

Ecological and biological determination of invasion success of non-native plant species in urban woodlands with special regard to short-lived monocarps

Marina Golivets

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Abstract Today's urban green space is exposed to a constant flow of newly introduced exotic plant species, resulting from multiple, intentional and inadvertent introductions. A substantial share of introduced plant species are represented by potential invaders of plant communities, which allows considering that the risk of rapid dispersion by aggressive plant species to be today's most serious threat to the urban biodiversity. Alien plant species with a short life span (monocarps, therophytes, annuals and biennials) are the most successful invaders across anthropogenically transformed landscapes. These species can have a significant impact on the functioning of previously disturbed ecosystems. At the same time, it is still unclear which mechanisms enable short-lived monocarps to invade under specific conditions of urban forest interiors. Therefore, I have conducted a literature analysis aiming at identifying possible biological and ecological determinants of monocarpic plants' invasive success in urban woodlands. The analysis was made at three qualitative levels taking into account characteristics of the urban environment, those of different types of urban woodlands as well as traits of non-native monocarpic species. Considering the city level, the main ecological factors are the high level of human-induced disturbance and propagule pressure on the urban-woodland interface sites. The level of invasion as well as invasibility of urban woodlands is mainly determined by the landscape context, whereas the habitat type, species composition and spatial structure play a less important role. In the forest environment, where competition for light and nutrients is the main shaping factor of the phytocoenosis, short-lived alien species must possess a certain level of competitive ability. These findings indicate that this ability may be due to such traits as high fecundity rates, effective dispersal mechanisms, early germination, high rate of growth and the overall big size of plants, presence of autonomous pollination and high shade-tolerance.

Keywords Urban woodlands · Invasive plant species · Invasion rate · Invasion success · Disturbance · Short-lived monocarps

M. Golivets (✉)

Megapolis Ecomonitoring and Biodiversity Research Centre, National Academy of Sciences of Ukraine,
Lebedeva str., 37, Kyiv 03143, Ukraine
e-mail: marina.golivets@gmail.com

Introduction

Urban woodlands present a range of habitats of different ecological quality and social value. Being the only refuge for many indigenous plant species, these areas are extremely important for maintenance of biodiversity in highly anthropogenically transformed environments (Alvey 2006). Unfortunately, disturbance caused by human activities have already resulted in suboptimal levels of habitat quantity and quality within most urban woodland patches (Honnay et al. 1999). The biological diversity of urban forest typically suffers from habitat fragmentation, recreational pressure and introduction of exotic species, which jointly contribute to the loss of native taxa and the overall alteration of ecosystem functioning.

Apart from land-use change and fragmentation, caused by development pressures, the most serious threat to urban biodiversity is the introduction of potentially invasive plant species. Plant invasion is a self-perpetuating and irreversible process, which may affect plant communities in various ways, from direct competition between native and alien species for nutrients, light, water and mutualists to changes in geochemical cycles and successional development. Urban green areas are exposed to the constant flow of newly introduced exotic plant species, resulting from systematic intentional and inadvertent introductions. It has been documented that forest patches embedded in the urban landscape have a significantly higher proportion of alien plant species than fragments located in forested or agricultural landscapes (Duguay et al. 2007).

Alien plant species with a short life span (monocarps, therophytes, annuals and biennials) are the most successful invaders across anthropogenically transformed habitats. Likewise, short-lived monocarpic plants are effectively associated with urban woodlands, while in rural woodlands, polycarpic species are mainly represented (Vallet et al. 2010). Their invasive success is usually related to high relative growth rate, short generation time and abundant seed production as those being mainly early-successional, disturbance-preadapted species (Rejmánek and Richardson 1996). At the same time, most annuals are poor competitors and have no adaptations for shade tolerance, and thus cannot reproduce effectively under tree canopy. Consequently, their penetration into the forest ecosystem is mainly restricted to edges (Honnay et al. 2002; Dobravolskaitė and Gudžinskas 2011). These general considerations are probably the main reason behind a poor research interest in the specific group of short-lived monocarpic woodland invaders. However, regardless of the general pattern, there is a growing number of non-native monocarps, which have become highly abundant in the herb layer of both intensively disturbed woodlands and relatively untouched natural ones (e.g., *Impatiens parviflora* DC. in Europe; *Alliaria petiolata* (M. Bieb.) Cavara & Grande and *Microstegium vimineum* (Trin.) A. Camus in North America). Moreover, research has empirically demonstrated that these species can have a significant impact on ecosystem functioning after the disturbance had occurred, thus being classified as “back-seat drivers” of ecosystem change (Stinson et al. 2006; Bauer 2012).

