A Synthetic Review of Adaptation Strategies and Invasion Pathways in Urban Flora: Linking Ecological and Evolutionary Mechanisms for Management

Ignacio Navarro

Department of Botany Research, University of the Philippines Los Baños, Andres M. Umali Avenue, Los Baños, Philippines

Abstract

Urban ecosystems represent one of the most rapidly expanding and novel environments on Earth, characterized by a unique set of abiotic and biotic stressors. These include habitat fragmentation, pollution, the urban heat island effect, altered hydrological regimes, and frequent anthropogenic disturbance. This review synthesizes current research on how native and non-native plant species adapt to these stringent conditions and explores the critical intersection between adaptation and invasion. We first delineate the key selective pressures of the urban environment and elaborate on the specific phenotypic and genotypic adaptations observed in urban flora, including traits related to thermotolerance, drought resistance, phenology, seed dispersal, and pollution tolerance. We then investigate the pathways through which non-native species are introduced and spread in urban settings, arguing that cities function as primary hotspots and dispersal hubs for biological invasions. A central thesis of this paper is that the same traits that pre-adapt species for urban environments often overlap with those characterizing successful invaders, creating a synergistic cycle where urban areas act as filters and accelerants for invasion. Furthermore, we discuss the concept of "urban evolutionary traps" and the potential for rapid evolutionary change in both native and non-native populations. The article concludes by integrating these concepts into a management framework, proposing that understanding urban adaptation is not merely an academic exercise but is crucial for predicting invasion dynamics, conserving native biodiversity, and implementing effective greening strategies for sustainable urban futures. We highlight the need for interdisciplinary research that combines genomics, ecology, and social science to address the complex challenges of urban plant ecology.

Keywords

Urban Ecology, Plant Adaptation, Biological Invasions, Phenotypic Plasticity, Rapid Evolution, Urbanization Gradients, Functional Traits, Dispersal Mechanisms

1. Introduction

The 21st century is the urban century. For the first time in human history, more than half of the global population resides in urban areas, a proportion projected to rise to nearly 70% by 2050. This massive demographic shift drives an unprecedented transformation of landscapes, converting natural and agricultural lands into complex, human-dominated matrices of impervious surfaces, buildings, and managed green spaces [1]. These urban environments impose a powerful and novel set of selective pressures on the species that inhabit them.

Urban flora-the assemblage of plant species within a city-is not a random subset of the regional species pool. It is a dynamic and filtered community comprising a mixture of remnant native species, cultivated ornamentals, and a vast array of spontaneous non-native species, some of which become invasive. The survival and proliferation of plants in cities depend on their ability to cope with a suite of challenges, including elevated temperatures (the urban heat island effect), soil compaction and contamination, altered nutrient cycles, atmospheric pollution, frequent physical disturbance, and fragmented habitats that disrupt gene flow and pollinator services [2].

In response to these pressures, plants exhibit a range of adaptation strategies. These can be rapid, occurring over just a few generations through evolutionary change, or they can be plastic, involving reversible phenotypic adjustments in response to environmental cues [3]. Concurrently, urban areas are major points of entry and establishment for non-native plant species. The global horticulture trade, transportation networks, and the creation of disturbed, resource-rich habitats provide constant propagule pressure and opportunities for introduced species to establish and spread. The invasion pathways are numerous and often intertwined with human activities.

This article aims to explore the intricate relationship between the adaptation strategies of urban flora and the pathways of biological invasion. We posit that cities are not just passive backdrops but active drivers of ecological and evolutionary change. The core objectives of this review are to:

• Synthesize the primary adaptive strategies plants employ to survive and reproduce in urban environments.

• Elucidate the major pathways through which non-native plants are introduced and become invasive in urban settings [4].

• Examine the trait overlap between successful urban adapters and invasive species, proposing that urban environments act as "filtering landscapes" that pre-adapt species for invasion.

• Discuss the implications of these processes for urban conservation, restoration, and management, and to identify key future research directions.

By bridging the fields of evolutionary ecology and invasion biology, this review seeks to provide a holistic understanding of the forces shaping the green fabric of our cities.

2. The Urban Environment: A Matrix of Selective Pressures

To understand plant adaptation, one must first characterize the environment. Urban environments present a mosaic of conditions that differ significantly from those in surrounding non-urban areas. These pressures act as filters, determining which species from the regional pool can persist and which functional traits are favored [5].

