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Alien plants in urban nature reserves: from red-list species to future invaders?

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Abstract

Urban reserves, like other protected areas, aim to preserve species richness but conservation efforts in these protected areas are complicated by high proportions of alien species. We examined which environmental factors determine alien species presence in 48 city reserves of Prague, Czech Republic. We distinguished between archaeophytes, i.e. alien species introduced since the beginning of Neolithic agriculture up to 1500 A. D., and neophytes, i.e. modern invaders introduced after that date, with the former group separately analysed for endangered archaeophytes (listed as C1 and C2 categories on national red list). Archaeophytes responded positively to the presence of arable land that was in place at the time of the reserve establishment, and to a low altitudinal range. In addition to soil properties, neophytes responded to recent human activities with the current proportion of built-up area in reserves serving as a proxy. Endangered archaeophytes, with the same affinity for past arable land as other archaeophytes, were also supported by the presence of current shrubland in the reserve. This suggests that for endangered archaeophytes it may have been difficult to adapt to changing agricultural practices, and shrublands might act as a refugium for them. Forty-six of the 155 neophytes recorded in the reserves are classified as invasive. The reserves thus harbour 67% of the 69 invasive neophytes recorded in the country, and particularly worrisome is that many of the most invasive species are shrubs and trees, a life form that is known to account for widespread invasions with high impacts. Our results thus strongly suggest that in Prague nature reserves there is a high potential for future invasions.

Keywords

Alien plants, archaeophyte, Czech Republic, nature reserve, neophyte, plant invasions, red list, urban

Introduction

Urbanization is the most dramatic form of natural habitat destruction making cities a rather hostile environment for natural wildlife. Conserving the native biodiversity in urbanized areas is therefore particularly challenging because remnants of natural habitats in urban areas are restricted to small and isolated patches. These often harbour fragmented populations of native plants and animals that face risks associated with small population sizes and pressures from heavily altered urban environments (Raupp et al. 2010, Jarošík et al. 2011). Maintaining biological biodiversity in urban landscapes has recently become a conservation priority and protecting natural remnants within cities is increasingly viewed as important (Celesti-Grapow and Blasi 2003, Turner et al. 2004, Palmer et al. 2008, Toth et al. 2009, Vermonden et al. 2009). Many cities are located in naturally species-rich areas (Kühn et al. 2004) and their heterogeneous environments (Zerbe et al. 2003) have the potential to support high numbers of species.

However, overall species diversity in entire cities has been intensively studied (Klotz 1987, 1988, 1990, Pyšek 1989, Knapp et al. 2008, 2010) and it has been repeatedly documented that urban environments and the associated life styles promote introductions of alien species (Pyšek 1998, Celesti-Grapow et al. 2001, 2006, Chocholoušková and Pyšek 2003, LaSorte et al. 2007, 2008, Ricotta et al. 2009). Plant invasions are strongly dependent on propagule pressure and pathways associated with human activities that are extremely pronounced in urban areas, and also create favourable conditions for the establishment of arriving species via disturbances (Hulme et al. 2008, Pyšek et al. 2010c, Essl et al. 2011). These factors contribute to plant species richness in cities that is higher than surrounding landscapes (Haeupler 1974), and overall alien species contribute to the remarkably high species richness of European cities (Pyšek 1993, 1998).

However, as in other protected areas, the conservation focus in nature reserves in urban areas is on the diversity of native species. Urban areas are where these "two diversities" come into the sharp conflict that results from the mismatch between human efforts to protect natural biodiversity and their activities that create ideal environments for alien species invasions. This matrix of urban development and nature reserves is therefore an appropriate testing ground to explore resistance patterns of natural vegetation against penetration by alien plants. It has been shown for other environments that nature reserves and protected areas possess some resistance against invasions (Pyšek et al. 2003, Foxcroft et al. 2011).

This study analyses patterns of species richness of alien vascular plants in the city of Prague, Czech Republic. Based on the same data set as in Jarošík et al. (2011) where the factors shaping the richness of native, including endangered, butterflies and plants were analysed, this paper focuses on alien plants. It aims to identify the factors that contribute to the levels of reserve invasions (in the sense of Hierro et al. 2005, Richardson and Pyšek 2006, Chytrý et al. 2008a) and that determine the numbers of archaeophytes and neophytes currently observed in nature reserves in Prague.

Methods

Study area

The city of Prague, Czech Republic, contains 88 nature reserves in an area of 496 km^2 (Kubíková et al. 2005). Complete plant species lists were available for 48 reserves, and resulted from a systematic surveys of flora in the late 1980s/early 1990s (Špryňar and Marek 2001; Appendix 1). The reserves analysed are evenly distributed across the metropolitan area, both in its central and peripheral areas between 14°13'51 and 14°43'80"N and 49°56'33" and 50°12'23"E, and were established between 1953 and 1990. The vegetation protected in the reserves ranges from plant communities of rocky outcrops and unused quarries to thermophilous grasslands and shrublands, and semi-natural woodlands (see Jarošík et al. 2011 for details). Nineteen of the reserves (mainly rocks and unused quarries) were originally established to protect geological or palaeontological sites and 15 to conserve rare plants (Kubíková et al. 2005). At present all of them represent sites protected from human influence other than tourism.