Today, it is still unclear which mechanisms enable plant species with a short life cycle to become established and effectively spread under specific conditions of forest interiors. In this vain, the current review aims at finding possible explanations of invasion success of alien monocarps in urban woodlands. Specifically, this review aims to address the following questions: 1) what are the main ecological determinants of invasion success of non-native short-lived plants along the nature-urban gradient; 2) which ecological factors determine the level of invasion and invasibility of urban woodlands by alien monocarpic species across different spatial scales; 3) whether there is a set of specific ecological and biological traits among non-native short-lived herbaceous species responsible for their invasions into woodlands.

Following the tradition of plant invasion ecology, the review incorporates research findings on adaptive strategies of exotic species with a short life cycle as well as those on invasibility of urban woodlands as the target habitats of invaders. In order to build a robust picture of the chosen subject, the review involves a number of studies devoted to ecology and biology of short-lived monocarpic plants, regardless their origin status and occurrence. However, the review is restricted to studies devoted to the temperate zone and thus the spatial restriction of the subject may result in some bias of the conclusions.

Key characteristics of urban environment in relation to non-native plant invasions

According to the ecological approach, the city or urban environment is regarded as an ecosystem, characterized by its history, structure and function, including both biotic and abiotic components, and the cycling and conversing of materials and energy (Sukopp 2002). Urban ecosystems consist of several subsystems, each representing a complex system of its own and influencing all others at various structural and functional levels (Alberti 2005). As a result, due to simultaneous work of socio-economic and biophysical factors, cities have their own spatial organization and distinctive patterns of change through time, which consequently leads to specific patterns of plant species behavior, population dynamics and the formation of communities (Sukopp 2002).

The floral diversity and plant species richness of plants are high in urban areas. The main determinant of this pattern is high environmental heterogeneity, which provides habitats for plants with all kinds of life strategies (Sukopp and Werner 1983; Gilbert 1989; Kühn et al. 2003). Moreover, cities are often species-rich in natural plants as they are often located in pre-existing biodiversity hot spots with a high geological diversity (Kühn et al. 2004). However, no one would disagree that today's intensive urban development promotes the lack of integration among urban habitat patches and communities within them (Trepl 1995) and the loss of native species (Bertin 2002; McKinney 2004). Concurrently, human factor environment provides “niche opportunities” for the vast majority of non-native species worldwide (*sensu* Shea and Chesson 2002).

The diffusion pattern of alien plant species throughout cities has been well documented. It is already known that the share of non-native plants significantly increases towards the city core (Kowarik 1995) and with the increase of city size (Klotz 1990; Pyšek 1998). Moreover, the positive correlation between the density of built-up areas and the presence of exotic species has been also well established (Ricotta et al. 2009).

