

Classifying the effect of urbanisation on non-indigenous species using the stage-based approach: A case study on *Phragmites australis*

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SUMMARY

Urban environments are centres for human activity and environmental change, providing an ecosystem that is frequently disturbed and outside the evolutionary path of local species. The combination of these factors, along with other characteristics of the human dominated environment, create an environment which is ideal for non-indigenous species to out-compete indigenous ones, potentially becoming invasive. The process by which a non-indigenous species is transported to a novel environment and becomes invasive can be analyzed using the stage-based approach to invasion ecology. The four stages identified in this framework are transport, establishment, spread, and impact, with different pressures affecting the non-indigenous species at each stage of the process. In this review, we identify how urbanization has the potential to facilitate the invasion of non-indigenous species with respect to each of these stages. We then apply this framework to *Phragmites australis*, an invasive reed which is widespread and invasive in many urban environments in North America.

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INTRODUCTION

The number of non-indigenous species around the globe has skyrocketed in recent decades due to an increase in events such as worldwide trade, immigration and travel and tourism. All of which can knowingly or unknowingly bring species from around the world to new environments (Cadotte et al., 2017). These species can have ecological, economic, and social implications on the invaded region if they are able to establish themselves in the foreign habitat. To curb the introduction and establishment of these species, we must consider the complex factors that influence their ability to

have a negative impact (Padayachee et al., 2017). Urban centres are geographic areas which are the frontlines for species introduction, establishment, and spread. By identifying the aspects of urban centres that so readily allow for the invasion of non-indigenous species, it will allow us to mitigate their future impact.

Urbanisation, defined as the emergence of cities as settled living spaces for people moving from rural areas (Prono, 2017), has become a hallmark of the 20th and 21st centuries. Since 2007, half of the world's population has lived within cities, with this proportion continuing to increase (Leon, 2008). It

is estimated by the United Nations that over three million people move to cities every week, and that in 2050, more than 68 percent of the world's population will live in cities (United Nations, 2014). The growth of these cities has led to urban sprawl and land use patterns that are both highly fragmented yet connected. This has become a

(Niemelä, 1999). Disturbance, very simply, facilitates invasion (Lockwood, Hoopes and Marchetti, 2007). The natural state of an environment is significantly more resistant to invasion than an urban one for a number of reasons, including much higher ecosystem integrity. Indigenous species have all evolved in the