Plant data

For each reserve, the total number of vascular plant species was recorded; only naturally occurring species were considered; planted shrubs and trees were excluded. The total number of plant species in all reserves was 1309 (about a half of the Czech flora; Kubát et al. 2002), mean species number per reserve was 291, ranging from 117 to 683.

Species were classified into native and alien, with archaeophytes and neophytes distinguished among the latter group (e.g. Pyšek et al. 2002b, 2004c, Preston et al. 2004). Archaeophytes are plant species introduced to the Czech Republic since the beginning of Neolithic agriculture up to 1500 A. D., mostly from the Mediterranean region and Western Asia, while neophytes arrived after that date and represent a much more variable group in terms of the areas of origin (Pyšek et al. 2002b, Lambdon et al. 2008). The effect of the time of arrival is still detectable at present and both groups markedly differ in their ecology and habitat affinities in Central Europe (Pyšek et al. 2004b, 2005, 2011, Chytrý et al. 2005, 2008a, b). In total there were 175 archaeophytes and 155 neophytes in the reserves analysed (mean per reserve 14.0 and 20.3, range 4–63 and 6–104, respectively).

Since some archaeophytes appear on national red lists despite their alien origin, (Holub and Procházka 2000, Cheffings et al. 2005, Zajac et al. 2009), we recorded the number of species that are considered endangered in the Czech Republic for each reserve following the red-list classification in Kubát et al. (2002). This group (further referred to as "endangered") included species classified in categories C1 (critically threatened taxa, corresponding to the IUCN category "critically endangered") and C2 (strongly threatened taxa, corresponding to the IUCN category "endangered"; see

Holub and Procházka 2000 for details). In total there were 15 endangered species in the reserves analysed (mean = 0.6, range 0–8).

The numbers of neophytes, archaeophytes and endangered archaeophytes recorded in reserves were used to calculate their proportions among total numbers of species, used in statistical analyses.

Explanatory variables

Explanatory variables describing factors that were assumed to affect the patterns of alien species occurrence in the reserves reflect geography (no. 1–7 below), habitat characteristics (8–9), substrate (10–12) and urbanization (13–16), and included: 1. reserve area (ha); 2. degree of reserve isolation (categorical: isolated, > 1 000 m from the closest reserve; clustered, < 300 m from the closest reserve; neighbouring, adjoining other reserves); 3. reserve age, expressed as years since the establishment; 4. aspect (north to north-east; plain; south-east and west; south and south-west; valley with all aspects present); 5. mid altitude, i.e., the mid value between minimum and maximum altitude; 6. altitudinal range, i.e. the difference between maximum and minimum altitude; 7. presence or absence of railway; 8. past habitat, reflecting the proportional representation of the following habitat types at the time of reserve establishment, with each type treated as an independent variable: forest, arable land, pasture, grassland, orchards, shrubland (including rocky outcrops) and built-up area; 9. present habitat, referring to the current state, using the same classification; 10. soil type (categorical variable with following levels: alluvial; acid; calcareous; neutral; acid and alluvial; acid and neutral; acid and calcareous; acid, neutral and calcareous); 11. presence or absence of bare rock; 12. presence or absence of a quarry; 13. minimum distance to natural habitat; 14. minimum distance to built-up area; 15. built-up perimeter, i.e. length of perimeter formed by built-up area; 16. natural perimeter, i.e. length of perimeter formed by other than built-up area.

The variables are the same as in Jarošík et al. (2011) where further details and means and ranges for continuous variables are given.

Statistical analysis

The response variables were proportional representations of species numbers of archaeophytes (mean 11.8%, range 2.4–21.5%), neophytes (mean 6.0%, range 2.0–17.4%) and endangered archaeophytes (mean 0.2%, range 0–1.3%) within all wild-growing species of vascular plants in each reserve. To prevent these proportions from species-poor reserves having undue influence, the proportions were weighted by the total numbers of species in each reserve (e.g. Pyšek et al. 2010a). The response variables were then analysed as a function of the environmental characteristics of the 48 nature reserves. These analyses were made by boosted trees (Friedman 2002) in a commercial statistical software TreeNet® v.1 (Friedman 1999, 2001). This data mining technique enables to make predictions and identify the most important predictors by screening a large number of candidate variables, without requiring any assumptions about the form of the relationships between predictors and the response variable, and without a priori formulated hypotheses (Hochachka et al. 2007). The method is more flexible than traditional statistical analyses also because it enables to reveal structures in the dataset that are other than linear, and to solve complex interactions. Importantly, the technique is nonparametric and thus not affected by spatial autocorrelations and by collinearity of the predictor variables (e.g. Jarošík 2011).