There are two main reasons behind the pattern of the spread of alien plant species. Those are the influx of propagules and human-induced disturbances, both having the highest rates in the most densely populated areas (Hobbs and Huenneke 1992; McDonnell et al. 1997; Lonsdale 1999; Davis et al. 2000; Mack and Lonsdale 2001; Shea and Chesson 2002). Highly intensive, deliberate and accidental introductions occur in the urban areas and supply a sufficient number of invading propagules, which results in high propagule pressure on sites. The second driver of the spread of non-indigenous plant species is disturbance defined as “any relatively discrete event in space and time, which disrupts ecosystem, community or population structure, changes resource and substrate availability, or the physical environment” (White and Pickett 1985). The role of disturbance both for native and alien plant diversity has been broadly studied. Disturbances of varying frequency, intensity and spatial extent produce heterogeneous mosaics of different successional stages (Lososová et al. 2006), and are important for maintaining diversity both within communities and at the landscape level (Hobbs and Huenneke 1992). Moreover, the disturbance degree explains up

to 55 % of the total variation in exotic plant species richness at the landscape scale across the globe (Rapoport 2000). The crucial role of disturbance in the plant invasion success is usually associated with the fact that it promotes releasing available resources and eliminate the number of competitors and natural enemies (e.g., soil pathogens), which results in creating safe microsites, and stimulates germination (D'Antonio et al. 1999; Hobbs and Huenneke 1992). However, if these factors were the only explanatory variables of a plant's performance success, there would not be any difference between invasion in the non-native range and colonization in the native range. On the contrary, it has been shown that disturbance has the bigger effect on a plant's abundance and performance in non-native ranges compared to the native sites (Hierro et al. 2006). One of the possible explanations is that human-induced disturbance regimes may be inappropriate to the life histories of native plants but suitable for life histories of invaders (Hobbs and Huenneke 1992).

Additional variables that explain the success of plant invasion in urban areas are the following. First, some of human-created ecotopes represent unique physical environments, which have no analogs in the nature, and in which successful establishment of non-native species and/or evolution of anthropogenic species from native and/or alien species occur (Kowarik 2003). Second, higher temperatures in urban areas known as the "heat island effect" allow exotic species to spread into the biogeographical regions where they wouldn't survive otherwise (McKinney 2006).

The therophyte life form strategy is one of the main determinants of invasion success into man-made habitats (Pyšek et al. 1995), and it is no surprise that short-lived monocarpic plants are highly represented in urban alien floras (Pyšek et al. 2003). High colonization rates and fast adaptation to environmental fluctuations of urban habitats, in other words, traits linked to ruderality are the main traits of short-lived invaders. Furthermore, the question arises whether those traits are sufficient condition for invading woodlands with a distinctive microclimate conditions and strong interspecific competition. Most probable, apart from high colonizing ability, a short-lived monocarp should possess a prominent level of competitiveness and stress-tolerance in order to become a successful invader in the forest. Besides the particular traits of short-lived species, there must be external factors, which promote monocarps' invasions into phytocoenoses shaped by woody vegetation. Thus, a more in-depth examination takes place further in the review in order to indentify the key determinants of the invasion success of short-lived monocarpic aliens in the urban forest interiors.

Factors determining urban woodlands' level of invasion and invasibility

In order to understand the adaptive mechanisms of particular groups of alien plant species, it is crucial to analyze information on the type and quality of invaded habitats. Urban woodlands are characterized by a specific landscape context suggesting that specific processes may influence ecosystem functioning (Honnay et al. 1999). Forested areas in dense urban environments represent a variety of habitats, which are usually defined on the basis of such factors as climate, past land-use history, type of primary vegetation, characteristics of soils and level of maintenance to preserve the integrity (Del Tredici 2010). Since socio-cultural factors play a crucial role in the invasion process, I chose the classification of urban woodlands by Kowarik and Körner (2005) as that being the most appropriate for our purposes. Four types of woodlands in terms of the agency of natural versus cultural mechanisms and their habitat continuity are recognized within the framework: i) remnants of "pristine" or primary forests; ii) forests shaped by silviculture; iii) planted tree stands in

greenbelts or urban spaces and iv) woodland succession on urban-industrial sites. Three woodland types excluding commercial forests are usually found within the city boundaries.