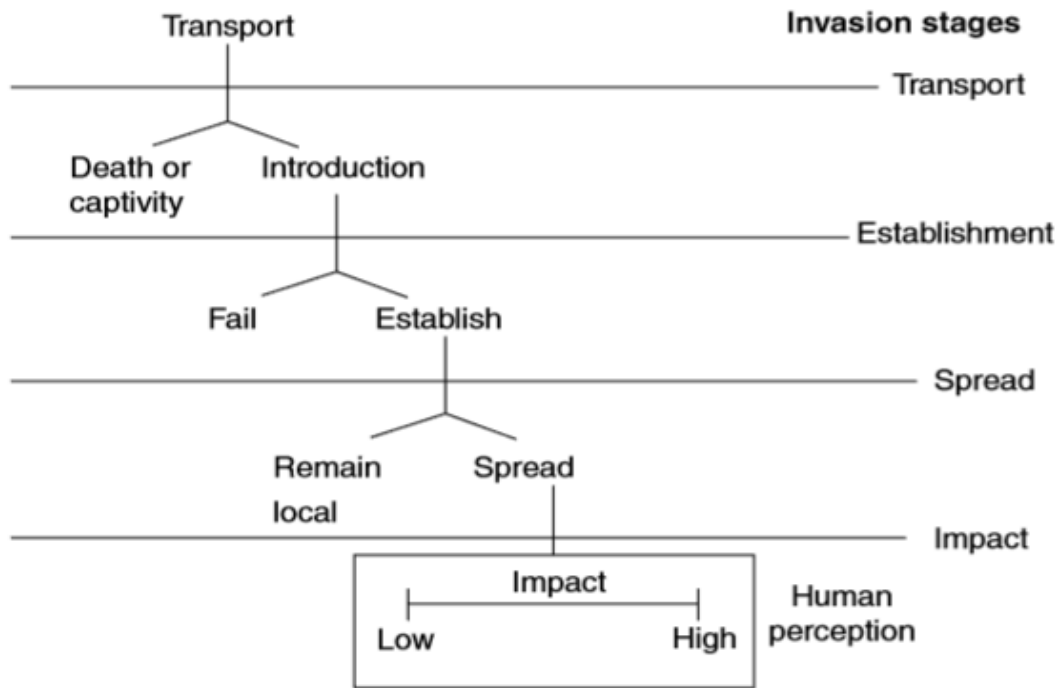


Figure 1: The stage-based approach to invasion ecology, as suggested by Lockwood, Hoopes, and Marchetti. This model depicts each stage of invasion, followed by the potential outcomes following each stage.

particularly large problem in North America, creating a major threat to indigenous species and the local environment. Along with urbanisation comes habitat destruction, which has a long-lasting effect on the ecosystem (Cadotte et al., 2017).

Urban centres act as islands; they represent areas that are isolated and have an incredibly different ecosystem than that of the surrounding area (Lechuga-Lago et al., 2017). Urbanisation creates mass human movements towards the urban centre; it results in an area that has a very high human population density, along with areas of industrial and commercial land-use. Disregarding that which is created by humans, urban areas generally have reduced levels of competition for invading species (Cadotte et al., 2017). Additionally, they represent early successional stages of an ecosystem and are characterized by high levels of disturbance

same ecosystem, thus, situations in which a non-indigenous species is more likely to dominate is one that is outside of their evolutionary path (Lockwood, Hoopes and Marchetti, 2007).

Urban centres provide starting points for non-indigenous species to enter a novel environment. It has been shown that the richness of non-indigenous species is greater in urban areas than in rural ones (Gaertner et al., 2017; Cadotte et al., 2017; Niemelä, 1999; Kühn, Wolf and Schneider, 2017). That being said, not all non-indigenous species entering a novel environment will become invasive. This depends on the level of impact that they have on both the local ecosystem(s) and the economy. The fact that urban environments are highly disturbed and impacted by humans does not negate them from the currently understood theories of ecology (Niemela, 1999). We aim to use

one of these theories to address the question of what aspects of urbanisation create an environment that allows non-indigenous species to thrive, and how it can affect the pathway that leads a species to being classified as invasive.

The stage-based approach to invasion ecology, as suggested by Lockwood, Hoopes, and Marchetti (2007) is a method for studying the process by which a species invades a novel ecosystem. It recognizes the fact that invasion is not a singular event, but a series of events that must occur to allow a species to successfully invade. The four stages identified in this framework are transport, establishment, spread, and impact (Figure 1). At each stage, the non-indigenous species can either succeed, and thus move onto the next stage of invasion, or can fail. The stage-based approach to invasion is beneficial in that it allows us to identify the different factors that can affect a species' ability to successfully invade a novel environment. The major barriers to invasion will differ at each stage; this approach allows us to identify when and how different factors impact this process. A large number of these factors are anthropogenic, and thus, acknowledging these stages allows us to identify whether humans are facilitating or inhibiting invasion of a species in a novel habitat.

Phragmites australis, also known as the common reed (henceforth referred as *Phragmites*) is a perennial grass that grows in dense stands, anywhere from one to six metres in height. It generally reproduces asexually via rhizomes, but it is also capable of producing seeds and reproducing sexually (Sturtevant et al., 2018). *Phragmites* is one of the most widespread perennial grasses in the world, yet haplotypes vary greatly between regions (McCormick et al., 2010).