Using trees, the data are successively split along coordinate axes of the predictors, represented by the environmental characteristics, so that at any node, the split is selected that maximally distinguishes the response variable, represented by the proportional representation of the species, in the left and the right branches (Breiman et al. 1984, De'ath and Fabricius 2000). This is done using binary recursive partitioning, with a best split made based on Gini impurity measure (e.g. Steinberg and Colla 1995, Cutler et al. 2007). In boosted trees (Friedman 1999, 2001), five hundred six-node classification trees were sequentially built from residual-like measures from previous trees. At each iteration, a tree was built from a default (50%) random subsample of the data set, producing a default incremental improvement in a model (0.01 learning rate at each iteration). The calculations were made with Huber-M regression loss criterion having breakdown 0.9, and minimum number of training observations in terminal nodes equal to three.

Five-fold cross-validation was used to obtain estimate of regression accuracy for each tree, and the best tree, having the smallest cross-validated mean absolute error, was chosen for interpretation. The quality of the best tree was expressed as R^2 value (Friedman 1999, 2001). Predictors of the best tree were ranked based on improvements of all splits associated with a given variable across all trees in the model, with the raw importance scores rescaled so that the most important predictor always got a score of 100. The resulting relative importance scores thus provided a relative measure of each predictor's contribution to the model's predictive power. Partial dependence plots (Friedman 2001, Hastie et al. 2001, Cutler et al. 2007) were used to graphically characterize relationships between the individual predictor variables and predicted probabilities of species presence.

The absolute numbers of archaeophytes, neophytes and endangered archaeophytes closely correlated with their proportional representation in the species pool of each reserve (Spearman's rank: archaeophytes r_s = 0.76; neophytes r_s = 0.70; endangered archaeophytes r_s = 0.99). However, it cannot be a priori excluded that the alien species respond very differently than native species to the predictors; if so, it may not be appropriate to weigh the proportions of alien species by the total number of wild growing species in each reserve, as it could change some of the conclusions presented. To verify that the results on proportions are generic, all analyses were repeated using numbers of alien species as the response variable. Comparing to previous analyses on proportions, there were no changes in conclusions, and thus only the results on proportions are presented.

Results

The most important factors affecting the proportion of archaeophytes among all species in a reserve were mainly the presence of arable land before the reserve was established, but also its altitudinal characteristics (Figure 1A): archaeophytes were more abundant when the reserve had a low altitudinal range (Figure 2). The proportion of neophytes consistently increased with the proportion of present built-up area and depended on soil type: neophytes were more represented on alluvial and neutral to calcareous soils than in reserves with acidic soils (Figure 1B and 3).

As with all archaeophytes, the proportion of endangered archaeophytes among all species in a reserve positively depended on the past presence of arable land (Figure 1C and 4A), but there was also an important effect of shrubland. The proportion of endangered archaeophytes abruptly declined in reserves with less than 30% of currently present shrubland (Figure 4B).

Discussion

Factors that determine the level of invasion of urban nature reserves

Prague nature reserves are important sanctuaries for native plants because they harbour approximately half of the native flora in the Czech Republic (Špryňar and Marek 2001, Kubát et al. 2002, Jarošík et al. 2011). Alien species in the reserves studied, on the other hand, constitute a much lower proportion of the total alien species richness in the country, but the figure differs with respect to the time of arrival: while the 175 archaeophytes represent 53% of all archaeophytes registered in the Czech Republic, the 155 neophytes found in reserves are only 15% of the 1046 neophytes (Pyšek et al. 2002b). On average, 17.8% of reserve floras are formed by alien species; this is much higher proportion than found in a larger set of 302 reserves in the whole of the Czech Republic where alien species make up on average 6.1% of the reserve flora (Pyšek et al. 2002a, 2004a).

Our study shows that the numbers of alien species in urban nature reserves can be predicted by relatively few factors. We used a number of variables that reflected site geography, land-use history and connectivity, and propagule pressure, but only five of them were needed to explain from 54 to 71% of the overall variability. That habitats were the most important factor for archaeophytes corresponds well to the recent results of studies on regional determinants of plant invasions in the Czech Republic and Europe that show habitat identity to play a decisive role, more important than propagule pressure and climate (Chytrý et al. 2008a, b, Pyšek et al. 2010b). For neophytes, the strongest effect of the proportion of built-up area reflects that it is a surrogate for propagule pressure by human activities. The effect of soil type corresponds to the well-known avoidance of acidic soils by neophytes and their affinity to resource-rich habitats (Chytrý et al. 2005, 2008b, Blumenthal et al. 2009). This is consistent with