Tree stands resulting from urban greenery are heavily shaped by local culture and traditions as they are designed and maintained according to aesthetic considerations. This type of woodland is characterized by high species diversity with a prominent influence of non-native plant species deliberately introduced for ornamental purposes (Kowarik and Körner 2005). They are characterized by open grown trees with a lower canopy closure than natural forest stands. Furthermore, these woodlands are exposed to the regular recreational activities, which result in soil disturbance, degradation of the herb layer, the breakage of branches, abrasion, and other mechanical injury resulting in wounds and damage to the crown. The consequence is the spread of more stress-tolerant plant species. This type of woodland possesses a high level of invasion; neophytes are more frequent invaders than archeophytes. Community gardens and parks serve as a pervasive source of potential invasive plant species particularly if they are located to adjacent woodlands (Dobravolskaitė and Gudžinskas 2011).

Sites formerly influenced by anthropogenic activities form a fine scale patch mosaic in the landscape (Vojta 2007). Spontaneous vegetation on abandoned urban land consists of native as well as deliberately and unintentionally introduced plants (Del Tredici 2010). Further species composition depends on whether human control of natural succession occurs or not. Secondary woodland present a unique type of vegetation that differs significantly from mature or old-growth forests by the presence of plant species indicating a high nutrient content and high pH of the soils, e.g. plants with a short life cycle (Vojta 2007).

Flora of undisturbed, natural forests is formed mainly by native species with a minor contribution of non-native plants. It has been traditionally thought that the typical forest microclimate, together with the lack of available resources (light in particular) and strong interspecific competition present together a relatively effective protection against plant invasions (Brothers and Spingarn 1992; Berezutsky 1999; Davis et al. 2000). However, several recent studies have indicated that natural forests, including relatively undisturbed ones, are not immune to pressure of invasive species, suggesting that the spread of invasive plant species into these forests is simply the matter of time (Godoy et al. 2011; Essl et al. 2011; Essl et al. 2012). Today, the percentage of non-native flora of temperate forests reaches up to 22 % (Mirkin and Naumova 2002), while in early 1970s, Kornaš (1971) named only ten neophytes spread into the forest in Poland. Alien plant species may undergo long time lags before they become invasive in the forest due to long life cycle of the species, low propagule pressure on site or long-term phenological and genetic adaptation to the new environment (Pyšek and Richardson 2007; Pyšek et al. 2009). Furthermore, there are a number of factors, which may contribute to widespread invasion debt, and, hence, mask invasibility of forests at the local and the landscape scales. Among them are long intervals between natural disturbances, the dispersal limitation of propagules through spatial fragmentation of forest patches and high local levels of propagule pressure (Von Holle and Simberloff 2005; Martin et al. 2009; Essl et al. 2012). Thus, the equilibrium state of plant invasion in most forest habitat patches may be considerably higher than currently observed (Essl et al. 2012). Moreover, there is evidence of rapid evolutionary changes in exotic plant species, particularly local adaptation to low light and selection towards shade tolerant phenotypes, which may foster the invasion process throughout different forest types (Godoy et al. 2011). Finally, today's forests often experience an increase in nutrient availability, which doubtlessly also contribute to the higher sensitivity of forests to plant invasions (Zerbe and Brande 2003).

Because most of non-native plant species are heliophytic and restricted to open sites, canopy openness of the forest site and the amount of open habitat in the surrounding landscape have been proved to have a significant positive influence on the proportion of alien plants in the forest (Charbonneau and Fahrig 2004). Similarly, there is an inverse relationship between total tree basal area/total tree layer cover and the proportion of exotic plant species per plot (Ohlemüller et al. 2006; Essl et al. 2012). Additionally, the structure of the vegetation of the forest edge affects the magnitude of the non-native plants' seed flux and the dispersal distance into the forest interior (Cadenasso and Pickett 2000).