The *Phragmites* haplotypes E and S are both considered indigenous to North America, where they have been present for more than 40 000 years (Saltonstall, 2002). Historical records from the 1800's describe *Phragmites* as being rare, yet within the past century it has become widespread along the Atlantic coast of the United States and spreading further north to the Great Lakes region and into Quebec (Saltonstall, 2002; Rickey and Anderson, 2004). The cause of this is thought to be the introduction of the European *Phragmites*, haplotype M, in the early nineteenth century to a port along the Atlantic Coast (Saltonstall, 2002; Brisson, de Blois and Lavoie, 2010; McCormick et

al., 2010). Haplotype M produces more root and stem mass and grows faster than haplotypes E and S (Rickey and Anderson, 2004; Lelong et al., 2007). Today, *Phragmites* is considered to be an invasive species (Saltonstall, 2002). Prior to the 1950's, around 92% of samples from *Phragmites* patches tested in Quebec were indigenous, whereas between 1990 and 2005, 95% were invasive (Lelong et al., 2007). *Phragmites* is now especially common in and along urban areas; it has been proposed that environmental disturbances have been a huge factor in its spread (McCormick et al., 2010).

Here, the factors that have allowed *Phragmites* to become invasive will be classified via the framework of the stage-based approach to invasion ecology. We will first review how an urban environment can impact invasions in general, and will then focus on how this environment has facilitated the invasion of *Phragmites*.

CLASSIFYING THE EFFECTS OF URBANISATION ON NON-INDIGENOUS SPECIES USING THE STAGE-BASED APPROACH

Concentrated human activity, characterized by high levels of disturbance, transport intensity, and environmental heterogeneity, all help to cause the increase in non-indigenous species richness relative to that of intact habitats beyond the city and agricultural limits (Cadotte et al., 2017; Padayachee et al., 2017). Recognizing the different stages to invasion and the role that humans play at each stage will allow us to identify how to best prevent and manage non-indigenous species. In the following section, the four categories of the stage-based approach will be used to classify how urbanisation facilitates invasion of non-indigenous species.

Transportation is the initial stage of the stage-based approach, consisting of the time it takes for a species to travel from its native range to a novel environment and be introduced as a non-indigenous species. It is an imperative stage, as all sequential stages rely on successful transportation (Padayachee et al., 2017). For many years, it has been shown that humans are a frequent vector for introducing species to foreign habitats. Urban environments are hotbeds of anthropogenic activity, and with human activity comes lots of

movement on both the local and international scale (Cadotte et al., 2017). As by-products of this movement is the frequent transport of new species, causing urban centres to be the frontlines for the introduction of non-indigenous species (Cadotte et al., 2017). Furthermore, the network of roads, railways, and other transport has allowed for the rapid spread of propagules (Gaertner et al., 2017). Understanding these pathways is essential to effectively respond to biological invasions (Padayachee et al., 2017).

Propagule pressure is a factor of utmost importance to the success of a non-indigenous species and is generally increased with human activity (Lockwood, Cassey and Blackburn, 2005). Gardens, ponds, lawns, parks, and other green areas found within urban environments are areas in which non-indigenous species can be purposefully introduced by humans, increasing propagule pressure (Cadotte et al., 2017). Multiple propagules can be introduced over time, such as unsuspecting residents planting non-indigenous plants for their garden. A frequent mode of establishment for non-indigenous species is via ornamental plantings in personal or municipal gardens (Cadotte et al., 2017).

The second stage is establishment, and through various human activities, urban environments provide many opportunities for non-indigenous species to establish. Urban environments are defined by a number of unique environmental conditions which do not exist naturally, such as changes to the soil, hydrological, climatic, and other ecological conditions (Cadotte et al., 2017). This disturbance and change to the environment, simply put, facilitates invasion (Lockwood, Hoopes and Marchetti, 2007). Disturbance is a characteristic which gives non-indigenous species an edge to establish themselves (Lockwood, Hoopes and Marchetti, 2007; Hui, Richardson and Visser, 2017). In addition, urban landscapes are highly fragmented. This creates novel ecosystems as well as artificial boundaries between those that are geographically very close to each other, which can lead to the local extinction of indigenous species (Hui, Richardson and Visser, 2017). The indigenous organisms that do persist in urban habitats end up being those that are most flexible and/or preadapted to similar conditions (Cadotte et al., 2017). Urban areas become islands of reduced competition, as the species living there

have escaped the enemies from their indigenous habitat, as described by the enemy release hypothesis. This reduced competition allows non-indigenous species to reallocate resources towards growth and development from defense, as seen by evolution of increased competitive ability (Cadotte et al., 2017; Keane and Crawley, 2002; Blossey and Notzold, 1995). To further support this case, natural intact ecosystems are significantly more resistant to establishment of non-indigenous species (Lockwood, Hoopes and Marchetti, 2007).

