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Adaptation of alien plant species in future urban environments: Ecological and planning implications – a review

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ABSTRACT

As a result of intensive urbanization processes, many urban ecosystems have undergone significant functional, morphological, and structural transformations. The introduction of inert, biologically inactive materials has influenced the alteration of land use and the functions of urban landscapes, thereby affecting the immediate natural resources (water, air, and soil). The degree of adaptation of a given plant species depends on the survival rate of its individuals, as well as on their ability to reach physiological maturity and the reproductive phase of the life cycle. The adaptability of plant species to new habitats (particularly urban ones) represents an important ecological indicator, as it reflects both the potential for broader utilization and the species' relationship to native biodiversity. Urban ecosystems often encompass a considerable number of unmanaged (abandoned) and, from an ecological standpoint, impoverished habitats – urban fallows which are especially susceptible to biological invasions. Such urban areas are of great importance for monitoring the processes of adaptation and behavioural dynamics of individual plant species, especially those of alien origin, i.e., species introduced into urban environments through anthropogenic activity. It is well known that certain groups of plants (weedy, invasive, and others) possess a highly developed ability to occupy, colonize, and establish populations even within such specifically altered habitats. A systematic understanding of the mechanisms of adaptation and acclimatization of plant species in urban environments, particularly those introduced through human activity, along with an examination of their ecological impacts within urban ecosystems as dynamic systems constantly exposed to change, provides a foundational basis for ecological urban planning. The objective of this study is to highlight the complexity of relationships and interactions between the city, as a physical and inert system, and plants, as living and biological systems. The general systematization of knowledge about the mechanisms of adaptation and adjustment of plant species in urban environments, especially those introduced through anthropogenic activity, and the analysis of their impacts on urban ecosystems, which are dynamic and constantly changing, provides a foundation for the ecological planning of cities. This paper aims to highlight the complexity of the relationships and interactions between the city as a physical, inert system and plants as living, biological systems.

Keywords: urban flora, adaptability, adaptation, planning implications, urban ecology, landscape engineering.

CHARACTERISTICS OF URBAN ENVIRONMENTS

Urban environments represent habitats altered under the direct influence of anthropogenic factors (Dubois and Cheptou, 2017). In these environments, conditions differ substantially from those in which plants, animals, and other organisms naturally grow or develop, as they are characterized by specific biophysical features resulting from human activities (McCarthy et al., 2010; Breust, 2013). Changes in urban environments caused by human activities are primarily driven by alterations in surface cover, that is, by modifications resulting from various types of urban land use (Figure 1), which in turn affect the exchange of matter and energy within such distinctive ecosystems (Gill et al., 2007).

Figure 1. Landscape transformations induced by urbanization (Borča-Greda, Belgrade)

Compared to natural ecosystems, urban ecosystems are distinctive systems characterized by multiple stress conditions arising from intense urbanization processes and a complex set of functional, morphological, and structural environmental changes (Antrop, 2004). Urbanization largely transforms natural ecosystems by replacing vegetation with anthropogenic, inert, and biologically inactive materials, such as concrete, asphalt, and glass, and with built structures that cover and penetrate the urban soil surface (Breuste, 2013). As these transformations affect fundamental natural resources such as water, air, and soil, human interventions through diverse land uses and temporal changes in land modification create conditions for the formation of unique urban ecosystems.

Urban environments should therefore be viewed as multidimensional and highly variable systems (Alberti et al., 2003).

ABIOTIC–PLANT ADAPTATION INTERACTIONS IN URBAN ENVIRONMENTS

Urban environments represent a unique set of abiotic conditions that strongly influence the survival, growth, and reproduction of urban plants. Factors such as elevated temperatures and reduced air humidity, altered light regimes, soil compaction and alkalization, changes in water availability in urban soils, as well as increased air pollution create a complex and highly dynamic selective environment that affects the survival and adaptability of urban plants. However, the interaction between abiotic factors and plant adaptive responses is often reciprocal: while abiotic factors influence modifications of the physiological, morphological, and reproductive characteristics of plants, the presence (particularly when dominant) and performance of urban plants can, in turn, modify urban environmental conditions. Understanding these interactions is essential for predicting which plant species will successfully adapt to environmental conditions in cities.

One of the most characteristic abiotic factors in cities is the urban heat island effect, i.e., the phenomenon whereby urban areas exhibit higher air and soil temperatures than their surrounding environments (Godefroid and Koedam, 2007; Buyantuyev and Wu, 2010; Jochner and Menzel, 2015; Cai et al., 2023).

