huebner et al. 2012). A small proportion of the urban flora will possess traits which satisfy these requirements (Aronson et al. 2007; Knapp et al. 2008). Together with high levels of propagule pressure and human intervention aimed at increasing alien plant survivorship, these species can proliferate within and around urban areas (e.g. Alston and Richardson 2006). For example, survivorship can be increased by reducing competition and increasing nutrient and water input, enabling alien plants to direct more energy to reproduction, greatly increasing the probability of forming self-sustaining populations.

While selective breeding or intraspecific hybridization of cultivars can reduce invasive potential (Anderson et al. 2006), such domestication efforts can also increase reproductive success (Culley and Hardimann 2008). Selection for desirable traits (such as showy appearance) can also inadvertently result in greater fecundity (Kitajima et al. 2006). Phenological changes associated with warmer urban conditions can result in earlier flowering and seeding and an expansion of the growing season, potentially placing alien plants at a reproductive advantage (Huebner et al. 2012).

The complex network of dispersal pathways and vectors in urban areas facilitates the movement of *some* alien plants.

Urban areas comprise a complex network of pathways and vectors that can facilitate plant movement within the urban matrix and into surrounding natural areas (Padayachee et al. 2017). Alien plants which possess traits suited to effective dispersal either along dispersal pathways such as roads and railways (e.g. wind-dispersed *Pennisetum setaceum*, Rahlao et al. (2010), and *Vincetoxicum rossicum*, DiTommaso et al. (2018)), or via movement of topsoil or garden waste (Hodkinson and Thompson 1997) are more likely to proliferate in urban areas. For example, long-distance dispersal by vehicles occurred more frequently for seeds of invasive alien plants than for native species (von der Lippe and Kowarik 2007). Moreover, rivers passing through urban areas can also promote alien species' spread (Planty-Tabacchi et al. 2001; Burton et al. 2005).

Alien plant species with fleshy fruits are more likely to expand their range in urban environments because of their ability to utilize bird dispersal (Aronson et al. 2007). Many alien plants do not possess the appropriate suite of traits required for efficient dispersal in urban areas. However, increased propagule pressure in urban areas can enable alien species with poor dispersal abilities to overcome urban dispersal barriers (e.g. by increasing the likelihood of seed dispersal).

Urban areas provide environmental conditions favourable for the spread of *some* alien plants

In urban areas, abiotic conditions such as climate, land use, pollution, and nutrient loads are dramatically altered through human intervention (Kowarik 2011). Cities provide a much greater array of diverse habitats and environmental conditions compared to natural areas of the same size (Sukopp and Starfinger 1999; Schmidt et al. 2014). This high level of heterogeneity means that there are many habitat patches (at different levels of disturbance) which can be exploited by alien plant species with different ecological demands. For example, roadsides serve as disturbance corridors that provide environmental conditions favourable for the establishment of alien plants (von der Lippe and Kowarik 2008; El-Barougy et al. 2018).

Habitat fragmentation greatly increases the amount of edge habitat, which can increase the susceptibility of vegetation patches to disturbances (Bar-Massada et al. 2014). Increased levels of human-mediated disturbance can increase the number of alien plant species in urban areas through the colonization of disturbed or newly created habitats (Kowarik 1995). However, high levels of disturbance can also act as a barrier to the establishment of some plant species not well adapted to the altered environmental conditions. Consequently, some alien taxa might be widespread along roadsides and other disturbed areas but struggle to invade natural ecosystems (e.g. *Centranthus ruber*, Holmes et al. 2018), and vice versa.

The influence of management

While the relative importance of the barriers to reproduction, dispersal, and environment for determining invasion success can be greater in urban areas compared to natural areas (Table 1), management interventions aimed at strengthening the geographic, cultivation and survival barriers can reduce the pool of potentially invasive plant species. As an example, the geographic barrier can be strengthened by policies that limit the importation of species and increase biosecurity measures. The cultivation barrier can be increased by policies that prohibit sale of some species. Finally, the survival barrier can be increased by municipal programs that promote the use of native over alien species to reduce the active support of less desirable species through gardening.

Impact classification schemes (EICAT and SEICAT)

A taxon with a high ecological impact in a rural or natural environment will not necessarily have the same impact in an urban environment, or impact at the same spatial and temporal scales. Generally, the magnitude of an alien species' impact (which can be highly variable and context-dependent, Ricciardi et al. 2013) is likely to increase from population and species to community and ecosystem effects along the invasion framework (Pyšek and Richardson 2010). This can occur in both natural and urban

ecosystems (Fig. 1), however in urban areas, these impacts can be more complex and manifest in different ways (e.g. greater socio-economic impacts). Aside from general shortcomings (for example, EICAT does not directly assess how many native species are affected; see Kumschick et al. 2020 for further details), the application of the ICAT Schemes in urban areas presents additional challenges.