It has already been stressed in this review, the presence of exotic species in any habitat, including forest is positively correlated with anthropogenic disturbance (Stapanian et al. 1998; Ross et al. 2002; Godefroid and Koedam 2003). This type of disturbance is always associated with a decline of native species richness and spatial fragmentation, and, thereby, influences the structure and composition of the vegetation of forest habitats. Interestingly, disturbance is thought to reduce competition between native plant species and alien "new-comers". Pyšek et al. (2002) linked the presence of disturbed areas with the positive relationship between the proportion of neophytes and native plant species richness. In accord with the authors, neophytes invade mostly disturbed, heterogeneous environments, where direct competition with native vegetation plays the minor role, and thus do not replace native species. Similarly, the positive correlation between the occurrence of annual *I. parviflora* and native forest species richness and diversity regardless the vegetation type was found in the study by Chmura and Sierka (2006). Though direct competition between indigenous and non-indigenous herbs seems to play a barely important role in forest ecosystems, there may be a significant negative effect of the spread of exotic species over a long-term period. It is possible, that the colonization of disturbed sites, including those of natural origin by alien plants may be a sufficient prerequisite to disable native forest herb species populations to replace themselves in a long run. Following this hypothesis, there will be a relatively short-lasting positive correlation between native and non-native species richness, and a gradual replacement of natives by exotics over the long perspective. For instance, Lysik (2008) reported that in the period of 10 years, *I. parviflora* have replaced native perennial species in 3 % of the study area in the protected beech forest in South Poland.

Thus, among the main predetermining factors of plant invasions into the natural forest at the local level are: i) sufficient level of soil/herb layer disturbance facilitating the penetration and creating safe microsites for newly introduced plant species; ii) canopy openness, which enables spread of propagules to greater distances and their successful establishment on the one hand, and, on the other hand, leads to decline of typical forest plant species, like vernal geophytes (Moore and Vankat 1986).

While studying biological invasions, landscape scale analysis is of great importance. Surrounding landscape, land-use history, connectivity, configuration and size of patches influence the level of plant invasion at a site (Vila and Ibanez 2011 for a review). The level of plant invasion of forest patches and, in particular, the richness of invasive neophytes grows in relation to the increasing amount of urbanized land in the surrounding landscape (Borgmann and Rodewald 2005; Jarošík et al. 2011) and the proximity and size of residential areas (Sullivan et al. 2005; Vidra and Shear 2008), which may be considered as surrogates of propagule pressure and changed disturbance regimes of natural ecosystems (Essl et al. 2011). It has repeatedly been shown that there is a strong negative correlation between the level of plant invasion and the size of forest fragments (Honnay et al. 1999; Ohlemüller et al. 2006). In particular, Honnay et al. (1999) demonstrated that small forest patches in the urban landscape matrix are known to harbor less native plants mainly due higher levels of anthropogenic disturbance and biological invasion in smaller patches compared to larger

ones. In addition, a significant positive relationship was found between the total number of alien plant species at the local spatial scale and the proportion of exotic tree plantations at the landscape scale (Essl et al. 2011). In general, the factors acting at the landscape scale seem to have more significant influence on the level of invasion in urban and suburban forests, compared to the ecological characteristics of an intact forest habitat (Sullivan et al. 2005; Ohlemüller et al. 2006).

Biological determinants of invasion success of short-lived monocarpic non-native species

The invasion success of a plant species depends on a number of biological and ecological traits, which are the result of the long-termed evolutionary history in the native range and its particular adaptation strategy in the secondary range (Ricotta et al. 2010). The most important traits are associated with the reproduction potential (e.g., short germination time, large seed number production, long fruiting period, etc.), annual life form, use of several vectors of long-distance dispersal, the ability to compete with native plant species, high stress tolerance and high phenotypic plasticity (Alpert et al. 2000; Daehler 2003; Pyšek and Richardson 2007; Pyšek et al. 2009). The invasion success of an alien species may be also associated with phylogenetic relatedness with native species suggesting some level of pre-adaptation to local environmental conditions (Richardson and Pyšek 2006; Donoghue 2008; Ricotta et al. 2010). A broad native range is considered as another explanatory variable of invasion success because of the higher likelihood of widespread species to be dispersed and to be adapted to various environmental conditions (Booth et al. 2003). Moreover, non-indigenous plant species can evolve greater invasiveness after their introduction due to: i) increased rate of evolution in small colonizing populations (Ohta 1973) and ii) hybrid populations resulting from multiple introductions from different source populations (Dlugosch and Parker 2008).

