Two faces of parks: sources of invasion and habitat for threatened native plants

Dvě tváře parků: zdroje invazí a biotop pro ohrožené druhy

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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 in various landscapes and socioeconomic contexts, in order to build complete inventories of alien taxa spontaneously spreading outside cultivation in parks or from their surroundings. We describe the richness, diversity, status, frequency and abundance of 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 invasive species are relatively low, and their population sizes are limited despite the great number of taxa cultivated in parks; (ii) many invasive plants arrived in parks from the surrounding urban and rural landscapes; and (iii) many parks act as refugia for threatened native taxa and vegetation types. We recorded 242 alien taxa, of which 21 were recorded for the first time outside cultivation, representing additions to the national alien flora, seven were cultivars of native taxa, and 26 were native taxa growing outside their natural distribution area in the Czech Republic. The most abundant taxon was the native *Hedera helix*, which often thrives 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 and 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. The 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.

Keywords: alien plants, chateau parks, escape from cultivation, nature conservation, ornamental plantings, plant invasion, public parks, Red List, threatened taxa

Introduction

Ornamental plants are commonly used in landscape architecture, floricultural industries and ethnobotany (Groening & Wolschke-Bulmahn 1989, Vogl et al. 2004, Wijnands 2005, Xia et al. 2006). However, the diversity and composition of cultivated ornamental

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flora in private or public areas and its significance for biological invasions in particular have only become a research topic in the last few decades (Dehnen-Schmutz et al. 2007a, b, Pergl et al. 2016, Klonner et al. 2017, van Kleunen et al. 2018). Traditionally, cultivated ornamental plants are mostly considered as garden escapes in studies on spontaneous floras in urbanized areas (Višňák 1995, Pyšek 1998, Sukopp 2002, Thompson 2002, Chocholoušková & 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 in ornamental plants is a major driver of alien species introductions including unintentional introductions of weeds in 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 are disappearing from the current landscape as a result of unsuitable management, habitat loss and global change (Alvey 2006, Celesti-Grapow et al. 2006, Niinemets & 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 centres (Ricotta et al. 2001) or suburban areas (Chocholoušková & Pyšek 2003, Kühn et al. 2004, Stewart et al. 2004), but also in the rural and post-industrial countryside (Dzwonko & Loster 1988, Konijnendijk et al. 2005, Sádlo et al. 2017).

Another category that needs to be considered within this study includes the so-called expansive species, i.e. native species that spread in human-transformed landscapes due to their ability to take advantage of changes in land-use (Prach & 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 impacts of invasive species (Pyšek & Richardson 2010, Vilà et al. 2011, Kumschick et al. 2015), including extinctions of native species (e.g. Downey & 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, 2020) 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 in parks or coming from the surroundings of parks; (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 parks. The data collected will allow us to quantify the main processes involved in alien taxa dynamics within parks, i.e. local escapes from cultivation, and their subsequent spread beyond the boundaries of parks and the invasion of alien taxa coming from surrounding landscapes.

Methods

Study sites and environmental variables

This 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. 1, 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.

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 simple landscape classification (Löw & Novák 2008; further referred to as 'modified landscape categories'). We distinguished areas in flatland (floodplains of big rivers; dry to mesic lowland on 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 much 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 2005a, Nielsen et al. 2014).

Nomenclature follows the checklist of the Czech flora (Danihelka et al. 2012) and the standardized names for 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 the native *C. avellana*. The taxa of *Forsythia*, including cultivars, were merged in the *F. suspensa* group since it is difficult to determine young non-flowering individuals.