Combining the ICAT Schemes might achieve a more comprehensive assessment of the negative ecological and socio-economic impacts from an invasion. Both schemes explicitly focus on deleterious impacts and do not set out to weigh deleterious against beneficial impacts to determine the net value of an introduction of an alien taxon (cf. Vimercati et al. 2020). However, an assessment of the positive impacts (benefits) provided by alien taxa is particularly important in urban areas where many species have been deliberately introduced to provide ecosystem services (e.g. for ornamental, horticultural, or land reclamation purposes with corresponding social, economic and environmental benefits) (Boland and Hanhammer 1999; Salisbury et al. 2015; Potgieter et al. 2017; Vaz et al. 2017), and where people have formed close connections with these species over time. For example, the invasive Norway maple, *Acer platanoides*, was commonly planted in large Canadian cities, such as Toronto, and is often seen as an iconic Canadian species by urban dwellers. So much so that the image of its leaf was mistakenly used on Canada's \$20 bill, instead of the native sugar maple, *Acer saccharum*, that adorns the Canadian flag.

Robust and comparable data on the impacts of most alien species are still lacking, and in many cases, uncertainties in impact assessments remain significant (Simberloff et al. 2013; Probert et al. 2020). The higher number and diversity of stakeholders in urban areas means there is a greater chance of strongly divergent perceptions and opinions regarding the impacts of alien species (Potgieter et al. 2019) – the perception of the impact of our example invader in Toronto (Box 1) depends on the degree of ecological engagement of the respondent (Livingstone et al. 2018). Complex socio-cultural and economic connections to human residents confound impact assessments and subsequent management thresholds (Gaertner et al. 2016). As the ICAT Schemes' classifications are governed by the best available data, achieving accurate impact classifications for specific alien taxa in urban areas can be difficult and expensive (Measey et al. 2020). It is also challenging to relate a change in human activity to a specific species because of the diversity of alien taxa and high levels of habitat heterogeneity in urban areas.

With ongoing dissemination of alien plant propagules, there are likely to be significant time-lags before any impact is realized (Mack et al. 2000). This has knock-on effects for impact classification as only published evidence is considered by the ICAT Schemes' assessors, resulting in a potentially lower impact and therefore a lower management priority being assigned to a species. Additionally, an in-depth review of the literature is not likely to comprehensively address all possible impacts (especially social impacts), which can be highly context-specific and dependent on the stakeholder group assessed, for example, wealthy landowners versus marginalized inner-city communities. Effective engagement with all relevant stakeholders is required to ensure a comprehensive assessment of all impact scenarios (Novoa et al. 2018).

Urban areas present increased economic and social opportunities for people compared to rural or natural areas (Elmqvist et al. 2013). As a result, people's capabilities and the

activities in which they can engage, are enhanced. There is therefore a greater likelihood for invasive alien plants to influence people's capabilities and realized activities, which ultimately affects their well-being. A clear understanding of the ways in which alien (and invasive) species affect biodiversity and ecosystem functioning, and the subsequent changes to the provision of ecosystem services (and disservices) is needed if the effects on human well-being are to be comprehensively assessed (de Groot et al. 2002; Kremen 2005; Haines-Young and Potschin 2010; Vaz et al. 2017; Vimercati et al. 2020). For example, in Cape Town, South Africa, invasion by Australian acacias, *Eucalyptus* and *Pinus* species displaces native vegetation, increasing the frequency and severity of wildfires, and reducing surface water flows (van Wilgen et al. 2012). The resulting loss in biodiversity, risk of damage to infrastructure, and decreasing water sources, all significantly impact the safety and well-being of the city's residents. Invasive alien plants can also sustain or enhance ecosystem functioning in their adventive range, for example, by increasing net primary production, pollinator support, decomposition rates, and nitrogen cycling (Ehrenfeld 2003; Corbin and D'Antonio 2004; Liao et al. 2008; Salisbury et al. 2015). This can lead to the maintenance or augmentation of ecosystem services or disservices with implications for human well-being (Charles and Dukes 2007; Eviner et al. 2012; Vaz et al. 2017). Empirical evidence evaluating this nexus is emerging but remains scarce in urban areas.

The way forward

With an abundance of invasion frameworks and a growing body of literature exploring the many facets of invasions in urban areas, it is important to consider whether current invasion frameworks apply to urban systems.