The third stage of the stage-based approach of invasion ecology is the spread of the species. As in the establishment phase, the ability for non-indigenous species to reallocate resources towards growth and development results in increased reproduction. For a non-indigenous species to be able to spread beyond the location of their initial establishment, they must out compete the indigenous species for which they share a similar niche. A large factor in their success depends on the degree of niche overlap between non-indigenous and indigenous species and their reproductive successes (Cadotte et al., 2017). Large overlap will create intense competition and the species with the higher average growth rate will prevail. While it is reasonable to expect all species' growth rates to decrease in an urban environment, indigenous species are likely hit harder. Urban environments have less natural heterogeneity and species will likely have different responses to the disturbances of urbanisation; this often shifts in favour of the non-indigenous species (Cadotte et al., 2017). Depending upon the degree of niche overlap, it is possible that a non-indigenous and an indigenous species could coexist in a natural habitat. When urbanisation is an added factor, indigenous species fitness and the differences in niches that were present naturally are reduced, often leading to competitive exclusion of the indigenous species and allowing the non-indigenous ones to further continue its spread (Cadotte et al., 2017).

In addition, urban areas are centres for movement and transportation, which allows non-indigenous species to be transported from their initial site of establishment to new cities (Gaertner et al., 2017). Although urban ecosystems are highly fragmented, they are connected through the extensive map of roadways and railways branching out from them. This high level of connectivity provides pathways for non-indigenous species to spread from one city

to another, providing the possibility of further spreading into the adjacent natural ecosystems.

The final stage in the stage-based approach is the impact of the species. It is in this stage that a species is subjectively determined to be either an invasive species or not, depending on their ecological, environmental, and economic impact. In urban environments, non-indigenous species richness is increased, but because a species may have established themselves in one or many isolated cities, it is possible that it will not spread beyond the city centres and impact indigenous habitats (Cadotte et al., 2017). In this case, a non-indigenous species may have a relatively low impact and thus not be deemed invasive.

APPLYING THE FRAMEWORK TO *PHRAGMITES AUSTRALIS*

Numerous sources have cited urbanisation and human-mediated activities as the source of spread and establishment for *Phragmites* (Jodoin et al., 2008; Amsberry et al., 2000), with many other papers citing other human mediated disturbances as a factor leading to its spread (McCormick et al., 2010; Lelong et al., 2007; Maheu-Giroux and de Blois, 2005). While it is not entirely clear why there was such a long lag time between the European *Phragmites* haplotype being introduced in North America and its spread and invasion, it is clear that urbanisation, along with human-mediated disturbances, catalyzed this event. Effects of urbanization that have benefited the spread of *Phragmites* can be identified at every stage of invasion.

Genetic analysis of many *Phragmites* patches has shown them to be relatively genetically diverse, indicating that the entire patch did not grow from a single rhizome, but instead from seeds (McCormick et al., 2010; Brisson, de Blois and Lavoie, 2010; Albert et al., 2015). Specifically, around 84% of *Phragmites* patches surveyed in the province of Quebec were found to have been established by seeds (Albert et al., 2015). *Phragmites* patches with greater genetic diversity are able to produce more viable seeds when compared to those with lower genetic diversity (McCormick et al., 2010; Brisson, de Blois and Lavoie, 2010). Once a non-indigenous haplotype is introduced, it allows for cross pollination with the other haplotypes present, slowly contributing to its spread. *Phragmites* seeds have very small

diaspores, further making them ideal for wind dispersal and have allowed for transport along far distances. This is especially prevalent along roadways, which provide long, straight corridors with cars and trucks acting as ideal transport vectors (Jodoin et al., 2008).

It has been suggested that the use of seeds as a means of invasion is, in part, what may have caused the lag time that was seen between the first establishment of *Phragmites* and its spread. As described by the Allee effect, it takes time for a population to grow large enough to have the genetic diversity required for sexual reproduction. While this would have been mitigated somewhat by the ability of *Phragmites* to reproduce clonally, it appears that its widespread prevalence is the result of successful seed production (McCormick et al., 2010).