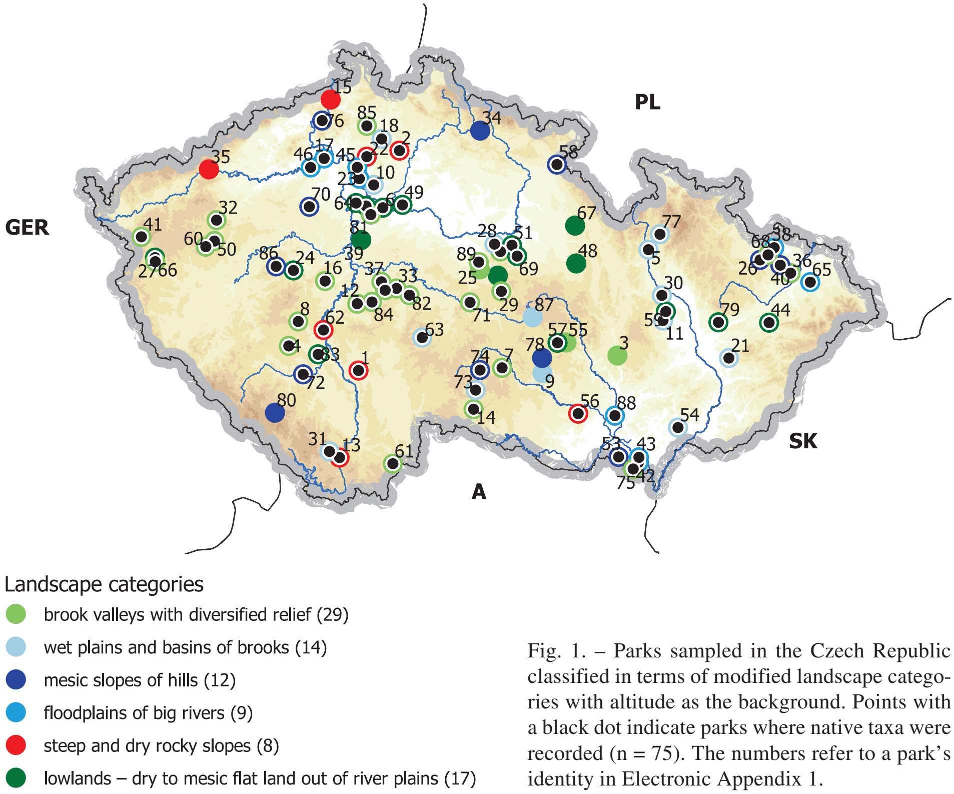

Fig. 1. – Parks sampled in the Czech Republic classified in terms of modified landscape categories with altitude as the background. Points with a black dot indicate parks where native taxa were recorded (n = 75). The numbers refer to a park's identity in Electronic Appendix 1.

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 in parks and escaped spontaneously from cultivation (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 parks due to unintentional introduction (often alien species) and (iii) remnants of the 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 provided by 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 in other areas in the Czech Republic but not in 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 and is extremely rare).

Alien spring geophytes were excluded due 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. (2012). 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 those that 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 originating from outside the park.

Alien status was assigned according to the Catalogue of alien plants of the Czech Republic (Pyšek et al. 2012). 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 (estimated for each taxon using the following scale: single locality, rare, scattered, locally abundant, and common across the whole Czech Republic), mode of introduction (intentional or unintentional) and region of origin. Some taxa were recorded as outside cultivation for the first time in the Czech Republic, thus representing new records for the country's alien flora (Hadinec & Lustyk 2017, Lustyk & 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 (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 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, ranging from rare occurrences (i.e. covering less than ~50 m^2 in total), to abundant at a few localities within a park or only sparsely abundant (i.e. ~50–5000 m^2 in total) to abundant taxa occurring in an area larger than 5000 m^2; and (iii) 'plantation context' for which two categories were distinguished: 'park escapes' (i.e. their parental populations were originally cultivated in the park) and 'other escapes', 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 & Šumberová 2004, Ekrt 2012). All Red List 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 represent 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 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 non-significant terms (using deletion tests from the maximal model), and retaining significant terms (e.g. Hejda et al. 2009, Pekár & 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, weighted by abundance and park attributes, was analysed using the canonical correspondence analysis (CCA) in Canoco 5 (Šmilauer & 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 Bonferroni 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 & 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 using a scree diagram. The PCA used to simplify existing climatic variables revealed that the first three axes explained 81% of the variance. The first axis (linear combination) was related to temperature and precipitation, the second to temperature, and the third axis to seasonality (Electronic Appendix 4).

