BIOL 540: A Review of Urban Species Invasions

Introduction

"Species invasions" covers populations that settle and establish in regions outside their native range, through intentional or unintentional introduction, or by natural means. A search on the Web of Science for "invasive species" yielded around 60,000 results, but in spite of pioneering work by Charles Elton as far back as the thirties, it has only become a significant topic of study in the last 25 years (given a ten-fold increase in papers per year since 1999 – Fig. 1&2). However, "urban invasion" on the web of science, gave around 2600 papers, showing a clear disparity and bias towards rural areas. Figures 1&2 show a comparison of the number of papers per year for the terms "invasive species" and "urban invasive species". They have similar gradients, but the number of papers is over ten-fold smaller for "urban species invasions" – the latest and largest values for "urban species invasion" equal the smallest values for "species invasion", suggesting that the field is around 25 years behind.

Urban invasion is a subset of species invasions - those within the boundaries of urban areas. This impact was even something of which Elton was aware—noting that alien species were more common in urban than rural areas (Elton, 1958). Urban invasions present interesting cases for two reasons: first is the distinct disturbance occurring in urban ecosystems; second is that this distubrance is not unique and is shared among urban sites — inducing homogenisation.

With regards to the first point, urban areas are ecosystems that are heavily impacted by humans. This results in increased species traffic (intentionally and unintentionally), as well as altered ecosystem functioning – changes in hydrology (water distribution and availability), refugia, and even climatic events (Johnson & Munshi-South, 2017). All of these facets combined result in new niches, natives are extirpated by human expansion, and invaders are presented with both the ecological oppurtunity and the propagule pressure to establish.

As to the second point, in non-urban areas, when disturbance occurs it is likely on a small scale and in a distinct way – it is unlikely that the same changes will occur in multiple unconnected non-urban areas. Urban areas present a situation in which intense disturbance occurs as a great scale, accompanied by environmental homogenisation. Many cities are located in riparian corridors that are disproportionately diverse before urbanisation (Naiman, et al., 1993), but as the urban sprawl develops, large areas of land are homogenised – an effect that occurs globally.

Not only are urban areas locations of increased species invasion, but the interconnectedness of urban areas, and their similarities pose a threat by facilitating invasive species spread, and homogenisation. Should these urban invaders then be able to spread out of the cities it would be clear that cities have the potential to act as a catalyst for invasions worldwide.

I see four ways one could study urban invasions: 1) a meta-analysis of case studies, and therefore the traits of urban invaders; 2) looking at the ecological theories and studies that explain the distinct nature of urban areas; 3) looking at propagule pressure – how species are introduced, and in what numbers; or 4) looking at all these aspects to forge a holistic response to the study of urban invasions. As mentionned, the number of urban area case studies is fairly meager, and the focus is rarely on more than two species. Thus, delving into a traits-based approach of urban invasion is fairly difficult. This impacts option (3), however, there is some information on both of these facets, as well as some novel ecological theories to explain the impact of urban areas. I elected to provide a holistic response to the question of the nature of urban invasions – this will result in a paper of greater breadth, lacking in as much depth as options (1) to (3). I have attempted to summarise the findings of effects that urban areas have on invasibility, and the life history of urban invaders. This involved assessing what factors of urban areas drive species invasions first,

through looking at the ecological mechanisms and the features of urban areas; and then what factors of invasive species permit invasion.

Methods

I began with a search for papers on both the Web of Science, and Google Scholar. I started searching for "*Urban Invasions*", which yielded 2659 papers like (Francis & Chadwick, 2015), (Kühn et al 2017), (Cadotte, et al., 2017), and (Gaertner et al, 2017). Given their recency, I looked further into papers they cited and subsequent papers that cited these. This allowed me to create my database of 28 papers. I then accumulated the case study data into Table 1, and looked at the ways ecological theories of invasion and urban areas intersected to provide a broad view of the nature of urban invasions.