Air temperatures in urban areas are typically several degrees higher than in surrounding rural zones, a pattern observed in most cities worldwide and throughout the year (Oke, 1973; Walker et al., 2015; Zipper et al., 2016). The heat island effect further influences other ecological factors, including hydrological characteristics (Breust, 2013), and the properties of urban soils (Schmid and Niyogi, 2013). Its intensity varies among cities and correlates positively with urban size (Imhoff et al., 2010; Clinton and Gong, 2013). Moreover, urban heat island intensity is affected by the physical characteristics of the urban landscape (topography, hydrology, and morphology) and climatic factors (wind speed, cloud cover, etc.) (Lou et al., 2007). Oke et al. (1991) demonstrated that urban geometry can exacerbate microclimatic stress by reducing surface cooling due to built-up density and by increasing long-wave radiation absorption from adjacent structures. High spatial fragmentation of the urban matrix also alters microhabitat conditions (Dubois and Cheptou, 2017); impermeable surfaces absorb more solar radiation compared to vegetated areas (Avissar, 1996).

In general, the formation of the urban heat island is influenced by the physical characteristics of cities, among which the most important are anthropogenic heat sources, the dominant presence of impervious surfaces, and the lack of green spaces (Brown et al., 2015).

The development of the urban heat island is particularly affected by the reduction of urban green spaces, as this decreases the intensity of evapotranspiration, an important mechanism for cooling the urban environment. In contrast, urban vegetation can mitigate urban heat through shading and water evaporation, thereby improving local microclimatic conditions (Bowler et al., 2010; Gill et al., 2007). Urban plants and green spaces create an oasis effect and reduce the warming of urban areas at both macro- and micro-scales (Chen and Wong, 2006). They act as corrective factors, cooling agents, and regulators of air temperature and humidity, and are therefore important for improving ecological conditions in cities (Givoni and La Roche, 2000; Stojanović et al., 2018).

Air temperature near green spaces may be lower by 2–8 °C (Taha et al., 1991), as plant leaves prevent solar radiation from reaching the ground. Due to the temperature differences between green spaces and their surroundings, air circulation occurs during warm summer days from green spaces toward built-up parts of the city, which contributes to the mitigation of high air temperatures (Bunuševac, 1962; Stojanović et al., 2018). Bernatzky (1989) determined in Frankfurt that smaller green spaces can reduce air temperature by 3–3.5 °C and increase relative air humidity by 5–10%.

Urban heat islands are also characterized by a greater presence of air pollutants, which, due to increased temperatures, tend to circulate and subsequently accumulate in the immediate surroundings. It has been established that the concentration of pollutants in urban air is approximately ten times higher than in the air outside the urban fabric (Taha, 1997). Air quality in cities is directly influenced by anthropogenic emissions, including suspended particles, nitrogen oxides, and ozone, which can cause physiological stress in plants. However, their impact can be partially mitigated by the establishment of urban vegetation, which has the capacity to filter pollutants from the air (Nowak et al., 2006).

Although anthropogenic impacts on urban soils may appear spatially limited, they represent a critical component of the overall urban environmental influence. The anthropogenic modification of soils should be understood as an integral aspect of human activity, as every intervention provokes an environmental response. Consequently, actions aimed at achieving specific goals often generate both intended and unintended, sometimes negative, outcomes (Anastasijević, 2011). A comprehensive understanding of urban plant requirements must therefore include an assessment of the soil's physical and chemical properties, as well as its volume, factors particularly vital for trees that must persist in urban soils for extended periods (Trowbridge and Bassuk, 2004). Urban soils serve multiple functions: they provide a medium for plant growth and development, a foundation for construction, and a recipient for water and pollutants (Bullock and Gregory, 1991). These soils differ in their physical, chemical, and biological characteristics, which are substantially modified by landscape disturbances associated with urban infrastructure development (Scharenbroch et al., 2005). Soils influenced by anthropogenic factors differ from natural soils primarily in the surface layer, which is altered, compacted, filled, or contaminated by human activity (Craul, 1992).

Urban soils are often highly degraded and are characterized by increased alkalinity due to the presence of construction materials, reduced organic matter content, compaction, and elevated concentrations of heavy metals and other potentially toxic elements (Craul, 1992; Pouyat et al., 2010).

The covering of urban soils with inert materials leads to reduced water infiltration and changes in the size and nature of soil porosity (Scalenghe and Marsen, 2009). Mechanical loads on soil surfaces also influence the structure of urban soils by altering their water-holding capacity. Studies by various authors (Craul and Klein, 1980; Vratuša, 1986; Jim, 1998; Vratuša, 1999a) have shown that urban soils tend to exhibit soil reactions somewhat different from those of natural soils. In most cases, pH values are higher in urban environments, meaning that soils with alkaline reactions generally predominate.

