Alien and invasive plant species in parks and gardens of the Czech Republic

Nepůvodní a invazní druhy rostlin v parcích a zahradách České republiky

PhD Thesis

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Abstract

Parks and gardens are generally known as a source of invasions of alien plants into natural habitats. However, the latest findings show that these green areas do not represent a high risk as a hotspot of invasion. On the contrary, they provide refuge for many threatened species and communities, which invasive taxa can attack from their outside neighbourhood. This thesis aims to evaluate the overall role of public parks in the invasion process: to reveal the plant species that escape from parks and identify the species whose invasion threatens parks (especially from the point of view of their natural values). Another goal of the work is to obtain comprehensive information about new, potentially invasive species that escape from ornamental plantings. The last goal is to define the most common species that invade parks and propose an optimal way of controlling them.

The work is based on a field survey of 89 park sites in the Czech Republic, where not only were escaping alien species from ornamental plantings monitored, but also the increase in alien species in park areas from surrounding areas (in this case, mainly invasive species). Based on the survey, two groups of aliens were defined. The first group consists of species that spread from park plantings; the second group is represented by aliens that spread independently of cultivation in parks. From these groups, the taxa that best represented each group were subsequently selected – (i) ornamental species that often spread from plantings and whose ecology and spreading mechanisms were not yet known (*Lychnis coronaria*, *Stachys byzantina*), and (ii) species that often invaded parks and created massive problematic stands requiring effective control (*Reynoutria* spp). These two species groups were approached separately in individual research included in the thesis.

Results show that: (i) alien and invasive species spread spontaneously from ornamental park plantings; (ii) the number of invading species both inside and outside the studied parks is not very high; (iii) the parks are, however, threatened by the number of invasive plant species from the surrounding urban landscape or private gardens; (iv) the alien species *L. coronaria* and *S. byzantina* have outstanding

generative reproduction capabilities and, therefore, high potential for invasive spread; and, (v) the invasive alien taxa *Reynoutria* spp. can be controlled more appropriately by more environmentally sensitive methods.

Abstrakt

Parky a zahrady jsou obecně chápány jako zdroj invazí nepůvodních rostlin do přírodních biotopů. Nejnovější poznatky však ukazují, že tyto zelené plochy nepředstavují vysoké riziko jako ohnisko invazí, ale naopak poskytují útočiště pro množství ohrožených druhů a společenstev, která mohou být invadována nepůvodními druhy z vnějšího okolí. Cílem práce je zhodnotit celkovou úlohu zámeckých parků v invazním procesu: odhalit druhy rostlin, které z parků zplaňují a identifikovat rovněž druhy, jejichž invaze parky naopak ohrožuje (zejména z hlediska jejich přírodních hodnot). Dalším cílem práce je získat komplexní informace o nových, potenciálně invazních druzích, které unikají z okrasných výsadeb. Posledním cílem je definovat nejčastější druhy, které v parcích invadují a navrhnout optimální způsob jejich likvidace.

Práce je založena na průzkumu 89 parků v České republice, kde bylo sledováno nejen zplaňování nepůvodních druhů z okrasných výsadeb, ale také přibývání nepůvodních druhů do parkových ploch z okolí (zde šlo zejména o druhy invazní). Na základě průzkumu byly tedy definovány dvě skupiny nepůvodních druhů. První skupinu tvoří druhy, které se šíří z parkových výsadeb, druhou skupinu představují druhy, které se šíří nezávisle na pěstování v parcích.

Z těchto skupin byly vybrány taxony, které jednotlivé skupiny nejlépe reprezentovaly – (i) okrasné druhy, které se často šíří z výsadeb a jejichž ekologie a způsob šíření dosud nebyly známy (*Lychnis coronaria*, *Stachys byzantina*), a (ii) druhy, které do parků invadují a mohou zde vytvářet problematické porosty vyžadující účinný management (*Reynoutria* spp.). Obě skupiny byly následně řešeny samostatně, v rámci jednotlivých výzkumů zařazených do práce.

Výsledky ukazují, že (i) nepůvodní a invazní druhy se spontánně šíří z okrasných parkových výsadeb, (ii) počet zplaňujících invazních druhů uvnitř i vně studovaných parků však není příliš vysoký, (iii) parky jsou výrazně ohroženy množstvím invazních druhů rostlin z okolní městské krajiny nebo soukromých zahrad, (iv) nepůvodní druhy *L. coronaria* a *S. byzantina* mají velmi dobré schopnosti generativního

rozmnožování a tedy i vysoký potenciál invazního šíření a (v) invazní nepůvodní taxony *Reynoutria* spp. lze likvidovat vhodnějšími a environmentálně šetrnějšími metodami.

I declare that I prepared the dissertation with the topic "Alien and invasive plant species in parks and gardens of the Czech Republic" independently using the sources cited in the bibliography.

Table of contents

1 General introduction

1.1 Cultural landscape as framework for alien species study

The cultural landscape of Central Europe has been influenced by human activity since the Neolithic period, which includes historical influences (coppice management, litter raking, grazing, etc.), contemporary effects (atmospheric deposition, eutrophication, climate change, etc.), and long-term influences (cultural and socio-economic, including agriculture). These are influences that shape the current cultural landscape in the long term. It is precisely based on their effects that the landscape can be divided into several types according to the degree of naturalness. The first type includes the remains of untouched (close to nature) ecosystems with no or minimal impacts of human activity (e.g., atmospheric deposition) – natural landscape (primaeval forests, bogland, rocky outcrops, etc.) (Löw and Míchal 2003; Kowarik 2005a). The second type is mainly represented by elements of the landscape that were created through traditional or modern agricultural or forestry practices – the cultural landscape (meadows, pastures, fields, coppice forests, etc.) (Löw and Míchal 2003; Kowarik 2005a). Kowarik (2005b) enriches the traditional division of the landscape (natural/cultural) with a third type of landscape, which is made up of non-native greenery that arose as part of garden plantings and their subsequent maintenance. The type includes all the results of horticulture work, which were used in the form of private or public gardens (including gardening colonies and cottage settlements) or parks during the garden history. The third type also includes urban greenery – street trees and shrubs. According to Kowarik (2005b), the fourth landscape type is a landscape with natural development (with spontaneous spreading), which occurs unintentionally, but nevertheless in connection with landscape planning or garden architecture. Spontaneous spreading (escaping plant species from artificial plantings) manifests in extensive lawns, pavement cracks, abandoned areas, or industrial sites (Kowarik 2005a). The escape of ornamental plant species from cultivation into the wild is one of the primary sources of potentially invasive taxa that can negatively affect an area's original flora and reduce the natural values of the invaded area (Hédl 2004; Pergl et al. 2016b). Alien species are generally known as one of the biggest threats to native species of plants (Wilcove et al. 1998). Since their number in the Czech Republic has constantly been increasing over the last twenty years (Pyšek et al. 2012a), they can be characterised as a global threat to nature conservation and overall biodiversity.

This thesis provides a comprehensive view of the role of parks (including public gardens) and ornamental plantings in spreading alien and invasive plants. As part of the first study, which focused on park plantings (Chapter 3), all alien taxa that spread spontaneously in parks were monitored – the subject of interest was species that spread from plantings and also species that entered parks from the surrounding (e.g., *Impatiens parviflora* or cultivated crops *Juglans regia* or *Prunus cerasifera*). Ornamentals without spontaneous spreading activity were not included in the analyses. Still, they can be an essential object for future studies – many of them could be suitable alternatives for dangerous aliens or invasive taxa in new ornamental plantings.

The study of escaping plant taxa from the cultivation of parks, gardens, and urban green areas (Chapter 3) produced pilot results, based on which suitable materials began to emerge for proposals for comprehensive approaches to specific plant species in horticultural practice. This botanical part of the research (inventory of plant species by field mapping) was carried out in 89 park areas (including gardens and urban greenery) across the Czech Republic to ensure a sufficient amount of floristic data from different phytogeographical areas (Kaplan 2012). Within the field mapping, the species were classified into the following categories based on their spontaneous spreading:

(i) escaped alien species without a specific link to the parks (including 106 species) – these alien species are already known as a common escapee in sites other than parks. These are often with invasive status (Pyšek et al. 2012b), and their ability to spontaneously spread is reflected in a significant invasion across the open landscape (*Reynoutria* spp., *Robinia pseudoacacia*, *Solidago canadensis* etc.);

(ii) native species escaped from cultivation out of the range of native distribution ("regionally alien taxa"; including 23 species) – these are native species in the Czech Republic which were grown in parks as ornamental species and subsequently escaped to their surrounding (*Hedera helix*, *Taxus baccata*, etc.);

(iii) alien species at the beginning of escaping from plantings (including 26 species) are alien cultivated species the escaping of which is just beginning. They are new spontaneously spreading species for the territory of the Czech Republic and have not yet been listed in the Catalogue of alien species (Pyšek et al. 2012b). Their wild populations are usually close to mother plants grown in a park (*Ilex aquifolium*, *Lonicera maackii*, *Toxicodendron radicans*, etc.);

(iv) alien species with potential for invasive spreading (including 77 species) – for the time being, these alien cultivated species have the status of casual or naturalized (see Pyšek et al. 2012b), and their number of locations is still limited; therefore, the link to ornamental plantings is demonstrable. Their escaping populations are stabilising and, for many, it is only a matter of time and management before they invade the surrounding landscape (*Abies grandis*, *Lychnis coronaria*, *Stachys byzantina* etc.).

For the subsequent studies, we selected representatives of the two most significant categories showing considerable spontaneous activity on park sites and the limitations of which can be essential for the future management of park areas.

For selected species of category iv, in which frequent spontaneous spread outside garden plantings was observed (*Lychnis coronaria*, *Stachys byzantina*), a study was conducted to analyse the invasive potential of both taxa. The ecology of the species was monitored, including generative reproduction and cytological variability (see Chapter 4). Based on the results of the study, it is possible to infer the negative impact of escaping plants on the surrounding landscape – e.g., hybridisation of *S. byzantina* with an endangered native species *Stachys germanica* – Endangered category (C2b) on the IUCN Red List of endangered species (Grulich 2017). Since it was found that both species are capable of very good generative reproduction, and therefore have a significant potential to invade natural habitats, they became, together with other "dangerous aliens", the subject of a current project entitled "Grow safely" (see Chapter 8). Within this project, the risks of growing alien species capable of escaping into the open landscape are presented, as well as the possibility of their full replacement by "safe species" or cultivars of similar qualities and aesthetic values, which do not escape into the open landscape – this approach can make ornamental plantings in parks and gardens less dangerous for surroundings, reduce the costs of management ornamental weeds, and open up this important topic for the public.

However, the high invasive potential of some taxa that spread spontaneously in or to parks has long been known – three invasive taxa of the genus *Reynoutria* (*R. ×bohemica*, *R. japonica*, and *R. sachalinensis*) were among the most common in parks. Knotweeds are known as one of the worst European invaders (Netwig et al. 2018), but the problem with their invasive spreading is global (e.g., Clements et al. 2016). The knotweed invades many riparian and anthropogenic habitats, where they can form massive stands that usually outcompete other plant species, resulting in the loss of biodiversity and limiting many ecosystem services (Abgrall et al., 2018; Murrell et al., 2011). However, the invasive taxa of *Reynoutria* can have a significant negative impact not only on the native vegetation in natural habitats (e.g., Gerber et al. 2008), where the knotweeds spread uncontrollably despite nature conservation management efforts but on artificial habitats such as parks, as well as gardens – in these sites, it can spread very well and form large monoculture knotweed stands (Chmura et al. 2013; Sołtysiak and Brej 2014). Several parks were even recorded where the coverage of knotweeds was so high that it limited the planted ornamental plants and movement in the park areas – they were chemically eliminated here, but unsuccessfully (see Fig. 1).

Fig. 1: *Example of unsuccessfully chemical control in Kravaře chateau park. Japanese knotweed (Reynoutria japonica) completely occupied the park area after reconstruction of the park, and now it is impossible to get rid of it even with chemical control.*

Knotweed can be controlled using many various methods, of which the most common is chemical or a combination of mechanical and chemical control (e.g., Bímová et al. 2003; Kabat et al. 2006; Jones et al. 2018), where late season spraying is used and which is widely considered as one of the most effective control methods. However, we wanted to use less herbicide and a suitable concentration for the specific taxon, so we tested each taxon in timing when the aboveground biomass was lower – in the early season, which led to a more efficient and environmentally sensitive method of knotweed control (see Chapter 5). Chemical control was tested on all invasive taxa of the *Reynoutria* genus on different sites, including urban greenery and park sites (see Fig. 2.).

Fig. 2: *The effective chemical control method was tested at different timing across the vegetation period, on three invasive knotweed taxa. The study sites included parks and urban greenery – this is an experimental site of Giant knotweed (Reynoutria sachalinensis) in the Konopiště chateau park.*

1.2 Parks and gardens as a specific element of the landscape

Urban nature is an element that creates significant social and psychological benefits for human society in residential areas and is, therefore, one of the key elements of urban sustainability (Chiesura 2004). Urban greenery contains a high number of alien plant species which, in combination with the native flora of parks, form hotspots of biodiversity, especially in the highly urbanised environment of large cities; and at the same time, they create an environment for the possible preservation of endangered and rare species or cultivars of ornamental plants (Li et al. 2006; Kümmerling and Müller 2012). The results of earlier research show that the species richness of urban and suburban parks increases primarily with the amount and diversity of seminatural habitats represented in a park and its area (Cornelis and

Hermy 2004). However, the main problem of urban garden plantings is that they can escape from cultivation with a subsequent invasive spread of introduced taxa into the open landscape, which can negatively affect the native flora in the area (Kowarik 2005a; Kümmerling and Müller 2012). Alien species mainly affect native flora through competition, but they can also hybridise with native species, which can lead to genetic drift or genetic erosion of native populations (Thompson 1991; Huenneke and Thomson 1995; Vilà et al. 2004; Largiadèr 2008). The likelihood of hybridisation is then mainly carried by seed mixtures commonly used in settlement and in plantations connected with open landscape (Štajerová et al. 2021). Another negative effect these species can cause is the intensive mineralisation and nitrification of habitats (e.g., *Robinia pseudoacacia*), which can lead to a widespread change of entire ecosystems (Vítková and Kolbek 2010).

The main competitive advantage of these intentionally introduced species is their ecology with specific characteristics, which include one of the most important ecological traits – the trait of reproduction, which can lead to their invasive success and competitive advantage over other species (Pyšek 2007; Pyšek et al. 2009). Examples include species that can spread vegetative and generative as well (e.g., *Ailanthus altissima*) or species which germinate at lower temperatures and are capable of earlier timing of germination and rapid seedling growth (Baskin and Baskin 1998), such as *Heracleum mantegazzianum* (Gioria and Osborne 2009). These traits directly support invasive spreading and are known for many alien or invasive perennials introduced to ornamental planting (e.g., Pyšek 2007). Horticulture is, therefore, generally considered one of the main causes of plant invasions and garden plantings as the primary source of invasions (e.g., Ni and Hulme, 2021; Dehnen-Schmutz and Touza 2008). On the other hand, hotspots of spontaneous spread can also be located in urban areas in places that are contrary excluded from cultivation or maintenance and where no management is applied (e.g., Lososová et al. 2012a; Vakhlamova et al., 2022). In unmaintained parts of a city, a higher proportion of alien species outside plantings was also found (species from other parts of Europe, the Mediterranean, and Western Asia most often escaped) in contrast to residential areas, where native species are more numerous (Kowarik et al. 2013).

In particular, the age of garden monuments and the historical development of specific areas have an effect on the species composition and landscaping of urban or chateau parks and gardens (including the presence of potentially invasive taxa) (Li et al. 2006). Garden concepts and landscape elements (solitary trees, vistas, water bodies, flower beds, lawns, etc.) are also greatly affected by historical colonization, which expanded the urban concept of cities, including urban greenery and parks, as part of the expansion. An example of colonial landscape architecture that significantly changed the original identity of cities is the English landscape, which influenced cities throughout the British Empire (America, Australia, etc.) (Ignatieva and Stewart 2009). Parks, landscaping, and urban greenery create a combination of not only natural but also historical, social, and aesthetic values and ecosystem services, which can lead to the declaration of the given places as cultural monuments of international importance and inclusion on the UNESCO World Heritage List (Park on the Ilm, Průhonice chateau park, etc.) (Kümmerling and Müller 2012). A park or urban greenery can then become a controlling variable, e.g., when valuing not only the cultural heritage but also the market price of real estate (mainly residential premises) within the framework of the hedonic price method, which makes it possible to include the non-market value of the quality of the surrounding environment (Votsis 2017). The quality of the surrounding environment is then assessed, among other things, according to the wide range of ecosystem services that park greenery offers (air filtration, micro-climate regulation, noise reduction, rainwater managementj, recreational opportunities, etc.) (Bolund and Hunhammar 1999). As part of the study of parks, it is, therefore, appropriate to consider socio-economic factors which are connected with the biological approach. For example, higher biological richness can be a decisive element for the aesthetic value of urban ecosystems and significantly increase park attendance – urban meadows with distinct structural diversity and a higher number of plant species are significantly more popular with visitors to park areas than species poorer meadows (Lindemann-Matthies et al. 2010; Southon et al. 2017). However, parks are also greatly affected by the recreational activities of visitors (walking, barbecuing, etc.) – recreational use can cause spatial, vegetational, or soil changes (fragmentation into sites with different soil or vegetation characteristics, changes in soil chemistry, etc.) (Sarah et al. 2015). Urban greenery and park areas are currently also influenced by the newly revived interest in collecting forest fruits, wild plants and mushrooms, which until recently was the prerogative of mainly rural agglomerations (McLain et al. 2012; Poe et al. 2013). Some parts of urban greenery can also be affected by urban agriculture or grazing (e.g., McLain et al. 2014; Hurley et al. 2015; Davis 2021) which, however, can create habitats for the spread of alien species, which can have a negative effect to ecosystem services (Charles and Dukes 2008; Vaz et al. 2018).

1.3 Invaded habitats and prevention of the spread of invasive alien species

Habitats and vegetation types with the highest proportion of alien species are usually characterised by a significant degree of disturbance or fluctuating input resources, especially nutrients and, in some cases, also light and water (Davis et al. 2000; Pyšek et al. 2012a). Anthropogenically influenced types of originally natural habitats and habitats requiring permanent management, which is either not intensive enough or has been interrupted, are most often invaded (Chytrý et al. 2005). Defence against the spread of invasive species usually consists of several eradication procedures that can limit the spread of alien taxa in the invaded habitats or completely eradicate invasive populations there (e.g., Pergl et al. 2016c) – prioritisation of infested stands is essential (due to limited financial resources, it is not possible to eradicate everything) as is the evaluation of the effectiveness of the applied management actions used for future management planning (Berchová-Bímová et al. 2019b).

However, the most effective and economically friendly is protection – prevention, within which it is possible, for example, to define localities potentially threatened by invasions or to determine species that could harm biodiversity (Wittenberg and Cock 2001; Thalmann et al. 2015). Subsequently, it is also possible to restrict the cultivation of certain species in specific locations, including informing the public about the inappropriateness of planting invasive species (gardening manuals, etc.) (Kowarik 2005b). Better communication about the issue of invasive species among the public, environmentalists, and gardeners could then lead to a reduction in the planting of problematic species, which would reduce the threat of escapes from garden compositions (Reichard and White 2001). Suggestions on the cultivation of alien and invasive plant species, which can escape from garden cultivations, have already been used within the framework of educational projects that aim to connect the information channel between gardeners and invasive biologists – e.g., Grow me instead in Australia, Be plant wise in UK, and "Grow safely" in the Czech Republic (see Chapter 8). Other projects are also trying to draw attention to escapees from gardens – citizen science can also be used to prevent the spread here, e.g., Plant Alert project, which collects data from gardeners and the wider public about ornamental plants spreading (Dehnen-Schmutz et al. 2022). Furthermore, it is also possible to consider monitoring and limiting cross-border internet trade with potentially invasive taxa (so-called e-commerce) which, in combination with private gardening, creates a new significant driver for the introduction of alien species (Humair et al. 2015). However, the biggest problem in defence against plant invasions is differentiation between non-invasive and invasive (potentially dangerous) species, which is essential for further prevention or eradication strategies (Hulme 2006). For these reasons, it is appropriate to continuously review the invasive status of individual taxa and repeatedly reconsider their spread, invasibility, and impacts on native species, vegetation, and natural habitats (Pyšek et al. 2002; Pyšek et al. 2012b; Pergl et al. 2016a; Pyšek et al. 2022), which results in changes in the status of particular species in the Black, Grey and Watch lists (Pergl et al. 2016a).

1.4 Development and changes in parks and gardens of the Czech Republic

Several plant species are described in most Czech botanical literature as "Escape and spreading in surrounding of gardens and parks" (e.g., Deyl and Hísek 2001, Kubát and Bělohlávková 2002). With this description, the selected species are placed in the role of dangerous refugees, i.e. species that will once and for all be identified as a real threat to the surroundings of monuments of garden architecture. A comprehensive study of the spontaneous spread of species from park and garden plantings, based on robust data and statistical analyses, has only recently been processed (see Chapter 3). Thus, the designation of taxa as endangered refugees was based only on casual observations, which could be influenced by several factors such as subjectivity of observers, specific garden practices, or other local contexts.

Gardens, parks, and urban greenery have, therefore, often historically been presented as hotspots of potential invasions, where ornamental species that were subject to fashionable trends were added throughout history (Kümmerling and Müller 2012). In this way, a mixture of species from practically all over the world was created in parks, of which some species really escaped dangerously, others adapted over a long time to the existing conditions (they escaped rarely), and others waited for climate change before escaping from ornamental gardens and spreading to the surroundings (Niinemets and Peñuelas 2008). Thus, there is a certain invasive potential here, but questions arise as to which species the potential is associated with and which factors affect it.

Public parks are affected by many factors that changed, shaped, and brought the original architectural work to its current form. The species composition, area, and location of parks in the landscape, combined with the architectural concept and the experience of the gardeners, are variables that had and still have a significant effect on the viability and invasive potential of the planted species. When socio-economic factors, which are also based on historical facts, are added to these direct effects, the matter becomes quite complicated – wars or marriages that enabled the migration of noble families from distant countries to Czech territory (including popular types of plants and garden arrangements), fashionable waves in the field of garden architecture (Renaissance, Mannerism, Baroque, Romanticism, etc.) and related reconstructions and modifications of garden compositions, the opening of gardens and parks to the public (18th century), or changes in land use around parks, which were started mainly by the industrial and demographic revolution in the 19th century (Cavallo et al. 2016). Subsequent urbanisation, which continues until today, then led to the development of settlements in the vicinity of parks, which brought pressure from higher population density (increased park attendance) and the construction of new transport corridors, which enabled the directional transfer of alien species from urban to surrounding landscapes (Zwaenepoel et al. 2006; von der Lippe and Kowarik 2007). Supporting the spread of invasive species, urbanisation, or the concentration of trade, travel and transport, also significantly affects biodiversity (Pyšek 1998; Säumel and Kowarik 2010). Parks were also affected by other property changes in the 20th century (land reform, confiscation, restitution, and privatisation), which led to further modifications, changes in use, revitalisation or, conversely, the abandonment of previously maintained areas. Just abandoned parks or parts of them (sites with little or no control of alien weeds) are often a suitable habitat for the spread of alien species and can create a hotspot of invasion to open landscapes (e.g., Kollmann and Bañuelos 2004; Štajerová et al. 2017).