Results

One issue that arose in the search was linguistic. Many papers discussing urban environments, even if published in ecological journals, used the term "pests". This is an ordinary language term that includes any organism that causes harm (physical or psychological) to humans, or damage to produce. Many pests are also invasive species: bed bugs, rats, mosquitoes, the emerald ash borer, and others for instance. While these are technically invasive pests, even in literature there is an aversion to calling them invasive, instead focusing on their detrimental impacts to humans. The line is further blurred as to what counts as an urban invader. While most species have native habitats outside of their range, some of them (cats, dogs, bed bugs, Aedes aegypti aegypti) have lived around humans for thousands of years. These serve as examples of possible long-term effects of species invasion – pseudo-commensalism with humans. This certainly impacted my research, as papers were undoubtedly missed because of terminology, and a more thorough effort would include the synonyms used in the literature.

The first aspect I considered were the results of *looking at* urban invasions. This can be contrasted with the results of urban invasions that I will consider afterwards. The former led to several ecological theories explaining the urban spread of species, as well as some traits of the few invaders considered; it also revealed that the study of invasions and, even moreso, urban invasions, is fraught with bias.

Two standout ecological theories relevant to urban invasion are the Urban Heat Island effect, and Anthropogenically Induced Adaptation to Invade. The Urban Heat Island effect (UHI effect henceforth) is a heat accumulation in urban areas due to human activity (Yang, et al., 2016), and further studies have shown this allows cities to mimic future global change (Lahr, et al., 2018). There are a host of factors that induce these microclimates: concrete structures that induce changes in hydrology, alter cloud density, decrease direct sunlight, and change soil structure (Kühn & Klotz, 2006). Urbanisation also affects the water availability, exacerbates drought conditions, and makes areas warmer (Borden & Flory, 2021) by localised greenhouse effects (Johnson & Munshi-South, 2017), resulting in hotter climates and rarer frost events than non-urban latitudinal counterparts. Microclimatic variation means once latitudes reach a certain temperature, the urban areas, already at higher temperatures and wherein invaders may have established, can facilitate the spread of invaders to the now warmer surrounding areas (Borden & Flory, 2021). These invasive species may previously have been kept at bay within the urban limits by colder, hostile environments surrounding the urban refuge, but the effects of climate change may liberate them (Lahr, et al., 2018). This could have untold effects on surrounding ecosystems.

Connected to this is humanity as the mediator of eco-evolutionary feedback through urbanisation (Alberti, 2015). The disturbance caused by urban environments, while providing stress and a source of instability for invaders, also promotes innovation (Alberti, 2015). I also

found several papers that discussed cases where urban invaders adapted for life within urban ecosystems shown in Table 1: urban evolution could compound the effects of urban invaders (Johnson & Munshi-South, 2017).

The second standout theory is the Anthropogenically Induced Adaptation to Invade hypothesis (AIAI hypothesis henceforth). This suggests human altered habitats in native ranges can induce adaptive changes in species that facilitate their invasion into novel, urban regions (Hufbauer, et al., 2011). This is a form of preadaptation: an adaptation to an environmental facet that enables success elsewhere by chance (Hufbauer, et al., 2011). The difference between AIAI and simple preadaptation is that the former is not only down to chance – there are similarities in the way urban ecosystems are structured, plus they are connected globally. This means a species adapted to an urban environment in one area should have traits that prove beneficial in urban ecosystems elsewhere (Hufbauer, et al., 2011). Not only this, but following establishment in other urban areas, it is possible for them to spread to surrounding, non-urban sites and outcompete natives such as the case of the Emerald Ash borer (Poland & McCullough, 2006). This may lead to *biotic homogenization* (McKinney & Lockwood, 1999) – this will be expanded upon in the section on the results of urban invasion.