The increased pH values of urban soils are largely a consequence of the presence of carbonate anthropogenic materials such as cement, mortar, concrete, and various types of bricks (Howard, 2017). Research by Vodyanitskii (2015) indicates that urban soils experience disturbances in matter cycling, including nutrient cycles typical of soils in natural systems. Studies also show that organic matter in urban soils differs in nature compared to that in natural soils, and that in urban environments it undergoes changes both in quantity and composition (Beyer et al., 2001).

Pouyat et al. (2002) emphasize that the type of urban land use directly and/or indirectly affects the content of C and N, resulting in altered total organic C and N levels compared to soils in natural systems. Urban soils generally act as continuous recipients of harmful elements and other pollutants. Wei and Yang (2010) and Karim et al. (2014) note that pollutants in urban environments originate from a wide range of sources, including industrial activity, coal and fuel combustion, vehicle emissions, municipal waste disposal, and others.

Woszczyk et al. (2018) points out that urban soils are particularly susceptible to acute contamination by various substances, with heavy metals being the most commonly present (i.e., elements with concentrations below 100 mg/kg). The accumulation of heavy metals in the surface layers of urban soils and their transformation into chemically active and mobile forms poses a significant risk to the urban environment, as they can reach groundwater and, consequently, enter food chains (Abrahams, 2002; Godt et al., 2006).

Many heavy metals, such as Fe, Zn, and Cu, belong to the group of microelements that play an important role in plant metabolism. However, at high concentrations, these elements are phytotoxic, while metals such as Cd, Pb, and others do not participate in physiological processes in plants, yet they are absorbed through roots and accumulate in plant tissues (Sharma and Dubey, 2005; Samuilov et al., 2016).

Urban green spaces have a particularly positive effect on the absorption and retention of various particles of potentially toxic elements, which are most commonly produced by intense urban traffic and industrial activity. Green spaces trap pollutant particles on leaves and plant tissues, as well as in the soil beneath the plants. Soils of green areas act as specific refugia for the absorption and deposition of harmful substances (dust, soot particles, heavy metals, etc.) (Vratuša, 2001; Trowbridge and Bassuk, 2004). As a result of these influences, the physical and chemical properties, structure, quality, fertility, and other characteristics of soils in urban green spaces are altered. A particularly important ecological contribution to the preservation of urban soils comes from green areas that are largely covered by urban vegetation, such as city parks or urban forests. Higher vegetation cover provides a larger surface for pollutant adsorption and, at the same time, greater potential for positive effects on the soil itself (more plant biomass, shading of the soil surface, creation of favorable microclimatic conditions that support soil processes, etc.) (Vratuša and Anastasijević, 2002).

Due to different land uses in cities, the existing terrain is altered, which in turn affects the patterns of stormwater runoff in terms of speed, volume, and flow direction (Katsifarakis et al., 2015). Furthermore, urban hydrological systems are modified by large areas covered with impervious materials, leading to increased surface runoff and reduced natural water infiltration (Walsh et al., 2005).

These changes in stormwater drainage can have several environmental consequences, the most significant of which are ecological: the occurrence of flooding, a decrease in groundwater levels caused by reduced infiltration of precipitation, increased soil erosion due to higher volumes and velocities of runoff, and elevated contamination of groundwater and soils. This is because stormwater carries a large portion of pollutants, including salts, sand, waste, particulate matter, and various contaminants from vehicle exhausts and dust.

Until recently, the problem of excess water on land surfaces was addressed by removing it and transporting it (via sewer systems, channels, etc.) to the nearest water body, without considering the impact of these discharged waters on the new environment. This practice had a cumulative effect on the environment and generally on water quality.

More recent stormwater management practices have recognized the need to regulate excess water primarily at its source (Dunnett and Clayden, 2007). Retention, storage, and infiltration of stormwater at the site of origin are made possible by the presence of urban green spaces and plantings (bioretention systems), as they act as natural porous infiltration systems and help minimize hydrological problems by preserving and maintaining previous stormwater drainage patterns (Echols and Pennypacker, 2015).

All these changes in the urban environment create selective pressures favoring plant species with high ecological tolerance, phenotypic plasticity, and strong colonization potential.

Consequently, many allochthonous and invasive plant species are particularly successful in urban environments, where disturbed habitats and altered ecological conditions provide favorable opportunities for their establishment and spread.