A regression tree was produced to assess the role of factors determining the frequency of taxa in the parks. The number of taxa was the response variable. To account for phylogenetic relationships of the recorded taxa, 1/sqrt of the number of taxa within the genus was used as a weighting 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, 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 & 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 resubstituting 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 an outlier in 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. 1), which occurred within six modified landscape categories. The parks were located both in flat 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. 1).

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 outside 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 belonged to 179 genera in 73 families. The most common genera were *Prunus* (incl. *Cerasus*, *Laurocerasus*, *Padellus*, *Padus*) (10), *Lonicera* (5), *Acer* (5), *Sedum* (4) and *Spiraea* (4), and prominent families *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.)

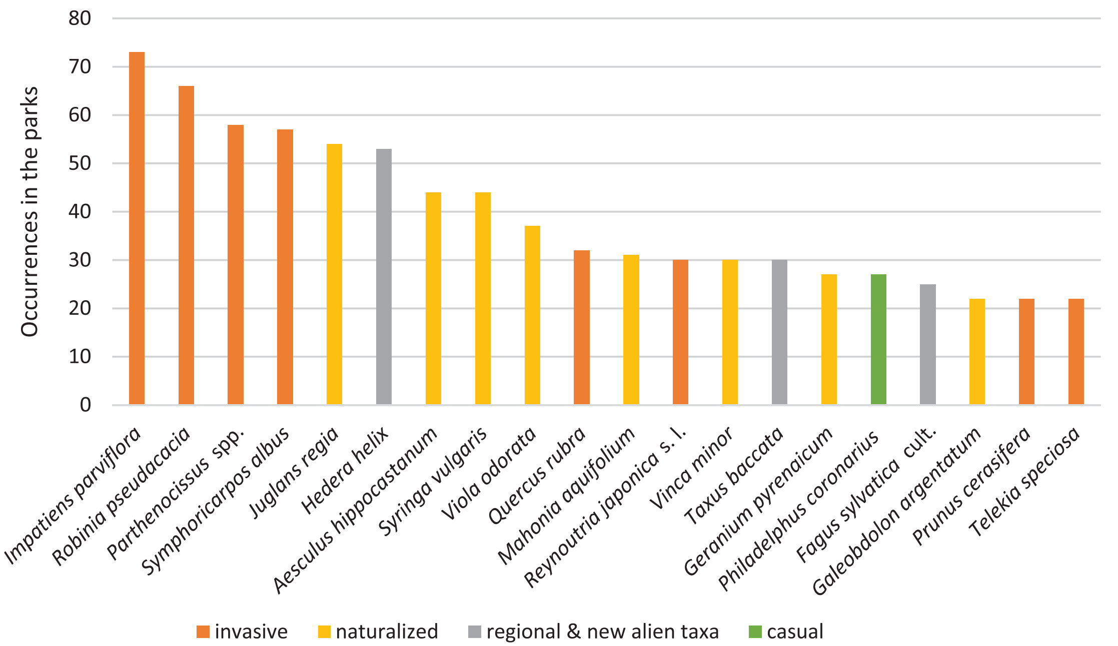

Fig. 2. – Number of occurrences of the top 20 taxa spreading within parks. The colours indicate invasion status.

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). Of all aliens recorded, 11.0±6.3 were classified as park escapes and 6.0±3.0 as other escapes.

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 5).

The most frequent taxon was *Impatiens parviflora*, which occurred in 73 parks (i.e. more than 65% of all those surveyed; Fig. 2). Other high-ranking taxa in terms of frequency were mostly woody species (Fig. 3). 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 with either means of spread, *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%) (Fig. 2).