At the same time, the shift in the role of a park is essential – initially a private garden (e.g., for the aristocracy), i.e. an area focused only on the subjective feelings and requirements of the owner, it is now transformed into a space of practical use with an impact on the general public, offering recreational and cultural values, including playgrounds or outdoor gyms (Kaczynski et al. 2008; Zhai and Baran 2016). If we understand this trend as urban, i.e. directly related to the expansion of buildings and higher population density, it is then possible to characterise the transformation of parks into golf or disc golf courses as post-urban (a significant trend in the Czech Republic – chateau parks in Štiřín, Kynžvart, Třešť, Konopiště, etc.), which returns the spaces into a limited group of people (sport or golf clubs, etc.). This type of commercial use of public parks leads to the denial of their existence of them and may contribute to their complete degradation (Šantrůčková 2016; Navrátil et al. 2016). The post-urban direction with commercial use, therefore, reduces the offer of recreational values, as a result of which the number of visitors decreases, homogenises park areas, and creates disturbances due to reconstructions, which make conditions not only for succession but also for invasion (DeCandido 2004). The number of park improvements, their extent and form (in history and in the present), including land use changes and spontaneous changes due to succession, significantly condition the state of biological diversity in chateau parks (Zipperer and Zipperer 1992; Sikorski et al. 2011). However, the import of alien plant species can occur in parks also within the framework of minor horticultural modifications, during which soil is moved (tearing, filling of soil, etc.) (Hodkinson and Thompson 1997). Another vector for the spread of alien plants in parks may be the species of birds present and their number, which may vary depending on the surrounding urban noise (González-Oreja 2017); the determining factor could therefore be the localisation of park areas (centre vs outskirts of the city) or distance from individual noise sources. Alien species are also transmitted through local watercourses, where their seeds and macro residues (cuttings) can spread downstream and invade, especially along river floodplains (Thomas et al. 2006; Säumel and Kowarik 2010). An advantage of invasive species have over non-invasive species is that they are able to float for a longer time when dispersed by water indicating that they can spread long distances along rivers (Moravcová et al. 2010). The risk of invasion here also increases depending on hydrological changes, especially on the flow or frequency of higher (flood) flows (Truscott et al. 2006). In addition, the occurrence and spontaneous spread of plant species are also significantly effected by the number of visitors to parks, the population density of urban areas, and the presence of transport networks (Lundholm and Marlin 2006; Rat et al. 2017). Anthropogenic activity, combined with invasions of non-native species and subsequent successional processes, can then lead to significant degradation of the natural (native) flora of parks and its replacement by alien species (DeCandido 2004). The spread of alien species can also result in biotic homogenisation (increasing similarity between the biota of different areas). However, in the slightly disturbed environment of urban parks and residential areas, much higher heterogeneity was found than in squares, streets, or early successional habitats (it was found that archaeophytes in particular are the bearers of homogenisation) (Lososová 2012b).

Another important factor affecting a park's flora is global climate change. Many species still used in horticultural practice occasionally spread from ornamental plantings or are directly invasive; due to global warming, there could be an expansion of the spectrum of alien species which will be able to invade areas with changed climate conditions (Niinemets and Peñuelas 2008). These may include species that have not yet naturalised – climate change is a threat here as it may lower the barriers to naturalisation for these ornamental alien species (Haeuser et al. 2018). However, the risk of naturalisation of alien species depends not only on climatic suitability but especially on the combination of climatic suitability and land cover, which can significantly increase the risk of escaping (Dullinger et al. 2017). Therefore is very important for the management of planting applied with respect to land cover and raising awareness of the issue of biological invasions in the context of climate change among gardeners and the public (Dullinger et al. 2017).

Depending on anthropogenic climate changes, native species must acclimatise, adapt, move, or become extinct. Although some species are indeed moving in response to climate change, their ability to keep up with increasingly rapid climate shifts is unclear for the future (Corlett and Westcott 2013).

2 Aims

The aim of the thesis and the included research is to: (i) understand the processes inside parks from the point of view of alien and invasive species; (ii) create an inventory of alien species that spread spontaneously in parks; (iii) evaluate the potential invasion threat inside (outside) parks; (iv) identify the invasive potential of selected alien species spreading from ornamental plantings; and, (v) find an appropriate and considerate method of chemical control for knotweeds, common invaders in parks.

3 Case study I: Two faces of a park: the source of invasions and habitats for threatened native plants

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Abstract

To study the role that public parks play as sources of invasions, we surveyed 89 sites in the Czech Republic, comprising chateau parks in urban areas and countryside across various landscapes and socioeconomic contexts, to build complete inventories of alien taxa spontaneously spreading in parks from cultivation or arriving from their surroundings. We describe the richness, diversity, status, frequency, and abundance of the park floras, explore the relationship between alien taxa, site factors, and management practices used in the parks, and assess the invasion potential of the recorded taxa and their interaction with threatened native taxa occurring in the parks. We found that (i) the numbers of escaping invaders are relatively low, and their population sizes are limited despite the great numbers of taxa cultivated in the parks; (ii) there are many invasive plants which arrived in the parks from the surrounding urban and rural landscapes; and (iii) many parks act as refugia for threatened native taxa and vegetation types. We found 242 alien taxa, of which 21 were recorded for the first time escaping from cultivation, thus representing additions to the national alien flora, seven were cultivars of native taxa, and 26 were native taxa planted outside their natural distribution area in the Czech Republic. The most abundant taxon was the native *Hedera helix* which often behaves expansively in its natural habitats; the most abundant alien taxa included the invasive neophytes, *Impatiens parviflora*, and *Robinia pseudoacacia*. Alien taxa classified as naturalized or invasive in the Czech Republic were recorded as escaping from cultivation in 69% of the parks sampled, while casual aliens in only 18%. We recorded 100 Red List taxa, including four critically threatened. Our study shows that parks play a similar role in invasions as other sites in urbanized landscapes, but they also provide habitats for many native taxa. Such conservation effect is made possible by regular management primarily focused on aesthetic functions, e.g., removing shrub and tree saplings in specific habitats to maintain open sites and steppe localities.

Introduction

Ornamental plants are commonly used in landscape architecture, floricultural industries, and ethnobotany (Groening and Wolschke-Bulmahn 1989; Vogl et al. 2004; Wijnands 2005; Xia et al. 2006). However, the diversity and composition of cultivated ornamental flora in private or public areas and its significance for biological invasions in particular have only become a research topic in the last decades (Dehnen-Schmutz et al. 2007a, b; Pergl et al. 2016b; Klonner et al. 2017; van Kleunen et al. 2018). Traditionally, cultivated ornamental plants were mostly considered as garden escapes in studies on spontaneous floras of urbanized areas (see Višňák 1995; Pyšek 1998; Sukopp 2002; Thompson 2002; Chocholoušková and Pyšek 2003, Celesti-Grapow et al. 2006; Aronson et al. 2015; Čeplová et al. 2015; Lososová et al. 2016). From the plant invasion perspective, the trade with ornamental plants is a major driver of alien species introductions, and this also concerns the unintentional introductions in the form of weed contaminants of commodities associated with the horticulture industry (Hulme et al. 2008; Lambdon et al. 2008; Pergl et al. 2017; van Kleunen et al. 2020).

On the other hand, public areas such as parks, urban forests, and other green areas that are maintained by regular management (e.g., removal of regenerating shrubs in open forests or steppe-like habitats) provide habitats for many threatened native species that disappear from the current landscape as a result of unsuitable management, habitat loss and global change (Alvey 2006; Celesti-Grapow et al. 2006; Niinemets and Peñuelas 2008; Koperski 2010; Haeuser et al. 2018). For example, some urban forests harbour many endangered species and species of a high conservation value (Alvey 2006), and meadows or dry grasslands in parks are rich in native species (Celesti-Grapow et al. 2006). Parks and urban forests can thus be viewed as local biodiversity refugia not only in city centers (Ricotta et al. 2001) or suburban areas (Chocholoušková and Pyšek 2003; Kühn et al. 2004; Stewart et al. 2004) but also in the rural and post-industrial countryside (Dzwonko and Loster 1988; Konijnendijk et al. 2005; Sádlo et al. 2017).

Another category that needs to be taken into account within this study system includes the so-called expansive species, i.e. native species that spread in human-transformed landscapes due to their ability to take advantage of land-use changes (Prach and Wade 1992; Pyšek et al. 2004). Expansive species are successful competitors, spread rapidly, prefer nutrient-rich habitats, and can usually use a wide range of resources (Thompson et al. 1995).

Previous studies on the impact of invasive species (Pyšek and Richardson 2010; Vilà et al. 2011; Kumschick et al. 2015), including extinctions of native species (e.g., Downey and Richardson 2016; Pyšek et al. 2017a, 2020) and their survival in cities and rural landscapes (Celesti-Grapow et al. 2006; Koperski 2010; Jarošík et al. 2011), point to the importance of addressing plant invasions in urban habitats, including public parks. The data collected in parks, gardens, and urbanized areas also make it possible to predict future naturalized and invasive aliens (Dullinger et al. 2017; Mayer et al. 2017; Haeuser et al. 2018; Kutlvašr et al. 2019) and can serve as a model for landscape ecology and metapopulation biology.

Here we aim to (i) build complete inventories of alien taxa spontaneously spreading in parks as escapees from cultivation or arriving from parks' surroundings; (ii) describe richness, diversity, status, frequency, and abundance of those alien floras; (iii) explore the relationship between alien taxa performance, various site factors and management practices used in the parks; (iv) assess the invasion potential of the recorded taxa; and (v) their interaction with threatened native taxa occurring in the parks. The collected data allow us to quantify the main processes involved in alien taxa dynamics within parks, i.e. local escapes from cultivation, some followed by subsequent spread beyond the park boundaries, and the invasion of alien taxa arriving to the parks from the surrounding landscapes.

Methods

Study sites and environmental variables

The study was conducted in the Czech Republic, a country located in the temperate broad-leaved deciduous forest zone (Chytrý 2012; Divíšek et al. 2014), with mean annual temperatures of 5.0–9.5 °C and annual precipitation of 320–1450 mm (Tolasz et al. 2007). There are ~700 chateau parks in the Czech Republic for which detailed dendrological and socioeconomic information is available (Hieke 1984, 1985; Pacáková-Hošťálková 2004).

We focused on the chateau and palace parks (further referred to as 'parks'), many of which serve as urban or countryside parks. We recorded the presence of alien taxa in 89 parks (incl. their close surroundings). In 75 of these parks, we also recorded the native and threatened plant taxa (Fig. 3, see Electronic Appendix 1 for a detailed description of the parks). The selected parks cover a representative range of environmental, geographical, and socioeconomic factors (in terms of accessibility to the public and maintenance). The parks studied ranged from 1.4 to 270 hectares in area and were located between 140–730 m a.s.l.

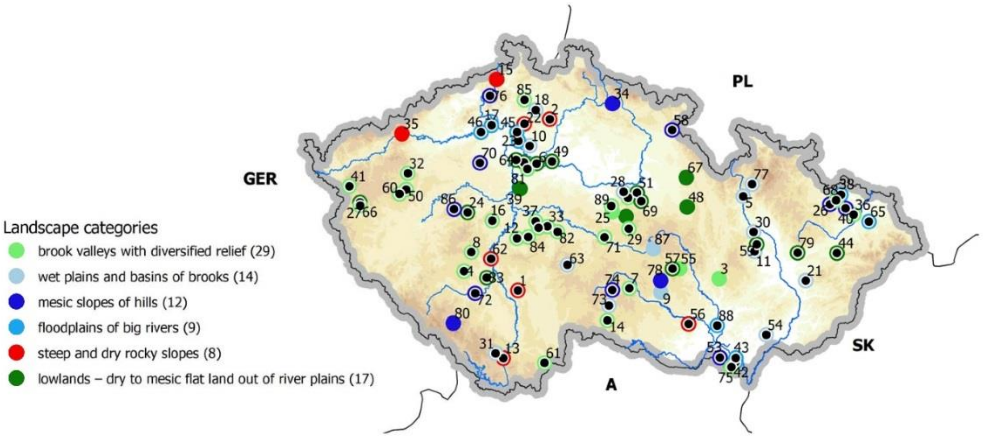

Fig. 3: *Sampled parks in the Czech Republic classified according to the modified landscape categories with altitude as the background. Points with a black dot represent parks where native taxa were recorded (n=75). The numbers refer to a park's identity in Electronic Appendix 1.*

The park area was defined by its visible borders (i.e. walls, hedgerows, and/or fences). The following parameters were compiled for each park from the literature:

the number of planted woody taxa (taken from Hieke 1984, 1985), park area including buildings and paved spaces, mean altitude (Pacáková-Hošťálková 2004) and climate (Karger et al. 2017; see Electronic Appendix 1 for the list of climatic variables). The position of the park was characterized with respect to the surrounding landscape, which was categorized according to a simplified landscape classification (Löw and Novák 2008; further referred to as 'modified landscape categories'). We distinguished areas in flatland (floodplains of big rivers; dry to mesic lowland out of river floodplains; wet plains and shallow basins of brooks) and undulating landscape (brook valleys with diversified relief; gentle hill slopes with deep mesic soils; steep and dry hill slopes with rocks and shallow soils).

The factors related to a particular park (further termed 'site factors') were characterized by estimates of areal proportions of the following categories reflecting park structure: (i) French formal garden (i.e. highly managed ornamental part of the park), (ii) English landscape park (i.e. nature-like part of the park with comparably less intense regular management), (iii) technical support areas (i.e. serving as maintenance background, with restricted access to visitors) and (iv) seminatural areas with weak or no garden management, including deer-parks (defined as land for the management and hunting of wild animals, woodland management and grazing) (Bassin 1979; Kowarik 2005c; Nielsen et al. 2014).

Nomenclature follows the checklist of the Czech flora (Danihelka et al. 2012), and the standardized names for the newly introduced taxa were taken from The Plant List (2013). To cope with the high number of cultivars, some taxa were synonymized. For example, the taxon *Corylus avellana* agg. cult. includes the alien *Corylus maxima* and purple-leaved cultivars of *C. avellana* but not native *C. avellana*. The taxa of *Forsythia*, including cultivars, were merged to *F. suspensa* group since it is difficult to determine young non-flowering individuals.

Delimitation of the taxa included in the study

The taxa meeting the following criteria were included in the survey: (i) alien taxa that were planted to parks and escaped spontaneously (i.e. they are currently cultivated, or were in the past, and dispersed to other areas within the park without human assistance); (ii) taxa that occur in the parks due to unintentional introduction (often alien species) and (iii) remnants from original vegetation before the park was founded (mostly native species).

To reveal taxa that occur in the parks as a result of intentional introduction, we used the current composition of cultivated taxa recorded by our field research, historical records, and catalogues (if available with the park's administration), as well as historical literature on the cultivation of woody taxa (Hieke 1984, 1985). Among alien taxa that were introduced intentionally, we also included those that are native to other areas in the Czech Republic but alien to the region where the park is located; these were termed 'regionally alien taxa' (e.g., mountain species cultivated in lowland parks or the native *Taxus baccata* that naturally occurs only in some deep valleys but is extremely rare).

Alien spring geophytes were excluded owing to their early and short-term occurrence. Lastly, we did not include taxa that were introduced unintentionally in modern times (e.g., *Conyza canadensis*) and taxa not escaping from cultivation. Residence time, used to separate taxa into archaeophytes and neophytes, was taken from Pyšek et al. (2012b). Native and threatened taxa, reflecting the presence of seminatural vegetation, were recorded to evaluate the parks' role in conservation.

Recording of alien taxa

Between June 2016 and September 2018, we recorded all alien taxa that were planted and escaped from cultivation or spread into the park from its surroundings; the latter were identified as taxa not found in cultivation within a given park. The arrival pathway of a taxon into the park was inferred from field surveys of taxa planted in the neighbourhood and botanical research in the park's surroundings; if a taxon was found in the close neighbourhood but not in the park, we considered it as arriving from outside the park.

Alien status was assigned according to the Catalogue of alien plants of the Czech Republic (Pyšek et al. 2012b). The status of regionally alien taxa was inferred from distribution maps in the Pladias database (Chytrý et al. 2017; Wild et al. 2019) and publications on the distribution of species of the Czech flora (Kaplan et al. 2015, 2016a, b, 2017a, b, 2018a, b, 2019b). These sources were also used to obtain information on life form, residence time, invasion status, regional abundance (i.e. estimated for each taxon using the following scale: single locality, rare, scattered, locally abundant, and common across the whole Czech Republic), mode of introduction (i.e. intentional or unintentional) and region of origin. Some taxa were observed as escaping from cultivation for the first time in the Czech Republic, thus representing new records for the country's alien flora (Hadinec and Lustyk 2017; Lustyk and Doležal 2018). Such taxa were assessed separately as their invasion status is not yet clear. Due to a low number of taxa in some categories of invasion status and the uncertain classifications of the pathway of arrival, we used the following merged groups: 'inv+nat' (i.e. including invasive and naturalized taxa) and 'regional aliens and new alien taxa' (pooled because the invasion status of all taxa in these two categories is not currently known).

Each alien taxon was classified with respect to the (i) mechanism of spread, with two categories according to Sádlo et al. (2018): 'movable diaspores' (i.e. escape from cultivation by spores, seeds, fruits or vegetative escape by separable and viable parts such as branch fragments) and 'sedentary clonal modules,' mostly belowground (i.e. clonal spread on-site) (Electronic Appendix 2); (ii) abundance in the park, classified to three levels ranging from rare occurrences (i.e. covering less than ~50 m^2 in total), to abundant in few localities within a park or only sparsely abundant (i.e. ~50–5000 m^2 in total), and abundant taxa occurring in an area larger than 5000 m^2; and (iii) 'plantation context' where two categories were distinguished: 'park escapees' (i.e. their parental populations were originally cultivated in the park) and 'other escapees', where it was impossible to decide whether the parental populations originated inside or outside the park (Electronic Appendix 2).

Native and threatened plants and habitat classification

The records of these taxa were used to infer the presence of natural habitats in parks that can host threatened taxa. Categories of threatened taxa were taken from the Red List of vascular plants (Grulich 2012). The threat status of all taxa was classified according to the new edition of Key to the flora of the Czech Republic (Kaplan et al. 2019a). On-site recording of the habitats was not possible due to intensive management at most parks (e.g., regular lawn mowing). Since making complete inventories of native taxa in individual habitats was not logistically feasible, we recorded native taxa in each park, disregarding common ubiquitous species. If available, published floristic data for individual parks was also used (e.g., Danihelka and Šumberová 2004; Ekrt 2012). All Red Listed taxa in categories C1–C4 (i.e. C1 – critically threatened taxa, C2 – endangered taxa, C3 – vulnerable taxa, C4 – lower risk taxa) that are native to the Czech Republic were recorded (further referred to as 'threatened plant taxa') (Grulich 2012).

The classification of habitats of threatened taxa was done based on the presence and dominance of native taxa according to Chytrý et al. (2017). We used 12 categories which represented groups of native taxa in specific habitats (i.e. rocky slopes; forest-steppe formations; mesic semi-open tree groves; mesic oak/oak-hornbeam forest; wet floodplain forest & nitrophilous fringes; mountain forest; short-cut lawns; mesic meadows; wet thistle meadows; continental inundated meadows; wetlands; ruderal vegetation; see Electronic Appendix 3).

Data analysis

For alien taxa the following approaches were used: (i) generalized linear model (GLM) for testing the proportion of spontaneously occurring taxa originating in the park vs. taxa arriving from outside the park, (ii) ordination methods for relating the environmental and other attributes of the parks to species composition, and (iii) regression trees to analyse the relationship between species traits and the frequency with which they occur in the parks.

The proportions among all aliens of taxa escaping from cultivation within the park and of those that arrived from the surroundings were analysed using a linear binomial model (Crawley 2012) with the above two groups as response variables (the higher value meaning a greater proportion of escaping taxa and vice versa). Attributes of the parks (i.e. altitude, park size, number of woody taxa, and casual, naturalized, invasive, and neophyte taxa) were independent variables, and the initial maximal model was set without interactions.

The minimal adequate model was determined by using a step-wise selection process of model simplification, beginning with the maximal model containing all factors and attributes of the parks, then proceeding by the elimination of nonsignificant terms (using deletion tests from the maximal model), and retaining significant terms (e.g., Hejda et al. 2009; Pekár and Brabec 2009; Crawley 2012). Data were analysed in R 3.0.2 (R Development Core Team 2019). Akaike's Information Criterion (AIC) was used for the evaluation of the models (Crawley 2012).

The relationship between species composition, weighed by abundance and park attributes, was analysed using the canonical correspondence analysis (CCA) in Canoco 5 (Šmilauer and Lepš 2014). Species data without singletons (157 taxa in total) were log-transformed and the following park attributes were used: altitude; park size; the percentage of the total area covered by French formal garden, English landscape park, seminatural, and technical support areas; climatic factors; and the number of woody taxa (specified in Electronic Appendix 1). The significant explanatory variables were selected by using forward step-wise selection from the full model with Bonferonni correction, and this was tested using the Monte Carlo permutation test with 499 unrestricted permutations. To describe the proportion of variance assigned to site attributes and climatic factors, variation partitioning analysis was used (Økland and Eilertsen 1994). In this analysis, primary climatic variables were replaced (because of a high level of collinearity) with uncorrelated linear combinations of principal component analysis (PCA) scores (see Dupin et al. 2011). Climatic variables were standardized before the analysis. Calculations were done in Canoco 5. The number of PCA scores retained for further analyses was determined by the scree diagram. The PCA used to simplify existing climatic variables revealed that the first three axes explained 81% of the variance (Electronic Appendix 6). The first axis (linear combination) is related to temperature and precipitation, the second to temperature, and the third axis to seasonality (Electronic Appendix 6).

A regression tree was produced to assess the role of factors determining the frequency of taxa in the studied parks. The number of taxa was a response variable. To account for phylogenetic relationships of the recorded taxa, 1/sqrt of the number of taxa within the genus was taken as a weighing factor. The dependent variable was the frequency of occurrences in the parks. The explanatory variables were residence time (i.e. archaeophyte vs. neophyte), invasion status, regional abundance, mode of introduction, a region of origin, mechanism of spread, and life form. Regression trees were constructed using binary recursive partitioning, with the default Gini index impurity measure used as the splitting index, in CART v. 8.0 (Breiman 1984; Steinberg and Colla 1995). To find the optimal tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was produced, and their resubstitution relative errors, corresponding to residual sums of squares, were estimated. Ten-fold cross-validation was used to obtain estimates of cross-validated relative errors.

Interactions between specific habitat types and park structure were analysed using linear regression. The number of habitat types with threatened taxa was the dependent variable, and the proportion of English landscape park and that of the seminatural part of the park were used as explanatory variables. The Nové Hrady locality was excluded from the analysis because it was a clear outlier harbouring many threatened taxa due to large parts of the park being a protected landscape area.

Results

Parks studied

We sampled 89 parks in the Czech Republic (Fig. 3), which occurred within six modified landscape categories. The parks were located both in flatland and hilly areas. Brook valleys with diversified relief (29 parks) and dry to mesic lowland out of river plains (17 parks) were the most common landscape categories (Fig. 3).

Alien species richness

In total, we found 242 alien taxa (escapes from cultivation within the parks and arrivals from the surroundings). Twenty-one of them were newly recorded as escaping from cultivation in the Czech Republic, seven were cultivars of native taxa, and 26 regional aliens (i.e. native taxa outside their natural distribution area in the Czech Republic). These species represented 179 genera in 73 families. The most represented genera were *Prunus* (incl. *Cerasus*, *Laurocerasus*, *Padellus*, *Padus*) (10), *Lonicera* (5), *Acer* (5), *Sedum* (4), and *Spiraea* (4), and prominent families comprised *Rosaceae* (37), *Asteraceae* (22), *Fabaceae* (11), *Lamiaceae* (11) and *Poaceae* (11) (Electronic Appendix 2). On average, there were 17.0±9.6 (mean ± S.D.) taxa per park that escaped from cultivation, of which 13.0±7.2 were neophytes and 3±2 archaeophytes (with a maximum of 37 neophytes and 12 archaeophytes). From all aliens recorded, 11.0±6.3 taxa were classified as park escapees and 6.0±3.0 as other escapees.

The most abundant taxa were *Hedera helix* (regional alien) and *Impatiens parviflora*; in 17 parks, their populations covered more than 5000 m^2 (Electronic Appendix 2).

Symphoricarpos albus and *Robinia pseudoacacia* were also abundant aliens with populations larger than 5000 m^2 in 10 and six parks, respectively (Electronic Appendix 4).