Regardless of the large body of research aiming at revealing a general “portrait” of an invasive plant, scientists have concurred with the opinion that finding a set of traits responsible for invasiveness and applicable to all vascular plants is an unachievable goal. The variation in invasiveness is primarily associated with species level. Thus, exploration of traits responsible for invasiveness should be fulfilled within smaller taxonomic and biogeographical groups, e.g. at the levels of particular functional types, life forms, species or even populations (Richardson and Pyšek 2006; Pyšek et al. 2009). This section takes a deeper look on the group of non-native plants with a short lifespan.

Short-lived monocarpic plants can be defined as: i) biological group of plants, which are differentiated on the basis of short lifespan; ii) variations of specific architectural model and life form as a complex of adaptive morphological traits; iii) type of life strategy. All of the mentioned specifications hold merit and complement each other (Markov 1989).

Short-lived monocarps are the most evolutionary advanced life form. This is a specific life strategy, which enclose a wide and diverse range of varieties within the general R-strategy, and that's why they are able to occupy ecological niches across different types of phytocoenoses with a regime of coenotic incompleteness. These species accumulate the greatest biomass growth, have short generation time, abundant seed production and can pass into the reproduction stage nearly at any moment of their ontogenesis (Markov 1987). These characteristics are considered to be important adaptations to nitrogen-rich conditions (Rejmanek and Richardson 1996). At the same time, short-lived exotic species successfully establish in nitrogen-poor environments. For example, James (2008) suggested leaf nitrogen

productivity to be the trait assuring invasion success of annual grasses by producing more root length and consequently capturing more nitrogen across a range of soils with different nitrogen availability.

It has been frequently stated that among the main characteristics ensuring successful invasion of a plant species is their ability to produce large amounts of propagules and easy germination along different environment gradients (Rejmánek 1996). As a rule, invasive plant species are characterized by production of a higher amount of propagules and having lighter and more rounded seeds compared to non-invasive plant species (Moravcová et al. 2010). In monocarpic plants, seeds are the only link between subsequent generations, and therefore traits related to regeneration must be considered as the core adaptive strategies of alien monocarps.

An important role in maintenance of highly dynamic short-lived monocarpic plant populations is played by soil seed banks (Matus et al. 2001). Soil seed banks i) buffer plant populations against temporal fluctuations of unpredictable environmental conditions and help to avoid the demographic effects of reproductive failure by spreading germination over time; ii) maintain genetic diversity in populations and have the effect of slowing differentiation in populations; iii) may serve as a source of genetic novelty by accumulating mutations (Levin 1990; Evans and Cabin 1995; McCue and Holtsford 1998; Clauss and Venable 2000). Invasive non-native plants often have large, persistent soil seed banks. Furthermore, seed banks of those species are often considerably larger in the secondary range than in the native range (Noble 1989).

Seed mass links regeneration, vegetative growth and survival. Seed size has a strong effect on fecundity, establishment success, competitive ability, and persistence in the seed bank (Rees et al. 2001). Seed size is inversely related to fecundity, resulting in enhanced colonization ability of small-seeded short-lived plants. In addition to high fecundity, small seeded species often have long-lived seeds (Rees 1993), form more persistent seed banks (Thompson et al. 1993), and suffer lower rates of predation (Guo et al. 1995), which all together contribute to high abundance rates. Small, long-lived and well-dispersed seeds are common traits of plant species adapted for rapid colonization of disturbed habitats (Rejmánek 1996). However, it is evident that such species are poor competitors because of lower establishment rates and smaller seed reserves compared to large-seeded species (Rees et al. 2001). The competitive ability of short-lived plants is determined by their capacity to reproduce efficiently in the presence of competitors, including perennials (Crawley and May 1987; Bonser and Ladd 2011).