Both of these theories relate to a more general theory of urban areas as "bridgeheads". Bridgeheads were popularised by Lombaert et al. in 2010; the theory suggests there are ecosystems that, once invaded, become centres of spread. A species may not initially be a great invasion risk, but, having invaded a certain ecosystem, it may suddenly become a high-risk invader. For example, the harlequin ladybirds native to China, eventually successfully invaded Europe, Africa, and South America, having establish in the south-east and north-west of the US (Lombaert, et al., 2010). Trees can be considered bridgeheads in urban areas (Paap, et al., 2017). Their role stems from the reduction of biodiversity in urban trees along with the potential for arboreal disturbance from anthropogenic contact, and the dispersal of pests using the notion of cities as thoroughfares (Paap, et al., 2017). These factors put urban trees at risk of facilitating spread, especially as they are often the only source of vegetation in a highly fragmented landscape. Urban vegetation may therefore be apt candidates to act as markers of invasion, or even to consider as "sentinel plantings" that might mitigate invasion (Paap, et al., 2017).

Another approach is to look at dispersal not just to and from, but within urban areas. This enables an integration of invasion ecology, and understandings of dispersal. Such an approach has shown that most invaders spread within cities by natural means (Padayachee, et al., 2017). The characteristics of individual cities were the main influencer of which vector species used (Padayachee, et al., 2017). Preventing the natural spread of species within cities and to new ecosystems is a challenging task, the prioritisation of prevention from establishment and introduction to urban areas in the first place is, therefore, essential (Padayachee, et al., 2017). This seems clear from the studies of AIAI and UHIs: once species infiltrate urban areas, and the natural processes of adaptation and selection are carried out, they pose a great threat to surrounding and homogeneous areas. By taking into account not only the ecological novelties of the urban landscape, but proposing solutions, and addressing the benefits such changes may incur, researchers are able to frame the issue of urban invasions in a clear way to policy makers.

One can consider the environmental factors that influence invasion success in two ways, as top-down and bottom-up processes (Shochat, et al., 2010). The former entails changes in predation pressure, and the latter changes in food density. Humans remove these hurdles since large natural predators are unable to survive in urban areas, and increased human density also increases the availability of food (Shochat, et al., 2010). The effects of these drivers allow invasive species with a high behavioural plasticity to outcompete even endemic synanthropic species (those

that benefit from proximity to humans) – and therefore humans act as relievers of selection pressure and facilitators of urban invasion. This was shown in a case study where three alien species accounted for 51% of the urban bird population of Baltimore, surviving even through competition with local human-friendly species. Further research has found for both plants and animals that the absence of larger competitors allows an enemy release effect to occur, permitting flexible, introduced species to establish, and take advantage of the conditions (Cadotte, et al., 2017). This has permitted researchers to conclude that urban areas facilitate species invasion.

The final result of the study of invasions were the biases revealed. Although Table 1 shows only a small subset of papers (11) most of these occurred in Northern Europe and America, and even the few papers show multiple studies of the same species. Up until 2010 most papers had been carried out in Europe, and those outside were only descriptive (Kühn & Klotz, 2006). Additionally, most of the studies on mechanisms until then were from studies of only the most harmful invaders (Pyšek, et al., 2008). Further there are strong geographical biases in favor of western Europe and the US with Asia and Africa heavily understudied (Pyšek, et al., 2008). Biases against urban invasion studies aside, there are clearly leanings in the study of invasion towards certain areas. While some argue that the theories of non-urban ecology are satisfactory for understanding urban ecology (Niemelä, 1999), and that the scale is a continuum from urban to rural, a difference in degree not kind, this is irrelevant if the field of non-urban invasions is lacking representation. These biases imply that more resources should be allocated to understanding and analyzing our cities as well as the non-urban areas surrounding them. We cannot accurately predict or build legislation without understanding the consequences of our action or inaction.

Next are the effects of species invasion gleaned from the papers. This includes biotic homogenisation, and invasional meltdown (Lechuga-Lago, et al., 2017) – where invasive species respond to a disturbance, cause further ecosystem change, and facilitate the establishment of additional invaders, in a positive feedback loop.