2.1 Abiotic Stressors

Urban Heat Island (UHI) Effect: Cities are typically several degrees warmer than their rural surroundings, a phenomenon caused by the absorption and re-radiation of heat by buildings and pavements, reduced vegetation cover, and anthropogenic heat sources. This creates a thermal gradient, with temperatures often decreasing from the city core to the periphery. Plants must cope with elevated mean temperatures, more frequent heatwaves, and warmer nights, which can affect photosynthesis, respiration rates, and phenology [6].

Altered Hydrology and Drought: Impervious surfaces prevent water infiltration, leading to increased surface runoff and reduced groundwater recharge. This often results in "flashier" hydrographs and longer periods of drought between precipitation events for vegetation in unirrigated sites. Consequently, drought tolerance is a highly selected trait in urban flora.

Soil Modification and Contamination: Urban soils are notoriously heterogeneous and often degraded. They can be compacted, which reduces aeration and root penetration, and have altered pH and nutrient profiles (e.g., higher phosphorus and salt levels from de-icing agents). They may also be contaminated with heavy metals (e.g., lead, zinc), polycyclic aromatic hydrocarbons (PAHs), and road salts [7].

Atmospheric and Light Pollution: Air pollutants like ozone, nitrogen oxides, and particulate matter can damage plant tissues and impede gas exchange. At night, artificial light from street lamps and buildings can disrupt photoperiod-sensitive processes, such as flowering and dormancy, potentially extending the growing season.

2.2 Biotic Stressors

Habitat Fragmentation: The urban landscape is a patchwork of green spaces (parks, remnants, gardens) isolated by a matrix of unsuitable habitat. This fragmentation reduces habitat area, increases edge effects, and can isolate plant populations, limiting pollen and seed dispersal and reducing genetic diversity [8].

Altered Species Interactions: Urbanization reshuffles ecological communities. Pollinator assemblages may change, leading to selection for self-compatibility or asexual reproduction. Herbivory pressures can shift, and competition from non-native species can intensify. The loss of mutualists or the introduction of novel pathogens can further challenge native plants.

2.3 Anthropogenic Disturbance

Frequent mowing, trampling, chemical application (herbicides, pesticides), and soil disturbance create a high-stress environment that favors species with specific life-history strategies, such as ruderals (short-lived, fast-growing species with high seed output) and species capable of vegetative regeneration [9].

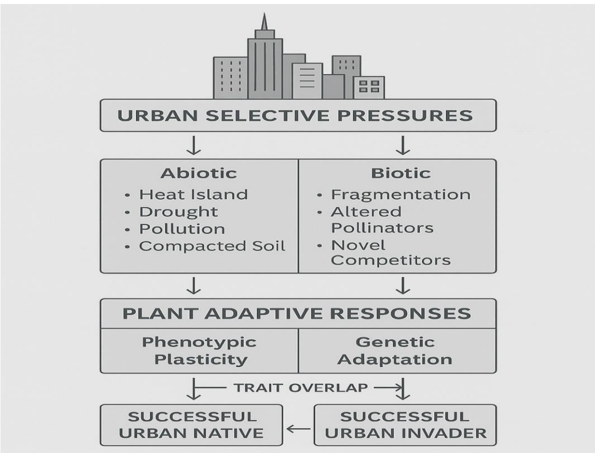

Figure 1. Conceptual Diagram of Urban Selective Pressures and Plant Responses

Figure 1 explains how urban environments shape plant evolution and adaptation by imposing a unique combination of abiotic and biotic selective pressures. At the top, the cityscape symbolizes the urban ecosystem, which exposes plants to abiotic stressors such as heat island effects, drought, pollution, and compacted soil, as well as biotic pressures including habitat fragmentation, altered pollinator communities, and competition with novel species. These selective forces drive two main types of plant adaptive responses: phenotypic plasticity, where plants adjust their traits flexibly to cope with stress, and genetic adaptation, where advantageous traits become genetically fixed over generations. The outcomes of these responses are shown at the bottom of the diagram: plants may emerge as "successful urban natives" or "successful urban invaders." The two-way arrow labeled "trait overlap" highlights that the traits enabling native species to persist in cities often resemble those that allow non-native invasive species to thrive, making urban environments hotspots for both adaptation and biological invasion.

3. Adaptation Strategies of Urban Flora

Plants surviving in cities are not merely passive victims of urban stress; they actively respond through a suite of morphological, physiological, phenological, and life-history adaptations. These responses can be plastic or evolutionary [10].

3.1 Phenotypic Plasticity: The First Line of Defense

Phenotypic plasticity-the ability of a single genotype to produce different phenotypes in different environments-is a crucial mechanism for coping with heterogeneous and unpredictable urban conditions.