A multitude of factors have allowed *Phragmites* to successfully establish in North America, yet the majority of them can be classified as a result of urbanisation. The high levels of disturbance provide frequent changes of ecosystems and empty niches which can be filled by a non-indigenous species (Lockwood, Hoopes, and Marchetti, 2007). It was not its initial establishment two centuries ago that caused *Phragmites* to be invasive, but its more recent spread. As a cause of this, we will first look at the factors that have allowed *Phragmites* to spread to new environments, followed by the factors that have allowed them to establish there.

Eastern North America is highly populated with major urban centres and extensive road and highway systems. This expansive road network and its frequent usage for travel is thought to have led to the spread of *Phragmites*, having been principally studied in the province of Quebec. The initial widespread presence of *Phragmites* in Quebec can be correlated with the expansion of the highway system that occurred in the province in the 1960's (Brisson, de Blois and Lavoie, 2010; Lelong et al., 2007). The expansive network of straight pathways with frequent traffic provide the perfect dispersal vector, along with disturbed land alongside the newly built roads. Roadways, and especially the drainage ditches alongside them, essentially act as a hugely connected linear wetland (Brisson, de Blois, and Lavoie, 2010). On top of this, construction of these roadways requires soil movement, which allows for the transportation of

rhizome fragments (Brisson, de Blois, and Lavoie, 2010; Lelong et al., 2007).

Once *Phragmites* has spread, it must once again establish in the novel environment. The drainage ditches created alongside roadways act not only as an ideal transport pathway, but as a habitat for *Phragmites* to establish. Drainage ditches are engineered to collect runoff and act as a barrier between the road and the surrounding ecosystem. This creates a connected ecosystem and a consistent habitat for *Phragmites* to establish, regardless of the ecosystem(s) on either side of it. In Quebec specifically, the organic clay soil along roadways adds to the similarities between natural wetlands and the local urban environment (Brisson, de Blois and Lavoie, 2010; Albert et al., 2015). During the highway expansion that took place during the 1960's, the water levels of the Saint Lawrence River were low, which created larger than usual wetland regions along its shoreline. This provided a secondary location for *Phragmites* to establish, alongside that of roadways (Brisson, de Blois and Lavoie, 2010).

Another aspect that can lead to the establishment of *Phragmites* is high nitrogen levels in local waterways and soils (Rickey and Anderson, 2004; Jodoin et al., 2008). This nitrogen is collected from runoff into drainage ditches. It has been shown

that areas with higher levels of nitrogen will also have a larger proportion of shoreline dominated by *Phragmites* (Minchinton and Bertness, 2003). Additionally, while the indigenous *Phragmites* haplotypes show no difference in biomass under varying nitrogen conditions, that of haplotype M did increase. These results suggest that under high nitrogen conditions, *Phragmites* would be capable of out-competing an indigenous species (Rickey and Anderson, 2004). In general, *Phragmites* responds more to increased nutrient levels than many of its competitors (Brisson, de Blois and Lavoie, 2010).

The extensive use of road salt as a de-icing technique causes ditches alongside roadways to be highly saline, a condition that can severely harm many plant species. The benefit for the spread of *Phragmites* in these conditions is two-fold. *Phragmites* is highly tolerant to saline conditions, naturally occurring in brackish wetlands. Secondly, these conditions inhibit the growth of other plants, reducing competition (Brisson, de Blois and Lavoie, 2010; Saltonstall, 2002; Jodoin et al., 2008).

The impact that *Phragmites* will have is highly dependent on what is present in the surrounding environment. If *Phragmites* remains solely along roadsides and in drainage ditches, then its impact