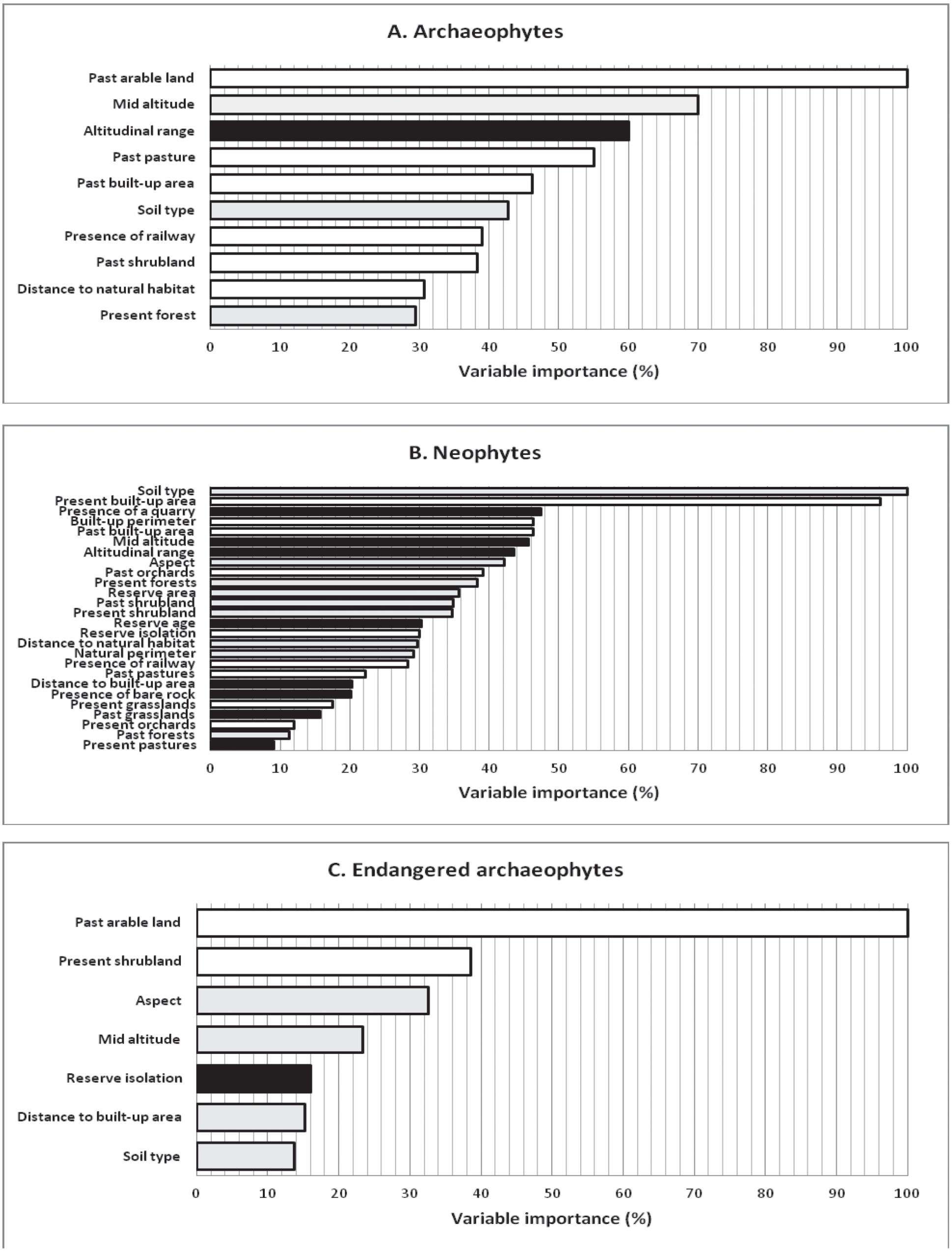

Figure 1. Rank of importance of the individual predictor variables from boosted regression trees for archaeophytes **A** neophytes **B** and endangered archaeophytes **C** Variable importance is scaled to have values between 0 and 100. Results for the best trees with R^2 = 0.71 **A** R^2 = 0.69 **B** and R^2 = 0.54 **C** White bars are predictors in which large values means positive effect, black barks in which large values mean negative effect, and grey bars are predictors with effect varying equivocally.

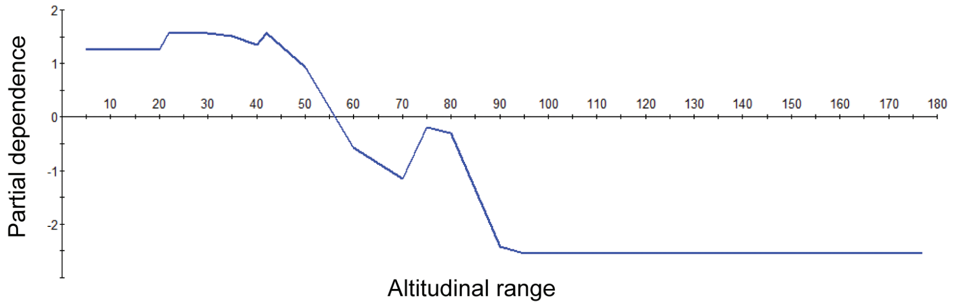

Figure 2. Partial dependence plot of representation of archaeophytes on altitudinal range. The partial dependence describes positive and negative dependences of the representation of archaeophytes on altitudinal range, averaging out the effects of the other predictor variables in the model.

the finding of Chytrý et al. (2008a) that habitat is disproportionally a more important determinant of the level of invasion by archaeophytes than neophytes, with propagule pressure also playing an important role in the latter group.