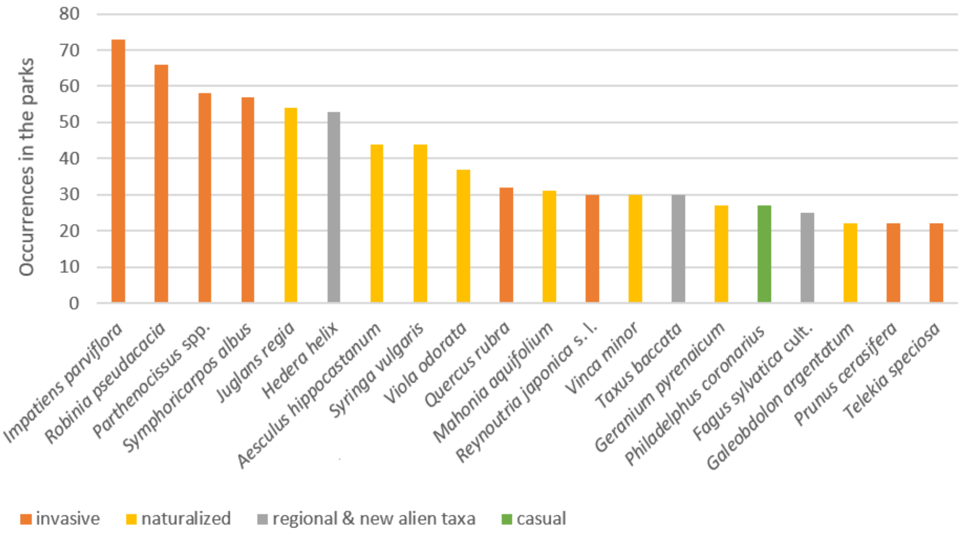

Fig. 4: *Number of occurrences for the top 20 taxa spreading within the parks. The colours are indicative of invasion status.*

The most frequent taxon was *Impatiens parviflora*, which occurred in 73 parks (i.e. more than 65% of all surveyed; Fig. 4). Other high ranking taxa in terms of frequency were mostly woody species (Fig. 5). Of the taxa recorded with the highest frequency, *Robinia pseudoacacia* (present in 59% of the parks), *Vinca minor* (27%), and *Galeobdolon argentatum* (20%) spread via vegetative means. In comparison, *Juglans regia* (48%), *Quercus rubra* (29%), and a regional alien *Taxus baccata* (27%) spread via generative diaspores and *Reynoutria japonica* s.l. (27%) by vegetative fragments. For 12 taxa, both means of spread are combined (see Electronic Appendix 2), among them *Parthenocissus* spp. (52%) and *Hedera helix* (47%) have the highest frequency (Electronic Appendix 2).

Alien taxa classified as naturalized or invasive in the Czech Republic were recorded as escaping from cultivation in 69% of the parks sampled, while casual aliens in only 18%. The most represented life forms were perennial (21.3%) and woody species (shrubs 18.3%, trees 19.9%). The most frequently recorded naturalized or invasive alien perennials were *Viola odorata* (33% of parks), *Reynoutria japonica* s. l. (27%), and *Geranium pyrenaicum* (24%) (Figs 4, 5).

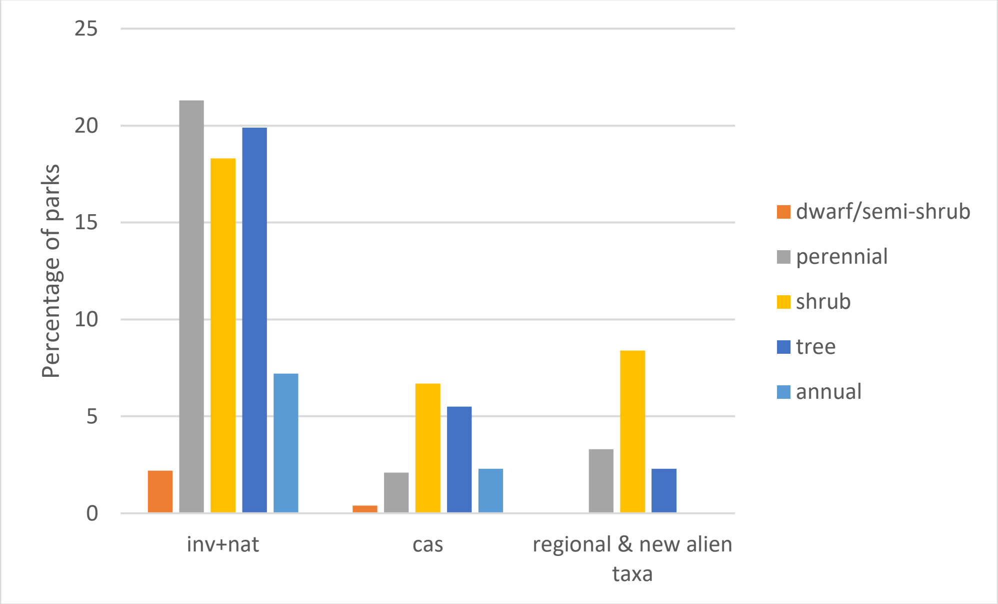

Fig. 5: *Frequency distributions of taxa grouped according to life forms and stage of the invasion process; invasive and naturalized (inv+nat) and casual (cas); regional aliens and newly recorded aliens are treated together (regional & new alien taxa).*

Native and threatened plants species richness

We recorded 421 native taxa and assigned them to 12 categories of prevailing habitat types (Electronic Appendix 3). Among them, 100 were Red-List taxa: four critically threatened taxa – C1, 23 endangered taxa – C2, 40 vulnerable taxa – C3, and 33 taxa with lower risk – C4. In total, there were 163 individual records of threatened taxa in the 75 parks sampled. The highest number of threatened taxa were found in Nové Hrady (24 taxa, excluded from the analysis as an outlier; Electronic Appendix 3). The most threatened species (C1) were *Carex buxbaumii*, *Dactylorhiza incarnata*, *Orchis palustris* (all three in Liblice), and *Pulicaria dysenterica* (Lednice park).

In terms of habitats, the highest number of threatened taxa (40) was found in wet lowland continental meadows, followed by wetlands (29) and ruderal habitats (26) (Electronic Appendix 3).

Patterns in the distributions of alien species

The forward selection of factors from the canonical correspondence analysis revealed that only altitude, English landscape and seminatural parts of the park can be linked to the observed composition of alien taxa (Table 1, Fig. 6). All variables explained 5.2% of the total variation in the data. The variables related to climate (PCA scores; Electronic Appendix 6) accounted for 61.9% of the explained variation (3.2% of the total variation; F = 1.7; P = 0.002) while park attributes accounted for 57% (3%; F = 1.6; P = 0.002) and 19% (1%; F = 1.8; P = 0.002) was shared between the groups. Explanatory variables related to climate (Electronic Appendix 6, Table 1) accounted for 61.9% of the explained variation (3.2% total variation; F = 1.7; P = 0.002) while park attributes accounted for 57% (3%; F = 1.6; P = 0.002) and 19% (1%; F = 1.8; P = 0.002) was shared between the groups.

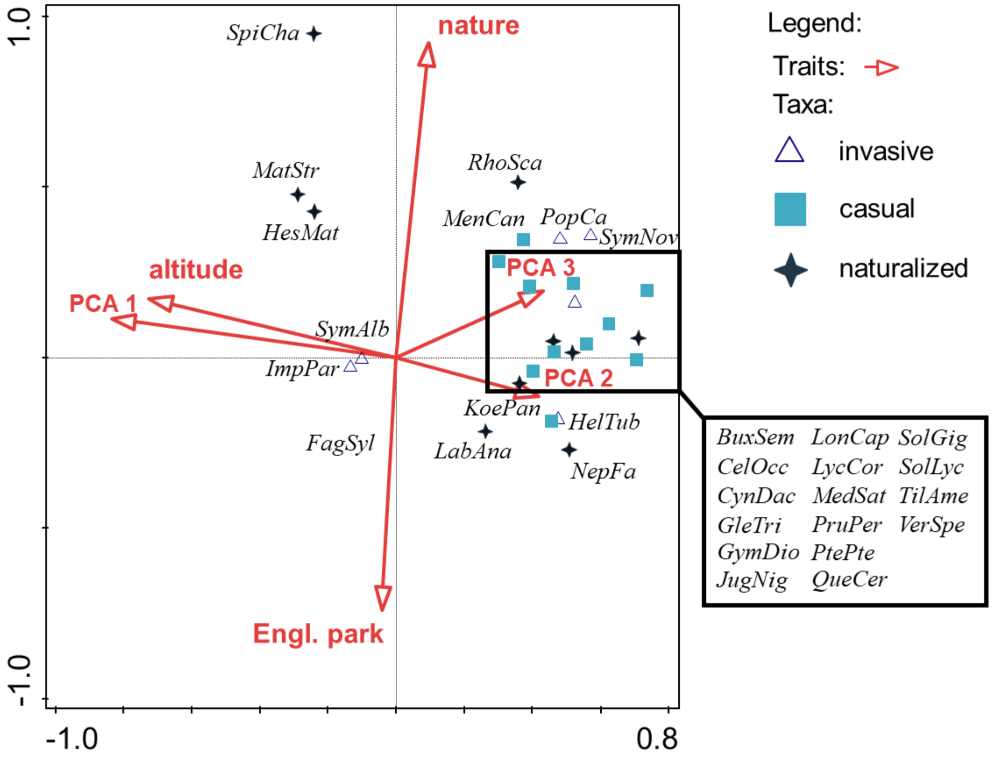

Fig. 6: *Canonical correspondence analysis of species compositions with the effects of park attributes and climate. Arrows: English park stands for the percentage area covered by this part of the parks, nature for the area covered by seminatural vegetation; PCA 1–3 represent PCA scores for climatic variables (see Electronic Appendix 6). The invasion status of taxa is shown by different symbols. Abbreviation of taxa:* BuxSem–*Buxus sempervirens*, CelOcc–*Celtis occidentalis*, CynDac–*Cynodon dactylon*, FagSyl–*Fagus sylvatica* cultivars, GleTri–*Gleditsia triacanthos*, GymDio–*Gymnocladus dioica*, HesMat–*Hesperis matronalis*, HelTub–*Helianthus tuberosus*, ImpPar–*Impatiens parviflora*, JugNig–*Juglans nigra*, KoePan–*Koelreuteria paniculata*, LabAna–*Laburnum anagyroides*, LonCap–*Lonicera caprifolium*, LycCor–*Lychnis coronaria*, MatStr–*Matteuccia struthiopteris*, MedSat–*Medicago sativa*, MenCan–*Menispermum canadense*, NepFa–*Nepeta ×faasenii*, PopCa–*Populus ×canadensis*, PruPer–*Prunus persica*, PtePte–*Pterocarya pterocarpa*, QueCer–*Quercus cerris*, RhoSca–*Rhodotypos scandens*, SolGig–*Solidago gigantea*, SolLyc–*Solanum lycopersicum*, SpiCha–*Spiraea chamaedryfolia*, SymAlb–*Symphoricarpos albus*, SymNov–*Symphyotrichum novi-belgii* agg., TilAme–*Tilia americana*, VerSpe–*Verbascum speciosum*.

Table 1: Variables affecting the distribution of alien taxa in the parks. Percentage of explained variation, P-values and P_{adj} (after Bonferroni correction) resulting from forward selection in partial canonical correspondence analysis are shown. The variables are rank according to the explained variation.

	Explained variation (%)	P-value	P_{adj}
Park attributes			
Altitude	2.9	0.002	0.014
Seminatural (percentage of area with seminatural vegetation)	2.1	0.002	0.014
English park (percentage of an English landscape park area)	1.8	0.004	0.028
Climate variables			
PCA 1	3.2	0.002	0.006
PCA 3	1.9	0.002	0.006
PCA 2	1.8	0.002	0.006

How frequent alien taxa were in parks depended on their status; invasive taxa occurred on average in 18.2± 21.7 (mean ± S.D.) parks while other (casual and naturalized) in 5.0±8.5. Invasive shrubs were the most frequently recorded group – *Parthenocissus* spp. and *Symphoricarpos albus* were present in 57 and 58 parks, respectively (Terminal node 4; Fig. 7). Among other life forms, species with sedentary clonal spread such as *Robinia pseudoacacia* or *Helianthus tuberosus* were the second most frequently recorded group, with an average of 42.6±30.8 occurrences (Terminal node 3; Fig. 7).

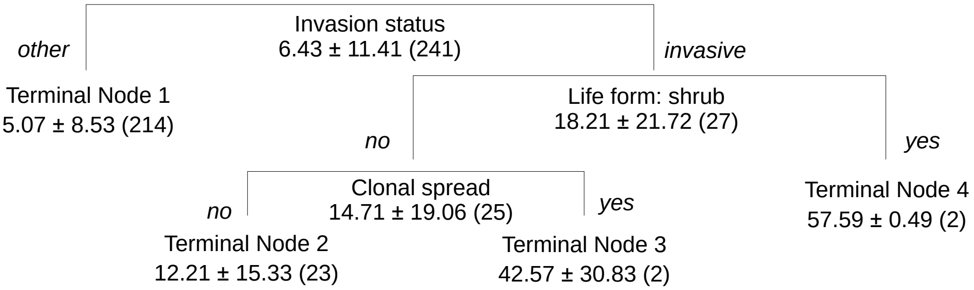

Fig. 7: *Regression tree showing important factors influencing the frequency of alien taxa recorded in the parks.*

Patterns in the distributions of threatened plants

The number of habitats in which at least one threatened taxa was recorded decreased with the proportion of area of English landscape park (Fig. 8A; $F_{1.73} = 12.19$, $P < 0.001$, $t = -3.491$) and increased with the proportion of park area covered by seminatural habitats (Fig. 8B; $F_{1.73} = 20.06$, $P < 0.001$, $t = 4.479$). Other components of the park's structure had no significant effect on the distribution of threatened taxa.

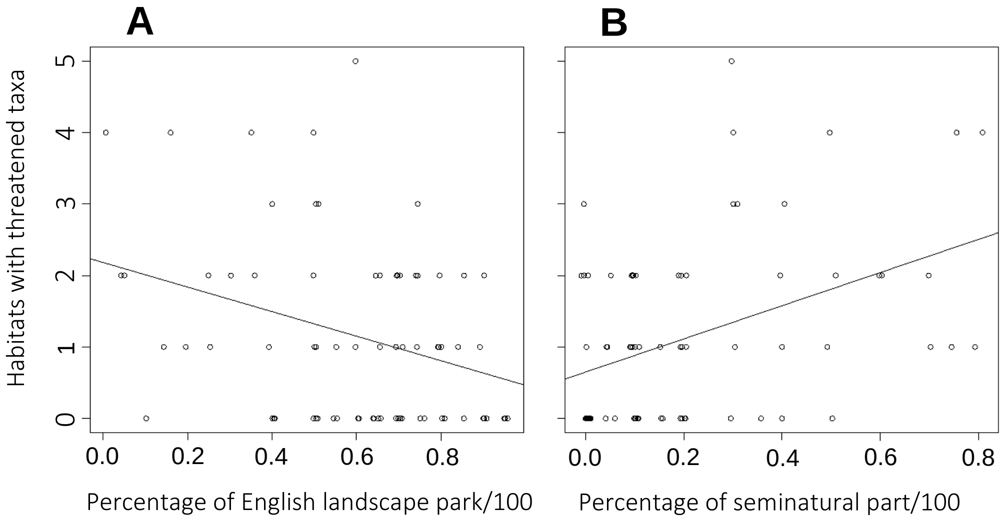

Fig. 8: *Relationships between the number of habitats harbouring threatened taxa for the proportion of parks structured by English landscape (A) and seminatural parts of parks (B).*

The role of parks in the invasion process

The number of escaping taxa significantly depended on the proportion of recorded taxa with different invasion status in the park (i.e. casual: $z = -4.131$, $P < 0.0001$; naturalized: $z = -3.354$, $P < 0.001$, invasive: $z = -5.458$, $P < 0.0001$, neophytes: $z = 4.777$, $P < 0.0001$), but not on park attributes. Using the Akaike's Information Criterion (AIC), we found that the final model provided best fit (AIC = 368.8; df = 5), unlike the maximal model (AIC = 371.7; df = 8) (see Electronic Appendix 7 for all model parameters). The relationship is increasing when alien plants spread from parks to the surrounding and decrease with increasing proportion of alien arriving into the parks among the entire park alien flora.

Discussion

Are alien species spreading from parks?

Our study provides two contrasting perspectives on spontaneous flora of chateau parks that are typical features of central-European landscapes. The parks represent sources of alien taxa escaping from cultivation but also serve as habitats harbouring threatened native taxa. Across the 89 surveyed parks, we recorded 242 alien taxa escaping from ornamental plantings. Some parks contain populations of locally invading species (e.g., *Cicerbita macrophylla*, *Tanacetum macrophyllum*, or *Scutellaria altissima*) that have not yet spread into the surroundings. Other escaping taxa are shared with home gardens, such as *Telekia speciosa* (Pergl et al. 2020), exhibiting a trend to expand in unmanaged sites. To assess whether parks serve as a source of alien plants for open landscapes, we combined our data with distribution data in the Pladias database. This source includes more than 13 million records of ~4900 taxa (species, subspecies, varieties, and hybrids) representing 3713 species from the Czech Republic (Kaplan et al. 2015, 2016a, b, 2017a, b, 2018a, b, 2019a, b; Wild et al. 2019). For 85 common alien taxa in the Czech Republic, we compared their distribution in Pladias with their distribution in the surveyed parks (Electronic Appendix 5).

This analysis revealed that, for example, *Impatiens parviflora* is a common invasive neophyte in the parks (Fig. 4). Still, as it is widespread in the whole country, the role of parks for its invasion is negligible because park occurrences account for only 3.5% of Pladias grid cells from which it is recorded (Electronic Appendix 5). In contrast, the taxa of *Parthenocissus* are reported from 20% (504) of grid cells in Pladias but occur in 71 grid cells in parks (14% of its overall distribution). Therefore, parks are important for its spread and this finding is also true for planting *Parthenocissus* in private gardens (Pergl et al. 2016b). In a similar vein, *Phytolacca esculenta*, an emerging alien in Europe (Martan and Šoštarić 2016), was recorded in 10 grid cells with parks out of 41 grid cells in Pladias (i.e. 24%) and *Gymnocladus dioicus* in 7 out of 9 (78%). Hence, their presence in parks is an important factor in spreading these taxa (Electronic Appendix 5).

The most represented family in parks was *Rosaceae* (37 taxa), while in the private gardens it was *Asteraceae* (Pergl et al. 2016b). In both studies, there was a high proportion of *Lamiaceae* and *Poaceae*. In the parks, *Fabaceae* taxa were over-represented compared to gardens due to the popularity of woody species belonging to this family in park compositions (Electronic Appendix 2; Pergl et al. 2016b). In terms of the overall taxonomic composition of alien plants in the Czech Republic (Pyšek et al. 2012b), the representation of *Asteraceae* and *Poaceae* in parks is comparable, while *Brassicaceae* is less frequent in parks and gardens than in the whole alien flora of the country.

Parks and other ornamental plantations are potential sources of future invasion (Dullinger et al. 2017; Haeuser et al. 2018). Based on our survey, we report 20 new alien taxa in the Czech Republic – *Acer opalus* subsp. *obtusatum*, *Aesculus parviflora*, *Campsis radicans*, *Caragana frutex*, *Festulolium* sp., *Gymnocladus dioica*, *Hibiscus syriacus*, *Ilex aquifolium*, *Kerria japonica*, *Lonicera maackii*, *Lonicera maackii* hybrids, *Menispermum canadense/M. dauricum*, *Parietaria lusitanica*, *Pinus ponderosa*, *Prunus triloba*, *Pterocarya pterocarpa*, *Rhododendron luteum*, *Tilia americana*, *Toxicodendron radicans*, and *Yucca filamentosa.* Based on Hlásná Čepková et al. (2016), we consider as an alien also *Vinca minor*, a species that was previously considered native. Additionally, the invasive behaviour of some species (e.g., *Lychnis coronaria* and *Stachys byzantina*) may lead to updating their invasion status as currently given in the national catalogue of alien flora (Pyšek et al. 2012b) (Electronic Appendix 2).

Woody species and perennial herbs: successful life forms to escape from cultivation

Many ornamental plants can easily escape from cultivation and spread, the most successful life forms being woody species and perennial herbs. Ten of the 20 most commonly escaping aliens in parks form clonal stands soon after being planted and can easily propagate by vegetative means. Trees are the most frequently planted life form in parks (Hieke 1984, 1985; Pacáková-Hošťálková 2004) and are also the most frequently escaping taxa, as previously reported for e.g., *Ailanthus altissima* and *Robinia pseudoacacia* (Kowarik and Säumel 2007; Cierjacks et al. 2013), with a potential for long-distance dispersal by rivers or transportation corridors. Globally, trees and shrubs make up 32% of naturalized taxa (Pyšek et al. 2017b). Another successful life strategy is a non-clonal tree with large seeds and robust seedlings, such as *Juglans regia* (Tomšovic 1990).

Our data shows that the most commonly escaping ornamental taxa are shrubs, many of them currently classified as casual aliens in the Czech Republic (Pyšek et al. 2012b). These shrubs reproduce vegetatively, form dense stands, tolerate a wide range of environmental conditions, and are rather resistant to management, which generally makes them successful invaders (Richardson and Rejmánek 2011). Examples of alien shrubs with a strong reproductive ability and invasion potential that spread spontaneously in parks (Möllerová 2005) include *Mahonia aquifolium*, *Symphoricarpos albus*, and *Syringa vulgaris* (Fig. 4). *Philadelphus coronarius*, classified as a casual alien in the Czech Republic (Pyšek et al. 2012b), seems to be at the onset of more extensive spread and cultivation in large parks can serve as a source (Hieke 1984, 1985).

Similarly to private gardens (Pergl et al. 2016b), many native ornamentals can escape from cultivation in parks. Traits that make these taxa competitive and facilitate the establishment and spread, such as tall and robust perennials with good seed germination or clonal spread, are favoured by gardeners regardless of whether such species are native or alien. Species possessing these traits have a strong potential, following the escape, to establish in other ornamental garden beds, and then in various seminatural habitats within and near parks (Barošová and Baroš 2009; Kutlvašr et al. 2019). *Vinca minor* and *Hedera helix* (which are native in some regions of the Czech Republic) are frequently planted in private gardens and escape from cultivation (Schulz and Thelen 2000; Dlugosch 2005; Pergl et al. 2016b). The high frequency of occurrence of these species in the chateau parks was observed before (Hieke 1984, 1985), and corresponds with a high invasion potential and negative impact on species diversity of woody vines (Schulz and Thelen 2000; Dlugosch 2005; Liu et al. 2008; Panasenko and Anishchenko 2018).

The role of park structure and management in naturalization

The characteristics of the park play a role in determining the occurrence and diversity of alien plants. More aliens were recorded in parks with large seminatural parts (Fig. 6), rather than in English landscape parks and French formal gardens where many ornamental species are planted in beds and swards (Mukerji 1997; Woudstra and Hitchmough 2000).

We show that the proportion between the numbers of alien taxa escaping from cultivation and those arriving from outside the parks depends on the invasion status of the park's alien flora. The more invasive taxa are present in the park, the greater the contribution of arrivals from the surroundings to its alien flora, and vice versa – the number of alien taxa arriving from the outside declines with greater representation of casual and naturalized aliens inside the park. This pattern may result from lower overall maintenance in abandoned parks with many invasive taxa, where the horticultural management is focused on selected invasive and problematic species (Lososová et al. 2012a). Management actions differ not only among parks but also concerning individual habitats within the same park (Schroeder and Green 1985; Welch 1991; Speak et al. 2015). Less intensive management is a factor in secluded parts of parks such as areas in the vicinity of park boundaries, ruderal habitats such as compost heaps, or wall remains where pioneer woody species and competitive perennials find suitable conditions to spread and invade (Jim 2008; Lososová et al. 2012b; Petřík et al. 2019).

Attributes of the parks and climatic factors

In several studies, altitude has been documented as an important factor affecting the presence and spread of alien taxa (e.g., Becker et al. 2005; Alexander et al. 2009; Pyšek et al. 2011b). Climatic variables were also reported as important; for example, the number of spreading neophytes was associated with temperature (Lososová et al. 2012a). Besides, several park attributes related to its structure (i.e. representation of the French formal garden, English landscape park, and seminatural vegetation, and the extent of technical support areas) also had a highly significant effect on alien taxa composition.