Biological invasions represent a complex societal issue. Consequently, impact assessments and subsequent management decisions should include input from a wide range of stakeholders to elucidate the positive and negative effects of invasive alien plants in urban areas (e.g. Potgieter et al. 2019; Vimercati et al. 2020). Transparent and replicable approaches are needed to document the different consequences of invasive alien plants for different groups of stakeholders. For example, Kumschick et al. (2012) provide a framework for the prioritization of invasive alien plants for management according to their impact. It includes both a scientific impact assessment and the evaluation of impact importance by affected stakeholders, and accounts for both positive and negative impacts of invasive alien plants (thereby accommodating potential conflicts of interest). Potgieter et al. (2018) use multi-criteria decision tools to develop a prioritization approach for managing invaded areas across an urban landscape. However, more work is needed to test the applicability of such frameworks to urban systems around the world and how suitable frameworks will need to be modified accordingly. For example, Kumschick et al.'s (2012) proposed 'impact categories' will need to be modified to address the full spectrum of potential impacts of invasive alien plants in urban areas.

Urban areas have a complex network of dispersal pathways and vectors that can facilitate the movement of alien plants. Existing pathway frameworks (e.g. Hulme et al. 2008; Wilson et al. 2009) are likely to effectively accommodate urban dispersal pathways, though a shift in emphasis on certain dispersal categories will be re-

quired. For example, horticulture (categorized as ‘cultivation’ *sensu* Wilson et al. 2009) is a prominent urban dispersal mechanism. Yet, more quantitative evidence is needed to elucidate the full suite of urban dispersal pathways and vectors.

Urbanization provides insights into how species will respond and interact under future global change scenarios (Lahr et al. 2018). So, future frameworks circumscribing the invasion process would benefit by including the urban dimension. Viewing invasive species’ success and impact as complex and variable in human-dominated landscapes will provide managers and policy makers with the necessarily complex frameworks to address alien species’ prioritization and control in an increasingly altered world.

Acknowledgements

This paper emerged from a workshop on ‘Frameworks used in Invasion Science’ hosted by the DSI-NRF Centre of Excellence for Invasion Biology in Stellenbosch, South Africa, 11–13 November 2019, that was supported by the National Research Foundation of South Africa and Stellenbosch University. Funding was provided by the Connaught Global Challenges Award, the Office of the Vice-President International, the School of Graduate Studies and the HKU-U of T Strategic Partnership Fund at the University of Toronto, and the Office of the Vice-Principal Research at the University of Toronto Scarborough. MWC wishes to further acknowledge funding from the Natural Sciences and Engineering Research Council of Canada (#386151).

References

- Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology and Evolution* 30(2): 114–126. <https://doi.org/10.1016/j.tree.2014.11.007>
- Alston KP, Richardson DM (2006) The roles of habitat features, disturbances and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. *Biological Conservation* 132(2): 183–198. <https://doi.org/10.1016/j.biocon.2006.03.023>
- Anderson NO, Galatowitsch SM, Gomez N (2006) Selection strategies to reduce invasive potential in introduced plants. *Euphytica* 148: 203–216. <https://doi.org/10.1007/s10681-006-5951-7>
- Ariori CO (2014) Plant invasion along an urban-to-rural gradient.
- Aronson MFJ, Handel SN, Clemants SE (2007) Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape. *Biological Invasions* 9(4): 465–475. <https://doi.org/10.1007/s10530-006-9053-1>
- Aronson MFJ, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, La Sorte FA (2016) Hierarchical filters determine community assembly of urban species pools. *Ecology* 97: 2952–2963. <https://doi.org/10.1002/ecy.1535>
- Averill KM, DiTommaso A, Mohler CL, Milbrath LR (2010) Establishment of the invasive perennial *Vincetoxicum rossicum* across a disturbance gradient in New York State, USA. *Plant Ecology* 211: 65–77. <https://doi.org/10.1007/s11258-010-9773-2>