The results also reflect that the two groups differ in long-term dynamics (Pyšek and Jarošík 2005). Archaeophytes, prehistoric invaders to Central Europe, respond to the presence of arable land that was in place at the time of the reserve establishment; this is in accordance with the results of a previous study from Prague nature reserves that found native plants generally responding to the past factors, unlike butterflies that were more affected by current landscape settings (Jarošík et al. 2011). From the nature conservation perspective this implies that future levels of reserve invasion by archaeophytes were "imprinted" at the time of their establishment. The effect of low altitudinal range that also significantly affected the numbers of archaeophytes may also be related to habitat structure in a reserve since hilly sites were traditionally considered less suitable for agriculture in a lowland region.

Neophyte introductions, however, continue at an accelerating rate in Europe (Lambdon et al. 2008, Hulme et al. 2009), and a substantial proportion of them were introduced when most reserves were already established. Neophytes, therefore, respond to more recent ongoing human activities with the current proportion of built-up area in our study serving as a proxy for this activity. Still, the historical signal, similar to that for archaeophytes, is present and manifested by the effect of soil properties.

Endangered archaeophytes: better not lose them

Though it is is questionable whether species of alien origin should be a part of red lists, these species are perceived by botanists as elements of local nature, especially when they are rare, and many of them are typical of traditional cultural landscapes in Europe and considered to be species of cultural and historical importance (Cheffings et al. 2005). From the management perspective, this attitude is justified because rare archaeophytes

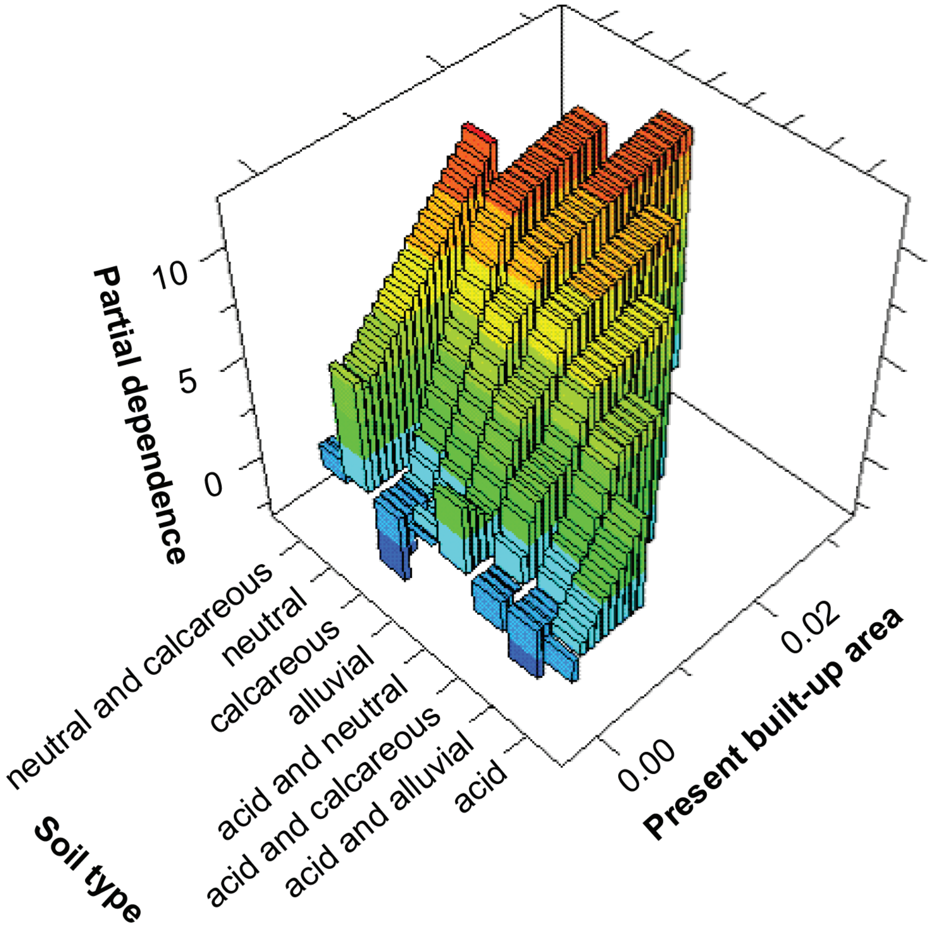

Figure 3. Bivariate partial dependence plots of representation of neophytes on present built-up area and soil type. Otherwise as in Figure 2.