Some thermophilous taxa could spread into seminatural vegetation due to climate change (Kowarik 2005b; Barošová and Baroš 2009). Such taxa were already reported to escape more often now than in the past. Niinemets and Peñuelas (2008) reported potentially invasive species commonly used in horticulture that are likely to spread due to global warming. However, the risk of naturalization of alien taxa depends on the interaction of climate suitability and land cover (Dullinger et al. 2017).

Parks harbouring threatened taxa

Seminatural habitats in the parks studied harboured some rare and threatened taxa (Fig. 8); this may include species that disappeared from the surrounding degraded landscapes (Corlett and Westcott 2013) and found refuge inside the parks where they occur in seminatural habitats such as species-rich forests or seminatural grasslands typical of English landscape parks (Šantrůčková et al. 2017). However, our data shows that seminatural vs. English-landscape parts of the parks have different effects on rare taxa – their occurrence increases in the seminatural and decline in the English parts of the parks. Rare and threatened taxa usually occur in the close-to-nature parts of the park with seminatural habitats persisting from early modern cultural landscapes before the park's establishment. This pattern is likely due to less intense horticultural activity in seminatural parts, compared to English landscape parks, and minor impacts from visitors in these remote areas, making them suitable for many rare and threatened taxa. The spread of alien taxa should be rather sporadic in such seminatural parks (Kingston et al. 2003; Myśliwy 2008). However, our results show that alien taxa spread there too, even more so than in the English park sites (see Fig. 6). The seminatural parts of the parks are similar to other human-disturbed habitats, such as post-mining sites with extremely dry, wet, nutrient-poor, and acidic habitats that host rare and threatened taxa and represent islands of suitable habitats in otherwise homogeneous surrounding landscapes (Prach and Pyšek 2001). In the Anthropocene, the parks thus serve as biodiversity islands in urbanized and agricultural landscapes (Wilson and Peter 1988; Boinot et al. 2019). Also, native plants in the parks and gardens could also serve as genetic reservoirs for future potential in-situ recovery of threatened and vulnerable species (Roberts et al. 2007; Stojanova et al. 2020).

Supplementary material

The list of electronic appendices which are available on https://www.preslia.cz/article/11:

Electronic Appendix 1: List of parks used in this study. The table includes geographical, climatic factors, and other park attributes. Columns: French formal garden, technical support areas, seminatural areas, and English landscape parks indicate the percentage extent of each part within the park. Amount of trees represents the number of woody taxa taken from Hieke (1984, 1985) and Pacáková-Hošťálková (2004). Climatic factors were taken from Karger et al. (2017): CHELSA_bio_01 – Annual Mean Temperature [°C*10]; 02 – Mean Diurnal Range [°C]; 03 – Isothermality; 04 – Temperature Seasonality [standard deviation]; 05 – Max Temperature of Warmest Month [°C*10]; 06 – Min Temperature of Coldest Month [°C*10]; 07 – Temperature Annual Range [°C*10]; 08 – Mean Temperature of Wettest Quarter [°C*10]; 09 – Mean Temperature of Driest Quarter [°C*10]; 10 – Mean Temperature of Warmest Quarter [°C*10]; 11 – Mean Temperature of Coldest Quarter [°C*10]; 12 – Annual Precipitation [mm/year]; 13 – Precipitation of Wettest Month [mm/month]; 14 – Precipitation of Driest Month [mm/month]; 15 – Precipitation Seasonality [coefficient of variation]; 16 – Precipitation of Wettest Quarter [mm/quarter]; 17 – Precipitation of Driest Quarter [mm/quarter]; 18 – Precipitation of Warmest Quarter [mm/quarter], 19 – Precipitation of Coldest Quarter [mm/quarter]. The number of taxa within life form, invasion status, residence time (neophytes/archaeophytes/uncategorized), escaping/arriving, and the total number of aliens per park is shown.

Electronic Appendix 2: List of recorded alien taxa in the parks. The columns represents: all abbreviations of used taxa, status of naturalization; include change of status against Catalogue of Alien Plants (Pyšek et al. 2012b), family (the codes are formed by initial letters of the family name), residence time status (archaeophyte/neophyte), invasion status (invasive/naturalized/casual and x for regional aliens, several cultivars), regional abundance (estimated for each taxon using the following scale: single locality, rare, scattered, locally abundant, and common across the whole Czech Republic), mode of introduction (unintentional/intentional), origin (M – Mediterranean region, E – Europe, As – Asia, Af – Africa, AmN – North America, AmC – Central America, AmS – South America, hybrid – hybrid origin, anec – anecophyte and native for regional aliens) – all of these data were taken from Pyšek et al. (2012b), columns of sedentary clonal modules and movable diaspores are classified as: 1–the best, 3–medium and 5–without or bad spreading, life form (annual, perennial, dwarf-semi shrub, shrub and tree) and number_of_escaping (from parks), number_of_arriving (to parks) and number of overall occurrences of the taxa. The numbers 1, 10, 100 represent 3 levels of abundances from rare occurrences (ca less of 50m^2 in total) (1), abundant in few localities within park or only sparsely abundant (ca 50–5000m^2 in total) to abundant taxa occurring in area larger than 5000m^2.

Electronic Appendix 3: List of the native and threatened plant taxa in each park with levels of threat – taken from Grulich (2012) and abbreviation of the groups of native taxa in specific seminatural habitats (cl-short-cut lawns; ohf-mesic oak/oak-horbeam forest; ff-wet floodplain forest & nitrophilous fringes; ro-rocky slopes; fs-forest steppe formations; mf-mountain forest; gr-mesic semi-open tree groves; m-mesic meadows; cm-continental inundated meadows; tm-wet thistle meadows; ru-ruderal vegetation; we-wetlands).

Electronic Appendix 4: Taxa with the highest abundances in the parks – "c" means less of 50m^2 in total); "b" is in few localities within park or only sparsely abundant (ca 50–5000m^2 in total) and "a" are taxa occurring in area larger than 5000m^2. There are summarized several information about showed taxa, complete attributes are listed in Electronic appendix 2.

Electronic Appendix 5: Comparison of the distribution in the parks (covered grid cells) and in the whole Czech Republic. The Czech Republic distribution – number of grid cells (5 longitudinal minutes × 3 latitudinal minutes) is taken from Pladias; Czech Republic is covered by 2551 grid cells (Wild et al. 2019).

Electronic Appendix 6: Analysis of PCA scores for climatic variables.

Electronic Appendix 7: The role of parks in the invasion process – model parameters.

4 Case study II: Two shades of grey: effect of temperature on seed germination of the escaping ornamental species *Lychnis coronaria* and *Stachys byzantina*

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Abstract

This paper describes germination and cytological variability in two popular ornamental and potentially invasive species, lamb's ear *Stachys byzantina* and rose campion *Lychnis coronaria*. Both xerophytic species have the potential to invade natural habitats across Europe and create viable naturalised populations, with subsequent impacts on native vegetation. To assess the species' invasiveness, seeds were collected from naturalised populations and germination was recorded under different temperature regimes. Flow cytometry, used to record cytological variability, indicated that all populations of both species were cytologically homogeneous. Germination success, an important means of distribution factor in both species, was significantly influenced by temperature, with final germination of *L. coronaria* being extremely high at temperatures > 15/10 °C (98.5%) and extremely low at temperatures < 10/5 °C (2.9%). The final germination in *S. byzantina* is the highest at 22/15 °C (55.6% germinated seeds), reduced to 40.3% at 15/10 °C and to 0.3% at temperatures lower than 10/5 °C. No significant differences in final germination were observed between escaping and non-escaping populations, although there were some differences between particular populations. Our results

indicate germination temperature limits of two species whose non-native areas include Central Europe. The observed germination allows for successful generative reproduction of both species over their non-native ranges, suggesting that these species are likely to become invasive species of European grasslands soon.

Introduction

Horticulture has been an integral part of human society for centuries (Relf and Dorn 1995; Zhou 1995; Kendle and Stoneham 2014). Recently, however, the increasing influence of horticulture has made it one of the major sources of alien plant species (Dehnen-Schmutz and Touza 2008; Klonner et al. 2017; van Kleunen et al. 2018; Vojík et al. 2020). These not only contribute significantly to regional floral communities (Köppler et al. 2014; Lososová et al. 2015; Pergl et al. 2016b), they also potentially threaten biodiversity and natural ecosystems, leading to the homogenisation of the Earth's biota (Vilà et al. 2011; Price et al. 2018; Morri et al. 2019; Pyšek et al. 2020). The control and eradication of such 'invasive species' are demanding and often unfeasible (Ewel and Putz 2004; Downey et al. 2010) and, as such, it is crucial to prevent the spread of potentially invasive species before they get a hold (van Kleunen et al. 2007). Whether a species becomes invasive depends not only on the species' ecology but also on the physical characteristics of the invaded habitat and the prevalent environmental conditions (Pyšek et al. 2012a). One of the most important ecological traits to assess when investigating the potential for invasion in early spreading species are their reproduction traits, i.e. whether they can be a 'master of all traits' or if they have specific characteristics leading to their success (Pyšek 2007; Pyšek et al. 2009). Species reproducing by seed tend to be associated with habitat conditions such as light availability and temperature regime, with low temperatures limiting germination and day length influencing seedling establishment (Pepe et al. 2020). However, species that are capable of germinating at lower temperatures, with earlier timing of germination and rapid seedling growth, will have a competitive advantage over other species (Baskin and Baskin 1998). Furthermore, species with wider distributional ranges can have competitive advantages due to adaptation to different conditions of their local populations across the range. The germination of these species is usually tested in the different temperature regimes to define their germination niche breadth (Brändle et al. 2003). This parameter, combined with others (ecological niche breadth, geographic range etc.), can result in ecotypic differentiation detectable by germination tests (Donohue et al. 2010). The ecotypic differentiation represents an opportunity for increasing species' fitness (e.g. Geber and Eckhart 2007). Recent studies focused on reproduction traits have often concentrated on variability within the genetic structure of plant populations (e.g. Saad et al. 2011). High genetic and cytological diversity of introduced populations increases species survival capacity (Puillandre et al. 2008; Estoup et al. 2016). If the introduced population is small, however, it may have a low level of variability, creating a bottleneck effect that could limit its invasion success (Puillandre et al. 2008). Nevertheless, some introduced species have become invasive with a low level of genetic/cytological diversity due to a so-called ‘genetic paradox of invasion’ (Hassan et al. 2003; Dlugosch and Parker 2008b; Estoup et al. 2016), whereby genome size and polyploidy in newly spreading alien species may be the first indication of increasing variability or ongoing evolutionary processes, which could then support invasion (Meyerson et al. 2020; Wan et al. 2020). Due to polyploidization, faster germination can occur (e.g. Bretagnolle et al. 1995), which can support the spread and thus increase the invasive potential of some populations. The effect of polyploidization on the germination of invasive and potentially invasive plants has already been demonstrated (e.g. Castro et al. 2007, Pegtel 1999).

Other characteristics aside from reproduction traits have also been identified as significantly affecting invasion/naturalisation probability in ornamental taxa (Pyšek et al. 2019). For example, the horticultural success of certain species is mainly related to their charisma (e.g. colour, shape and size of bloom, or time of flowering), which affects not only global public perception but also introduction by humans and resistance to management following their escape (McNeely 2001; Shackleton et al. 2019; Jarić et al. 2020). The invasion potential of ornamental species following introduction will then be linked to their ability to grow under low maintenance (e.g. abandoned sites) and their adaptability to local conditions (e.g. temperature, humidity), such characteristics also giving the species a greater ability to escape from horticulture (Williams et al. 2010; Flory et al. 2011; Vojík et al. 2020; Kutlvašr et al. 2020). There have also been several recent cases of ornamentals spontaneously spreading due to global warming, highlighting the potential of climate change to facilitate invasions (Dullinger et al. 2017; Haeuser et al. 2018).

In this study, we describe germination and cytological variability in two popular ornamental and potentially invasive species, lamb's ear *Stachys byzantina* and rose campion *Lychnis coronaria*, whose status are casual and naturalised, respectively, in the Czech Republic (Pyšek et al. 2012b) and have spread into human-made habitats (e.g. mown lawns or grasslands). Both species are popular ornamentals worldwide due to their grey-felted leaves and easy maintenance, and have been planted in a wide range of habitats, including public parks and private gardens as well as courtyards (Dimke et al. 2008; Wade 2010; Cullen et al. 2011; Glawe and Koike 2018). Records of both species escaping from cultivation have increased in recent years, with such escapes going on to form viable populations in both artificial and semi-natural habitats (Barošová and Baroš 2009; Kutlvašr et al. 2019; Vojík et al. 2020), including narrow and broad-leaved dry grasslands and acidophilous dry grasslands. Consequently, these species can be considered as newly emerging alien species that could easily become invasive. Moreover, in the case of *S. byzantina*, hybridisation may be possible with an endangered native species, *Stachys germanica* – *Endangered* category (C2b) on the IUCN Red List of endangered species (see Grulich 2017), which is known from the literature (Dunn 1997) and which has recently been recorded in the Czech Republic (Danihelka in prep.). Hybridisation, alongside effective generative reproduction, could significantly accelerate the invasive success of *S. byzantina* by producing high performance genotypes that could rapidly colonise even unfavourable sites (see Buhk and Thielsch 2015).

Though both species originate in the Middle East, they differ in their native range (POWO 2019). It has been shown repeatedly that the probability of naturalisation success is affected by the size of a species' geographical range and its habitat range niche (e.g. Rejmánek 1996; Pyšek et al. 2009). With a native distribution centred on the Mediterranean and Central Asia, *L. coronaria* has a sizeable native range with a broad ecological amplitude (Hejný 1997; CABI 2019; Chytrý et al. 2021) unlike *S. byzantina*, which is an endemic species to Iran (Asnaashari et al. 2010). While the basic descriptive characteristics regarding biology and ecology are known for both species (see Hejný 1997; Chytrý et al. 2021), details on population variability and their ability to spread remain largely unknown.

To identify reasons for the recent spread of both species, we undertook a series of tests to assess cytological variability and *in vitro* seed germination potential. In doing so, we asked a series of questions: (1) What is the genome size variability among populations of two individual species *S. byzantina* and *L. coronaria*? (2) Is the germination of either species affected by temperature? (3) Are there any differences between escaping and non-escaping populations in seed germination? (4) Where is the temperature limit of generative reproduction of the species?

Material and Methods

Study species

Stachys byzantina C. Koch (*Lamiaceae*) is a perennial, long-felted, 20–80 cm tall herb. It is diploid (2n = 30; Hejný 1997; Lindqvist and Albert 2017; Wild et al. 2019). Originally an endemic Iranian mountain species (Asnaashari et al. 2010), it has widened its native area to include north Turkey and the Crimean Peninsula (POWO 2019). It has been introduced to Central and Western Europe, North America, Canada and New Zealand (POWO 2019). Germination characteristics of *S. byzantina* are not available; however, generative and clonal reproduction has been observed in the field (Vojík et al. 2020). Based on numerous field observations, it is obvious that the species is a polycarpic perennial, which is stated to be probably myrmecochorous (Chytrý et al. 2021) with Allium dispersal type (mostly autochory; see Sádlo et al. 2018). Information about self-fertilization is unknown but could be expected because of self-fertilization ability in the related species *Stachys germanica* (Minachilis et al. 2021).

Lychnis coronaria (L.) Desr. (*Caryophyllaceae*) is a short-lived, white felted, monocarpic perennial plant, generally grown as a biennial or annual, 30–60 (–100) cm tall (Jiang et al. 2016; Moravcová et al. 2010). It is diploid (2n = 24; Hejný 1997; Jeelani et al. 2011; Zonneveld 2019). It originates from the Mediterranean, Middle East and the whole of Central Asia. The northern boundary of the native range reaches southern Slovakia. It is non-native in Central and Western Europe and North and South America (Brazil, Chile; Hejný 1997; POWO 2019). The final germination percentage of *L. coronaria* is 100% under tested laboratory conditions (12 hours in light/12 hours in the dark; 25/10 °C, 20/5 °C and 15/5 °C), with seedling establishment reaching almost 60% (Moravcová et al. 2010). Life-history strategy of the species was classified as CSR (Klotz and Kühn 2002) with an Allium dispersal type (mostly autochory; Sádlo et al. 2018; Klotz S. & Kühn I. 2002), non- myrmecochorous (Chytrý et al. 2021). Information about self-fertilization is unknown but could be expected due to self-fertilization in related species *Lychnis flos-cuculi* (Dulya and Mikryukov 2016).

Population genome size variability

Within sampling design for assessment of genome size, we used 7 populations for *L. coronaria* and 10 populations for *S. byzantina* (see Supplementary table); all these populations were also selected for germination experiments (at random) – for genome size analysis, fresh leaves were used from particular maternal plants in populations from the Czech Republic. The two populations from the native range (LC5 – Istanbul, TR and SB10 – Tehran, IR) were germinated first and then seedlings were used for the genome size analysis.

To assess genome size homogeneity, the DNA weight per nucleus (genome size; expressed in picograms [pg]) was determined for each study population (see Supplementary table) using flow cytometry, based on a two-step procedure using Otto I and II buffers (Otto 1990). As its genome size (2C DNA = 3.38 pg) is close to that of the species studied, the common daisy *Bellis perennis* was used as an internal reference standard (Schönswetter et al. 2007). In each case, 1 cm^2 of fresh leaf tissue from the study species and from *B. perennis* were macerated together with a sharp blade and placed in a Petri dish containing 0.1 ml of ice-cold Otto I buffer (0.1 M citric acid monohydrate, 0.5% v/v Tween 20) for approx. 90 s, after which the suspension was filtered through a 42 µm nylon mesh. Nuclei within the filtered suspension were then stained with 1 ml of Otto II buffer (0.4M $Na_2HPO_4 .12H_2O$) supplemented with 1 ml of DAPI stock solution (DAPI 10 mg dissolved in 100 ml H_2O) + 50 µl ß-mercaptoethanol (2 µL/mL). Each sample was then incubated at room temperature for 10 min and analysed using a Sysmex-Partec CyFlow SL equipped with a green solid-state laser flow cytometer (532 nm, 100 mW output power; Sysmex Partec GmbH, Görlitz, Germany).

Seed collection and germination experiments

Two germination experiments were undertaken, the first assessing the effect of temperature regime on seed germination, and the second assessing differences in final germination between escaping and non-escaping populations. The populations were selected randomly in the Czech Republic at sufficient distances from each other (more than 500 m) to not collect the seeds from one population repeatedly (detailed locations are in Supplementary table). Seeds were collected from the 10 most viable and fully matured plants per population. The required number of healthy-looking and fully sized seeds was selected for germination experiments (i.e. *L. coronaria*: 360, *S. byzantina*: 270 seeds). The seeds from the Czech Republic were collected at the end of the growing period 2017 (*L. coronaria*) and 2018 (*S. byzantina*). Moreover, the seeds from three distant populations were also collected in defined years – one from the native range of *L. coronaria* in 2017 (LC7; Istanbul, Turkey), one from the non-native range of *S. byzantina* in 2018 (SB9; Dublin, Ireland), and one from the native range of *S. byzantina* in 2018 as well (SB10; Tehran, Iran). Because the longevity of the seeds can be significantly different (e.g. between families or localities; Walters et al. 2007), we used fresh seeds for the experiments, which were first dried at room-temperature (ca. 20 °C) for a week. Furthermore they were dark-stratified at 5°C for six weeks to simulate the winter period in Central Europe (e.g. Mandák et al. 2006; Kołodziejek 2019), then surface-disinfected in 70% (v/v) ethanol for 1 min and immersed in 50% (v/v) bleach solution for 1 min as well (< 5% sodium hypochlorite; Ślesak et al. 2017). The seeds were then incubated in Petri dishes on three-layers of filter paper dampened with distilled water. Seeds were kept under a simulated daily light regime consisting of 14 hours light and 10 hours dark with four different temperature regimes, 22/15 °C, 15/10 °C, 10/5 °C and 5/3 °C. The 5/3 °C regime was used only for *L. coronaria* as our previous screening experiment had shown that *S. byzantina* seeds stop germinating at 10/5 °C. Each population sample consisted of 30 seeds in three replicates for each group (escaping vs non-escaping) or treatment (temperature regimes). All germinated seeds were counted and recorded at two-day intervals for 30 days. The experiment was performed in complete randomized blocks and the individual temperature regimes were applied in a factorial design.

To evaluate the effects of temperature regime on seed germination, we collected seeds from four *L. coronaria* populations and four *S. byzantina* populations. The populations were selected on semi-shaded human-made habitats (e.g. backyards, gardens and parks) in environmental conditions typical for central Europe (average precipitation 450–712 mm, 7–9 °C; see Supplementary table) for reducing the differences among populations. Three germination traits were measured: i) final germination, calculated as the total number of germinated seeds at the end of the germination period, ii) germination rate, calculated as the number of germinated seeds in each time interval, and iii) germination delay (hereinafter GD), calculated as the number of days until the first germination recorded (Cerabolini et al. 2004; Pepe et al. 2020).

To compare differences in final germination between escaping and non-escaping populations (only this germination trait was measured here), seeds were collected from maternal plants, i.e. even in the case of escaping populations maternal plants growing in gardens were sampled (the cultivated source populations). The sampling design was the same as for the first trial and the populations were selected independently on environmental conditions. Both groups (escaping vs. non-escaping) were sampled in the same year for particular species (*L. coronaria* – 2017, *S. byzantina* – 2018). Eight *S. byzantina* populations were sampled, four escaping and four non-escaping, and six *L. coronaria* populations, four escaping and two non-escaping (see Supplementary table). Escaping populations were characterised by intensive spontaneous spreading into surrounding semi-natural grasslands, while non-escaping populations showed no sign of spreading, despite suitable habitats for spontaneous spreading being available. Differences in final germination between escaping and non-escaping populations were tested using seeds grown in the 22/15 °C regime, as this was shown to be optimal for both species during the first experiment of this study, where it was tested in different temperature regimes (see above).

Data analysis

Differences in final germination between temperature regimes were tested by comparing observed ‘final germination’ counts using generalized linear mixed-effect models (GLMM) for the negative binomial family. Temperature regimes were included as a fixed factor. The same models were used to assess differences in final germination between escaping and non-escaping populations of each species, using the number of germinated seeds as the response variable and escaping/non-escaping as the predictor (fixed effect). GLMMs were also used for GD analyses using the number of days until first germination recorded as a response variable and different temperature regimes as a predictor (fixed effect). Particular populations were included as a random effect and hierarchically nested within the fixed effect in all GLMMs. Full models were simplified using posterior comparisons and the most plausible models were selected based on the Akaike information criterion (Akaike 1978; Crawley 2012), using backward selection.

Differences in germination rate were tested using MANOVA (multivariate ANOVA) due to the violation of the sphericity assumption (assumption for the use of repeated measures ANOVA), where the number of germinated seeds at a particular time was used as the response variable, temperature regimes were multivariate used as predictors (Mardia et al. 1979; Lepš and Šmilauer 2016). All analyses were performed using R software (R Development Core Team 2019) and Statistica 13 (TIBCO 2017), with differences considered significant at $P \leq 0.05$.

Results

Population genome size variability

Flow cytometric analysis confirmed genome size homogeneity in all populations of both species in their non-native range (Fig. 9), with *S. byzantina* populations ranging from 1.55 to 1.63 pg (2C-values), and *L. coronaria* populations ranging from 6.40 to 6.58 pg (2C-values) (see Supplementary table).