THE INFLUENCE OF URBAN ENVIRONMENT ON CITY PLANTS

In comparison with natural ecosystems, urban ecosystems are characterized by a distinct biodiversity of plants, animals, and other organisms (Francis and Chadwick, 2015). High species diversity in urban ecosystems is often supported by the intentional creation of artificial habitats such as parks, gardens, and green corridors. This diversification has been further shaped by the extensive introduction of alien species into urban environments through human activity (Pyšek 1998; Niemelä 1999; Lososova et al., 2012; Dubois and Cheptou, 2017; Štajerová et al., 2017). Despite the high species diversity, urban ecosystems are environments dominated by conditions that can be described as stressful (most often expressed through stresses caused by extreme temperature fluctuations, low soil moisture, and significant air and soil pollution). These conditions differ substantially from those under which such plants naturally grow and develop. The harmful effects of urban environments on woody plants are particularly pronounced when the stress is both intense and short-term. However, certain stressful influences of urban environments can also have positive effects, as they stimulate adaptive responses in plants, such as increased tolerance to drought, flooding, heat, and pollution (Kozlowski and Pallardy, 2002; Borden and Flory, 2021). For instance, the phenomenon of the urban heat island, while extremely stressful for plants during periods of high temperature, may be beneficial during colder months, as it can extend the vegetation period or accelerate physiological processes in urban plants (Mimet et al., 2009; Calfapietra et al., 2015). Since every plant species existing within an urban setting is exposed to stress, plant selection for urban planting should always consider the species' existing level of adaptation to the prevailing environmental conditions.

To understand how species respond to these stresses, it is necessary to clarify the concept of adaptation. Adaptation is a concept related to how plants survive and reproduce under specific environmental conditions (Hill et al., 1998), which is reflected in the synchronization between their developmental phases (phenophases) and the ecological characteristics of a given habitat (Aslamarz et al., 2009). However, this definition does not fully encompass the complexity of the term. Over the years, many authors have addressed adaptation and adaptability (Dietrichson, 1964; Tigerstedt, 1994; Solecki et al., 2011; Futuyma, 2009), therefore, two concepts are recognized in the literature: Adaptation and Adaptability (McDonnell and Hahs, 2015). These terms are often interpreted as synonyms; however, when their definitions are examined, clear distinctions can be observed. The term Adaptation is defined as a genetic change, that is, as an evolutionary process driven by natural selection (Hill et al., 1998; Futuyma, 2009 Futuyma and Kirkpatrick, 2017), while Adaptability refers to the ability of an organism to respond to changing environmental conditions. Adaptability can be considered at both the population and individual level. At the individual level, it refers to organisms whose physiology enables them to withstand a range of environmental conditions. At the population level, it represents the ability to respond genetically to environmental changes, which is only possible if there is sufficient variability within the population to cope with such changes (Hill et al., 1998).

In general, all organisms are adapted to specific environments; however, the challenge lies in determining the degree of their adaptation (i.e., adaptability). The main criteria for assessing individual adaptedness include survival ability, attainment of physiological maturity, and the capacity to reproduce during the life cycle (Hill et al., 1998). When discussing the adaptability of individual plants to urban environments, it should be understood that this refers not only to adaptation to ambient conditions, but also to their capacity to tolerate the stressors prevailing within them. A plant individual can be considered highly adapted to urban environmental conditions if comparative analyses of its morphometric characteristics and phenological phases (in relation to local climatic conditions) reveal similarities to those achieved in its natural habitats.

While evaluating native species' adaptability is essential, urban ecosystems also contain many alien species whose behaviour and impacts must be assessed. The degree of adaptability of certain plant species to urban environments indicates their potential for broader use in urban planting.

However, since urban areas are environments with a high rate of alien species introduction, understanding the behaviour of such species (not only their adaptability) is equally important, as they may also exert negative impacts on the environments into which they are introduced (Richardson et al., 2000). An alien species is defined as a species introduced into a new environment from a biogeographical region outside its natural range (Pyšek and Richardson, 2008).

ALIEN URBAN PLANTS SPECIES

The classification of alien flora can be based on several criteria, including the period of their introduction, the pathways or mechanisms by which species were introduced, and their degree of naturalization and integration into the local flora.