are unlikely to exert any impact. Moreover, it is generally difficult to draw the line between the archaeophyte and native status, resulting sometimes in uncertain labelling (Pyšek et al. 2002b, Lambdon et al. 2008). In some cases the decision to assign a species the archaeophyte rather than native status is based on the fact that native range or habitat of the given species is unknown, and criteria applied are mostly indirect. A strong argument for protecting rare archaeophytes follows from the fact that many archaeophytes have native world ranges which are not known or are highly uncertain, and some archaeophytes are regarded as alien throughout their known global range (so-called anecophytes; Zohary 1962). As pointed by Cheffings et al. (2005), if such species were excluded from conservation efforts on account of their non-native status, it would lead to them being ignored almost everywhere and they would effectively fall through the conservation net.

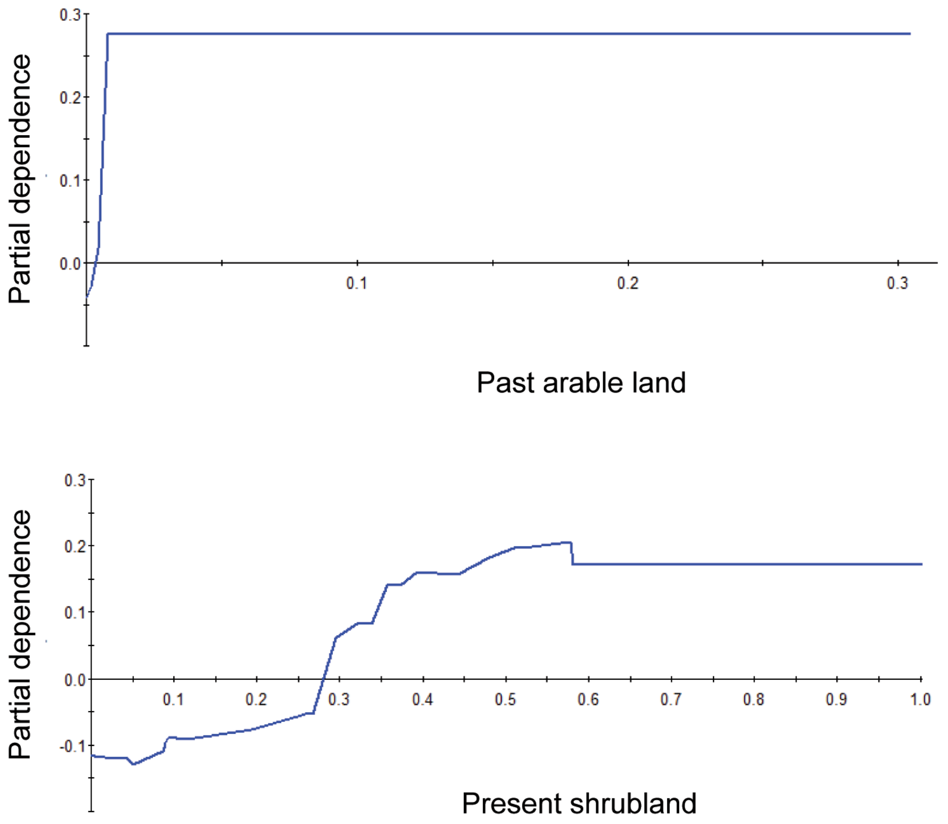

Figure 4. Partial dependence plots of representation of endangered archaeophytes on past arable land (A) and current shrubland (B). Otherwise as in Figure 2.

Endangered archaeophytes, in addition to the same affinity for past arable land as other archaeophytes, are supported by the presence of current shrubland in a reserve. This seems to indicate that there are species among this group for which it might have been difficult in the past to adapt to changing agricultural practices and that new technologies might have negatively impacted their population dynamics (Kropáč 2006). For such species, shrublands serve as refugia. This is further supported by the fact that it is current, not past shrublands that play a role. This finding points out that from the viewpoint of conservation of endangered archaeophytes, nature reserves could be more important than previously thought.

From endangered to endangering: rare archaeophytes and invasive neophytes

Our results suppport previously raised concerns about studies that analyse patterns of regional plant invasions and lump all aliens regardless of the time of immigration. It has been repeatedly shown that archaeophytes and neophytes are ecologically distinct groups that differ in habitat affinities, historical dynamics, pollination patterns and response to climate (Pyšek et al. 2004b, 2005, 2011). This is even more pronounced in nature reserves where the categories of alien species stand on opposite sides from the conservation point of view, ranging from threatened species included on red lists to potentially dangerous invaders that are targeted by management efforts. Obviously, species numbers used to infer general patterns that can lead to universal management recommendations (Jarošík et al. 2011) are one side of the coin, but to realize the immediate threat at the local scale, species identities need to be taken into account.