- Bar-Massada A, Radeloff VC, Stewart SI (2014) Biotic and abiotic effects of human settlements in the wildland – urban interface. *Bioscience* 64: 429–437. <https://doi.org/10.1093/biosci/biu039>
- Bartuszevige AM, Gorchov DL (2006) Avian seed dispersal of an invasive shrub. *Biological Invasions* 8: 1013–1022. <https://doi.org/10.1007/s10530-005-3634-2>
- Bigirimana J, Bogaert J, De Cannière C, Bigendako M-J, Parmentier I (2012) Domestic garden plant diversity in Bujumbura, Burundi: role of the socio-economical status of the neighborhood and alien species invasion risk. *Landscape and Urban Planning* 107(2): 118–126. <https://doi.org/10.1016/j.landurbplan.2012.05.008>
- Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien taxa based on the magnitude of their environmental impacts. *PloS Biology* 12: e1001850. <https://doi.org/10.1371/journal.pbio.1001850>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26(7): 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Boland P, Hanhammer S (1999) Ecosystem services in urban areas. *Ecological Economics* 29(2): 293–301. [https://doi.org/10.1016/S0921-8009\(99\)00013-0](https://doi.org/10.1016/S0921-8009(99)00013-0)
- Burton ML, Samuelson LJ, Pan S (2005) Riparian woody plant diversity and forest structure along an urban-rural gradient. *Urban Ecosystems* 8: 93–106. <https://doi.org/10.1007/s11252-005-1421-6>
- Cadotte MW, Campbell SE, Li S-P, Sodhi DS, Mandrak NE (2018) Preadaptation and Naturalization of Nonnative Species: Darwin's Two Fundamental Insights into Species Invasion. *Annual Review of Plant Biology* 69: 661–684. <https://doi.org/10.1146/annurev-arplant-042817-040339>
- Cadotte MW, Yasui SLE, Livingstone S, MacIvor JS (2017) Are urban systems beneficial, detrimental, or indifferent for biological invasion? *Biological Invasions* 19: 3489–3503. <https://doi.org/10.1007/s10530-017-1586-y>
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15(1): 22–40. <https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Chapman D, Purse BV, Roy HE, Bullock JM (2017) Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography* 26: 907–917. <https://doi.org/10.1111/geb.12599>
- Charles H, Dukes JS (2007) Impacts of invasive species on ecosystem services. In: Nentwig W (Ed.) *Biological Invasions (Ecological Studies, Vol. 193)*. Springer-Verlag, 217–237. https://doi.org/10.1007/978-3-540-36920-2_13
- Cilliers SS, Williams NSG, Barnard FJ (2008) Patterns of exotic plant invasions in fragmented urban and rural grasslands across continents. *Landscape Ecology* 23: 1243–1256. <https://doi.org/10.1007/s10980-008-9295-7>
- Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037. <https://doi.org/10.1007/s10530-005-3735-y>
- Colautti RI, MacIsaac HJ (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions* 10: 135–141. <https://doi.org/10.1111/j.1366-9516.2004.00061.x>

- Colautti RI, Parker JD, Cadotte MW, Pyšek P, Brown CS, Sax DF, Richardson DM (2013) Quantifying the invasiveness of species. *NeoBiota* 21: 7–27. <https://doi.org/10.3897/neobiota.21.5310>
- Corbin J, D'Antonio CM (2004) Effects of invasive species on soil nitrogen cycling: implications for restoration. *Weed Technology* 18: 1464–1467. [https://doi.org/10.1614/0890-037X\(2004\)018\[1464:EOESOS\]2.0.CO;2](https://doi.org/10.1614/0890-037X(2004)018[1464:EOESOS]2.0.CO;2)
- Culley TM, Hardimann, NA (2008) The role of intraspecific hybridization in the evolution of invasiveness: A case study of the ornamental pear tree *Pyrus calleryana*. *Biological Invasions* 11: 1107–1119. <https://doi.org/10.1007/s10530-008-9386-z>
- Cunningham SA (2000) Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* 14(3): 758–768. <https://doi.org/10.1046/j.1523-1739.2000.98609.x>
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534. <https://doi.org/10.1046/j.1365-2745.2000.00473.x>
- Davis AJS, Singh KK, Thill J-C, Meentemeyer RK (2016) Accounting for residential propagule pressure improves prediction of urban plant invasion. *Ecosphere* 7(3): e01232. <https://doi.org/10.1002/ecs2.1232>
- De Groot RS, Wilson MA, Boumans RMJ (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* 41: 393–408. [https://doi.org/10.1016/S0921-8009\(02\)00089-7](https://doi.org/10.1016/S0921-8009(02)00089-7)
- Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007) A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions* 13: 527e534. <https://doi.org/10.1111/j.1472-4642.2007.00359.x>
- Díaz S, Pascual U, Stenseke M, Martín-López B, Watson RT, Molnár Z, Hill R, Chan KMA, Baste IA, Brauman KA, Polasky S, Church A, Lonsdale M, Larigauderie A, Leadley PW, van Oudenhoven APE, van der Plaats F, M Schröter, S Lavorel, Aumeeruddy-Thomas Y, Bukvareva E, Davies K, Demissew S, Erpul G, Failler P, Guerra CA, Hewitt CL, Keune H, Lindley S, Shirayama Y (2018) Assessing nature's contributions to people. *Science* 359: 270–272. <https://doi.org/10.1126/science.aap8826>
- Di Castri F (1990) On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: Di Castri F, Hansen AJ, Debussche M (Eds) *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, 3–16. https://doi.org/10.1007/978-94-009-1876-4_1
- DiTommaso A, Lawlor FM, Darbyshire SJ (2005) The biology of invasive alien plants in Canada. 2. *Cynanchum rossicum* (Kleopow) Borhidi [= *Vincetoxicum rossicum* (Kleopow) Barbar.] and *Cynanchum louiseae* (L.) Kartesz & Gandhi [= *Vincetoxicum nigrum* (L.) Moench]. *Canadian Journal of Plant Science* 85(1): 243–263. <https://doi.org/10.4141/P03-056>
- DiTommaso A, Stokes CA, Cordeau S, Milbrath LR, Whitlow TH (2018) Seed-dispersal ability of the invasive perennial vines *Vincetoxicum nigrum* and *Vincetoxicum rossicum*. *Invasive Plant Science and Management* 11: 10–19. <https://doi.org/10.1017/inp.2018.8>
- Donaldson JE, Hui C, Richardson DM, Robertson MP, Webber BL, Wilson JR (2014) Invasion trajectory of alien trees: The role of introduction pathway and planting history. *Global Change Biology* 20(5): 1527–1537. <https://doi.org/10.1111/gcb.12486>