Caprobotus edulis is a good case study for invasional meltdown in dune ecosystems (Lechuga-Lago, et al., 2017). This study has profound implications for invasions in general. Researchers found that not only were the *C. edulis* overwhelmingly present in areas of human disturbance - urbanised areas of coast front; but *C. edulis* even altered the hydrology and nutrient make up forcing out native species. This additional disturbance caused by *C. edulis* establishment then facilitated the invasion of both other *C. edulis* individuals and allowed the establishment of non-dune species due to the shifts in dune structure (Lechuga-Lago, et al., 2017). This is one of many dynamic and multifaceted effects of invasion in vulnerable habitats, they can have farreaching consequences, especially in urban areas, where pockets of vegetation are often exclusively inhabited by invaders (Kühn & Klotz, 2006), and the little green space there is can prove vitally important across trophic levels.

The case studies in Table 1 not only show some of the traits that are beneficial to urban invaders (tolerance for humans, generalist mesopredators, high dispersal ability, quick response to disturbance), but also cases of urban evolution. The list is not comprehensive, but does show species adapting to establish in urban areas, for instance the cases discussed by Borden & Flory (2021), and Thompson, et al. (2018). It is possible that this capability (the capacity for urban evolution) allowed the species to become fully established. For instance, the Brown Anole developed short hind limbs and tails, and became behaviourally adapted to seek out higher perches that in its native Bahamian range to adjust to the urban lifestyle (Putman, et al., 2020).

Biotic homogenisation is the process whereby a widespread species replaces an endemic species. There are many factors behind this, but one is invasion. Initially the focus of biotic

homogenisation was "winners and losers" - how human action could lead to regional, and global scale homogenization (McKinney & Lockwood, 1999). This was expanded upon, and the discussion entered the realm of species invasion (McKinney, 2006). Invasion and homogenisation relate not only to humans facilitating the domination of species that can live among us, but also homogenising the landscape through urbanisation to further assist invaders. In a case study of Bariloche, Argentina in 1993, introduced plants in rural areas around the city made up 10 to 20% of species richness, while in the city they comprised 100% of the vegetation (Niemelä, 1999). This is not only due to disturbance by pollution run off from cars, de-icing, and fertilisers, but additionally to the disturbances tied to the UHI effect. This link between urbanisation and homogenisation can be seen best through the urban gradient, onto which can be transposed a gradient of homogenisation: the suburbs are home to more widespread native species (McKinney, 2006), but even these areas are invaded by mesopredator mammals, and ground-foraging, omnivorous and frugivorous birds that exploit the fragmented structure of the suburbs (McKinney, 2006). It is cities though that are home to the greatest homogenisation, not only on a local scale but globally too. Since these habitats often have comparable structures and states of disequilibrium from the surrounding environment, they entice a certain species – generalist, human-tolerant, synanthropic species that have invaded and adapted to the urban lifestyle (McKinney, 2006).

Finally, papers alluded to the damage caused by urban species, but for none I found was it the primary concern. One example was the effects of urbanised mosquitos whose adaptations make them a threat as the hosts of disease (Aubry, et al., 2020); another was the impact of emerald ash borers and their devastation to ash trees (Poland & McCullough, 2006); thirdly, one mentioned the damage caused by Japanese knotweed (Francis & Chadwick, 2015) – although this was a case of a species adapted to hostile conditions that found a niche in urban areas, thus allowing it to burrow into concrete and ruin infrastructure of urban areas. These effects could themselves form a paper, although a lack of case studies would impede the depth of such a paper, I believe.