In total, 15 threatened archaeophytes were recorded in nature reserves studied, eight of them considered critically endangered (C1 category): *Conringia orientalis* (occurring in 3 reserves), *Erysimum repandum*, *Marrubium vulgare*, *Torilis arvensis* (2), *Adonis flammea*, *Misopates orontium*, *Polycnemum arvense* and *P. majus* (1). Additional seven species belong to the endangered (C2) category: *Adonis aestivalis* (5), *Veronica triloba* (3), *Anthriscus caucalis*, *Stachys annua*, *Veronica agrestis* (2), *Geranium molle* and *Sclerochloa dura* (1).

On the other hand, 46 of the 155 neophytes recorded in reserves (Appendix 2) are classified as invasive (Pyšek et al. 2002b). Also, the above figure about the percentage of all neophytes recorded in the set of reserves studied among their total number in the Czech Republic, 15%, changes dramatically if expressed for a subgroup of invasive neophytes: Prague reserves harbour 67% of the 69 invasive neophytes recorded in the country (Pyšek et al. 2002b). Therefore, the potential threat to Prague nature reserves by alien plants may be in fact greater than inferred from species numbers. The list from reserves includes the majority of noxious invaders of the Czech flora, species that often exert a high impact on vegetation and species diversity of invaded communities, e.g. *Heracleum mantegazzianum*, *Reynoutria japonica*, *Helianthus tuberosus*, *Lupinus polyphyllus*, *Solidago gigantea*, *S. canadensis* (Hejda et al. 2009). Invasive species in Prague reserves include diverse life forms and it should be seen as warning that there are many species of shrubs and trees, a life form that is known to account for many widespread invaders, often with a high impact (Křivánek and Pyšek 2006, Pyšek et al. 2009): *Robinia pseudoacacia* (recorded in 38 reserves), *Symphoricarpos albus* (24), *Mahonia aquifolium* (21), *Quercus rubra* (18), *Syringa vulgaris* (17), *Lycium barbarum* (10), *Populus ×canadensis* (4), *Ailanthus altissima* (3), *Rhus hirta* (2) and *Amorpha fruticosa* (1). Considering that none of the reserves was free of alien species, that the most invaded reserves harboured up to as much as 17.4% of neophytes and 32.3% of all aliens, and which species are most represented, our results strongly suggest that in Prague nature reserves there is a warning potential for future invasions unless appropriate control measures are imposed by nature conservation authorities. To make targeted practical recommendations specific to particular reserves with distinct environmental and vegetation settings, studies on current status of individual invasive species and their dynamics over time are needed, ideally initiated by state/municipal administration.

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Appendix 1. Numbers of species in Prague nature reserves and characteristics of reserves. Ttotal includes both native and alien species. Only characteristics of the reserves that affect the proportion of archaeophytes and neophytes sre shown (see Methods for details). Soil types present in a reserve: al – alluvial; ac – acid; ca – calcareous; n – neutral.

Reserve	Species numbers				Reserve characteristics						
	Total	Archaeophytes	Neophytes	Archaeophytes endangered	Age (yrs)	Area (ha)	Altitudinal Range (m)	Past arable (%)	Present shrubland (%)	Present built-up (%)	Soil type
1. Baba	368	67	29	1	21	7.3	80	0.00	97.68	0.00	ac
2. Barrandovské skály	160	14	14	1	21	11.6	100	0.00	51.86	0.05	ca
3. Bažantnice v Satalicích	158	24	17	0	52	15.8	10	0.00	0.00	0.00	ac
4. Bohnické údolí	202	12	10	0	21	4.6	60	0.00	0.00	0.00	ac
5. Podhoří	363	57	30	2	21	8.4	75	0.00	57.86	0.00	ac
6. Zámky	379	64	23	1	21	5.2	60	0.00	51.05	0.00	ac
7. Branické skály	160	21	13	0	35	9.1	50	0.00	48.02	0.00	ca
8. V Hrobech	187	24	6	0	15	1.3	10	0.00	98.46	0.00	ac
9. Šance	225	9	6	0	21	116.8	177	0.00	0.43	0.00	ac
10. Čimické údolí	341	49	23	1	35	11.2	30	9.17	8.90	0.00	ac
11. Dalejský profil	280	46	18	1	21	22.8	50	0.00	19.32	0.00	ac-ca
12. Divoká Šárka	683	104	47	4	39	25.4	105	2.56	32.07	1.58	n
13. Dolní Šárka	248	29	12	1	21	6.2	70	0.00	65.69	0.00	n
14. Homolka	192	11	4	0	21	13.5	60	0.00	33.90	0.00	ca
15. Hrnčířské louky	221	15	10	0	15	29.3	20	0.17	44.27	0.00	ac-al
16. Chuchelský háj	271	21	11	0	21	19.8	90	0.00	0.00	0.00	n-ca
17. Jabloňka	158	14	17	0	35	1.3	70	0.00	100.00	0.00	ac-n
18. Jenerálka	357	44	10	2	35	1.5	30	0.00	35.76	0.00	ac
19. Zlatnice	188	12	13	0	35	3.3	50	0.00	0.00	0.00	ac-n
20. Nad mlýnem	266	32	11	0	35	4.0	40	15.66	8.84	0.00	ac
21. Klapice	254	6	6	0	15	16.2	106	0.00	11.63	0.00	ca
22. Královská obora	362	54	63	0	15	104.5	42	0.00	26.78	3.10	al
23. Lochkovský profil	205	16	4	1	15	39.1	95	0.00	29.49	0.00	ca
24. Meandry Botiče	117	16	11	0	35	6.7	15	0.00	93.58	0.60	ac-al