Morphological Plasticity: For instance, plants in trampled areas may develop a more prostrate growth form. In response to shade from buildings, species may exhibit shade-avoidance syndromes, such as increased stem elongation and larger leaf area [11].

Physiological Plasticity: Plants may adjust their photosynthetic pathways or osmotic potential in response to drought or salinity. Some species can increase the production of heat-shock proteins or antioxidant enzymes to mitigate thermal and oxidative stress.

The Role of Plasticity in Invasion: For many non-native species, high phenotypic plasticity is considered a key "invasion tool", allowing them to establish and thrive across a wide range of urban habitats upon introduction [12].

3.2 Genetic Adaptation and Rapid Evolution

There is growing evidence that urban populations can undergo rapid evolutionary change, diverging genetically from their rural counterparts over just a few dozen generations.

Thermotolerance: Studies on common weed species like *Crepis sancta* have shown that urban populations have evolved earlier flowering times and altered seed dispersal mechanisms in response to warmer temperatures and fragmented habitats.

Drought and Salinity Tolerance: Research on white clover (*Trifolium repens*) has documented the convergent evolution of reduced hydrogen cyanide (HCN) production-a anti-herbivore defense-in urban populations across multiple cities, potentially due to pleiotropic trade-offs with drought tolerance [13].

Heavy Metal Tolerance: Classic examples include the evolution of tolerance to zinc, copper, and other heavy metals in grasses like *Agrostis capillaris* and *Festuca ovina* on mine tailings and, by extension, in contaminated urban soils. This tolerance often involves mechanisms like metal exclusion, sequestration in roots, or chelation.

Altered Seed Dispersal and Dormancy: In fragmented habitats, the cost of dispersing seeds into unsuitable pavement or lawn may be high. This has led to the evolution of reduced seed dispersal in plants like the dandelion (*Taraxacum officinale*) and *Crepis sancta* in cities.

3.3 Life-History Shifts

Urban environments often favor a "live fast, die young" strategy. Short generation times, early and prolific reproduction, and a high capacity for clonal growth are common traits among successful urban species, both native and non-native. This ruderal strategy allows plants to capitalize on temporary, disturbed habitats before the next disturbance event occurs.

4. Invasion Pathways in Urban Landscapes

Urban centers are epicenters of global trade and human movement, making them primary gateways for non-native species. The pathways of introduction and spread are diverse and often facilitated by human activities.

4.1 Intentional Introductions: The Horticulture Trade

The commercial horticulture industry is arguably the most significant pathway for introducing non-native plants into urban areas. Ornamental plants are selected for traits such as showy flowers, fast growth, pest resistance, and environmental tolerance-traits that often correlate with invasiveness. When these species escape from gardens and parks via seeds or vegetative fragments, they can establish self-sustaining populations in nearby natural areas. Examples include trees like the Norway maple (*Acer platanoides*) and shrubs like butterfly bush (*Buddleja davidii*) [14].

4.2 Unintentional Introductions

Contaminants: Weed seeds can be introduced as contaminants in soil, with agricultural produce, or in packing materials.

Transportation Corridors: Roads, railways, and ports act as conduits for the dispersal of propagules. Seeds can be carried on vehicle undercarriages, in ship ballast soil, or along railway ballast. These corridors often feature disturbed, high-light environments that are ideal for the establishment of ruderal invasive species [15].

4.3 The Role of Urban Green Spaces

Different types of urban green spaces play distinct roles in the invasion process:

Botanical Gardens and Arboreta: Historically, these institutions have been a source of invasive species, as they intentionally cultivate a wide range of exotic plants, some of which may escape.

Parks and Gardens: These managed landscapes provide a constant source of propagules from ornamental plantings.

Ruderal and Vacant Lots: These highly disturbed, unmanaged sites often serve as the initial "beachheads" for invasive species, where they can establish large populations before spreading into more intact habitats.