- Douglass C, Weston L, DiTommaso A (2009) Black and pale swallow-wort (*Vincetoxicum nigrum* and *V. rossicum*): the biology and ecology of two perennial, exotic and invasive vines. *Management of invasive weeds*. Springer, 261–277. https://doi.org/10.1007/978-1-4020-9202-2_13
- Dubois J, Cheptou PO (2017) Effects of fragmentation on plant adaptation to urban environments. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160038. <https://doi.org/10.1098/rstb.2016.0038>
- Ehrenfeld J (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503–523. <https://doi.org/10.1007/s10021-002-0151-3>
- El-Barougy RF, Cadotte MW, Khedr AHA, Nada RM, Maclvor JS (2017) Heterogeneity in patterns of survival of the invasive species *Ipomoea carnea* in urban habitats along the Egyptian Nile Delta. *Neobiota* 33: 1–17. <https://doi.org/10.3897/neobiota.33.9968>
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the USA* 97(13): 7043–7050. <https://doi.org/10.1073/pnas.97.13.7043>
- Elmqvist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (2013) Urbanisation, Biodiversity and Ecosystem Services: Challenges and Opportunities. Springer, Dordrecht. <https://doi.org/10.1007/978-94-007-7088-1>
- Ernst C, Cappuccino N (2005) The effect of an invasive alien vine, *Vincetoxicum rossicum* (Asclepiadaceae), on arthropod populations in Ontario old fields. *Biological Invasions* 7: 417–425. <https://doi.org/10.1007/s10530-004-4062-4>
- Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. *BioScience* 55: 399–407. [https://doi.org/10.1641/0006-3568\(2005\)055\[0399:TDIUC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2)
- Gaertner M, Larson BM, Irlich UM, Holmes PM, Stafford L, van Wilgen BW, Richardson DM (2016) Managing invasive species in cities: A framework from Cape Town, South Africa. *Landscape and Urban Planning* 151: 1–9. <https://doi.org/10.1016/j.landurbplan.2016.03.010>
- Gilbert OL (1989) *The Ecology of Urban Habitats*. Chapman & Hall, London. <https://doi.org/10.1007/978-94-009-0821-5>
- Gleditsch JM, Carlo TA (2011) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions* 17: 244–253. <https://doi.org/10.1111/j.1472-4642.2010.00733.x>
- Groom Q, Desmet P, Reyserhove L, Adriaens T, Vanderhoeven S, Oldoni D, Baskauf S, Chapman A, McGeoch MA, Walls R, Wiczorek J, Wilson JRU, Zermoglio P, Simpson A (2019) Improving Darwin Core for research and management of alien species. *Biodiversity Information Science and Standards* 3: e38084. <https://doi.org/10.3897/biss.3.38084>
- Haase D, Larondelle N, Andersson E (2014) A quantitative review of Urban Ecosystem Service Assessments: Concepts, Models, and Implementation. *AMBIO* 43: 1–413. <https://doi.org/10.1007/s13280-014-0504-0>
- Haines-Young R, Potschin M (2010) The links between biodiversity, ecosystem services and human well-being. In: Raffaelli DG, Frid CLJ (Eds) *Ecosystem Ecology: A New Synthesis*. Cambridge University Press, 110–139. <https://doi.org/10.1017/CBO9780511750458.007>