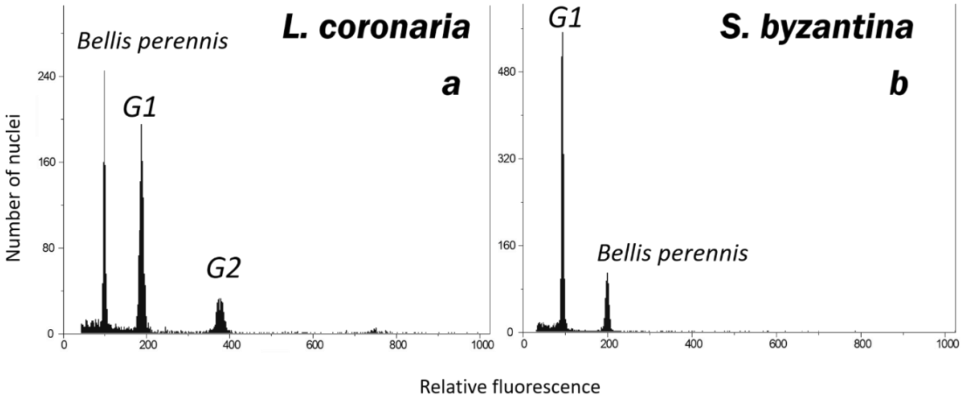

Fig. 9: *Flow cytometric histograms (nuclei stained with propidium iodide) for Lychnis coronaria and Stachys byzantina, with Bellis perennis used as an internal reference standard for both species (placed at 100 relative fluorescence for L. coronaria (a) and at 200 relative fluorescence for S. byzantina (b)). The G1 peak represents nuclei with DNA 2C, while the G2 peak represents nuclei with DNA 4C (G2 phases of the cell cycle with double the amount of DNA present represents noise in the sample). The cytogrammes of all sampled individuals of each species are similar, thus the populations are homogenous in genome size.*

Seed germination

Lychnis coronaria

Temperature had a highly significant impact on final germination, with posteriori comparisons distinguishing two levels of significance, i.e. <10/5 °C (x̄ ± SE; 0.88 ± 1.83; SE: Standard Error of Mean) and > 15/10 °C (29.54 ± 0.91) (average per Petri dish; Fig. 10a). While germination at temperatures < 10/5 °C was low, with final germination at 2.9% (21 of 720 seeds germinating), final germination at temperatures > 15/10 °C was exceedingly high at 98.5% (709 of 720 seeds germinating).

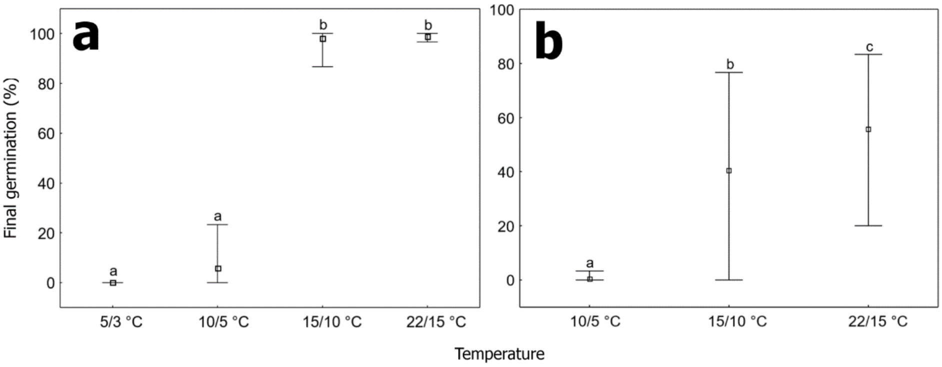

Fig. 10: *Influence of temperature on final germination of both species: Lychnis coronaria (a) showing two contrasting responses between treatment levels 5/3 °C and 10/5 °C vs. 15/10 °C and 22/15 °C; Stachys byzantina (b) did not germinated in level 5/3 °C. Squares = means of final germinated seeds, whiskers = min-max; different letters at the end of each treatment row indicate a statistically significant difference (P < 0.05).*

GD was significantly affected by temperature. Seeds germinated later at lower temperatures, with a GD of three days at 22/15 °C, three days at 15/10 °C, nineteen days at 10/5 °C, and no germination at 5/3 °C. The seed germination rate over the first twelve days differed significantly, primarily due to population LC2 having a lower germination rate at 22/15 °C, though this difference later vanished (Fig. 11).

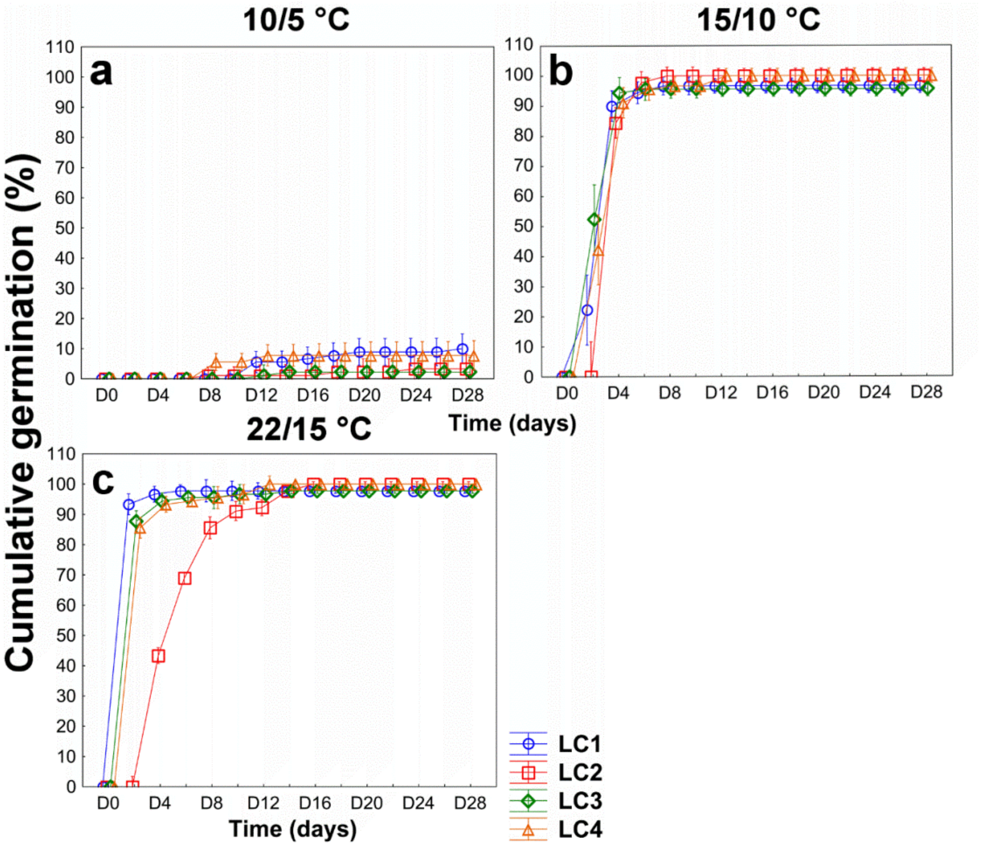

Fig. 11: *Time course for Lychnis coronaria seed germination under different temperature regimes (a: 10/5 °C; b: 15/10 °C; c: 22/15 °C). The results for the 5/3 °C temperature regime are not shown as no seeds germinated, giving a final germination of 0%. LC1–LC4 represent particular localities of sampled populations (see Supplementary table). Vertical bars denote +/- standard errors.*

All detailed results are merged in Table 2.

Table 2: Results of all germination trials of Lychnis coronaria; df = degrees of freedom; Significant effects (P < 0.05) are indicated in bold

Tested parameter	df	Test statistics	P-value
Temperature regime	1, 43	z = 15.894	**< 0.001**
Germination rate	42, 93	F = 4.335	**< 0.001**
Germination delay	2, 43	z = -12.784	**< 0.001**
Escaping	1, 5	z = 0.157	> 0.05

Stachys byzantina

As with *L. coronaria*, temperature had a highly significant impact on final germination. Likewise, germination was low at temperatures < 10/5 °C, with a final germination of 0.3% (1 of 360 seeds germinating), but increased with increasing temperature, with final germination at 15/10 °C reaching 40.3% (145 of 360 seeds germinating) and the highest final germination being recorded at 22/15 °C at 55.6% (200 of 360 seeds germinating) (Fig. 10b). No seeds germinated at 10/5 °C (apart from one seed from the SB3 population).

GD was significantly affected by temperature. Seeds germinated later at lower temperatures, with a GD of two days at 22/15 °C, seven days at 15/10 °C and just one seed germinating at 10/5 °C.

There were significant differences in seed germination between temperatures over time, with the strongest effect observed at higher temperatures, i.e. 12.08 ± 8.21 at 15/10 °C and 16.70 ± 5.93 at 22/15 °C (average per Petri dish). Populations SB1 and SB4 both displayed a higher germination rate than the other populations, with almost all seeds germinating during the first ten days of the experiment (Fig. 12).

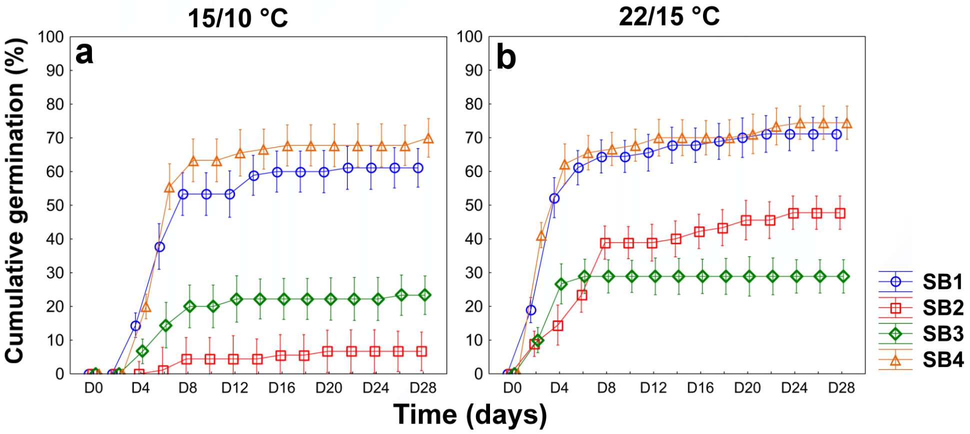

Fig. 12: *Time courses of Stachys byzantina seed germination under different temperature regimes (a: 15/10 °C; b: 22/15 °C) (results for 10/5 °C temperature regime are not shown as only one seed germinated, giving a final germination of 0.3%). SB1–SB4 represent particular localities of sampled populations – see Supplementary table. Vertical bars denote +/- standard errors.*

Difference in final germination between escaping and non-escaping populations

There was no significant difference in final germination between escaping and non-escaping populations of particular species.

All detailed results are merged in Table 3.

Table 3: Results of all germination trials of Stachys byzantina; df = degrees of freedom; Significant effects (P<0.05) are indicated in bold

Tested parameter	df	Test statistics	P-value
Temperature regime	2, 30	z = 4.959	**< 0.001**
Germination rate	28, 40	F = 4.367	**< 0.001**
Germination delay	2, 30	z = -6.901	**< 0.001**
Escaping	1, 7	z = -0.073	> 0.05

Discussion

Detailed studies of generative reproduction and population ecology, including studies of genetic and cytological variation, have proved to be promising tools providing important information on the determinants of species invasiveness (Moravcová et al. 2010; Suda et al. 2015; Pyšek et al. 2018). Standardised studies on the germination characteristics of plant taxa (Grime et al. 1981; Grime et al. 1988), for example, help clarify the capacity for spreading and the potential for establishment of new populations (Pyšek and Richardson 2007).

In the present study, we describe cytological variability and germination in two newly spreading species, *S. byzantina* and *L. coronaria*. The seeds of both species displayed optimal germination at temperatures between 15/10 °C and 22/15 °C, with *S. byzantina* closer to 22/15 °C (Figs. 11 and 13). Hence both species, which have similar spreading potential but different native ranges, proved highly successful at germinating under temperature conditions typical of Central Europe (Iran, Ireland, and Turkey were only sampled for testing cytological homogeneity). Differing environmental conditions are usually the main reason plants fail to survive or spread in their non-native range (Richardson et al. 1994; Mack 1996; Richardson et al. 2000); thus, their ability to germinate successfully in this temperature range allowed them to overcome a major barrier between their native and non-native ranges. Though *L. coronaria* was previously classified as non-invasive in the basic IAS screening study of Moravcová et al. (2010), the species has recently begun spreading, with multiple observations of the species escaping from plantations (Kutlvašr et al. 2019; Vojík et al. 2020). Similarly, *S. byzantina* was originally classified as casual in the study of Pyšek et al. (2012b), but has recently shown similar spreading behaviour as *L. coronaria* in the field.

Germination, and timing of germination, depend heavily on a combination of factors, including light, temperature, and dormancy (Hoyle et al. 2015), with external temperature and available light in particular regulating the enzymes directly involved in germination (Baskin et Baskin 1998). Consequently, these two key factors formed the basis of our study into the germination capabilities of *S. byzantina* and *L. coronaria*.

For *Lychnis coronaria*, a species with extremely high final germination at 22/15 °C (almost 99% of seeds germinated; see Fig. 11), rapid germination within the first six days of the experiment, and a germination rate that does not differ between populations of the species, our results were similar to those of Moravcová et al. (2010). However, we disagree with their suggestion that this species does not display invasive behaviour. The species' high final germination under conditions typical of its non-native range and its rapid growth both increase its ability to invade new environments (Beerling and Perrins 1993; Gioria et al. 2016), and numerous recent recordings of localised spreading in the field (Vojík et al., in prep.) clearly indicate the high invasive potential of the species. An early and/or rapid germination strategy (Ross and Harper 1972; Gioria and Pyšek 2017) is especially typical for ornamental plants originating from arid or semi-arid environments. Indeed, the same strategy is found in a number of fast-growing invasive annuals, including Himalayan balsam *Impatiens glandulifera,* and some of the most invasive monocarpic perennials, including giant hogweed *Heracleum mantegazzianum* and Chilean rhubarb *Gunnera tinctoria* (Gioria and Osborne 2009; Gioria and Osborne 2013). The potential for *L. coronaria* to spread invasively is also supported by its high seed production, with a two-year-old plant releasing 19 000 seeds on average (counted on plants growing in experimental garden bed). Therefore, *L. coronaria* must be considered as a new and potentially dangerous invasive species in this country.

Stachys byzantina, was estimated to show highest germination at around 22/15 °C, similar to related species of dry grasslands *S. germanica* (highest germination 20/15 °C; Dunn 1997). Our results confirmed this expectation, with highest germination (55.6%) indeed occurring at 22/15 °C, while almost no seeds germinated (0.3%) at temperatures < 10/5 °C. Furthermore, the two populations examined (SB 1, SB 4) differed from each other – their final germination rate at 22/15 °C was 72.8% and at 15/10 °C was 65.6% (Fig. 12), which is about 30% higher than the germination rate of the rest of the tested populations. The explanation may be an adaptation to human-made habitats in urban areas. Urban environments and phenomena (e.g. urban heat and dry islands) strongly influences species adaptation (Williams et al. 2015; McDonnell and Hahs 2015); species are changing their ecological and reproductive traits to become more invasive (Dubois and Cheptou 2017). Such phenomenon has been described in several highly invasive European species, including the highly invasive common ragweed *Ambrosia artemisiifolia* (Gorton et al. 2018). However, we did not study the influence of maternal population growth conditions on germination and it could be the reason for the described difference among populations of the species, in spite of similar site conditions of maternal plants (described in detail in Material and Methods).

The final germination was relatively high and contradicts the expected reproduction limits typical for rare, often endemic, species (Pavlik et al. 1993; Kaye 1999), though these can vary between specific sites (e.g. with altitude) or with the age of the populations sampled (Giménez-Benavides et al. 2005). Until recently, it was believed that a small native range would not include many safe sites for sexual propagules (germination conditions), and that this would limit species from spreading in other part of the world (Massey and Whitson 1980). However, there are now numerous examples of rapid and heavy invasion by such species, e.g. *I. glandulifera* (Beerling and Perrins 1993), suggesting that a species' individual ecological characteristics and its ability to evolve may be all that is needed to produce invasive behaviour (Dlugosch and Parker 2008a).

We also analysed the cytological variability of both *S. byzantina* and *L. coronaria* to determine differences in ploidy levels among their populations. We did not assess genetic diversity as it was expected to be high in both species due to their predominant generative reproduction mode (Crawley 1996). Nevertheless, genome size variability is a fast screening method for detecting changes in ploidy level or ongoing evolution that can affect seed germination and/or growth rate (Pegtel 1999; Schween et al. 2005; Münzbergová 2006). Polyploidy, for example, can cause differently sized seeds, changes in viability, and changes in a species' ability to germinate under stressful conditions (Stevens et al. 2020). Such changes to genome size can significantly influence the ability of an alien species to spread and potentially become invasive (Suda et al. 2015; Pyšek et al. 2018). Our results indicated that both species were cytologically homogenous with no evidence of polyploidy, with all populations of either species having a similar species-specific genome size (*S. byzantina* 1.55–1.63 pg; *L. coronaria* 6.40–6.58 pg), levels similar to those given by Zonneveld (2019). Furthermore, reference samples taken from the species' native range around Istanbul in Turkey (LC 7) and Tehran in Iran (SB10) showed the same ploidy levels as those from the non-native range (Supplementary table).

Comparison of escaping and non-escaping populations

Based on field observations (visual detection of escapes), we expected to see a difference in cytological variability and final germination between escaping and non-escaping populations. Surprisingly, our results failed to show any significant difference in variability and germination rate for either species examined (see Fig. 13), suggesting that germination and genome size are not key factors for escape from plantations. However, spreading into surrounding habitats could be caused by changes in local site conditions, such as management or disturbance regime (Buckley et al. 2007). Both species have now been recorded escaping from urban habitats, especially parks and gardens (Hejný 1997; Barošová and Baroš 2009; Pergl et al. 2016b; Kutlvašr et al. 2019; Vojík et al. 2020). While both species are currently classified as naturalised (*L. coronaria*) or casual (*S. byzantina*) (Pyšek et al. 2012b), they are likely to become problematic species as they spread into natural or semi-natural habitats, with rural semi-dry grasslands as well as semi-natural species-rich grasslands and steppes particularly at risk. *L. coronaria* is a particularly competitive species due to its ability to produce a huge number of viable seeds that can be spread in different ways (e.g. hydrochory, epizoochory), allowing it to spread into faraway habitats (Moravcová et al. 2010). *S. byzantina* can spread successfully by either seed or vegetative dispersal. It is also likely that *S. byzantina* could erode the genome of the endangered native species, *S. germanica*, through hybridisation (see

Introduction); this process is generally considered one of the most serious impacts of invasive species on native biota (Largiadèr 2008; Muhlfeld et al. 2014).

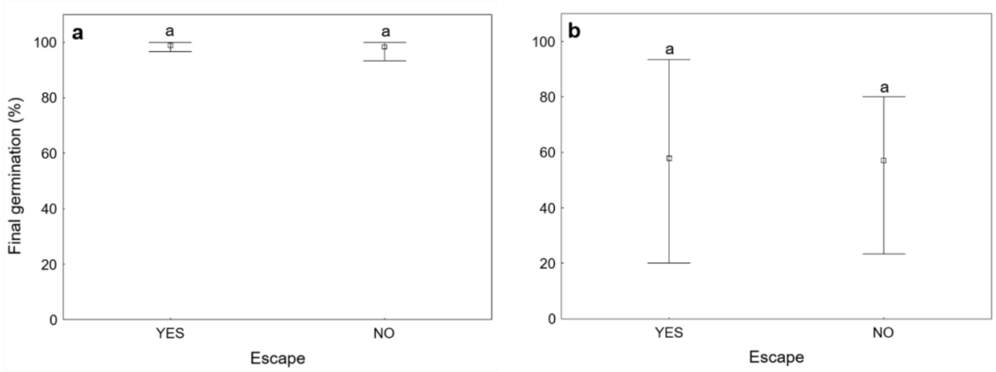

Fig. 13: *Analysis of final seed germination between escaping and non-escaping populations of Lychnis coronaria (a) and Stachys byzantina (b). Squares = mean of germinated seeds, whiskers = min-max; the same letters at the end of the treatment row show statistically non-significant differences (P > 0.05).*

Overall, our results suggest that generative spreading of both *L. coronaria* and *S. byzantina* is directly influenced by environmental factors, such as mean and spring temperature, both of which are likely to increase due to global climate change (Hansen et al. 2006; Anderson et al. 2008). In addition, indirect phenomena such as dry and warm islands in urban habitats (Roth et al. 1989; Lokoshchenko 2017; Yang et al. 2017; Hao et al. 2018) may be increasing the likelihood of these species escaping and spreading further. As such, both species may now pose a real threat to native species, particularly those in Central European mesic and xeric grasslands.

Supplementary material

Supplementary table: Selected populations of *Lychnis coronaria* (LC) and *Stachys byzantina* (SB) used in the study. Localities in white rows were used for both experiments, while those in shaded rows were only used for experiment 2, i.e. testing escaping (E) vs. non-escaping populations (N). The last row (SB10) was used just for detection of SB' genome size from primary area. CZ = Czech Republic, TR = Turkey, IE = Ireland, IR = Iran; Av. precip. = average precipitation, Av. temp. = average temperature. Climatic conditions from Culek et al. 2013 or Merkel 2019.

Locality	Destination	Coordinates	Av. precip. (mm)	Av. temp. (°C)	Genome size	E/N
LC1	Sloup, Central Bohemia, CZ	49.88781, 14.38009	564	8.3	6.402	E
LC2	Havlíčkův Brod, CZ	49.60433, 15.57965	712	7	6.553	N
LC3	Úvaly, CZ	50.07339, 14.72797	550–650	7.5–9	6.55	E
LC4	Prague, Opatov, CZ	50.02535, 14.5093	550–650	7.5–9	6.493	E
LC5	Istanbul, TR	41.00823, 28.97835	747	14.1	6.395	N
LC6	Prague, Agro, CZ	50.1305594, 14.3724772	450–500	8–9	6.452	E
LC7	Líšnice, Milevsko, CZ	49.422110, 14.383082	600	7	6,577	N
SB1	Hořovičky, CZ	50.15569, 13.53108	480–500	7.6–8	1.627	N
SB2	Čelákovice, CZ	50.16697, 14.77223	473–560	8.7–9	1.589	N
SB3	Prague, Vyšehrad, CZ	50.06373, 14.41665	450–500	8–9	1.612	E
SB4	Prague, Jahodová, CZ	50.05802, 14.5093	550–650	7.5–9	1.613	E
SB5	Prague, Suchdol, CZ	50.1301233, 14.3731692	450–500	8–9	1.58	N
SB6	Prague, Výhledy, CZ	50.1335474, 14.3768298	450–500	8–9	1.602	E
SB7	Úvaly, CZ	50.0705159, 14.7174431	550–650	7.5–9	1.616	E
SB8	Skalsko, CZ	49.8925350, 14.5404872	564	8.3	1.592	N
SB9	Dublin, IE	53.29496, -6.13895	767	9.7	1.547	E
SB10	Tehran, IR	35.7417725, 51.1733011	372	15.6	1.62	N/A

5 Case study III: Time to kill the beast – importance of taxa, concentration and timing during application of glyphosate to knotweeds

Martina Kadlecová, Martin Vojík, Josef Kutlvašr, Kateřina Berchová Bímová

Adapted from Weed Research 62 (2022) 215 – 223

Abstract

Knotweeds (*Fallopia* spp., syn. *Reynoutria* spp.) are among the most invasive plants globally, mainly due to their ability to regenerate from rhizomes and their extremely high biomass production. Spraying with glyphosate is a common control method, yet little is known about its effectiveness on underground rhizomes. In addition, there are concerns about the negative environmental impact of glyphosate. Therefore, it is essential to use appropriate dosages and application times to avoid overuse. Based on a pot trial and field experiments, we assessed the effectiveness of glyphosate concentration, application time and influence of glyphosate on rhizomes from different soil depths to determine their effect on the aboveground and belowground parts of knotweed plants of different taxa. The study demonstrates that sampling rhizomes is a more consistently accurate indicator of knotweed regeneration rate than sampling shoots. Regeneration of shoots and rhizomes was affected differently by glyphosate spraying depending on the application time. The effect on rhizomes was much greater with early season spraying than late season spraying, which primarily reduced shoot biomass. However, no differences were found between rhizome vitality at different soil depths. *F. sachalinensis* was

sufficiently controlled by early season foliar spray with 5% glyphosate (3.65 kg a.i. ha^{-1}) in contrast to *F. japonica* and *F. ×bohemica*. For rapid and targeted control, early season foliar spray with 8% glyphosate (5.85 kg a.i. ha^{-1}) is needed and, in the case of the hybrid, for a minimum of two consecutive seasons.