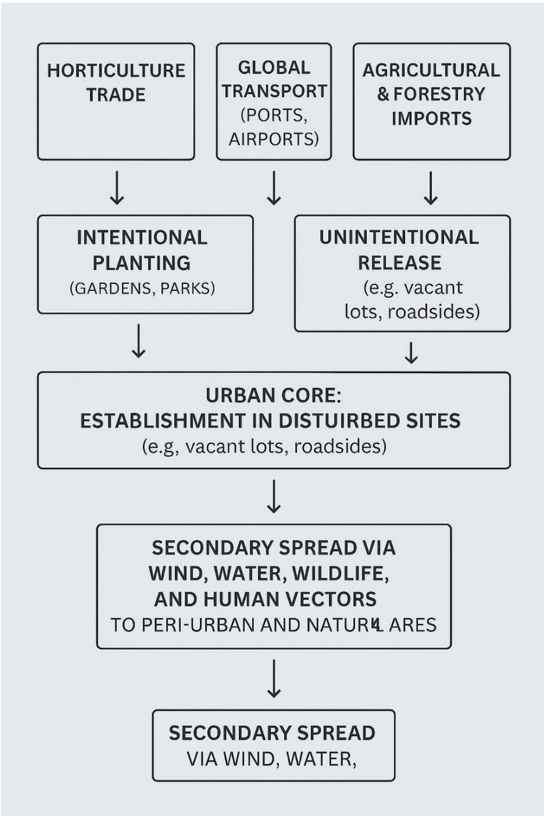

Figure 2. Pathways of Plant Introduction and Spread in Urban Landscapes

Figure 2 illustrates the typical invasion pathway through which non-native plant species enter, establish, and spread from urban environments into surrounding natural areas. The process begins with three major introduction pathways: the horticulture trade, global transport networks such as ports and airports, and the import of agricultural or forestry products. These pathways lead either to intentional planting in gardens and parks or to unintentional releases in disturbed spaces such as vacant lots and roadsides. Once introduced, plants establish themselves in the urban core-particularly in highly disturbed sites that provide open, resource-rich conditions favorable for colonization. From these initial footholds, the species undergo secondary spread facilitated by wind, water, wildlife movement, and human activities. This dispersal allows them to move from the urban center into peri-urban landscapes and eventually into natural ecosystems, where they may become invasive. Overall, the diagram highlights how urban areas function as both introduction hubs and stepping-stone environments for biological invasions.

5. The Nexus: Where Adaptation and Invasion Meet

The processes of adaptation and invasion are not independent; they are deeply intertwined in urban ecosystems. The very traits that enable a plant to survive the harsh, fragmented urban environment are often the same traits that define a successful invader.

5.1 Trait Overlap and Pre-adaptation

The "ideal" urban plant is often ruderal, stress-tolerant, plastic in its response to environment, and has efficient dispersal mechanisms. This suite of traits, sometimes described as the "global invasive syndrome," means that species pre-adapted to urban stresses are more likely to become successful invaders once they escape. For example, the ability to tolerate drought, poor soils, and pollution in a city park may equip a species to invade xeric, nutrient-poor habitats elsewhere. Conversely, many of the world's most invasive species thrive in urban areas precisely because they possess these pre-adapted traits [16].

5.2 Cities as Training Grounds and Launchpads

This creates a synergistic cycle:

- Filter: Urban environments filter for species with "weedy" and invasive traits from the global species pool introduced via horticulture.

- Accelerant: For non-native species that establish, the urban environment can act as a crucible for rapid adaptation, further honing their competitive abilities and environmental tolerances.

- Source: The now well-adapted and often abundant urban populations serve as a massive seed source for secondary invasion into adjacent peri-urban and natural ecosystems.

In this framework, cities are not just sinks for invasive species but are active generators and amplifiers of invasion risk.

5.3 Evolutionary Traps and Management Challenges

While adaptation can be beneficial for species persistence, it can also create "evolutionary traps." For example, a native plant that adapts to warmer urban temperatures by shifting its flowering phenology may become mismatched with its pollinators, which may not have shifted similarly. Furthermore, management actions can inadvertently select for more resilient weeds. Repeated mowing, for instance, selects for prostrate growth forms, and herbicide application can lead to the rapid evolution of herbicide resistance in urban weed populations. Understanding these evolutionary dynamics is critical for long-term management success [17].

6. Implications for Conservation and Urban Planning

The interplay between adaptation and invasion has profound implications for how we design, manage, and conserve urban ecosystems.

Native Biodiversity Conservation: Conservation efforts in urban areas must focus on preserving large, well-connected habitat patches to support viable populations of native species and mitigate the effects of fragmentation and invasion. Assisted migration or the use of locally adapted genotypes may be necessary to help native species keep pace with rapid urban warming.

Sustainable Urban Greening: There is a growing movement towards using native species in urban landscaping. However, this review suggests that simply using "natives" is not enough; we must consider the specific functional traits and genetic provenance of the plant material used. Using native genotypes pre-adapted to local urban stresses can increase planting success and reduce maintenance needs [18].

Biosecurity and Horticultural Regulation: Given the dominant role of the horticulture trade, a proactive approach is needed. This includes implementing "weed risk assessment" protocols for ornamental plants before they are introduced to the market, promoting the use of non-invasive alternatives, and educating gardeners and landscapers about the risks of invasive species.