- Hawkins CL, Bacher S, Essl F, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Vilà M, Wilson JR, Genovesi P, Blackburn TM (2015) Framework and guidelines for implementing the proposed IUCN environmental impact classification for alien taxa (EICAT). *Diversity and Distributions* 21: 1360–1363. <https://doi.org/10.1111/ddi.12379>
- Helmus MR, Mahler DL, Losos JB (2014) Island biogeography of the Anthropocene. *Nature* 513: 543–546. <https://doi.org/10.1038/nature13739>
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24: 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>
- Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. *Journal of Applied Ecology* 34(6): 1484–1496. <https://doi.org/10.2307/2405264>
- Holmes PM, Rebelo AG, Irlich UM (2018) Invasive potential and management of naturalised ornamentals across an urban environmental gradient with a focus on *Centranthus ruber*. *Bothalia* 48: a2345. <https://doi.org/10.4102/abc.v48i1.2345>
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414. <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- IUCN (2020) IUCN EICAT Categories and Criteria. The Environmental Impact Classification for Alien Taxa (EICAT): 1st edition. IUCN, Gland, Switzerland and Cambridge, UK. <https://doi.org/10.2305/IUCN.CH.2020.05.en>
- Khanna P (2016) *Connectography: Mapping the future of global civilization*. Random House.
- Kitajima K, Fox AM, Sato T, Nagamatsu D (2006) Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. *Biological Invasions* 8: 1471–1482. <https://doi.org/10.1007/s10530-005-5839-9>
- Knapp S, Dinsmore L, Fissore C, Hobbie SE, Jakobsdottir I, Kattge J, King JY, Klotz S, McFadden JP, Cavender-Bares J (2012) Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology* 93: S83–S98. <https://doi.org/10.1890/11-0392.1>
- Knapp S, Kühn I, Wittig R, Ozinga WA, Poschlod P, Klotz S (2008) Urbanization causes shifts in species' trait state frequencies. *Preslia* 80: 375e388.
- Kowarik I (1995) On the role of alien species in urban flora and vegetation. In: Pyšek P, Prach K, Rejmánek M, Wade M (Eds) *Plant Invasions: General Aspects and Special Problems*. SPB Academic Publishing (Amsterdam): 85e103.
- Kowarik I (2005) Urban ornamentals escaped from cultivation. In: Gressel J (Ed.) *Crop ferality and volunteerism*. CRC Press (Boca Raton): 97–121. <https://doi.org/10.1201/9781420037999.ch7>
- Kowarik I (2011) Novel Urban Ecosystems, biodiversity, and conservation. *Environmental Pollution* 159(8–9): 1974–1983. <https://doi.org/10.1016/j.envpol.2011.02.022>
- Kowarik I, Von Der Lippe M, Cierjacks A (2013) Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. *Preslia* 85: 113–132.

- Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology. *Ecology Letters* 8: 468–479. <https://doi.org/10.1111/j.1461-0248.2005.00751.x>
- Kricsfalusi VV, Miller GC (2008) Invasion and distribution of *Cynanchum rossicum* (Asclepiadaceae) in the Toronto region, Canada, with remarks on its taxonomy. *Thaiszia Journal of Botany* 18: 21–36.
- Kumschick S, Bacher S, Bertolino S, Blackburn TM, Evans T, Roy HE, Smith K (2020) Appropriate uses of EICAT protocol, data and classifications. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) *Frameworks used in Invasion Science*. *NeoBiota* 62: 193–212. <https://doi.org/10.3897/neobiota.62.51574>
- Kumschick S, Bacher S, Dawson W, Heikkilä J, Sendek A, Pluess T, Robinson TB, Kühn I (2012) A conceptual framework for prioritization of invasive alien species for management according to their impact. *Neobiota* 15: 69–100. <https://doi.org/10.3897/neobiota.15.3323>
- Ladd D, Cappuccino N (2005) A field study of seed dispersal and seedling performance in the invasive exotic vine *Vincetoxicum rossicum*. *Botany* 83: 1181–1188. <https://doi.org/10.1139/b05-093>
- Lahr E, Dunn RR, Frank SD (2018) Getting ahead of the curve: cities as surrogates for global change. *Proceedings of the Royal Society B* 285: 20180643. <https://doi.org/10.1098/rspb.2018.0643>
- Le Maitre DC, Gush MB, Dzikiti S (2015) Impacts of invading alien plant species on water flows at stand and catchment scales. *AOB Plants* 7: plv043. <https://doi.org/10.1093/aobpla/plv043>
- Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B (2007) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* 177: 706–714. <https://doi.org/10.1111/j.1469-8137.2007.02290.x>
- Livingstone SW, Cadotte MW, Isaac ME (2018) Ecological engagement determines ecosystem service valuation: A case study from Rouge National Urban Park in Toronto, Canada. *Ecosystem Services* 30: 86–97. <https://doi.org/10.1016/j.ecoser.2018.02.006>
- Livingstone SW, Isaac ME, Cadotte MW (2020) Invasive dominance and resident diversity: unpacking the impact of plant invasion on biodiversity and ecosystem function. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1425>
- Mace G, Collar N, Gaston K, Hilton-Taylor C, Akcakaya H, Leader-Williams N, Milner-Gulland EJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* 22(6): 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Maluck J, Donner RV (2015) A Network of Networks Perspective on Global Trade. *PloS ONE* 10: e0133310. <https://doi.org/10.1371/journal.pone.0133310>
- McLean P, Gallien L, Wilson JR, Gaertner M, Richardson DM (2017) Small urban centres as launching sites for plant invasions in natural areas: insights from South Africa. *Biological Invasions* 19: 3541–3555. <https://doi.org/10.1007/s10530-017-1600-4>