An early germination strategy may significantly enhance short-lived monocarpic species performance in the woodland environment. This characteristic helps to temporally reduce competition with native herbs for light and nutrients, and ensures seed maturation.

Bolker and Pacala (1999) highlighted the importance of a rapid exploitation strategy within annual plant communities. So called “exploiter-species”, characterized by local dispersal, fast growth, early maturation, and small size of adults, efficiently utilize gaps in vegetation. As it has been already shown, the quick and efficient exploitation of space and resources is of overriding importance for invaders. However, this strategy is unlikely to benefit alien species spreading into woodlands. First, there is no direct competition between native forest and exotic plant species in gaps, and second, a small size of plants is a disadvantage rather than a benefit under low light conditions.

Among the most significant adaptations of short-lived monocarps to unpredictable environments are self-pollination and seed polymorphism (Symonides 1988; Eckert et al. 2010). Uniparental reproduction allows small populations to grow faster than if they were outcrossing and reduce the duration of post-introduction bottlenecks (Barrett 2011).

Therefore, the capability of self-pollination is considered as an important determinant of invasion success among short-lived plant species, including those penetrating the forest environment. For instance, Vervoort et al. (2011) documented a high rate (over 80 %) of selfing for the widespread woodland invader *I. parviflora* linked with a full self-compatibility.

Shade-tolerance is another important trait of woodland invasive species. As it has been already mentioned, the majority of alien monocarpic species are light-demanding and, thus, cannot efficiently spread under the tree canopy. At the same time, those few monocarps known to be invasive in woodlands, are highly shade-tolerant and/or can take an advantage of disturbance-created gaps in the canopy.

In summary, there are a number of biological traits of monocarpic non-native plant species, which enable them to invade woodland interiors. It can be hypothesized that plants which combine the traits of early-successional and late-successional plant species, can be considered as the most effective potential invaders of urban woodlands. Subsequently, high fecundity, early germination, high rates of growth and dispersal on the one hand, and the overall big size of plants (Fenesi and Botta-Dukat 2010), high shade-tolerance and relatively large seeds are the most essential characteristics for establishment in woodland communities. The presence of autonomous pollination also seems to be a crucial feature during the first stages of the invasion process.

Conclusions

Plant invasion presents itself as a human-mediated process, which is determined by landscape context, rates of disturbance and propagule pressure across different spatial and temporal scales, initial habitat characteristics as well as biological and ecological traits of invasive plant species. The urban environment is characterized by habitat heterogeneity, the abundance of disturbance-generated establishment opportunities, changed climatic conditions and strong horticultural tradition, which collectively results in floristically species-rich urban ecosystems with a substantial component of potentially invasive alien plant species. Among others, short-lived monocarpic non-native plant species are highly represented across anthropogenically transformed habitats, including different types of urban woodlands. Although the role of short-lived plants may be ephemeral, they play a significant role in forest ecosystem functioning: they are widespread and due to sheer number deserve a higher research interest. Taking into account the hazardous state of urban woodlands and the lack of knowledge about the real invasibility (which surely differs from the current level of plant invasion) of forests, it is crucial to understand invasive potential of particular life forms, e.g. short-lived monocarps.

Short-lived alien plant species are characterized by high relative growth rate, short generation time, abundant seed production and large persistent seed banks, which enable them with a high colonizing potential. At the same time, these traits are among the most important explanatory variables of high invasive potential. However, the competitive ability of many alien annuals is quite poor, and their populations are usually maintained by repeated disturbances, both natural and human-caused. In the forest environment, where competition for light and nutrients is the main shaping factor of the phytocoenosis, annual alien species must possess a certain level of competitive ability, which may be due to such traits as high fecundity, early germination, high rate of growth and the overall large size of plants, presence of autonomous pollination and high shade-tolerance.

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