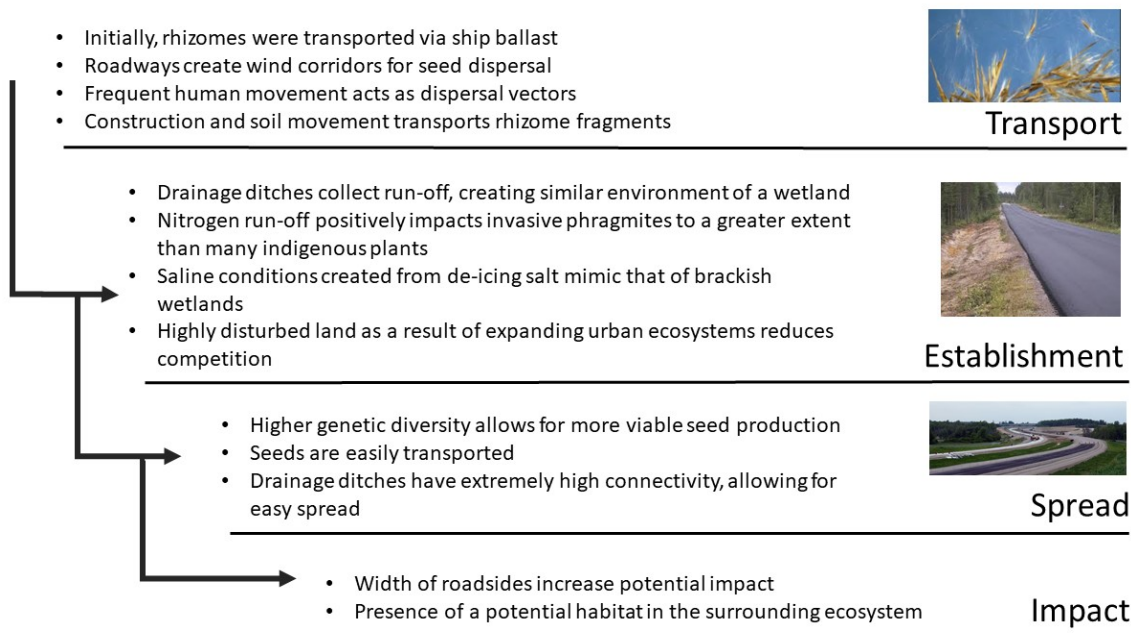


Figure 2: A summary of how urbanisation facilitates *Phragmites* invasion at each stage of the stage-based approach to invasion ecology.

is relatively small (Jodoin et al., 2008). Additionally, if the area surrounding the initial zone of establishment is a very different ecosystem, then the spread of *Phragmites* will be reduced. As an example of this, roadways with smaller roadsides and those that border forests are affected to a lesser degree than those that border marshes or other wetlands (Jodoin et al., 2008). That being said, because of the high level of connectivity and proportion of surrounding urban areas, the areas in which it is feasible to restrict *Phragmites* to roadsides are not frequent.

Many of the factors that have allowed *Phragmites* to become so widespread are consequences of the growing urban environment, as summarized in Figure 2. When referring to the multiple stages of invasion, the urban environment has perhaps impacted the ability of *Phragmites* to spread more than any other stage. The urban environment provides increasing connectivity that facilitates the rapid movement of not only people, but of other species as well. In addition to this, the characteristics of the urban environment allow for *Phragmites* to easily establish after its spread to a novel environment.

CONCLUSION

It is clear that urban environments do not fit within the typical category of a natural ecosystem, but are without a doubt a very critical aspect of attempting to prevent and manage the invasion of non-indigenous species. With the rapid growth of urbanisation and global movement, the number of non-indigenous species in urban areas will continue to grow and to be a focal point of non-indigenous introduction, establishment, spread, and impact. Using the stage-based approach, the effects of urbanisation have been classified into each stage, in an attempt to increase the understanding of urban environments and continue to build the database of knowledge for the anthropogenic ecosystem. Then using this framework, it was applied to *Phragmites* in the hope of better understanding their recent rapid spread in North America. By increasing the literature and knowledge on non-indigenous species in urban environments, a better method to prevent and manage non-indigenous and invasive species in urban environments can be constructed. We recommend using this review to continue research on how *Phragmites* spread can best be

mitigated. Additionally, this framework can be applied to other urban invaders to further the body of research in the field of invasion biology and improve the efficacy of treatments used for them.

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AUTHOR CONTRIBUTIONS

MW focused their research on the effects of urbanisation and MAS specifically on *Phragmites*. That being said, each person contributed equally to the project and all writing was done by both parties.

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