Conclusion

The consensus across the papers was that urban areas pose a unique threat. These areas are not only disturbed in such a way that they create ecological space for invaders, but they may even provide invaders with the means for preadaptation to other urban areas, provide refuge and preempt climatic change, reduce both top-down and bottom-up stressors that usually control invasion, and, finally, provide the means to spread to, and therefore homogenise the diversity of other urban – homogeneous – areas. My collection of papers is only a start – there are many more papers out there, undoubtedly with unique case studies or experimentation that yields new threats by or answers to urban invasion; and secondly, as agreed upon by many of the authors I have read (Fig. 3) there is not enough data in the field of invasions, especially in urban invasions, or even a clear idea of what "urbanisation" specifically entails (Cadotte, et al., 2017). More case studies are needed that cover more species than just the best-known, most serious invaders; more experimental papers are required to precisely understand the effects, and more effort must be made to prevent invaders entering cities in the first place.

Cities can be thought of as catalysts. Through the same conditions invaders have exploited (Kühn, et al., 2017) to increase in numbers for the last 200 years (Seebens, et al., 2017), cities have accelerated the rate of invasion, not only by the possibility of urban evolution, but also by providing niche space for the generalist invaders, habitat release, and acting as a global circulatory system to further spread of these species around the globe. It seems that if we are not more conscientious about the effects of our urban areas, they could incur damage more serious than they already have and are.

Figures

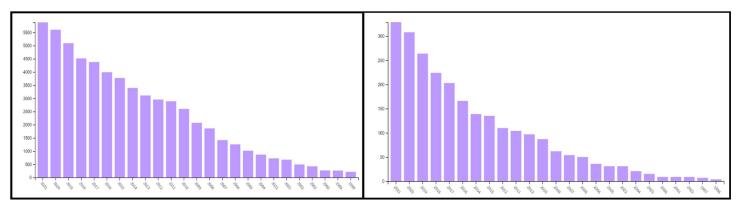


Figure 1&2 – two graphs from the Web of Science analysis of published papers with the terms "invasive species" and "urban invasive species" – left and right respectively. Note the difference in the y axes.

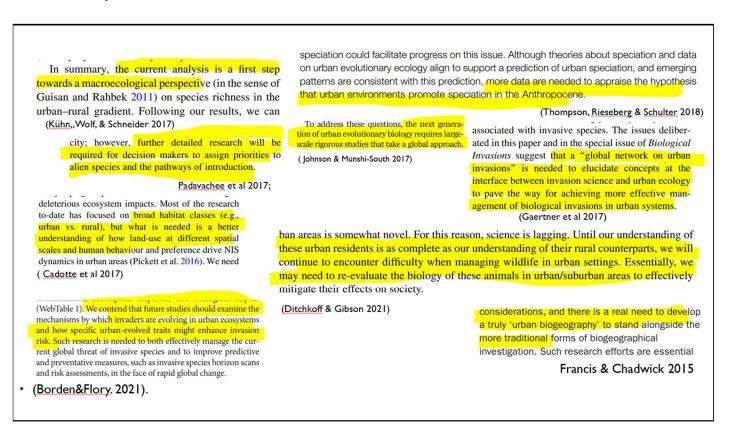


Figure 3 – this shows a collection of concluding remarks from some of the papers I read. The highlighted yellow sections all make similar points – that the field of invasion ecology, and specifically urban invasion, is a field lacking data and money. If we are to learn more and tackle the issue of urban invasive species, we must heed the advice of the experts.