Alien species are those that do not occur naturally in a specific area but appear there as a result of introduction from outside their native range, whether the introduction happens intentionally or accidentally through human activity. In Central Europe, alien species are traditionally classified into two groups: archaeophytes and neophytes. Archaeophytes are species that were introduced before 1500, regardless of whether the introduction was intentional or accidental, and irrespective of their potential invasiveness. Neophytes are species that were introduced after that period (Richardson et al., 2000; Pyšek et al., 2002; Pyšek et al., 2004; Ordonez et al., 2010). A plant species introduced to a new area typically undergoes a series of stages (Figure 2), which can be defined as follows: 1. Native species – a taxon existing in its natural habitat prior to any human-mediated transportation; 2. Alien (non-native) plant species – a species that has been introduced or transferred to a new area as a result of human activity, regardless of whether the introduction was intentional or accidental; 3. Casual alien species – a species capable of generative and/or vegetative reproduction but unable to maintain a population over an extended period; its continued presence depends on repeated introductions; 4. Naturalized species – a species that has succeeded in forming self-sustaining populations without direct human intervention; 5. Invasive species – a species that has successfully adapted (acclimatized) to environmental conditions in the newly occupied area, is capable of producing fertile offspring (naturalization), and occurs in large numbers over extensive distances from the original plant. Such species possess the ability to spread widely across large areas (invasion) (Richardson et al., 2000; Pyšek et al., 2004; Lambdon et al., 2008; Јарић, 2009; Pyšek and Richardson, 2008; Ureta, 2011).

Alien plant species are introduced into new environments for a variety of reasons, with the most significant being botanical, aesthetic, and economic purposes (Jovanović, 1950; Petrović 1951). Across Europe, it is estimated that approximately 62.8% of alien taxa were deliberately introduced, primarily for applications in landscape architecture, horticulture, forestry, and agriculture (Keller et al., 2011). Hu et al., (2023) emphasize that urban parks serve as key areas for the introduction of ornamental alien plant species.

Most non-native species in Europe originate from North America and Asia (Weber, 1997). Species diversity within a single square kilometre of a city can be remarkably high, making urban areas attractive for ecological and biodiversity research (Kinzing et al., 2005; Douglas, 2012; Štajerová

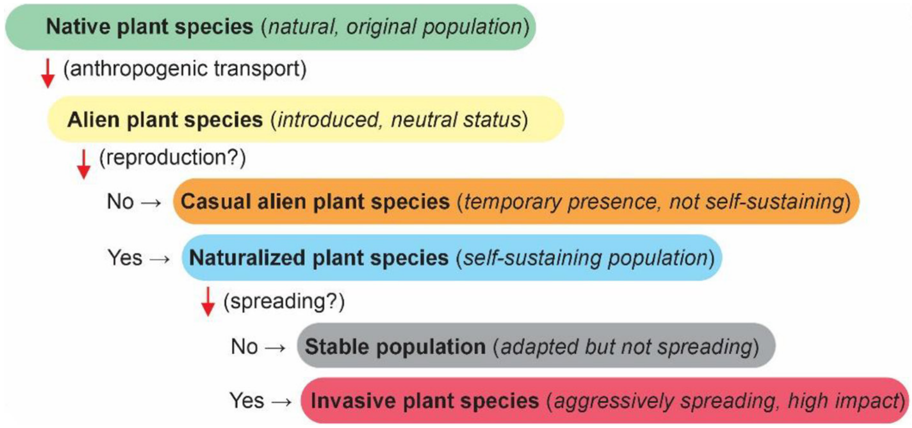

Figure 2. Invasion pathway of alien plant species

et al., 2017). Since their founding, cities have received large numbers of tree and shrub taxa from other regions and continents (Jovanović, 1950; Pyšek, 1998; Roy et al., 1999; Kühn and Koltz, 2006; Pyšek et al., 2010). In Central European cities, exotic species account for approximately 40% of the total urban flora, with neophytes representing 25% of this total (Lososová et al., 2012).