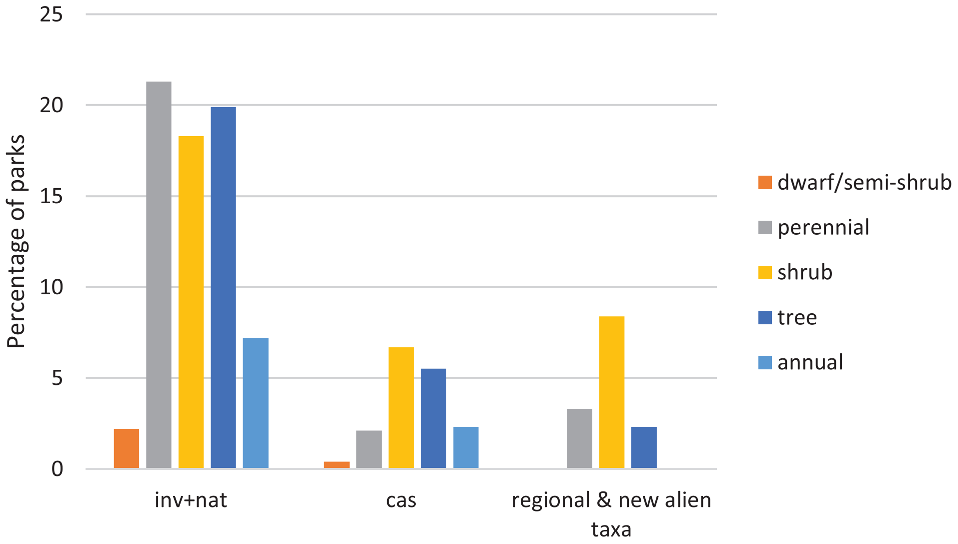

Fig. 3. – Frequency distributions of taxa grouped according to life forms and stage of the invasion process; invasive and naturalized (inv+nat) and casual (cas); regional aliens and newly recorded aliens are treated together (regional & new alien taxa).

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 – C1, 23 endangered – C2, 40 vulnerable – C3, and 33 of 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 recorded 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 at Liblice), and *Pulicaria dysenterica* (Lednice park).

In terms of habitats, the highest number of threatened taxa (40) was recorded 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 composition of alien taxa (Table 1, Fig. 4). All variables explained 5.2% of the total variation in the data. The variables related to climate (PCA scores; Electronic Appendix 4) 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.

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, naturalized) in 5.0±8.5.

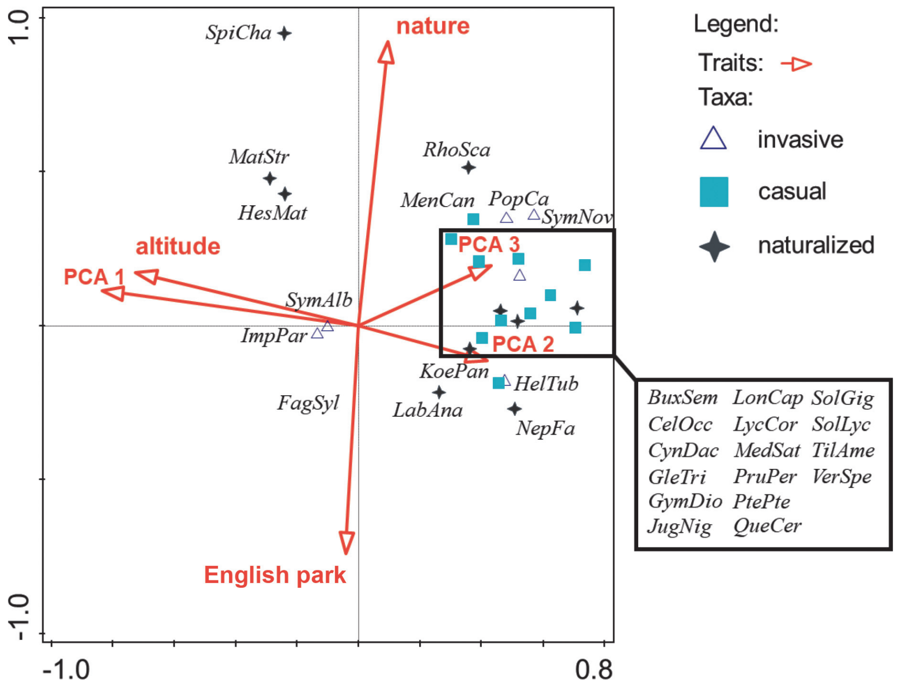

Fig. 4. – Canonical correspondence analysis of species compositions with the effects of park attributes and climate. Arrows: 'English park' stands for the percentage area covered by this part of the parks, 'nature' for the area covered by seminatural vegetation; PCA 1–3 represent PCA scores for climatic variables (see Electronic Appendix 4). 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 (no symbol), 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*/*M. dauricum*, 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. The variables are ranked according to the explained variation.