- Measey J, Wagener C, Mohanty NP, Baxter-Gilbert J, Pienaar EF (2020) The cost and complexity of assessing impact. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) *Frameworks used in Invasion Science*. *NeoBiota* 62: 279–299. <https://doi.org/10.3897/neobiota.62.52261>
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being*. Island Press, Washington, D.C.
- Moodley D, Geerts S, Richardson DM, Wilson JR (2013) Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. *PLoS ONE* 8: e75078. <https://doi.org/10.1371/journal.pone.0075078>
- Mumford L (1961) *The city in history: Its origins, its transformations, and its prospects*. Houghton Mifflin Harcourt.
- Nentwig W, Bacher S, Pyšek P, Vilà M, Kumschick S (2016) The generic impact scoring system (GISS): A standardized tool to quantify the impacts of alien species. *Environmental Monitoring and Assessment* 188: 1–315. <https://doi.org/10.1007/s10661-016-5321-4>
- Novoa A, Shackleton RT, Canavan S, Cybele C, Davies S, Dehnen-Schmutz K, Fried J, Gaertner M, Geerts S, Griffiths C, Kaplan H, Kumschick S, Le Maitre D, Measey J, Nunes AL, Richardson DM, Robinson TB, Touya J, Wilson JR (2018) A framework for engaging stakeholders on the management of alien species. *Journal of Environmental Management* 205: 286–297. <https://doi.org/10.1016/j.jenvman.2017.09.059>
- Padayachee AL, Irlich UM, Faulkner KT, Gaertner M, Procheş S, Wilson JR, Rouget M (2017) How do invasive species travel to and through urban environments? *Biological Invasions* 19: 3557–3570. <https://doi.org/10.1007/s10530-017-1596-9>
- Padayachee AL, Procheş Ş, Wilson JR (2019) Prioritising potential incursions for contingency planning: pathways, species, and sites in Durban (eThekweni), South Africa as an example. *Neobiota* 47: 1–21. <https://doi.org/10.3897/neobiota.47.31959>
- Pickett ST, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R (2008) Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics* 32: 127–157. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114012>
- Planty-Tabacchi AM, Tabacchi E, Salinas Bonillo MJ (2001) Invasions of river corridors by exotic plant species: patterns and causes. In: Brundu G, Brock J, Camarda I, Child L, Wade M (Eds) *Plant Invasions: Species Ecology and Ecosystem Management*. Backhuys, Leiden, 221–234.
- Potgieter LJ, Gaertner M, Irlich UM, O'Farrell PJ, Stafford L, Vogt H, Richardson DM (2018) Managing urban plant invasions: a multi-criteria prioritization approach. *Environmental Management* 62: 1168–1185. <https://doi.org/10.1007/s00267-018-1088-4>
- Potgieter LJ, Gaertner M, O'Farrell PJ, Richardson DM (2019) Perceptions of impact: Invasive alien plants in the urban environment. *Journal of Environmental Management* 229: 76–87. <https://doi.org/10.1016/j.jenvman.2018.05.080>
- Potgieter LJ, Gaertner M, Kueffer C, Larson BMH, Livingston S, O'Farrell P, Richardson DM (2017) Alien plants as mediators of ecosystem services and disservices in urban systems: a global review. *Biological Invasions* 19: 3571–3588. <https://doi.org/10.1007/s10530-017-1589-8>
- Probert AF, Volery L, Kumschick S, Vimercati G, Bacher S (2020) Understanding uncertainty in the Impact Classification for Alien Taxa (ICAT) assessments. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Rich-