Alien species in a novel environment may adapt to the prevailing conditions and develop normally in the new habitat, or they may become naturalized species, establishing self-sustaining populations without further spread. In some cases, they may become invasive, dispersing spontaneously over extensive areas (Richardson et al., 2000; Pyšek and Richardson, 2008). The introduction of alien taxa into urban ecosystems should not rely solely on their ornamental or economic value. Insufficient knowledge of their behavior in new environments may lead to undesired ecological consequences. Decisions regarding the use of alien species should be informed by the age of individual specimens, growth habit, development, reproductive capacity, regeneration potential, and experiences from other regions (Jovanović, 1950). Richardson et al. (2000) note that only a small proportion of alien species reproduce and spread beyond the sites into which they were introduced. In some cases, alien species adapt so successfully that they perform better in the introduced habitat than in their native range. Charles S. Elton (1958) was among the first to highlight the consequences of introducing alien taxa into new environments in his seminal work „The Ecology of Invasions by Animals and Plants", emphasizing the risks associated with insufficient knowledge of introduced species (Pyšek and Hulme, 2011; Simberloff, 2011; Kitching, 2011). The lack of comprehensive data on the ecological adaptability and impacts of alien species (Pyšek and Richardson, 2008) underscores the importance of their study in urban environments. Urban ecosystems are especially vulnerable to biological invasions because they are highly disturbed and have experienced significant environmental alteration (Davis et al., 2000; Chocholoušková and Pyšek, 2003; Celesti-Grapow et al., 2006; Chytrý et al., 2008; Lososová et al., 2012; Glišić et al., 2014). Alongside cultivated green spaces, cities contain unmanaged areas that represent impoverished habitats, characterized by limited light, water, and mineral availability ets. (Maskell et al., 2006; Botham et al., 2009; Štajerová et al., 2017). Urban green spaces are highly exposed to propagules from alien species (Figure 3) that grow both in landscaped and unmanaged areas, as well as from propagules of weeds (Montaldi et al., 2024). Over time, some of these species may spread from cultivated areas into unmanaged urban plots and even natural environments (Pyšek, 1998; Arson et al., 2007; Loram et al., 2008; Hanspach et al., 2008; Lososová et al., 2012; Štajerová et al., 2017).

The most significant adverse effect of alien plant species in a new environment lies in their invasive potential (Mengistu, et al., 2025). The invasiveness of alien plant species is defined as their ability to: be transported to a new environment, adapt to the new environmental conditions (acclimatize), reproduce successfully and produce viable offspring, and spread over large distances from parent plants, occupying substantial areas. The invasive potential of alien plant species is considered a major threat to global biodiversity.

Figure 3. Seedling of *Ailanthus altissima* (Mill.) Swingle (Fam. *Simaroubaceae*) along the Sava Promenade, New Belgrade (Belgrade)

According to the European program that serves as a database for research on invasive alien species in Europe (DAISIE, 2025), only a small number of countries have officially designated alien plant species as invasive, while in many others, the status of alien invasive plants has not yet been determined. Understanding the behavior of alien plant species in new environments is particularly important in urban areas, as cities are regarded as primary points of introduction and dispersion for many alien, especially invasive, plant species.

The spread of invasive alien species is a process strongly influenced by human activity, since the main pathways of their expansion are those created by humans such as roads, highways, railways, and other transport corridors (Figure 4) (Gelbard and Belnap, 2003; Arson et al., 2007; Villa et al., 2007; Kalusová et al. 2013; Sołtysiak and Brej, 2014; Padayachee et al., 2017; Stojanović et al., 2017b; Štajerová et al., 2017). Studies conducted in Belgrade confirm these patterns. For example, a survey of 38 green spaces along 15 main city roads recorded 15 invasive or potentially invasive woody species, including *Acer negundo* L., *Ailanthus altissima* (Mill.) Swingle, *Amorpha fruticosa* L., *Robinia pseudoacacia* L., *Ulmus pumila* L. etc. (Stojanović et al., 2017b). Interestingly, fewer invasive species were found along roads passing through highly urbanized central zones, whereas a greater number occurred along roads in less urbanized or park-managed areas.

In another study of 43 streets in central Belgrade, a total of 4.883 trees were recorded. Non-invasive species accounted for 4.830 individuals (98.9%), while invasive or potentially invasive species numbered only 53 individuals (1.1%) (Mešiček et al., 2014). The share of invasive and potentially invasive tree species within the street tree populations of central Belgrade is very small and can be considered almost negligible. Nevertheless, because these species occur in more than one-third of the surveyed streets with street trees (14 out of 43), their regular monitoring and control remain necessary. Additionally, this study recorded 28 different tree taxa, of which 5 belong to the group of invasive and potentially invasive species, accounting for 17.86% of the total number of taxa recorded in central Belgrade. Among the invasive and potentially invasive tree species, the most prevalent is *Quercus borealis* Michx., *Robinia pseudoacacia* L., *Ailanthus altissima* (Mill.) Sw. etc. Eight years later Lisica et al. (2024) conducted a survey in Belgrade's oldest municipality, Stari Grad, identified 16 tree taxa, of which one species, according to the list of invasive species of the Republic of Serbia, is classified as invasive, *Ailanthus altissima* (Mill.) Swingle, representing 12.5% of the total recorded taxa.