Monitoring and Early Detection: Resources should be directed towards monitoring high-risk invasion hubs within cities, such as ports, botanical gardens, and major transportation corridors, for new introductions. Early detection and rapid response are the most cost-effective strategies for managing invasions.

A comprehensive understanding of urban plant adaptation and invasion pathways relies on a multi-faceted methodological approach. Recent advances have combined field observations with cutting-edge laboratory techniques and computational tools. Common garden experiments, for instance, are pivotal in disentangling genetic adaptation from phenotypic plasticity. By cultivating plants from urban and rural populations under controlled conditions, researchers can quantify heritable differences in traits such as flowering time, stress tolerance, and biomass allocation. Similarly, reciprocal transplant experiments, where individuals are swapped between urban and non-urban sites, can reveal local adaptation and the fitness consequences of specific traits in different environments.

Molecular tools, including genomics and transcriptomics, have opened new frontiers. Genome-wide association studies (GWAS) and RNA sequencing allow scientists to identify the specific genes and regulatory pathways underpinning adaptive traits like heavy metal tolerance or altered phenology. For invasion biology, DNA barcoding and population genetics are used to trace the origin of invasive populations and reconstruct their introduction history, revealing whether multiple introductions have contributed to genetic diversity and invasion success.

In terms of spatial analysis, remote sensing and Geographic Information Systems (GIS) are indispensable for mapping urban heat islands, habitat fragmentation, and the distribution of invasive species. Coupled with long-term ecological monitoring, these tools help establish correlations between urban intensity and specific floristic changes. Furthermore, trait-based models integrate functional traits-such as specific leaf area, seed mass, and plant height-to predict which species are likely to adapt to urban stresses or become invasive, moving the field towards a more predictive science.

Case Studies: Adaptation and Invasion in a Philippine Context

The unique biogeographic and socio-economic context of Southeast Asian cities, such as Manila and Cebu in the Philippines, provides compelling case studies. The intense urbanization, coupled with a tropical climate and high native biodiversity, creates a complex arena for plant adaptation and invasion. One notable example is the invasion of the American weed *Chromolaena odorata* (hagonoy) in peri-urban areas of Metro Manila. This species capitalizes on disturbed habitats along roadsides and abandoned lots, traits that are pre-adaptive to the urban environment. Its prolific seed production and allelopathic compounds allow it to outcompete native early successional species, demonstrating the invasion pathway from intentional introduction for soil stabilization to widespread escape and naturalization.

On the adaptation front, preliminary observations suggest that native species like *Mimosa pudica* (makahiya) exhibit significant phenotypic plasticity in Manila's urban parks. Individuals growing in compacted, heavily trampled soils show a more prostrate growth form and quicker leaf-folding response compared to their rural counterparts. Another potential case is the endemic *Pandanus tectorius* (pandan), which is increasingly confined to isolated urban forest fragments. Genetic studies could reveal whether these populations are experiencing reduced gene flow and are adapting to the specific microclimates of these fragments. The Philippine horticulture trade also introduces a steady stream of potentially invasive ornamentals, such as *Sansevieria trifasciata* (snake plant) and various *Dieffenbachia* cultivars, whose invasion potential in the local context remains understudied. These case studies underscore the need for region-specific research to inform local conservation and biosecurity measures.

7. Conclusion and Future Directions

Urban environments are dynamic theaters of ecological and evolutionary change. The stringent selective pressures of city life drive rapid adaptation in both native and non-native flora, while human activities create direct pathways for the introduction and spread of species from across the globe. The convergence of adaptation strategies and invasion pathways in urban areas creates a feedback loop that can accelerate biotic homogenization and increase invasion risk regionally.

Future research should focus on:

- Genomic Studies: Utilizing genomic tools to identify the genetic basis of urban adaptation and to distinguish between plastic and evolutionary responses.

- Trait-Based Frameworks: Developing a more predictive trait-based framework to identify which native species are most vulnerable to urban stresses and which non-native species pose the greatest invasion risk.

- Global Comparisons: Conducting coordinated, multi-city studies across different biogeographic regions to understand how climate, culture, and urban form influence adaptation and invasion pathways.

- Human Dimension: Integrating social science to understand the drivers of horticultural choices and public perception of native versus non-native plants.

By embracing the complexity of urban plant ecology, we can move beyond viewing cities as ecological wastelands and instead see them as living laboratories. The insights gained are critical not only for conserving biodiversity within our cities but also for mitigating the broader environmental impacts of urbanization on a global scale.

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