	Species	Classification	Paper	Urban Adaptation - behaviour, morphology, and life history	Effect	Location of Invasion Study
Plants	hottentot fig, sour fig or ice plant	Caprobotus edulis	Lechuga-Lago et al 2017	Induces water stress (<i>C. edulis</i> is able to store water and outcompete other dune species).	Invasional Meltdown. C. Edulis reacts to disturbed conditions (recreational areas with high human impact) and alters soil hydrology in a way that further promotes the establishment of nondune species	Galicia, Spain
	Virginia Pepperweed	Lepidium virginica	Borden & Flory 2021; Thompson, Rieseberg & Schluter 2018		Greater dispersal abilities, and greater resource uptake ability to take adavantage of light availability	
	Scotch Broom	Cytisus scoparius	Borden & Flory 2021; Thompson, Rieseberg & Schluter 2018	Directional selection for larger flowers in urban populations, but not in rural		
	Japanese Knotweed	Fallopia Japonica	Francis & Chadwick 2015	Has the capacity to grow through hard substrates due to its natural range being at high altitudes, therefore able to grow through concrete	infrastructure damage to buildings across cities	UK
Insects	Cabbage White Butterfly	Pieris rapae	Borden & Flory 2021; Thompson, Rieseberg & Schluter 2018	Greater wing size in urban populations, allowing greater dispersal due to fragmentation. Ubran invaders can therefore spread further and faster posing a risk to non-urban areas		
	Common Bed Bug	Cimex lectularius	Francis & Chadwick 2015	synurbic - maintain greater populations in urban areas than in their natural habitats		
	Domestic A	Aedes aegypti aegypti	Aubry et al 2020	Oviposits in artificial containers and preferentially bites humans. Domestication was accompanied by an increased innate ability to acquire and transmit ZIKA virus	increased risk of zika transmission	They compared Subsaharan African Aedes with those in the Americas and Southeast Asia to compare how the domestic subspecies performed.
	Emerald ash borer	Agrilus planipennis	Poland & McCullough 2006	Ash trees are among the most common trees planted in north america	Death of up to 15 million ash trees in USA. Became problematic upon release from urban area into rural wildlife	Detroit, Michigan; Windsor, Ontario
	London Underground Mosquito	Culex pipiens complex	Thompson, Rieseberg & Schluter 2018	Urban populations have diverged for many life history traits associated with a life in the underground	potential epidemiological risk	London, UK
	Peppered moth	Biston Betularia	Ditchkoff et al 2006; Thompson, Rieseberg & Schluter 2018	Greater frequency of 'melanic' morph in polluted areas		Manchester, UK
Reptiles	Green Anole Lizard	Anolis carolinensis	Lailvaux 2020; Putnam, Pauly & Blumstein	Found near refuge mostly, suggesting they don't stray from hiding places. Also are more tolerant of human disturbance	outcompete local fence-lizard populations. Biotic homogenisation	Originally from Cuba, travelled to the US 12-6 million years ago. Now have been introduced to California, Hawai'l, Guam and Okinawa
	Brown Anole Lizard	Anolis sagrei	Putnam, Pauly & Blumstein; Lailvaux 2020	Found near refuge mostly, suggesting they don't stray from hiding places. Also are more tolerant of human disturbance. Additionally they more readily autotomize their tails, and have a higher propsenity to do so when resource availability is high. Uses more narrow perches than in native range to respond to the vegetation differences - Bahamian Brown Anoles also have shorter hind length.	outcompete local fence-lizard populations. Biotic homogenisation	Southern California, USA; Bahamas
	Crested Anole	Anolis cristatellus	Borden & Flory 2021; Thompson, Rieseberg & Schluter 2018	Longer limbs and more toepads in urban areas. Developed more lamellae and can climb and run more effectively on smooth surfaces than it can in natural areas	outcompete local Green Anole population	Florida, USA
	Asian House gecko	Hemidactylus frenatus	Borden & Flory 2021	Outcompetes urban local species. Greater ability to grip to smooth srufaces	Can spread to nearby non-urban forests given sufficient time and propagule pressure. Possibily arose by AIAI - due to their presence in urban areas within their native ranges.	Australia
	Italian Wall Lizard	Podarcis siculus	Putnam, Pauly & Blumstein	Found near refuge mostly, suggesting they don't stray from hiding places. Also are more tolerant of human disturbance	outcompete local fence-lizard populations. Biotic homogenisation	Southern California, USA