For this reason, as many studies show that cities represent significant areas with notable presence of alien invasive species, the European Union established the European Alien Species Information Network (EASIN, 2025) as an initiative of the Joint Research Centre of the European Commission. The goal is to provide easy access to information on alien species in Europe. EASIN functions as a service based on geographic data provided by partners such as the Global Biodiversity Information Facility, the Global Invasive Species Information Network, the Regional Euro-Asian Biological Invasions Centre, and others. In addition to this information network, numerous conventions and programs aim to protect biodiversity (e.g., Convention on Biological Diversity, Global Invasive Species Programme, European Network on Invasive Alien Species Gateway, Invasive Alien Species in North and Central Europe). Despite considerable scientific effort worldwide, knowledge regarding the ecological adaptability of alien species in Europe remains

Figure 4. Presence of invasive plants along major urban roads: a) *Ailanthus altissima* (Mill.) Swingle (Fam. *Simaroubaceae*) spontaneously colonizing the protective belt along the E-75 highway (Belgrade); b) *Gleditsia triacanthos* L. (Fam. *Fabaceae*) planted as part of the green belt along Zrenjaninski Road (Belgrade); c) *Robinia pseudoacacia* L. (Fam. *Fabaceae*) naturally occurring and later cultivated as part of the urban roadside greenery (Belgrade)

incomplete (Pyšek, 2003; Lambdon et al., 2008; Pyšek and Richardson, 2008).

In urban environments, alien plant species are mostly studied in the context of their phenology and response to global climate change (Abu-Asab et al., 2001; Ahas et al., 2002; Donnelly et al., 2006; Menzel et al., 2006; Luo et al., 2007; Dunnell and Travers, 2011; Keller and Shea, 2021). Particular attention is given to alien species that have already shown invasive tendencies or have the potential to do so (Davis et al., 2000; Pyšek et al., 2002; Chocholoušková and Pyšek, 2003; Pyšek et al., 2004; Celesti-Grapow et al., 2006; Lambdon et al., 2008; Jarić, 2009; Ordonez et al., 2010; Simberloff, 2011; Kitching, 2011; Pyšek and Hulme, 2011; Lososová et al., 2012; Glišić et al., 2014; Štajerová et al., 2017).

Studying the naturalization of alien species is important because all naturalized species have the potential to become invasive. The process of naturalization, however, varies across different habitat types. Although most invasive plant species worldwide maintain naturalized populations in the regions where they occur, they become invasive in only a limited number of those regions (Richardson and Pyšek, 2012).

The biological invasiveness of alien species represents a global environmental change driven by anthropogenic factors. Such changes lead to the loss of economic value of habitats, biodiversity, and ecosystem functioning due to the spread of invasive species (Mack et al., 2005; Pimentel et al., 2000, Hulme, 2003; Weber, 1997; Richardson and Pyšek, 2006; Lambdon et al., 2008; Mešiček et al., 2016). According to Richardson et al. (2000), Pyšek (2003), Lambdon et al. (2008), and Јарић (2009) successful invasion of a habitat by an alien species is determined by the interactions among the plant (its ecological characteristics, successful germination, growth, and reproduction), environmental conditions (soil moisture, nutrients, space), and the degree of ecosystem disturbance into which the species is introduced.

THE SIGNIFICANCE OF URBAN PLANTS IN THE CITY OF THE FUTURE

In response to global changes, ecological principles are increasingly incorporated in urban planning and adaptation, focusing primarily on climate change and intensive urbanization (Stojanović, 2017a). One method to mitigate urban heat islands is the use of green infrastructure in city planning. Urban greenery serves multiple functions: modifying air temperature and humidity, reducing the impact of urban heat islands through evapotranspiration, and absorbing heat while emitting radiation more slowly than surrounding built surfaces (Chen and Wong, 2006; Chang et al., 2007; Zoulia et al., 2009; Stojanović et al., 2018b; Kecman et al., 2025). Therefore, increasing urban green space, particularly in densely built urban cores, is considered an important adaptive response, especially to climate change.

On the other hand, Kozlowski and Pallardy (2002) emphasize that some harmful effects of the urban environment can also have positive impacts on plants. For example, a gradual increase in stress factors (such as drought, elevated air temperatures, etc.) can lead to physiological adaptation in plants, in contrast to the sudden and intense exposure to such stress.