	Explained variation (%)	P-value	P_{adj}
Park attributes			
Altitude	2.9	0.002	0.014
Seminatural (% of area with seminatural vegetation)	2.1	0.002	0.014
English park (% of area with English landscape)	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

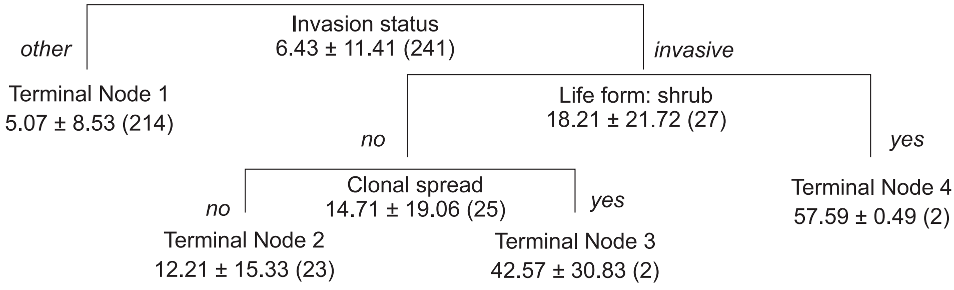

Fig. 5. – Regression tree showing important factors influencing the frequency of alien taxa recorded in the parks.

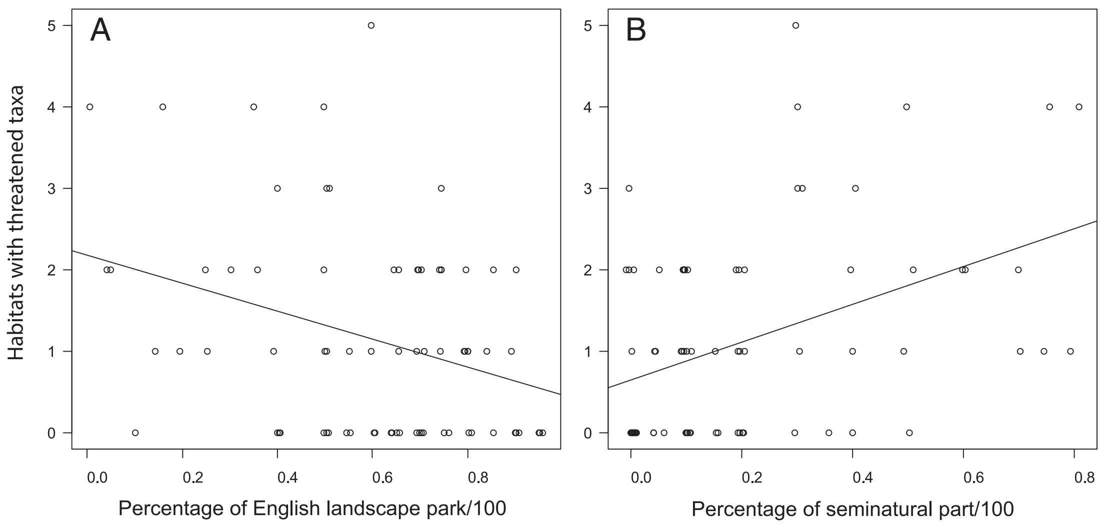

Fig. 6. – Relationships between the number of habitats harbouring threatened taxa and the proportion of the parks consisting of English landscape (A) and seminatural parts (B).

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. 5). 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. 5).

Patterns in the distributions of threatened plants

The number of habitats in which at least one threatened taxon was recorded decreased with the proportion of the area assigned to English landscape (Fig. 6A; $F_{1.73} = 12.19$, $P < 0.001$, $t = –3.491$) and increased with the proportion of park area covered by seminatural habitats (Fig. 6B; $F_{1.73} = 20.06$, $P < 0.001$, $t = 4.479$). Other park attributes had no significant effect on the distribution of threatened taxa.