Introduction

The spread of invasive alien weeds is one of the main threats to the environment today (Neve et al. 2018). Knotweeds are among the worst European invaders (Netwig et al. 2018) and cause serious problems worldwide (e.g., Clements et al. 2016). Knotweeds have spread uncontrollably despite nature conservation management efforts. They are invaders of riparian and anthropogenic habitats, where they form perennial stands that can outcompete other species completely, resulting in loss of biodiversity and limiting many ecosystem services (Abgrall et al. 2018; Murrell et al. 2011). Localities in urban habitats, parks, and gardens may be particularly hard-hit by large monoculture knotweed stands (Chmura et al. 2013; Sołtysiak and Brej 2014), and can represent hotspots for future spread (Vojík et al. 2020). Recently, an increasing spread has also been registered in agricultural fields with potato or maize (Skinner et al. 2012). There is evidence of such a risk for Central Europe as well (Fig. 14).

Fig. 14: *Spread of invasive F. ×bohemica into a maize field.*

Herbicides are routinely used as the most effective control method for invasive plants (Kabat et al. 2006; Majd et al. 2019; Rudenko and Hulting 2010). However, the application does not always lead to the total eradication of invasive stands (Rinella et al. 2009). Incomplete eradication can lead to new spread (Blossey 1999). Optimal control methods can be developed by identifying the appropriate herbicide dose and optimal plant response to spraying at different developmental stages (Benbrook 2016; van Bruggen et al. 2018). The dose of herbicide that ensures optimal control effectiveness is related to environmental conditions (temperature, soil moisture etc.); specific plant traits such as species, plant stand size or developmental stage; and the application time. The growth season sees an increase in plant biomass as well as the changes in physiological response to herbicides. For example, the biomass of knotweed stands is considerably higher in autumn than in spring or early summer, and different taxa exhibit different levels of sensitivity to herbicide control (e.g., Jones et al. 2018) due to physiological characteristics (Bashtanova et al. 2009). Further, a high amount of biomass increases the amount of herbicide needed for sufficient control, which in turn increases the risk of environmental and increases environmental contamination.

The most broad-spectrum of the currently approved herbicides used for weeds control, particularly for knotweeds, is glyphosate (N-(phosphonomethyl)-glycine-isopropylamine (IPA) salt) (Jones et al. 2018), commonly sold in the commercial formulation, Roundup - Active, Rapid, etc. (Bayer Crop Science). Instructions for its application generally recommend the lowest applicable dose in natural ecosystems to minimize the risk of any potential impact on the environment or human health; however, studies considering taxa-specific response, physiology, and appropriate glyphosate doses for knotweed are missing.

Various knotweed control methods have been attempted (Dommanget et al. 2013, 2019; Kabat et al. 2006). Most of them combine mechanical control with the use of herbicides (Kabat et al. 2006; Bashtanova et al. 2009; Jones et al. 2018). However, mechanical cutting of aboveground biomass, such as mowing, only results in weakening of the stands and not complete eradication (e.g., Scott and Marrs 1984). Knotweeds, like many perennials, can store carbohydrate in their underground rhizomatic systems. Such resource allocation creates an enormous propagule source underground combined with extremely high rhizome bud regeneration ability. For this reason, stand-alone digging up of whole stands is most effective, but technically difficult and only applicable to smaller knotweed stands (Barták et al. 2010). Digging and cutting the rhizomes into small segments leads to rapid rhizome segment regeneration. Followed-up with spraying with glyphosate appears to be most effective but technically difficult method (Bímová et al. 2003). In Europe, late season spraying is widely considered as one of the most effective control methods. This involves spraying of glyphosate (5-10% liquid concentration) in autumn (Barták et al. 2010; Kabat et al. 2006). During the late vegetation season, assimilates are stored in the rhizomes, and it is believed that this process helps transport the glyphosate to rhizomes and kill them. Within this process, the plants must not be ripped, dug, or mechanically damaged. The effectiveness of late season spraying in reducing aboveground biomass is high and has been described (Jones et al. 2018; Kabat et al. 2006). Nevertheless, little or no information is available on the effect of this method on rhizomes in clonal plants and subsequent regeneration from rhizome buds (Bímová et al. 2003; Pyšek et al. 2003), despite the importance of the knowledge of rhizome regeneration rate in evaluating control efficiency over the following seasons. Other common methods include cutting and follow-up spraying with glyphosate or spraying in the mid-summer vegetation season (Barták et al. 2010). In such cases, the efficiency is usually evaluated by counting newly regenerated shoots, often neglecting the underground parts (Jones et al. 2018). As mentioned above the rhizome systems of the taxa are complex in architecture and provide long persistence; they are able to penetrate almost all types of substrates and can be found at a distance of 20 m from a maternal stand (Beerling et al. 1994). Plants can regenerate from tiny fragments of rhizomes (1 cm, 0.7 g) containing at least one node with a bud (Adachi 1996; Brock and Wade 1992). Although there is a large body of knowledge, no studies have focused on the response of underground plant parts to particular control methods. Despite proper application, glyphosate is not always distributed to deep-seated rhizomes and thus could lead to plant regrowth.

Studies on knotweed control also suffer from a lack of taxa comparison. Studies have mainly focused on the control of *F. japonica* Houtt. var. *japonica* (Japanese knotweed; Kabat et al. 2006), in spite of apparent differences in the biology of particular taxa. As such, related taxa could respond differently to control treatments, as suggested by Bímová et al. (2003). Previous studies on the regeneration ability of *Fallopia japonica* var. *japonica* (herein *F. japonica*) and *F. sachalinensis* (F. Schmidt) Nakai (giant knotweed), and their hybrid *F.* ×*bohemica*

Chrtek et Chrtková (Bohemian knotweed) (Bímová et al. 2003; Kabat et al. 2006; Ringselle et al. 2021) and their competitive fitness (e.g., Parepa et al. 2014) indicate apparent differences, with rhizomes of *F. japonica* and *F. ×bohemica* having a recovery capacity nearly twice that of the aboveground stems. Furthermore, while *F. ×bohemica* is considered the most regenerative taxon of the genus, *F. sachalinensis* tends to regenerate better from stems (Bímová et al. 2003). Hence, the taxa-focused method should be developed to optimize control effectiveness.

To fill this gap, this study used a combination of pot trial and field experiments to find the optimal knotweed control method for particular taxa. The objectives of the study were to consider shoot emergence and rhizome regeneration ability after summer (early season) and autumn (late season) application of the foliar spray glyphosate. We tested commonly used dose of glyphosate (5%, 3.65 kg a.i. ha^{-1}) and the highest dose (8%, 5.85 kg a.i. ha^{-1}) suggested by the producer of Roundup®Active for the most resistant weeds. The study also compared effects of glyphosate treatments on rhizomes at different depths, as a possible important factor influencing the control effectiveness.

Material and methods

Three taxa of the genus *Fallopia* were selected (i.e. *F. japonica*, *F. ×bohemica*, *F. sachalinensis*) and subjected to various glyphosate treatments. Roundup®Active, containing the active ingredient glyphosate ($C_3H_8NO_5P$) 170 g/L SL (IPA salt) was applied by foliage spraying at 5% (3.65 kg a.i. ha^{-1}) and 8% (5.85 kg a.i. ha^{-1}) concentration dose during early season and late season, when the plants were at different developmental stages to determine the response of above/underground parts for comparison the efficacy of different doses of glyphosate.

The average spray volume, doses, and mean amount of aboveground biomass are shown in Table 4. No adjuvants were used.

Table 4: Details of spray volume, application dose (kg a.i. ha^{-1}), and size of aboveground biomass by treatment group. Taxa: FB – *F. ×bohemica*, FJ – *F. japonica*, FS – *F. sachalinensis*

Application timing	Taxa	Spray volume (litres ha^{-1})	Mean of application dose 5% (kg a.i. ha^{-1})	Mean of application dose 8% (kg a.i. ha^{-1})	Aboveground biomass (kg.ha^{-1})
Early season	FB	500	3.1	5.0	4394.0
	FJ	375			3976.5
	FS	225			2955.3
Late season	FB	625	4.2	6.7	8288.0
	FJ	550			7841.5
	FS	300			5479.6

This study was based on one *ex-situ* pot trial and two *in-situ* field experiments. All experimental plots and sample collection plots were located in Central Bohemia in the Czech Republic (see Supplementary material – Fig. S1).

Garden pot trial – comparison of treatment times, glyphosate concentration and taxa

Experimental plants were obtained from rhizomes that had been transported to a greenhouse, cleaned, and put to regenerate in water until new shoots formed. The regenerated rhizomes were placed in separate pots filled with a mixture of perlite and sand (1:1). All rhizomes were 25 cm long, consisting of approximately ten nodes with rhizome buds and one newly regenerated shoot. The experiment was conducted between May and October 2015, during which the plants were fertilized three times and watered regularly. Replication comprised 15 plants of each taxon treated with different concentration of glyphosate (5%, 8%), and 15 plants left unsprayed as a control. Spraying was carried out in early season and late season. Two sprayings using a classic knapsack sprayer (Titan 16 VITON ®, Marolex, Czech Republic) were conducted for each of these periods. Early season spraying was performed in the last week of May and three weeks later. Late season spraying was performed in the first week of September and three weeks later. After four weeks (i.e. in July for early season spraying and October for late season spraying), the rhizomes were cut into segments (each consisting of one node with two adjacent internodes), washed, and moved to containers with distilled water, where regeneration was observed under greenhouse conditions. Rhizome bud regeneration was recorded every second day for one month. The segments were considered to be regenerating if they produced new shoots from rhizome buds. The number of newly regenerated shoots was counted for each segment and used as a response variable for data analysis.

Field experiments – comparison of treatment times, glyphosate concentration, taxa and the effects of glyphosate at different rhizome depths

The first field experiment was conducted from August 2015 to October 2017. Glyphosate was applied at two concentrations (8%, 5%) to experimental treatment plots (9 m^2 on average) of each taxon at separate localities (i.e. three repeats, different localities for each taxon). A plot of similar size, which served as the control plot for each taxon, received no glyphosate spray. The glyphosate was applied to the whole knotweed stand (i.e., spraying aboveground biomass) at each locality using a knapsack sprayer, with the initial spraying carried out in the first week of September and the second spraying three weeks later. Data were collected using a 4 m^2 plot in the centre of each test plot four weeks after the second spraying. In each plot, the number of partial clumps and number of shoots before spraying were counted (and later used as a covariate), and the number of newly regenerated shoots after spraying treatment was counted and used as a response variable in the data analysis. The plots were again examined over the following two seasons when newly emerged shoots were subjected to the same glyphosate concentrations (spot spraying).

The second field experiment was conducted between May and October 2018. Based on previous results, glyphosate was only applied at 8% concentration. Experimental plot organisation followed the methodology of the first field experiment (i.e. 9 m^2, three repeats, different localities for each taxon), while the glyphosate season application followed the methodology of garden pot trial (i.e. two treatment times). Four weeks after the second spraying, new shoots were counted in both treatment plots, and rhizomes were dug from different depths (10 – 40 cm) from the inner 1 m^2 of each experimental plot. Regeneration of harvested rhizomes followed the same method as in the garden pot trial (i.e. cut into segments and rhizome bud regeneration recorded). The number of regenerated buds was counted for each segment and used as a response variable for further data analysis.

Data analysis

Several main factor ANOVA (Analysis of variance) models were employed to detect differences in the percentage of regenerated rhizomes (arcsine transformed) with taxa, concentration of glyphosate, season, and depth of rhizome layer as predictors. GLM (Generalized linear models) were employed to analyse the differences in the number of newly regenerated shoots with taxa, glyphosate concentration, and season as predictors. The initial number of partial clumps and shoots were used as covariates in the model. The minimal appropriate model was obtained using posterior contrasts (Quinn and Keough 2002) and AIC criterion (Akaike 1998). In addition, RM (Repeated Measure) ANOVA model, was applied to interpret the between-year decrease of shoots. In the RM ANOVA model, the response variable was log-transformed ($Y' = 1 + Y$). Year (RM factor), concentration, and taxa were used as predictors. Tukey's HSD tests followed the ANOVA models.

All statistical tests and output graphics were performed using R (R Development Core Team 2019) and Statistica 13 (TIBCO 2017) statistical software with respect to current statistical issues (Onofri et al. 2010). Differences were considered significant at $P \leq 0.05$.

Results

While spraying with glyphosate significantly reduced both shoot occurrence (GLM, $z = -6.93$, df = 23, $P < 0.0001$) and rhizome regeneration (ANOVA, $F_{(2, 264)} = 677.76$, $P < 0.0001$) regardless of the concentration applied, there were significant differences in the number of new shoots produced (GLM, $z = -2.73$, df = 8, $P = 0.01$) and regeneration rate of rhizomes (ANOVA, $F_{(2, 264)} = 677.76$, $P < 0.0001$, Tukey HSD test 5% vs. 8% < 0.0001).

Tested treatments and shoots occurrence

The number of shoots per plot decreased significantly faster after spraying with 8% concentration ($F_{(4, 36)} = 31.33$, $P < 0.0001$). After spraying with 5% concentration, the number of newly emerged *F. ×bohemica* shoots varied from 3 to 5 per plot, in *F. japonica* from 1 to 3 shoots, and in *F. sachalinensis* from 0 to 2 shoots. In contrast, no significant difference in the number of new shoots was observed between taxa after spraying with 8% concentration (GLM, z = 0.000, df = 8, P = 1.00) and the overall number of new shoots decreased almost to zero (mean number of shoots varied from 0 to 0.33 per sample plot, Fig. 15).

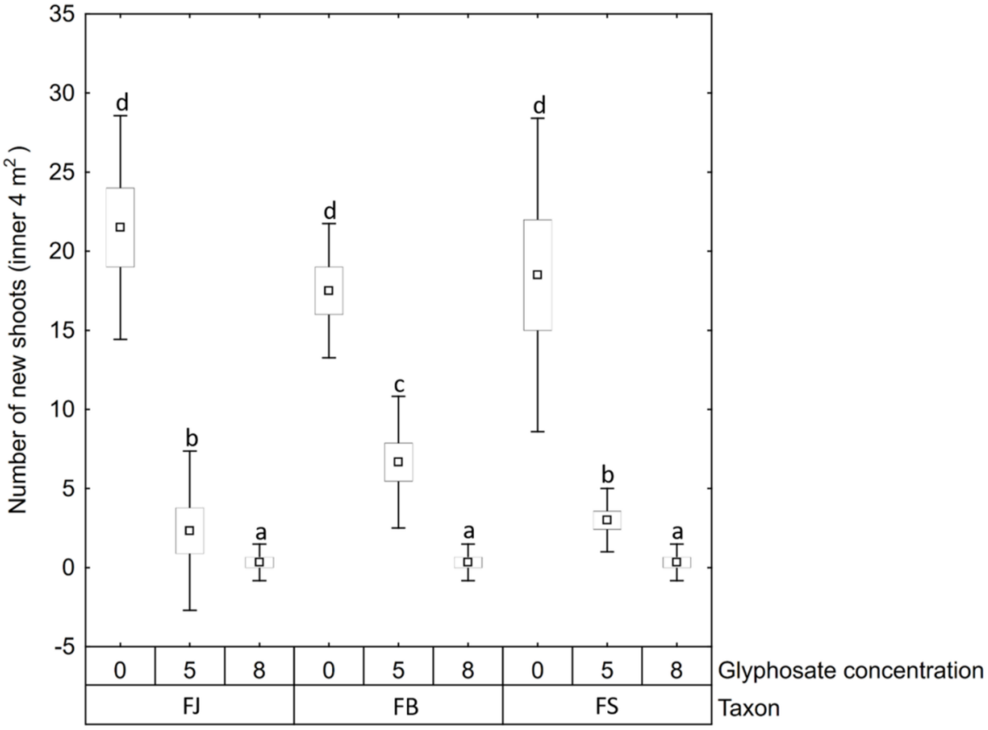

Fig. 15: *Influence of different treatments on the newly regenerated shoots (field experiment) in inner 4 m*^{2} *after one season's spraying; glyphosate concentration 5 = 5%, 8 = 8%, 0 = without treatment; taxon:* FJ = *F. japonica*, FB = *F.* ×*bohemica*, FS = *F. sachalinensis*. *Squares = mean, boxes = mean ± SE, whiskers = mean ± 2SD, boxes sharing a letter are not significantly different (Tukey-adjusted comparisons; P < 0.05).*

There was no significant interaction between the three years of study for particular treatment and taxa (RM ANOVA, $F_{(8,\ 36)} = 1.22$, P = 0.30). If single factors were tested, there was a statistically significant decrease in shoot numbers in the second and third years in all treatments except control (RM ANOVA, $F_{(2,\ 36)} = 38.68$, $P < 0.001$). There were no new shoots in the final year in plots sprayed with both concentrations in *F. sachalinensis* and 8% concentration in *F. japonica* (Supplementary material – Fig. S2, Table S1).

After spraying with 8% concentration, no differences were found in the number of newly regenerated shoots between seasons (GLM, z = 1.27, df = 17, *P* = 0.21) and particular taxa (GLM, z = 0.28, df = 17, *P* = 0.80) (Fig. 16; Supplementary material – Table S2).

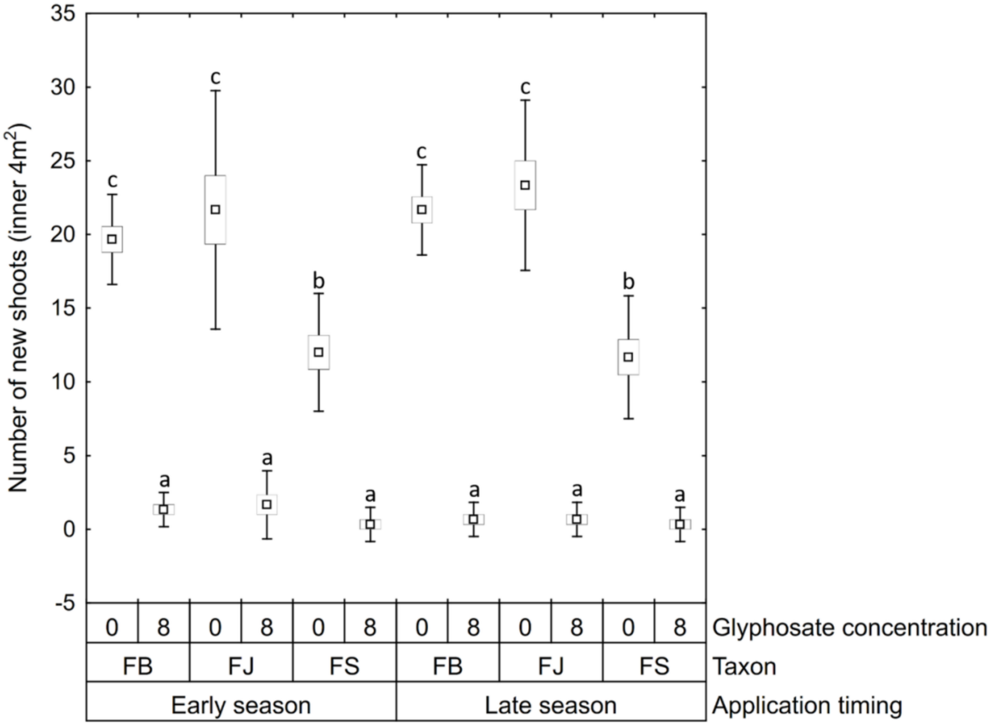

Fig. 16: *Influence of different treatments on the newly regenerated shoots (field experiment) in inner 4 m^2; glyphosate concentration 8 = 8%, 0 = without treatment; taxon:* FJ = *F. japonica*, FB = *F.* ×*bohemica*, FS = *F. sachalinensis*. *Squares = mean, boxes = mean ± SE, whiskers = mean ± 2SD, boxes sharing a letter are not significantly different (Tukey-adjusted comparisons; P < 0.05).*

Tested treatments and rhizome regeneration

There was a clear pattern of taxa-specific rhizome reactions to studied concentration ($F_{(2,\ 264)}$ = 8.20, *P* < 0.0001), *F. sachalinensis* rhizomes regenerated equally after spraying with both concentration (mean c5% =10.22%, c8% = 7.46%; c = concentration) other taxa were more reduced by 8% glyphosate (*F. japonica* – mean c5% = 18.69%, c8% = 9.47%), *F. ×bohemica* – mean c5% = 19.68%, c8% = 11.8%) (Fig 17).

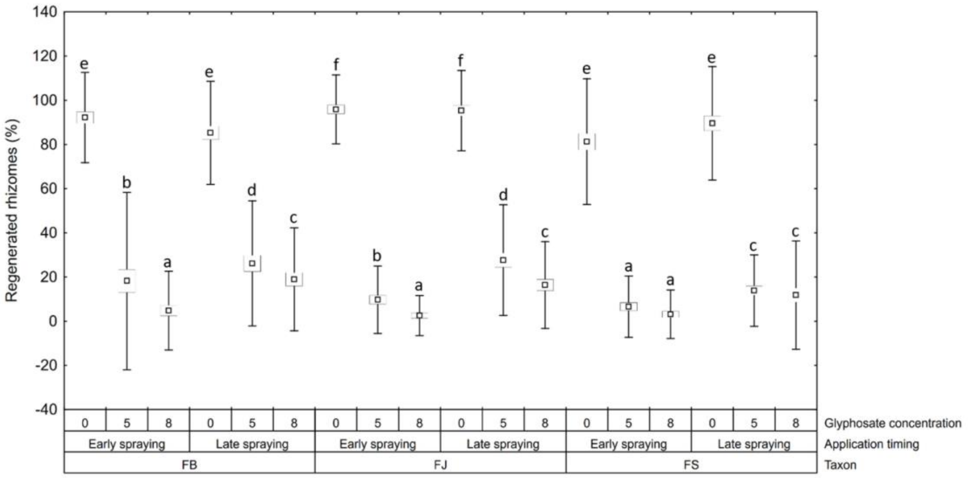

Fig. 17: *The percentage of regenerated rhizomes (garden pot trial) among F. ×bohemica* (FB), *F. sachalinensis* (FS) *and F. japonica* (FJ) *based on different application timing and treatment (glyphosate concentration 5 = 5%, 8 = 8%, 0 = without treatment). Squares = mean, boxes = mean ± SE, whiskers = mean ± 2SD, boxes sharing a letter are not significantly different (Tukey-adjusted comparisons; $P < 0.05$).*

The application season significantly affected rhizome regeneration rate (ANOVA, $F_{(1,\ 264)} = 28.59$, $P < 0.0001$), with a lower regeneration rate in early season spraying compared with late season spraying. While *F. ×bohemica* and *F. japonica* rhizome regeneration rates were significantly higher (mean early: 13.2% and 9.72%; mean late: 26.15% and 27.65%) than *F. sachalinensis* (mean early: 6.57%, mean late: 13.88%) after spraying with 5% glyphosate concentration (Tukey HSD, $P = 0.01$), there was only a small difference in the rhizome regeneration rate between all taxa using 8% glyphosate concentration (for specific results, see Supplementary material – Tables S3 and S4).

The effect of different depths of rhizomes in the soil on regeneration rate was not statistically significant ($F_{(3,\ 71)} = 0.662$, $P = 0.58$) (for details see Supplementary material – Table S5).

Discussion

Glyphosate concentration, shoots occurrence and rhizome regeneration

The results indicate that taxa respond differently to glyphosate concentrations treatments. In the 8% glyphosate concentration, there was little difference between taxa because the treatment strongly suppressed the growth of both shoots and rhizomes in all taxa (albeit it could not stop mainly the hybrid growth completely). However, in the 5% treatment, there was a clear difference between taxa with the hybrid surviving far better (producing 6.67 shoots in overage) than the parent species *F. japonica* (2.33) and *F. sachalinensis* (3.0). Consequently, the 5% concentration is not effective enough for the hybrid.

Similar results were obtained for the regeneration rate of rhizomes; the rhizome regeneration results showed that even an 8% glyphosate concentration could not stop knotweed growth completely, although it reduced growth significantly.