Exposure of plants, especially woody species, to extreme environmental conditions during critical developmental stages often affects their growth. Adaptive responses include tolerance to drought, flooding, heat, pollution, and other stressors. Calfapietra et al. (2015) argue that urban plants should be considered not merely as entities passively enduring environmental stress, but as dynamic participants in urban ecosystems that actively influence their surrounding conditions. For better adaptability of alien species in urban environments, plant selection for urban greening should consider traits favoring adaptation to novel conditions, such as: functional period, growth rate, tree height, trunk height free of branches, crown width, crown shape and structure, transplanting capability, low leaf mass, disease and pest resistance, ornamental value, and overall adaptability (Trowbridge and Bassuk, 2004, Harris et al., 2004).

Thus, adaptation can be interpreted as a mechanism for survival and reproduction in specific environments (Hill et al., 1998; Aslamarz et al., 2009). These mechanisms manifest through the synchronization of plant developmental phases (phenophases) with local climatic conditions (Dietrichson, 1964; Aslamarz et al., 2009; Keller and Shea, 2021). Studying the phenology and reproductive traits of individuals provides data on species' adaptability to urban conditions. Historical records of species introduction and current presence in green spaces also provide insight into the adaptability and behavior of alien species in new environments.

Existing experience highlights the importance of having data on the adaptability of alien species to prevailing environmental conditions. Many species introduced to new habitats were not initially assumed to adapt successfully or spread beyond planted areas. Invasiveness is often identified only after species have expanded in new environments. Therefore, understanding plant species before their introduction or extensive use represents sound planning and management practice. To reduce the risk of alien plant invasions, contemporary research focuses on pre-introduction risk assessment, precise identification, and preventive control of potentially invasive species (Verbrugge et al., 2019).

Another perspective on alien species in urban environments, particularly relevant for future urban greening, emphasizes that urban ecosystems are increasingly affected by global challenges (climate change, extreme temperatures, prolonged droughts, floods, overpopulation). The origin of urban greenery, native or non-native, becomes secondary compared to its ecological and societal benefits. Many urban residents value the presence of green spaces, regardless of whether they are native, planted, or non-native. Greenery improves ecological conditions, offers psychological, health, aesthetic, cultural, and social benefits (Smardon, 1988; Vratuša and Anastasijević, 1999; Fuller et al., 2007; Chen etal., 2009; Georgi and Dimitriou, 2010; Gidlöf-Gunnarsson and Öhrström, 2011; Anastasijević et al., 2015; Stojanović et al., 2018a), and provides recreational opportunities, it is important to recognize the entire spectrum of services that urban greenery provide (Figure 5) (Niemelä et al., 2011). For example, Del Tredici (2010) notes that cosmopolitan assemblages of spontaneous plants in most urban areas provide essential ecosystem services, which are likely to become increasingly important under projected climate change (Figure 6). Spontaneous vegetation, uncultivated or unplanned plants growing in vacant lots, sidewalks, brick walls, and other urban habitats, is often overlooked (Ilie and Cosmulescu, 2023).

Managing spontaneous urban vegetation to enhance its ecological and social value can be a more sustainable strategy than attempting to restore historical pre-urban ecosystems. Such vegetation can achieve many of ecological goals of traditional restoration with lower costs and higher likelihood of long-term success (Choi 2004; Sagoff, 2005). However, the influence of urban environments on the occurrence patterns and composition of spontaneous plants remains insufficiently understood (Chen and Wang, 2025), making it necessary to consider the entire biological resource of cities, including ruderal areas, which can significantly contribute to urban ecological functionality (Del Tredici, 2010).

To suppress the presence of invasive plant species in urban areas, it is considered good practice that parts of the city directly affected by invasive plants, as well as zones where their spread is anticipated, should be planted with ecologically suitable species, primarily native ones, since these are already adapted to specific environmental conditions, often grow almost spontaneously,

Figure 5. Aesthetic value of the planted diversity of native and non-native plant species along highway E-75, Belgrad

Figure 6. Spontaneous flora along Belgrade roadways as a basis for selecting sustainable urban plant populations

and are easy to plant, cultivate, and maintain in a functional state. If existing vegetation is present in the affected area, its floristic composition and bioindicator species should be analyzed in order to provide recommendations for the introduction of new species. The analysis of existing plant species can offer a clearer and more precise understanding of the prevailing environmental conditions in a given area (Stojanović et al., 2011). Native plant species are undoubtedly the most important component of the local natural ecosystem. Furthermore, it is necessary to develop cities and settlements that are adapted to biodiversity, cities that enable the adaptation of all living organisms not only through the provision of essential resources and suitable living conditions, but also through the creation of favorable environments in which diverse species can adjust to both the acute and chronic challenges imposed by urban settings (McDonnell and Hahs, 2015).

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