	European Starling	Sturnus vulgaris	Shochat et al		Biotic homogenisation - Their ability to efficiently take up resources, and fill in niches in the urban community allows few syanthropic species to dominate in urban areas	Baltimore, USA
Birds	House sparrow	Passer domesticus	Shochat et al		Biotic homogenisation - Their ability to efficiently take up resources, and fill in niches in the urban community allows few syanthropic species to dominate in urban areas. Bioaccumulation of lead may have adverse effects on predators	Baltimore USA
	House Finch	Haemorhus mexicanus	Able & Belthoff 1998; Ditchkoff et al 2006; Thompson, Rieseberg & Schluter 2018	Urban birds have evolved larger bills and stronger bites than non-urban birds, which causes them to differ in song. They are also better able to access human-supplied feeders. Display shifts in migratory behaviour - from totally sedentary to migrating up to 80km within 20 years of introduction		Eastern USA from California.
	Florida Scrub Jay	Aphelocoma coerulescens	Ditchkoff et al 2006	More efficient at foraging that its non- urban counterparts. Commence breeding up to 3 weeks earlier than normal.		
Mammals	Rock dove (or pigeon)	Columba livia	Francis & Chadwick 2015	synurbic - maintain greater populations in urban areas than in their natural habitats	Biotic homogenisation - Their ability to efficiently take up resources, and fill in niches in the urban community allows few syanthropic species to dominate in urban areas	Baltimore, USA
	Racoon	Procyon lotor	Ditchkoff et al 2006	Aggregated dsitribution focused on communal feeding sites. Adapted to primarily consume artifical food.	May lead to an increase in disease, due to the nature of the food consumed, and the high density of racoons in cities	
	Cats	Felis catus	Ditchkoff et al 2006	generalist uncontrolled predators can cause great damage to populations of urban wildlife	Kill an estimated 258-822 million lizards per year	
	Dogs	Canis lupus familiaris	Ditchkoff et al 2006	generalist uncontrolled predators can cause great damage to populations of urban wildlife		
	Red Fox	Vulpes vulpes	Johnson & Munshi-South	synurbic - maintain greater populations in urban areas than in their natural habitats	Transmission of disease	
Amphibians	Cuban Treefrogs	Osteopilus septentrionalis	Borden & Flory 2021			spread as far north as Ontario from their natural habitat of florida

Table 1 – starting on page 7 – this is the table that I made by collecting the case studies from the papers. I labelled which paper the studies came from, and the location and features of the organisms if they were discussed. I also included the effect of their invasion if it was present. While there aren't enough case studies to draw solid conclusions regarding traits of invaders, it does show that some triats (dispersal ability, plasticity, and generalism) are traits that crop up often. There are both instances of urban evolution, and the pernicious effects of invaders apparent from the table.

References

Alberti, M., 2015. Eco-Evolutionary dynamics in an urbanising planet. *Trends in Ecology & Evolution*, pp. 114-126.

Aubry, F. et al., 2020. Enhanced Zika virus suceptibility of globally invasive Aedes Aegypti populations. *Science*, 370(6519), pp. 991-996.

Borden, J. & Flory, S., 2021. Urban Evolution of Invasive Species. *Front Ecol Environ*, pp. 184 - 191.

Cadotte, M., Yasui, S., Livingstone, S. & MacIvor, J., 2017. Are urban systems beneficial, deterimental or indifferent for biological invasions? *Biological Invasions*, pp. 3489 - 3593.

Crosby, A. W., 1986. *Ecological Imperialism: the Biological Expansion of Europe 900-1900*. Cambridge; New York: Cambridge University Press.

Ditchkoff, S. S. S. & Gibson, S., 2006. Animal behaviour in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems*, pp. 5-12.

Elton, C., 1958. The ecology of invasions by plants and animals.. London: Methuen.

Francis, R. & Chadwick, M., 2015. Urban invasions: non-native and invasive species in cities. *Geography*, pp. 144-151.

Gaertner, M. et al., 2017. Non-native species in urban environments: patterns, processes, impacts and challenges. *Biological Invasions*, pp. 3461-3469.