The role of parks in the invasion process

The number of escaping taxa significantly depended on the proportion of the taxa with different invasion status recorded 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 the best fit (AIC = 368.8; df = 5), unlike the maximal model (AIC = 371.7; df = 8) (see Electronic Appendix 6 for all model parameters). The relationship increases when alien plants spread from parks into the surroundings, and decreases with decrease in the proportion of aliens arriving into the parks among the entire park alien flora.

Discussion

Are alien species spreading from parks?

Our study provides two contrasting perspectives of the spontaneous flora in chateau parks that are typical features of central-European landscapes. The parks are sources of alien taxa escaping from cultivation but also serve as habitats for threatened native taxa. Of the 89 parks surveyed, we recorded 242 alien taxa escaping from ornamental plantings. Some parks contain populations of locally invasive 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), which tends to spread at unmanaged sites. To assess whether parks serve as a source of alien plants in 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 parks (Electronic Appendix 7).

This analysis revealed that, for example, *Impatiens parviflora* is a common invasive neophyte in parks (Fig. 2), but as it is widespread in the whole country, the role of parks in its invasion is negligible because park occurrences account for only 3.5% of Pladias grid cells in which it is recorded (Electronic Appendix 7). In contrast, the taxa of *Parthenocissus* are reported from 20% (504) of the 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 *Parthenocissus* planted in private gardens (Pergl et al. 2016). In a similar vein, *Phytolacca esculenta*, an emerging alien in Europe (Martan & Šoštarić 2016), was recorded in 10 grid cells with parks out of 41 grid cells in Pladias (i.e. 24%) and *Gymnocladus dioica* in 7 out of 9 (78%). Hence, their presence in parks is an important factor in the spread of these taxa (Electronic Appendix 7).

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

Parks and other ornamental plantations are potential sources of future invasions (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 also consider *Vinca minor*, a species that was previously considered native, as an alien. In addition, the invasive behaviour of some species (e.g. *Lychnis coronaria* and *Stachys byzantina*) may lead to updating their status as currently given in the national catalogue of alien flora (Pyšek et al. 2012) (Electronic Appendix 2).

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

Many ornamental plants easily spread outside cultivation, the most successful life forms being woody species and perennial herbaceous plants. Ten of the 20 most commonly escaping aliens in parks form clonal stands soon after being planted and 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 & Säumel 2007, Cierjacks et al. 2013), which can potentially be transported long-distances by rivers and along 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 indicates that the most commonly escaping ornamental taxa are shrubs, many of which are currently classified as casual aliens in the Czech Republic (Pyšek et al. 2012). 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 & 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. 2). *Philadelphus coronarius*, classified as a casual alien in the Czech Republic (Pyšek et al. 2012), seems to be at the onset of a more extensive spread and cultivation in large parks could serve as a source (Hieke 1984, 1985).

Similar to private gardens (Pergl et al. 2016), many native ornamentals can grow outside cultivation in parks. Traits that make these taxa competitive and facilitate 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 for establishing in other ornamental garden beds, and then in various seminatural habitats within and near parks (Barošová & 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 are often found growing outside cultivation (Schulz & Thelen 2000, Dlugosch 2005, Pergl et al. 2016, Perring et al. 2020). The high frequency of occurrence of these species in chateau parks that was observed before (Hieke 1984, 1985) is associated with a high invasion potential and negative impact on the species diversity of woody vines (Schulz & Thelen 2000, Dlugosch 2005, Liu et al. 2008, Panasenko & Anishchenko 2018).

The role of park structure and management in naturalization

The characteristics of parks play a role in determining the occurrence and diversity of alien plants. More aliens were recorded in parks with large seminatural areas (Fig. 4), rather than in English landscape parks and French formal gardens, in which many ornamental species are planted in beds and swards (Mukerji 1997, Woudstra & Hitchmough 2000).

We show that the ratio of the number 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 there are 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 outside declines as that of the casual and naturalized aliens inside the park increases. 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 differs not only among parks but also for the different habitats within the same park (Schroeder & 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 remains of walls where pioneer woody species and competitive perennials find suitable conditions for colonization (Jim 2008, Lososová et al. 2012b, Petřík et al. 2019).