- ardson DM (Eds) Frameworks used in Invasion Science. *NeoBiota* 62: 387–405. <https://doi.org/10.3897/neobiota.62.52010>
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau M-L, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the USA* 107(27): 12157–12162. <https://doi.org/10.1073/pnas.1002314107>
- Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35: 25–55. <https://doi.org/10.1146/annurev-environ-033009-095548>
- Rahlao SJ, Milton SJ, Esler KJ, Barnard P (2010) The distribution of invasive *Pennisetum setaceum* along roadsides in western South Africa: the role of corridor interchanges. *Weed Research* 50: 537–543. <https://doi.org/10.1111/j.1365-3180.2010.00801.x>
- Rebele F (1994) Urban ecology and special features of Urban Ecosystems. *Global Ecology and Biogeography Letters* 4(6): 173–187. <https://doi.org/10.2307/2997649>
- Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (Ed.) *Vegetation Ecology*. Blackwell Publishing, Oxford, 332–355.
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282. <https://doi.org/10.1890/13-0183.1>
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6: 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Ricotta C, Celesti-Grapow L, Kühn I, Rapson G, Pyšek P, La Sorte FA, Thompson K (2014) Geographical constraints are stronger than invasion patterns for European urban floras. *PloS ONE* 9(1): e85661. <https://doi.org/10.1371/journal.pone.0085661>
- Ricotta C, La Sorte FA, Pyšek P, Rapson GL, Celesti-Grapow L, Thompson K (2009) Phylogeology of urban alien floras. *Journal of Ecology* 97: 1243–1251. <https://doi.org/10.1111/j.1365-2745.2009.01548.x>
- Ruiz GM, Carlton JT (2003) Invasion vectors: a conceptual framework for management. In: Carlton JT, Ruiz GM (Eds) *Invasive Species: Vectors and Management Strategies*. Island Press, Washington DC, 459–504.
- Sæbø A, Borzan Z, Ducatillion C, Hatzistathis A, Lagerström T, Supuka J, García-Valdecantos JL, Rego F, Van Slycken J (2005) The selection of plant materials for street trees, park trees and urban woodlands. In: Konijnendijk CC, Nilsson K, Randrup TB, Schipperijn J (Eds) *Urban Forests and Trees. A reference book*. Springer Verlag, Berlin, 257–280. https://doi.org/10.1007/3-540-27684-X_11
- Salisbury A, Armitage J, Bostock H, Perry J, Tatchell M, Thompson K (2015) Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *Journal of Applied Ecology* 52: 1156–1164. <https://doi.org/10.1111/1365-2664.12499>
- Schmidt KJ, Poppendieck H-H, Jensen K (2014) Effects of urban structure on plant species richness in a large European city. *Urban Ecosystems* 17: 427–444. <https://doi.org/10.1007/s11252-013-0319-y>

- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Shochat E, Lerman SB, Anderies LM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in Urban Ecosystems. *Bioscience* 60: 199–208. <https://doi.org/10.1525/bio.2010.60.3.6>
- Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Sodhi DS, Livingstone SW, Carboni M, Cadotte MW (2019) Plant invasion alters trait composition and diversity across habitats. *Ecology and Evolution* 9: 6199–6210. <https://doi.org/10.1002/ece3.5130>
- Sukopp H (2004) Human-caused impact on preserved vegetation. *Landscape and Urban Planning* 68: 347–355. [https://doi.org/10.1016/S0169-2046\(03\)00152-X](https://doi.org/10.1016/S0169-2046(03)00152-X)
- Sukopp H, Starfinger U (1999) Disturbance in Urban Ecosystems. In: Walker LR (Ed.) *Ecosystems of disturbed ground: Ecosystems of the world*. Elsevier, Amsterdam, 397–412.
- van Wilgen BW, Forsyth GG, Prins P (2012) The management of fire-adapted ecosystems in an urban setting: the case of Table Mountain National Park, South Africa. *Ecology and Society* 17(1): 1–8. <https://doi.org/10.5751/ES-04526-170108>
- Vaz AS, Kueffer C, Kull CA, Richardson DM, Vicente JR, Kühn I, Schröter M, Hauck J, Bonn A, Honrado JP (2017a) Integrating ecosystem services and disservices: insights from plant invasions. *Ecosystem Services* 23: 94–107. <https://doi.org/10.1016/j.ecoser.2016.11.017>
- Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) *Frameworks used in Invasion Science*. *NeoBiota* 62: 525–545. <https://doi.org/10.3897/neobiota.62.52793>
- von der Lippe M, Kowarik I (2008) Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Diversity and Distributions* 14: 18–25. <https://doi.org/10.1111/j.1472-4642.2007.00401.x>
- Wilby RL, Perry GLW (2006) Climate change, biodiversity and the urban environment: a critical review based on London, UK. *Progress in Physical Geography: Earth and Environment* 30(1): 73–98. <https://doi.org/10.1191/0309133306pp470ra>
- Williams NSG, Schwartz MW, Vesik PA, McCarthy MA, Hahs AK, Clemants SE, Corlett RT, Duncan RP, Norton BA, Thompson K, McDonnell MJ (2009) A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology* 97(1): 4–9. <https://doi.org/10.1111/j.1365-2745.2008.01460.x>
- Wilson JR, Datta A, Hirsch H, Keet J-H, Mbobo T, Nkuna KV, Nsikani MM, Pyšek P, Richardson DM, Zengeya TA, Kumschick S (2020) Is invasion science moving towards agreed standards? The influence of selected frameworks. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) *Frameworks used in Invasion Science*. *NeoBiota* 62: 569–589. <https://doi.org/10.3897/neobiota.62.53243>
- Wilson JR, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136–144. <https://doi.org/10.1016/j.tree.2008.10.007>