Glyphosate and rhizome system

Numerous authors have pointed out the complexity and high biomass of the knotweed rhizome system and the problems associated with its eradication (Bashtanova et al. 2009; Bímová et al. 2001; Bímová et al. 2003). Brock (1995) reported that rhizome biomass can reach up to 1500 g/m^2. As such, systemic herbicides do not affect all parts of the rhizome system. The non-affected parts can regenerate and thus, prevent complete eradication of the knotweed. This could be a significant factor influencing the success of control. Therefore, we focused on the glyphosate efficacy on rhizomes excavated from different depths of soil. We assumed that the deep-laid rhizomes would be affected less by glyphosate spraying than these growing close to stems. Surprisingly, no difference was found in influencing the regeneration of rhizomes at different depths. The probable reason is the very complex architecture of the rhizome system, with rhizomes growing up to 7 m in different directions. Even within a knotweed stand, rhizomes can be at different distances from the above-ground stems and, therefore, far from the site of herbicide application. Individual taxa vary greatly in the structure of their rhizome system (Berchová, unpublished data); this may be the reason for the difficulty in getting rid of the hybrid *F. ×bohemica*, which has relatively strong (like

F. sachalinensis) and, simultaneously, long, deep growing and branched rhizomes like *F. japonica*.

The timing of spraying

Jones et al. (2018) described phenological changes in *F. japonica* growth, resource allocation, and rhizome source-sink strength during the growing season. Based on the study of phenological processes and extensive field-based assessment of control treatments, the authors suggest using biannual summer and autumn foliage spraying with glyphosate or autumn shoot injection. Both methods are based on the flow of resources in autumn, reaching a maximum in the rhizome-shoot direction. Rhizome bud activity is then triggered and exhausted. The results of our two season experiment show that knotweed rhizome regeneration was significantly reduced after early season spraying, whereas late season spraying reduced the aboveground biomass almost completely, but rhizome bud regeneration was less affected. This was seen also in the pot trial under standardized conditions (see Supplementary material – Tables S3 and S4). In the field experiment, high efficiency was achieved with autumn spraying of the aboveground biomass. Bímová et al. (2001) suggested cutting rhizomes into small segments followed by spraying foliage after the rhizomes regenerated, which corresponds with the reports of Jones et al. (2018). Unfortunately, excavation and cutting of rhizomes is technically arduous and not applicable at all localities. Furthermore, autumn treatment methods require higher amounts of herbicide due to the enormous amount of knotweed biomass. As a result, the evaluation of control treatment efficiency should concentrate on rhizome regeneration over the following seasons rather than shoot regrowth.

The regeneration rate of rhizomes after autumn spraying could be due to several reasons. Most probably, rhizome buds do not regenerate in late autumn, even if they are not influenced by glyphosate, due to dormancy, and they start to regenerate in the next vegetation season. Like other perennials (e.g., Liew et al. 2013), rhizomes of knotweed could be dormant as an adaptation to seasonal cold temperatures. This process can be influenced by carbohydrate storage and other physiological processes. However, further study is needed in order to understand the process of carbohydrate storage in knotweed so as to understand its processes (Klimešová et al. 2017). Carbohydrate storage is influenced by season, flowering, aboveground biomass distribution regime, and nutrient richness of the substrate.

Moreover, it is a species-specific process (Martínez-Vilalta et al. 2016). The flow of assimilates and the amount of carbohydrates in storage organs directly affects glyphosate influence and the regeneration ability of rhizomes after glyphosate application. We suppose that the lower regeneration rate in autumn can be affected by a combination of plant growth characteristics during the season – amount of carbohydrates and rhizome bud regeneration dynamics. In the early season, a plant could have a lack of carbohydrates in its rhizomes because they have been used for spring aboveground biomass growth. The early season growth of knotweeds is extremely fast, and they form a huge amount of biomass within a short time (Lavoie 2017). When the aboveground biomass is destroyed by glyphosate, the remaining carbohydrates are exhausted from rhizomes to form new shoots. When these new shoots are destroyed once again by glyphosate, the plant does not have enough carbohydrates to form the third cohort of new shoots and it dies. The plants could also regenerate less from rhizome buds during the late season because, in autumn, the plant is not desperate to produce aboveground biomass. Daily temperatures and light levels are declining at this time, and these are thought to be critical factors for knotweed rhizome regeneration (Bashtanova et al. 2009; Dommanget et al. 2013). Preliminary results of our further field experiments (unpublished) show that formation new shoots are higher in the following seasons after late season spraying compared to early season spraying, which has been found also in other species (e.g., Bergkvist et al. 2017).

Knotweed control treatment and evaluation

Results from both the garden pot trial and field experiments agree with the conclusion of Jones et al. (2018), that no available control method weakens the knotweed rhizome system entirely after the one-year control treatment application. Our results indicated the highest resilience to all control methods in the hybrid *F. ×bohemica*, which is consistent with its previously observed high regeneration ability (Bímová et al. 2001; Pyšek et al. 2003).

However, the results provide evidence that glyphosate spraying significantly affects the regeneration ability of rhizomes differently than the regeneration of shoots. Shoot regeneration did not differ between seasons; rhizome regeneration rate is higher in the late season than in the early season. As a result, the evaluation of control treatment efficiency of knotweed taxa should concentrate on rhizome regeneration rather than shoot regrowth over the following seasons. We believe that the change in the common methods of evaluating efficiency, which includes measuring the regeneration ability of the rhizome instead of counting the aboveground shoots, will be a better parameter of evaluation.

The study results also support a taxa-specific approach to control. Below, we suggest the control algorithm for knotweed elimination based on the results of the study and previously published facts (Fig. 18) (Bímová et al. 2001, 2003; Kabat et al. 2006; Barták et al. 2010; Jones et al. 2018).

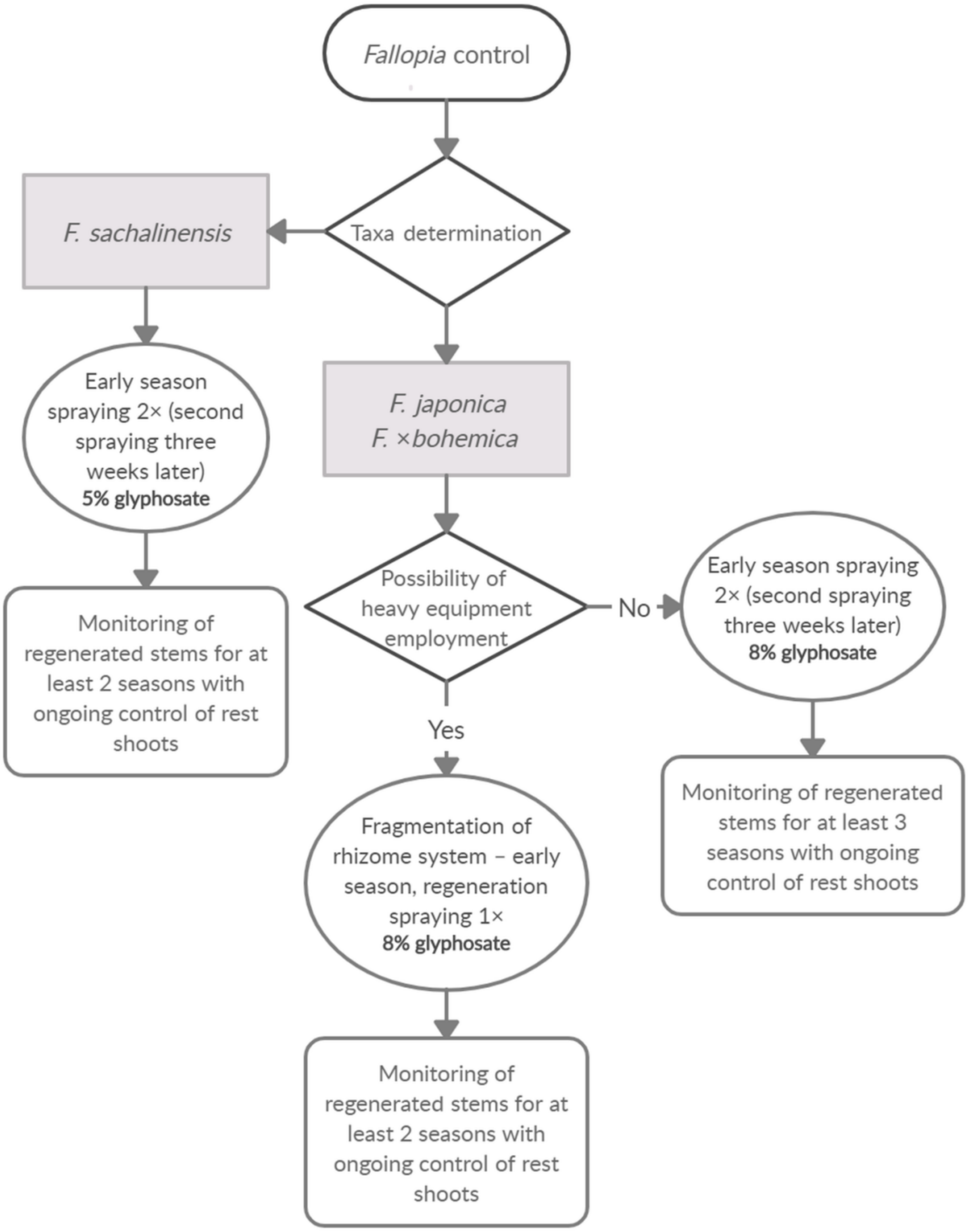

Fig. 18: *Algorithm of a recommended management procedure for successfully eliminating all taxa stands of knotweed* (*Fallopia* spp.); *5%, 8% glyphosate concentration = water solution of Roundup®Active.*

We suggest stand-alone foliage spraying in mid-summer, followed by monitoring and targeting local foliage spraying in autumn as the optimal control method; it saves costs and is more environmentally friendly. The dose of glyphosate should be taxa-specific, with 5% glyphosate (3.65 kg a.i. ha^{-1}) for *F. sachalinensis* and 8% glyphosate (5.85 kg a.i. ha^{-1}) for *F. ×bohemica* and *F. japonica* var. *japonica*.

Supplementary material

Supporting information figures

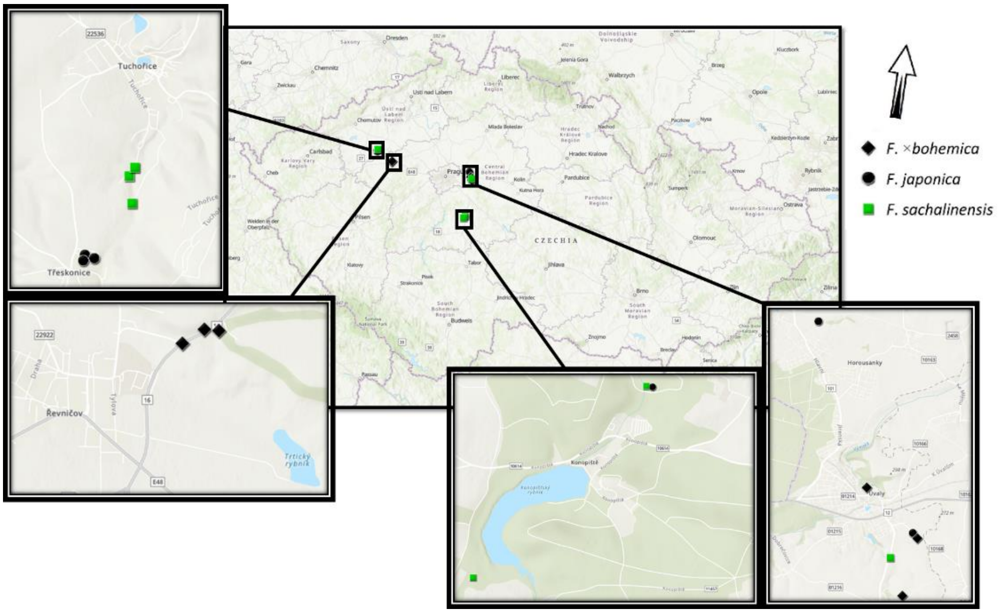

Fig. S1: *Location of the field study sites with experimental plots. Garden pot trial took place in a greenhouse – ex-situ; populations of all field study taxa are shown on the map.*

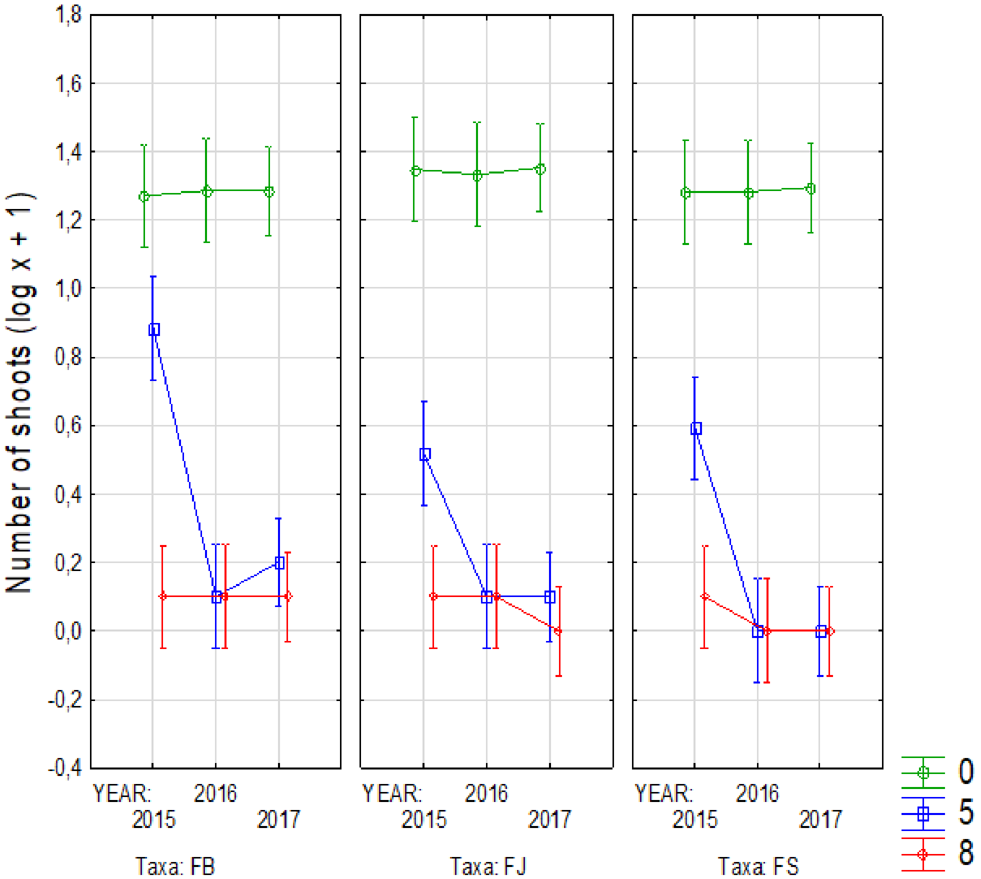

Fig. S2: *Shoot number decrease in three years of field experiment after applying different glyphosate concentrations (8%, 5%, 0% – control);* FB – *F.* ×*bohemica*, FJ – *F. japonica*, FS – *F. sachalinensis.*

Supporting information tables

Table S1: Number of newly regenerated shoots (field experiment) after late season spraying and under different treatments. FB – *F.* ×*bohemica*, FJ – *F. japonica*, FS – *F. sachalinensis*; Number of new shoots – mean of number of newly emerged shoots in inner 4 m^2 plot per three replicates; SE – standard error of mean; different letters at the end of treatment row show statistically significant difference using Tukey HSD test ($P < 0.05$).

Glyphosate concentration	Taxon	Number of shoots (Mean ± SE)			Significant difference
		2015	2016	2017	
8%	FB	0.33 ± 0.06	0.33 ± 0.06	0.33 ± 0.06	BC
5%		6.67 ± 0.06	0.33 ± 0.06	0.67 ± 0.06	BC
0%		17.67 ± 0.17	18.33 ± 0.17	18.33 ± 0.12	A
8%	FJ	0.33 ± 0.06	0.33 ± 0.06	0.00 ± 0.00	C
5%		2.33 ± 0,06	0.33 ± 0.06	0.33 ± 0.06	BC
0%		21.67 ± 0.55	21.00 ± 0.62	21.66 ± 0.36	A
8%	FS	0.33 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	C
5%		3.00 ± 0.11	0.00 ± 0.00	0.00 ± 0.00	C
0%		18.67 ± 0.61	18.33 ± 0.39	19.00 ± 0.44	A

Table S2: Number of newly regenerated shoots (field experiment) under different treatments. Taxa: FB – *F.* ×*bohemica*, FJ – *F. japonica*, FS – *F. sachalinensis*; Number of new shoots – mean of number of newly emerged shoots in inner 4 m^2 plot per three replicates; SE – standard error of mean; different letters at the end of treatment row show statistically significant difference using Tukey HSD test ($P < 0.05$).

Glyphosate concentration	Application timing	Taxon	Number of new shoots	SE	Significant difference
8%	Early season	FB	1.33	0.33	A
		FJ	1.67	0.67	A
		FS	0.33	0.33	A
0%		FB	19.67	0.88	C
		FJ	21.67	2.33	C
		FS	12.00	1.15	B
8%	Late season	FB	0.67	0.33	A
		FJ	0.67	0.33	A
		FS	0.33	0.33	A
0%		FB	21.67	0.88	C
		FJ	23.33	1.67	C
		FS	11.67	1.20	B

Table S3: Rate of regenerated rhizomes (average percentage calculated from the per cent recovery of each rhizome) in garden pot trial under different treatments. FB – *F. ×bohemica*, FJ – *F. japonica*, FS – *F. sachalinensis*; the rate of regenerated rhizomes (%) – mean of regenerated rhizomes per 15 replicates; SE – standard error of mean; different letters at the end of treatment row show the significant difference using Tukey HSD test ($P < 0.05$).

Glyphosate concentration	Application timing	Taxon	Regenerated rhizomes (%)	SE	Significant difference
8%	Early season	FB	4.80	2.30	A
		FJ	2.55	1.17	A
		FS	3.13	1.41	A
5%		FB	13.20	2.30	B
		FJ	9.72	1.97	B
		FS	6.57	1.79	A
0%		FB	92.15	2.64	E
		FJ	96.57	2.25	F
		FS	81.26	3.67	E
8%	Late season	FB	18.96	3.00	C
		FJ	16.39	2.53	C
		FS	11.79	3.16	C
5%		FB	26.15	3.66	D
		FJ	27.65	3.24	D
		FS	13.88	2.09	C
0%		FB	85.25	3.01	E
		FJ	95.28	2.35	F
		FS	89.55	3.32	E

Table S4: Rate of regenerated rhizomes (average percentage calculated from the percent recovery of each rhizome) in field experiment under different treatment. Taxa: FB - *F.* ×*bohemica*, FJ - *F. japonica*, FS – *F. sachalinensis*; Rate of regenerated rhizomes (%) – mean of regenerated rhizome buds (for details see Material and Methods); SE – standard error of mean; different letters at the end of treatment row show statistically significant difference using Tukey HSD test (*P* < 0.05).

Glyphosate concentration	Application timing	Taxon	Regenerated rhizomes (%)	SE	Significant difference
8%	Early season	FB	28.90	6.74	B
		FJ	24.52	6.98	B
		FS	17.16	1.80	A
0%		FB	89.24	6.40	E
		FJ	85.70	3.96	E
		FS	63.07	13.64	D
8%	Late season	FB	38.76	8.82	C
		FJ	36.71	6.21	C
		FS	24.19	5.26	B
		FB	89.24	6.40	E
0%		FJ	90.28	8.56	E
		FS	62.82	9.80	D

Table S5: Success of the regeneration of rhizomes in field experiment (average percentage calculated from the per cent recovery of each rhizome) for each study taxa (FB - *F. ×bohemica*, FJ - *F. japonica*, FS – *F. sachalinensis*) in various rhizome depth and under different treatment. N – number of successfully regenerated buds.

Taxon	Rhizome depth (cm)	Glyphosate concentration	Early season		Late season	
			Regenerated rhizomes (%)	N	Regenerated rhizomes (%)	N
FB	10-20	8%	31.54	82	38.19	78
		0%	89.47	83	89.97	87
	20-30	8%	26.87	71	37.90	92
		0%	94.80	99	90.74	54
	30-40	8%	27.11	22	38.50	69
		0%	80.55	15	88.31	46
FJ	10-20	8%	21.90	52	34.35	79
		0%	88.55	46	89.69	88
	20-30	8%	30.00	30	36.89	92
		0%	83.90	31	90.44	92
	30-40	8%	21.65	20	38.89	48
		0%	81.80	11	91.67	45
FS	10-20	8%	15.21	53	27.46	75
		0%	66.70	56	62.45	47
	20-30	8%	19.30	31	22.86	75
		0%	62.50	54	65.39	36
	30-40	8%	18.60	21	24.17	25
		0%	60.25	19	60.61	29

6 General discussion

6.1 Alien plant species – the subject of studies in parks and gardens

The topic of alien and invasive or expansive plant species in public parks and gardens forms one of the main directions in which invasive biology is moving today. In the Czech Republic, there are many alien species (including regionally alien taxa; see Chapter 1) which are expected to expand significantly due to being planted in public parks and gardens. Many of these species are referred to in the specialist literature as clearly having escaped from gardens and parks; however, this are often based on historical or inconclusive observations.

Based on a detailed inventory of spontaneously spreading alien plant species, robust data was obtained for compiling a list of escaping species (see Vojík et al. 2020). For recorded alien species, information was found about their ability to spontaneously spread or cause problems, for example, due to landscape changes or park improvements (a significant connection was observed between park improvements and the massive spread of alien species, e.g., knotweeds). Collected information about specific escaping species and the frequency and site of their escapes is an essential benefit for the establishment of new garden compositions, but also for the continuous management of public greenery, which is the central issue to controlling alien species (Štajerová et al. 2017). Within each site of escapes, variables related to particular parts of parks (site factors) were also recorded as well as values of (i) mechanism of spread, (ii) abundance in the park, and (iii) plantation context (see Vojík et al. 2020). With the help of these variables, it was possible to discover in which parts of the parks the most escapes occurred and how extensive spreading is usually involved. Based on this dataset is possible to generalise which park sites could be highly invaded – it can be used for future analysis of the relationship between environmental and socio-economic factors in public space. Recorded environmental variables can also suitably complement the input parameters of the methodology for classification of anthropogenically affected habitats, which connects biological and social (cultural) variables of the analysed landscape (see Sádlo et al. 2020).

The surveys carried out in the parks also brought a list of species which are starting to spread relatively recently from park plantings, or their spontaneous spread was neglected previously. This group includes, for example, the following species: *Aesculus hippocastanum*; *Galeobdolon argentatum*; *Hibiscus syriacus*; *Juglans nigra*; *J. regia*; *Lychnis coronaria*; *Robinia pseudoacacia*; *Stachys byzantina;* and *Syringa vulgaris* (see Vojík et al. 2020). We often lack knowledge of the biological or ecological traits of these species, which may be key to their fitness, competitive advantages, and invasive spread (van Kleunen et al. 2010). Since the rate of growth and germination of seeds are the biological traits that can give alien species a significant advantage over native species (Pyšek et al. 2009), the ecology study used germination and growth experiments. Two ornamental species (*Stachys byzantina* and *Lychnis coronaria*) were selected for studying the ability of generative reproduction. Both of these seem to be at the beginning of their invasive spread. Still, seminatural habitats have also been found with spontaneous spreading of these species – such sites could form hotspots of invasive spread in the future. Both species have a high potential for spreading, are not limited by the abiotic conditions of the non-native range and have a broad ecological niche – they are found in a wide range of different habitats (mown lawns, lighted post-culture forests – e.g., around defunct gardening colonies, ecotone zones, etc.). Model species are especially threatening the seminatural communities of open habitats with rare and often protected flora, where the presence of competitively stronger alien species would reduce plant community diversity. Within the germination experiments of selected species, germination speed, total germination, germination dependence on temperature, germination delay, and the difference in total germination between escaping and non-escaping populations of both species were monitored (Vojík et al. 2022). However, the overall seed vitality of both species across the studied sites and tested temperatures was very good – the final germination of *L. coronaria* was extremely high at temperatures > 15/10 °C (light/dark periods; 98.5 % germinated seeds), and in the case of *S. byzantina* was the highest at 22/15 °C (55.6 %), reduced to 40.3 % at 15/10 °C. The data obtained should serve mainly as a notice about newly spreading ornamental species with high invasive potential, but also as a warning for gardening work and future designs of ornamental beds, in which the species are still often inappropriately used (see Fig. 19).