Attributes of parks and climatic factors

In several studies, altitude is 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. 2011). Climatic variables are also reported as important; for example, the number of neophytes is associated with temperature (Lososová et al. 2012a). In addition, several attributes of parks related to their structure (i.e. area of French formal garden, English landscape park, seminatural vegetation and the extent of technical support areas) also had a highly significant effect on the composition of the alien taxa.

Some thermophilous taxa could spread into seminatural vegetation due to climate change (Kowarik 2005b, Barošová & Baroš 2009). Such taxa are already reported escaping more often now than in the past. Niinemets & Peñuelas (2008) report 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 between climate and land cover (Dullinger et al. 2017).

Parks harbouring threatened taxa

Seminatural habitats in the parks studied harboured some rare and threatened taxa (Fig. 6); this may include species that disappeared from the surrounding degraded landscapes (Corlett & Westcott 2013) but are able to survive inside the parks in seminatural habitats, such as species-rich forests or seminatural grasslands typical of English landscape parks

(Šantrůčková et al. 2017). However, our data indicates that seminatural vs English-landscape parts of parks have different effects on rare taxa, where 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 parks with seminatural habitats persisting from early modern cultural landscapes before the park was established. This pattern is most likely due to less intense horticultural activity in seminatural parts, compared to English landscape parks and minor impacts of 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 areas of English park (see Fig. 4). The seminatural parts of 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 are islands of suitable habitats in otherwise homogeneous surrounding landscapes (Prach & Pyšek 2001). In the Anthropocene, the parks thus serve as biodiversity islands in urbanized and agricultural landscapes (Wilson & Peter 1988, Boinot et al. 2019). Also, native plants in the parks and gardens could serve as genetic reservoirs for future potential in-situ recovery of threatened and vulnerable species (Roberts et al. 2007, Stojanova et al. 2020).

See www.preslia.cz for Electronic Appendices 1–7

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Souhrn

Studovali jsme výskyt nepůvodních rostlin v 89 parcích v České republice. Mezi studované lokality byly zahrnuty parky v městských oblastech, zámecké a palácové zahrady i venkovské parky v různých krajinných a socioekonomických podmínkách. Naším cílem bylo (i) zachytit všechny nepůvodní taxony, které se spontánně šíří z parkových výsadeb, nebo se do parků dostávají z blízkého okolí, (ii) podrobně popsat jejich druhovou bohatost, hojnost a četnost zplanění, (iii) zjistit vztah mezi výskytem nepůvodních druhů, lokálními proměnnými a managementem používaným v parcích, (iv) posoudit invazní potenciál zaznamenaných taxonů a (v) odhalit jejich vliv na ohrožené původní druhy vyskytující se v parcích. Mnoho invazních druhů se do parků šíří z okolní krajiny a mnoho parků naopak představuje útočiště pro ohrožené původní druhy. Celkem bylo nalezeno 242 nepůvodních taxonů – 21 druhů jsou nové přírůstky do katalogu nepůvodních druhů České republiky, 26 bylo původních taxonů, pro něž park leží mimo areál původního výskytu v České republice (regionálně nepůvodní druhy), a sedm bylo kultivarů původních taxonů. Nejhojnějším druhem byl regionálně nepůvodní druh *Hedera helix*, který se často chová expanzivně i na přirozených stanovištích. Nejhojnějšími nepůvodními druhy byly invazní neofyty *Impatiens parviflora* a *Robinia pseudoacacia*. Naturalizované a invazní taxony zplaňovaly v 69 %, přechodně zavlečené poté pouze v 18 % parků, ve kterých se vyskytovaly. V parcích bylo zaznamenáno 100 taxonů Červeného seznamu ohrožených druhů ČR, z čehož čtyři druhy spadají do kategorie kriticky ohrožených. Naše studie ukazuje, že parky mají v invazním procesu podobnou roli jako jiné podobné lokality v urbanizované krajině, ale poskytují také útočiště mnoha původním druhům. Nabídku příhodných biotopů pro ohrožené druhy umožňuje zejména pravidelný management, který je zaměřen především na estetické funkce, např. odstraňování náletových stromů a keřů na specifických stanovištích s cílem zachovat otevřené či stepní lokality, kde se ohrožené druhy často vyskytují.

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