Gleidistch, J., 2017. The Role of Invasive Plant Species in Urban Avian Conservation. In: *Ecology and Conservation of Birds in Urban Environments*. New York: Springer International Publishing, pp. 413-425.

Hufbauer, R. et al., 2011. Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-alteredhabitats within the native range can promote invasions. *Evolutionary Applications*, pp. 89-101.

Johnson, M. & Munshi-South, J., 2017. Evolution of life in urban environments. *Science*, pp. 1-11.

Kühn, I. & Klotz, S., 2006. Urbanisation and homogenisation - comparing the floras of urban and rural areas in Germany. *Biological Conservation*, pp. 292-300.

Kühn, I., Wolf, J. & Schneider, A., 2017. Is there an urban effect in alien plant invasions? *Biological Invasions*, pp. 3505-3513.

Lahr, E., Dunn, R. R. & Frank, S. D., 2018. Getting ahead of the curve: cities as surrogates for global change. *Proc. R. Soc.*.

Lailvaux, S., 2020. It's Not Easy Being Green: Behaviour, Morphology, and Population Structure in Urban and Natural Populations of Green Anole (Anolis carolinensis) Lizards. *Frontiers in Ecology and Evolution*, p. 315.

Lechuga-Lago, Y., Novoa, A., Le Roux, J. & Gonzalez, L., 2017. Understanding the influence of urbanisation on invasibility: Caprobrotus edulis as an exemplar. *Biological Invasions*, pp. 3601-3611.

Lombaert, E. et al., 2010. Bridgehead effect in hte worldwide invasion of the biocontrol harlequin ladybird. *PloS one*, p. e9743.

McKinney, M. L., 2006. Urbanization as a major cause of biotic homogenisation. *Biological Conservation*, pp. 247-260.

McKinney, M. & Lockwood, J., 1999. Biotic Homogenization: a few winner replacing many losers in the next mass extinction. *Trends in Ecol Evol*, 14(11), pp. 450-453.

Naiman, R., Décamps, H. & Pollock, M., 1993. The role of riparian corridors in maintaining regional diversity. *Ecological Applications*, 3(2), pp. 209-212.

Niemelä, J., 1999. Is there a need for a theory of urban ecology?. *Urban Ecosystems*, pp. 57-65.

Paap, T., Burgess, T. I. & Wingfield, M. J., 2017. Urban trees: bridge-heads for forest pest invasions and sentinels for early detection. *Biological Invasions*, pp. 3515-3526.

Padayachee, A. L. et al., 2017. How do invasive species travel to and through urban environments?. *Biological Invasions*, pp. 3557-3570.

Poland, T. M. & McCullough, D. G., 2006. Emerald Ash borer: invasion of the urban forest and teh threat to North America's ash resource. *Journal of FOrestry*, pp. 118-124.

Putman, B., Pauly, G. & DT, B., 2020. Urban invaders are not bold risk-takers: a study of 3 invasive lizards in Southern California. *Current zoology*, pp. 657-665.

Pyšek, P. et al., 2008. Geographical and Taxonomic biases in Invasion Ecology. *Trends in Ecology & Evolution*, pp. 237-244.

Seebens, H. et al., 2017. No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8(1), pp. 1-9.

Shochat, E. et al., 2010. Invasion, Competition, and Biodiveristy Loss in Urban ecosystems. *Bioscience*, pp. 199-209.

Thompson, K., Rieseberg, L. & Schulter, D., 2018. Speciation and the city. *Trends in Ecology and Evolution*, pp. 815-26.

Yang, L., Qian, F., Song, D.-X. & Zheng, K.-j., 2016. Research on Urban Heat-Island Effect. *Procedia Engineering*, 169(Special Issue: Fourth International Conference on Countermeasures to Urban Heat Island, 30-31 May and 1 June 2016), pp. 11-18.