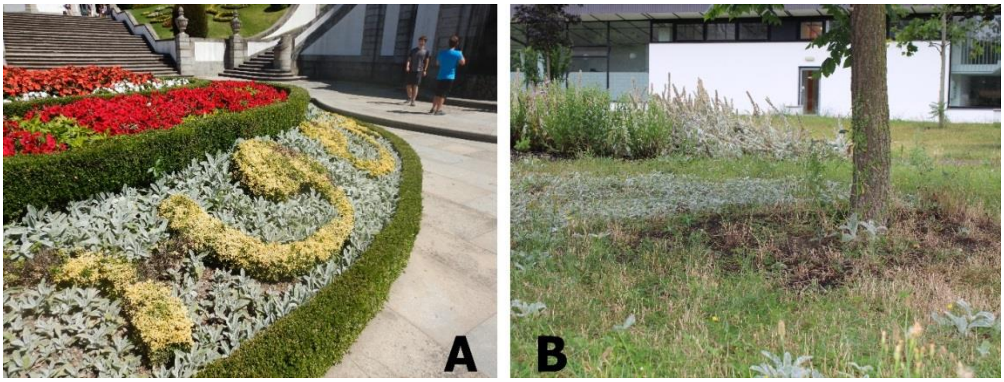

Fig. 19: Surroundings habitats should be considered when designing species for ornamental plantings: e.g., *Stachys byzantina* should be used only in the case where there is low chance to escape (A). The species can spread generatively and invade surrounding areas when not limited by habitat or management (B).

In addition to generative reproduction, species can also create propagule pressure by vegetative spread – e.g., *Stachys byzantina* can very quickly create very dense stands by vegetative growth, to which its root system is also adapted (Vojík et al. in prep.).

However, vegetative reproduction using the rhizome system is typical, especially for invasive taxa *Reynoutria japonica*, *R. ×bohemica*, and *R. sachalinensis*, which are no longer used for garden plantings. However, we can still often meet relicts of their long-term planting. They are frequent invaders of parks, which usually thrive there and cause many problems after their spread. All three taxa were widespread in parks (they were found in more than a third of inventoried parks; see Vojík et al. 2020), so it can be assumed that problems with their spread and the formation of massive stands in parks and their surroundings will increase. Due to its viability and resistance to liquidation attempts, it was, therefore, necessary to find an effective control method that would not be a significant burden on the environment, which can include threatened plant species and seminatural habitats in parks. Based on these requirements, we tested the chemical control with a lower impact on the environment (lower amounts of glyphosate were used) and at a more suitable time. Our results show the importance of determination of knotweed taxa and the use of early season spraying – *R. sachalinensis* was sufficiently controlled by early season foliar spray with 5 % glyphosate in contrast to *R. japonica* and *R. ×bohemica*. For them, early season foliar spray with 8 % glyphosate is needed; in the case of *R. ×bohemica*, for a minimum of two consecutive seasons (Kadlecová et al. 2022).

6.2 Habitats in parks as hotspots of invasion and harbours of threatened species

The initial study shows that parks can be potential hotspots for the invasion of plant species into the open landscape and refugia for threatened native taxa and vegetation types as well (Vojík et al. 2020). Therefore, parks can play the role of refugia sites of local biodiversity in city centres (Ricotta et al. 2001), suburban areas (Chocholoušková and Pyšek 2003; Kühn et al. 2004; Stewart et al. 2004), and rural or post-industrial countryside (Dzwonko and Loster 1988; Konijnendijk et al. 2005; Sádlo et al. 2017). The vegetation diversity of the study parks was determined based on native taxa records. Twelve categories were defined which represented groups of native taxa in specific habitats (i.e. rocky slopes; forest-steppe formations; mesic semi-open tree groves; mesic oak/oak-hornbeam forest; wet floodplain forest & nitrophilous fringes; mountain forest; short-cut lawns; mesic meadows; wet thistle meadows; continental inundated meadows; wetlands; ruderal vegetation; see Vojík et al. 2020). In these habitats, 100 Red-List taxa were recorded: four critically threatened – C1; 23 endangered – C2; 40 vulnerable – C3; and 33 of lower risk – C4. In total, there were 163 individual records of threatened taxa. The most threatened species (C1) were *Carex buxbaumii*, *Dactylorhiza incarnata*, *Orchis palustris* (all of these at Liblice), and *Pulicaria dysenterica* (Lednice park). In the case of the habitats, the highest number of threatened taxa (40) was recorded in wet lowland continental meadows, followed by wetlands (29) (Vojík et al. 2020). However, it is evident from the literature that forest habitats or dry grasslands can also be a refuge for threatened species in parks (Kümmerling et al. 2012).

Since the management of habitats across one park is usually different (including the intensity) (Schroeder and Green 1985; Welch 1991; Speak et al. 2015), artificial habitats were classified into several categories based on the park structure and intensity of applied management (see Chapter 3, Methods – Study sites and environmental variables). Based on this classification, the proportion of park area covered by seminatural habitats (minimum or no horticulture management) increases the number of habitats with threatened taxa, which represents the biodiversity of the native species there (Vojík et al. 2020). However, the intensity of management has been connected to the occurrence of alien taxa as well – less intensive management in secluded parts of parks, such as areas in the vicinity of park boundaries, ruderal habitats (compost heaps, or remains of walls), represents suitable conditions for the colonisation of pioneer woody species, competitive perennials, and weeds (Jim 2008; Lososová et al. 2012b; Petřík et al. 2019). Since both these parts of parks (seminatural and secluded or ruderal) can be located close to each other, park management should be more focused on controlling these often abandoned sites, which can become hotspots of invasion to seminatural parts with endangered habitats (include threatened species) or to the surrounding landscape, where invasive spreading can cause the decline of species richness and overall natural value of an area (e.g., Hédl 2004). In the case of an invasion of these valuable areas (inside or outside of parks), invasive species could displace the original vegetation from existing habitats and subsequently change the overall ecological regime of the habitats (Richardson et al. 2000). There could also be successful hybridisation of alien species with their native relatives, which causes erosion of the gene pool of native species (Marková and Hejda 2011); this is the case of *S. germanica* × *S. byzantina* (Dunn 1997). Thus, the combination of control of weeds at abandoned park sites and, for example, appropriately chosen species in ornamental park assemblages (the species without invasive potential – see related project "Grow safely" – Chapter 8) could successfully create conservation of refugia of native vegetation and threatened plant species in parks.

The selection of suitable species for horticultural assemblages seems today to be one of the main ways to avoid later problems with invasions. The majority of introduced species do not exhibit invasive behaviour, and their future spontaneous spread is, therefore, unlikely (Williamson and Fitter 1996). One of the main tools of invasive biology is, therefore, primarily to detect potentially invasive taxa (Mlíkovský and Stýblo 2006), the spread of which can be reduced. Preventing biological invasions is also advantageous from an economic point of view, as the funds spent on prevention are always lower than the funds spent on fighting an ongoing invasion (McNeely et al. 2001). A risk assessment system is used to detect potentially invasive taxa, which assesses and subsequently evaluates the invasive potential of individual species (Weber and Gut 2004). Also of importance are species for which invasive potential has not been determined – ornamental species for which no spontaneous spread has been detected can be collected on white lists, which serve as a basis for open trade with these species, but also for proposals for new garden plantings, with a reduced risk of escape from cultivation (Dehnen-Schmutz 2011). Within the Czech Republic, the following species grown in parks and gardens could be included on the white list: *Artemisia stelleriana*, *Inula helenium* and *Rudbeckia fulgida* (the complete list of recommended "safe" species for ornamental planting can be found on the project website "Grow safely" – see Chapter 8). Using these alternatives could significantly reduce the impact of plant invasions in the Czech Republic in the future, not only in the surroundings of ornamental plantings but also in the open landscape.

6.3 Public parks in the context of invasive, natural, and cultural processes

The Czech Republic is particularly prone to plant invasions due to its dense population and frequent linear structures that facilitate the transmission of diaspores in the landscape (roads, railways, rivers, etc.) (Pyšek and Sádlo 2004). Rivers and other small watercourses can represent the main migration corridor for alien species that escape from chateau parks or, on in contrast, invade them. Another significant pathway of introduction can be in parks, e.g., stowaways arriving with heavy machinery or contaminated soils due to landscaping (Pyšek et al. 2011a).

However, these spreading pathways can be main drivers not only for alien species but for expansive native species as well. These native dominants populate similar anthropogenic habitats as non-natives and can have similar negative effects on species diversity (Hejda et al. 2021). The expansive species apply a similar life strategy to the invasive species – they spread quickly, prefer nutrient-rich habitats, and use high opportunities of resources for extreme growth (Marková and Hejda 2011). In the case of chateau parks and gardens, these can be common species of eutrophic and ruderal habitats, such as *Urtica dioica* and *Calamagrostis epigejos*, or historically widely cultivated and widespread ornamental species that are native to the Czech Republic (e.g., *Aquilegia vulgaris*) (Rebele and Lehmann 2001; Kubát and Bělohlávková 2002). In addition, among the native dominants of the parks, species that are native to some parts of the Czech Republic can also be counted – "regionally alien taxa" (see Chapter 1; e.g., *Clematis vitalba* and woody species such as *Hedera helix* or *Taxus baccata*; Vojík et al. 2020)

Except for these biological elements (including the botanical view), parks should also be viewed as part of the urban environment, i.e. cultural landscape. Therefore it should be taken into account that these areas are complex (in terms of natural and especially cultural diversity), heterogeneous (in differences in local conditions), and, above all, significantly variable over time (Šantrůčková and Weber 2016). It is difficult to apply approaches to this environment from rural and natural landscapes, which are the traditional starting point of the entire ecology. Forman (2016) has already drawn attention to the demonstrable differences between urban and natural ecology principles. The fundamental difference between these two environments is due to human influence, both in quantity (cities are more densely populated than the countryside) and quality (urban activities differ from natural and seminatural activities traditionally associated with agriculture and forestry). For a full understanding and subsequent description of biological processes in the urban environment, it would be appropriate to consider human ecology, which can help grasp the complex issues of the urban environment (Sádlo et al. 2020). Human ecology is an interdisciplinary science (used in geography, anthropology, sociology, psychology, environmentalism, etc.) which looks at people as biological organisms and, at the same time, social beings in interaction with their environment (Bubolz and Sontag 2009; Calonge-Cano et al. 2017). Despite efforts to unify approaches, human ecology has been a strongly fragmented field since its inception (Bruhn 1974). One extreme is sociological theories without broad context to local reality, the other extreme is practical urbanism (building a city), and the third is a biological point of view – in this case, botany, which uses the city only as terrain for research into purely botanical contexts. From a botanical point of view, urban flora was studied, e.g., in the following studies (Lososová et al. 2012a) and (Lososová et al. 2012b). An exception to the purely botanical studies is the that of Sukopp, who assessed the city as a whole and found that there is different vegetation in the centre of the cities than in the peripheral settlements. Another exception is urban studies with social and cultural overlap (Thompson 2002). In an attempt to cover the maximum number of aspects that affect the anthropogenic landscape, a methodology for the management of native and alien plants in monuments of horticultural art was drawn up – chateau parks and gardens were a model example here, but the methodological approach can be applied for all functional types of greenery with a defined degree of human impact (Sádlo et al. 2020). As part of the effort to anchor botanical knowledge in the continuum of private and public space, a classification of urban habitats with varying degrees of accessibility and cultural influence was also compiled as part of the methodological approach (Sádlo et al. 2020).

We studied urban landscape from the perspective of invasion processes, cultural introductions, and survival mechanisms of existing vegetation. As an example of an urban landscape, a well-defined and well-diversified body of public parks was chosen, enriching the existing study of alien plants in private gardens and their surroundings (Pergl et al. 2016b). Based on the complexity of the studied environment, a number of variables were recorded as part of the mapping and inventory of the parks, which were intended to describe the botanical records as much as possible, but also the sites of individual escapes (see Chapter 6.1 and 6.2; Vojík et al. 2020).

Another aspect of public parks that needs to be addressed results from their historical development – parks are demonstrably a hotspot of biodiversity and, depending on their original garden composition and subsequent development, we can find the relics of seminatural vegetation there (Šantrůčková et al. 2017) with threatened species (see Chapter 6.2; Vojík et al. 2020). Resulting from this fact, in addition to biological values, socio-economic values are also significantly increased – nature areas are considered important places to relax or rest with friends. Moreover, the natural environment can shape local identities, especially when natural parts are protected by law (Adamczewska 2015). Of the parks included in this study, there were sites like Lednice, Liblice, and Nové Hrady where nature protection is implemented by law – all of these places are important for local identities, especially Lednice park with many threatened species in the natural habitats (see Vojík et al. 2020). Thus, for many visitors, appreciation of the natural conservation dimensions of parks or gardens is a reason to visit (Ward et al. 2010); however, in the majority of cases, visitors prefer mutually complementary use (e.g., knowledge and relaxation) with equilibrating the cultural and environmental values enabling a broader spectrum of visitors' activities (Navrátil et al. 2016). Within the significant amount of cultural ecosystem services that parks offer us (Šantrůčková et al. 2017; Šantrůčková et al. 2019), it would therefore be appropriate that the benefits are not threatened by invasions of alien plants, the onset of which can be significantly reduced. An appropriate procedure here is the prevention of the introduction of alien species that can negatively affect the surrounding landscape – e.g., the use of local herb mixtures of seeds without alien species that can spread spontaneously (Štajerová et al. 2021); limiting the use of species that have invasive potential in garden plantings (e.g., related project "Grow safely" – Chapter 8) and protect the parks from outside invasions. Because horticulture has been confirmed as one of the most important pathways of introduction of alien species in the case of both public and private gardens (Pergl et al. 2016b; Vojík et al. 2020), the suggestion is to continue educational activities, which should target not only the professional public (gardeners) but also the general public, who manage the forms and compositions of private gardens. Within the education of professionals (horticultural) and the general public, awareness should also be raised about biological invasions in the context of climate change (Dullinger et al. 2017). Newly naturalised or escaping aliens, in combination with the anticipated destabilisation of native plant communities based on the disequilibrium of climatic conditions and increased frequencies of extreme climatic events, such as droughts (Diez et al. 2012; Svenning and Sandel 2013), could present a major threat in few years, especially in natural parts of parks or in the surroundings of parks. In the mapping and inventorying of Czech public parks between 2016 and 2018, 21 new escaping aliens were found (see Vojík et al. 2020), and it was discovered that many aliens increased their escaping activity (e.g., *Juglans nigra*, *J. regia*, *Lychnis coronaria*, *Stachys byzantina*; Vojík et al. 2022), and some of them quickly (e.g., *Paulownia tomentosa*) compared to the reference state described in the Alien Catalogue (Pyšek et al. 2012b). It indicates that the naturalisation process is dynamic, and invasion status can be shifted in less than one decade. Because the warming climate approximates the non-native range conditions to suitable climatic conditions from native ranges, other plant species introduced from warmer parts of the world will probably have optimal conditions for spreading soon as well (Niinemets and Peñuelas 2008; Bradley et al. 2012; Dullinger et al. 2017). Therefore is appropriate to study biological traits such as the generative reproduction of specific alien species (e.g., Vojík et al. 2022) – the results help define invasive potential and prevent the wide spread of alien species by human activities such as horticulture. The planting of potentially invasive species should be applied only with a stratified approach considering the site of planting, surroundings of the plantation, and biology/ecology of the species. Otherwise there may be a massive spread of originally ornamental species that will affect the entire landscape – e.g., the case of *Reynoutria* spp. For these species, the main effort was to improve approaches to their control, which will enable successful disposal and, at the same time, minimal chemical burden on the surrounding environment (Kadlecová et al. 2022). In order to protect the environment of parks (incl. conservation of threatened park species and vegetation) and allow planting and managing aliens, the solutions could be adaptation of horticulture's activities to these expert findings, and careful selection of newly planted species and their planting sites.

7 Conclusions

The research presented in this Ph.D. thesis is focused on connecting field knowledge (observation) with in situ and ex situ experiments, which are based on the global issue of plant invasions (including the reduction of biodiversity and the threat to native species and vegetation). Based on field data, it is now possible to answer the questions of which species spontaneously spread in parks and which threat they represent to the surrounding landscape. The data obtained provides information on the behaviour and spread of alien species in parks, which are generalised according to the amount and specifics of individuals escaping. In combination with other data obtained (Vojík et al. 2022; Kadlecová et al. 2022), it is then possible to detect potential threats from species whose invasive activity has not yet been considered, as well as direct threats from species whose invasive activity is well known.

The knowledge gained will be helpful for the further study of invasion processes in urban habitats (including parks and gardens) and the practical protection of natural and cultural landscapes at local and global scales. The facts discovered, especially the list of escaping ornamental aliens, will also be helpful for the assessment of invasive threats inside parks and in their surroundings, as well as for proposals for horticultural management, cultivation, and eventual eradication of specific alien species, which can significantly limit the spread of aliens into the open landscape. Furthermore, the data obtained, and especially the results of partial studies of the invasive potential of specific species (*Stachys byzantina*, *Lychnis coronaria*) show the importance of study of ecology potentially invasive species and their traits. These results will be a good basis for future designs of garden compositions, where the results will be already reflected, and the studied species will not be planted near habitats that could be invaded. The results of another experiment, aimed at the control of knotweeds (*Reynoutria* spp.), which are frequent invaders in urban habitats and parks, were then processed into a methodology which appears as an appropriate and considerate method of chemical control of knotweeds, not only for parks and urban places, but for seminatural sites as well.

The thesis results show that park areas could become a harbour for disappearing or already disappeared rare plants or habitats of the given area (Vojík et al. 2020), which will be appropriately separated from garden compositions with alien ornamental plants that could endanger them by their spontaneous spread. Using detailed knowledge of the biology and ecology of individual alien species, as well as information on their ability to spread to particular types of park areas, it is possible to enable the coexistence of threatened and alien plant species in these monuments of garden architecture. If there will is a limit to the cultivation of ornamental species to only plants that do not show invasive activity, the planting sites are appropriately chosen (far from potentially invadable habitats), and invasive plants that come to parks from outside are effectively eliminated, permanently sustainable green park areas can be achieved without the burden of high costs for the disposal of massive stands of alien taxa. Parks would thus become a stable and, in the future, irreplaceable element of urban or rural greenery, which is also a source of necessary ecosystem services, at a time when climate changes are more pronounced and their impact more global.

8 Related projects

The thesis was created as part of the project "Biotic threats to garden monuments: algae, cyanobacteria and invasive plant species" (Project no. DG16P02M041, Ministry of culture 2016–2020); the study targeted the chemical control of knotweed taxa was partly funded by the Internal Grant Agency of the Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Kamýcká 129, Praha – Suchdol, 165 00, Czech Republic (Project no. 20184224; 2018–2019) and by the Technology Agency of the Czech Republic (Project No. TH02030523; 2017–2019).

The results of the thesis were further used as a basis for a currently solving project "Grow safely – do not support invasive species" (Project no. 3211100006; Support provider: Norwegian funds, State Environmental Fund; 2022–2024); https://ragopestuj.fzp.czu.cz/en) and project “Elimination of invasive plant species in practise” (Project no. 3211100010; Support provider: Norwegian funds, State Environmental Fund; 2022–2024; https://ragoinvaze.fzp.czu.cz/en).

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10 Curriculum vitae & List of publications

Martin Vojík

Born: 13. 5. 1991

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Education

2016 – present: Ph.D. studies

Applied and Landscape Ecology, Faculty of Environmental Sciences

Czech University of Life Sciences Prague, Czech Republic

Thesis: *Alien and invasive plant species in parks and gardens of the Czech Republic*

2014 – 2016: Master study program

Regional Environmental Administration, Faculty of Environmental Sciences

Czech University of Life Sciences Prague, Czech Republic

Thesis: *Long-term changes of forest vegetation – the comparison of present species composition and biodiversity with the historical records*

2011 – 2014: Bachelor study program

Landscape Technical and Administration Services, Faculty of Environmental Sciences

Czech University of Life Sciences Prague, Czech Republic

Thesis: *Natural forest vegetation of the Bojovský potok valley (Central Bohemia)*

List of publications

Vojík, Martin, M. Kadlecová, J. Kutlvašr, J. Pergl a K. Berchová Bímová. 2022: Two shades of grey: effect of temperature on seed germination of the escaping ornamental species *Lychnis coronaria* and *Stachys byzantina*. *Plant Ecology* 223 (9): 1121-1135.

Kadlecová, Martina, **M. Vojík**, J. Kutlvašr a K. Berchová Bímová. 2022: Time to kill the beast – Importance of taxa, concentration and timing during application of glyphosate to knotweeds. *Weed Research* 62: 215–223.

Hejda, Martin, J. Sádlo, J. Kutlvašr, P. Petřík, M. Vítková, **M. Vojík**, P. Pyšek a J. Pergl. 2021: Impact of invasive and native dominants on species richness and diversity of plant communities. *Preslia* 93: 181–201.

Vojík, Martin, J. Sádlo, P. Petřík, P. Pyšek, M. Man a J. Pergl. 2020: Two faces of parks: sources of invasion and habitat for threatened native plants. *Preslia* 92 (4): 353-373.

Sádlo, Jiří, J. Pergl, M. Pejchal, I. Perglová, P. Petřík, L. Štefl a **M. Vojík**. 2020: Management původních a nepůvodních rostlin v památkách zahradního umění. BÚ AV ČR.

Berchová-Bímová, Kateřina, M. Kadlecová, **M. Vojík** a J. Vardarman. 2019: Hodnocení efektivity likvidace invazních druhů rostlin, Fakulta životního prostředí, Česká zemědělská univerzita Praha.

Berchová-Bímová, Kateřina, J. Červený, M. Kadlecová, M. Kopecký, J. Patoka, E. Pecharová, D. Petrus, O. Simon, J. Vardarman a **M. Vojík**. 2019: Monitoring ohrožení zájmových lokalit invazními nepůvodními druhy – Metodika MŽP, *Lesnická Práce*, Kostelec n. Č. lesy.

Vojík, Martin, a K. Boublík. 2018: Fear of the dark: decline in plant diversity and invasion of alien species due to increased tree canopy density and eutrophication in lowland woodlands. *Plant Ecology* 219 (6): 749-758.

Grants and projects

2022 – 2024	Grow safely – do not support invasive species – funded by Norway Grants and State Environmental Fund of the Czech republic (QK21020022)
2022 – 2024	Elimination of invasive plant species in practise (3211100010) – funded by Norway Grants and State Environmental Fund of the Czech republic
2021 – 2026	Center for Landscape and Biodiversity – DivLand (SS02030018)
2019 – 2026	Integrated LIFE project for Natura 2000 in the Czech Republic, LIFE-IP: N2K Revisited – One Nature (LIFE17 IPE/CZ/000005)
2019 – 2021	DarkDivNet – global network to explore the dark diversity of plant communities
2018 – 2022	Responsible water management in built-up areas in relation to the surrounding landscape – SWAMP (EF16_026/0008403)
2018 – 2020	Development of new methods for the elimination of invasive knotweed taxa (IGA 20184224)
2017 – 2019	Development of Invasive Alien Species Geoinformation Portal – funded by TAČR (TH02030523)
2017 – 2019	Ecological impacts of alien and native plants on vegetation: does origin matter? – funded by GAČR (GA17-19025S)
2016 – 2020	Biotic threats to garden monuments: algae, cyanobacteria and invasive plant species – funded by programme NAKI II (MK ČR DG16P02M041)

11 Participation in conferences

(i) NEOBIOTA 2022 (Tartu, Estonia)

(ii) 4th Croatian Symposium on Invasive Species 2021 (Zagreb, Croatia)

(iii) NEOBIOTA 2020 (Vodice, Croatia)

(iv) EMAPi 2019 (Prague, Czech Republic)

(v) CASEE 2019 (Sarajevo, Bosnia and Herzegovina)

(vi) NEOBIOTA 2018 (Dublin, Ireland)

(vii) EMAPi 2017 (Lisbon, Portugal)