Reserve	Species numbers				Reserve characteristics						
	Total	Archaeophytes	Neophytes	Archaeophytes endangered	Age (yrs)	Area (ha)	Altitudinal Range (m)	Past arable (%)	Present shrubland (%)	Present built-up (%)	Soil type
25. Milíčovský les a rybníky	435	33	17	0	15	93.3	30	0.00	10.07	0.20	ac-al
26. Modřanská rokle	333	54	29	0	15	124.9	80	0.00	3.13	0.09	ac
27. Okrouhlík	137	23	9	0	21	0.6	20	0.00	0.00	0.00	ac
28. Pitkovická stráň	173	14	4	0	34	0.5	20	0.00	3.92	0.00	ac
29. Počernický rybník	251	38	21	0	15	41.8	5	0.00	69.18	0.00	ac
30. Podbabské skály	264	51	19	1	21	0.8	30	0.00	35.71	0.00	ac
31. Cholupická bažantnice	264	51	19	1	21	13.8	12	0.00	0.00	0.00	ac
32. Obora v Uhříněvsi	326	52	24	0	21	34.9	22	0.00	4.33	0.34	ac-al
33. Prokopské údolí	606	84	29	8	25	101.5	110	0.78	39.33	0.38	ac-ca
34. Radotinské údolí	552	64	22	3	50	103.3	80	6.90	3.79	0.00	ca
35. Rohožník a lom v Dubči	332	48	18	0	15	3.5	20	0.00	8.70	0.00	n
36. Tiché údolí a Roztocký háj	381	26	15	0	52	114.2	105	0.46	5.12	0.00	n-ca
37. Sedlecké skály	211	22	5	0	21	7.5	70	0.00	37.33	0.00	ac
38. Slavičí údolí	263	16	7	0	15	38.3	105	0.00	0.00	0.00	ac-ca
39. Trojská	195	42	15	0	21	1.3	35	0.00	100.00	0.00	ac
40. Údolí Kunratického potoka	283	21	12	0	15	152.0	80	0.00	10.55	0.13	ac
41. Vizerka	350	33	12	0	15	3.1	40	0.00	25.89	0.00	ac
42. Havránka	401	59	34	0	21	4.2	50	0.00	58.10	0.00	ac-n
43. Zmrzlík	335	46	15	0	15	16.4	80	30.46	10.28	0.01	ac-ca
44. Klánovický les	435	46	35	0	21	225.5	20	0.00	0.00	0.00	ac
45. Obora Hvězda	460	55	29	1	15	84.2	50	0.00	9.40	0.77	ac
46. Staňkovka	171	7	5	0	15	44.5	160	0.00	3.76	0.00	ac
47. Vinořský park	202	27	23	0	21	34.1	20	0.00	0.00	0.00	ac
48. Xaverovský háj	268	27	14	0	21	97.2	30	0.00	3.01	0.00	ac

Appendix 2. List of invasive neophytes recorded in Prague nature reserves. Species are ranked according to the decreasing number of reserves in which they were recorded (n = 48). Plant names according to Kubát et al. (2002).

Species	Family	Life form	Number of reserves invaded
Impatiens parviflora	Balsaminaceae	Annual	40
Robinia pseudacacia	Fabaceae	Tree	38
Symphoricarpos albus	Caprifoliaceae	Shrub	24
Mahonia aquifolium	Berberidaceae	Shrub	21
Quercus rubra	Fagaceae	Tree	18
Sisymbrium loeselii	Brassicaceae	Annual	18
Solidago canadensis	Asteraceae	Perennial	18
Conyza canadensis	Asteraceae	Annual	17
Echinops sphaerocephalus	Asteraceae	Perennial	17
Syringa vulgaris	Oleaceae	Shrub	17
Epilobium ciliatum	Onagraceae	Perennial	16
Geranium pyrenaicum	Geraniaceae	Perennial	14
Solidago gigantea	Asteraceae	Perennial	14
Bidens frondosa	Asteraceae	Annual	13
Galeobdolon argentatum	Lamiaceae	Perennial	13
Galinsoga parviflora	Asteraceae	Annual	12
Galinsoga quadriradiata	Asteraceae	Annual	12
Lycium barbarum	Solanaceae	Shrub	11
Heracleum mantegazzianum	Apiaceae	Monocarpic	10
Cytisus scoparius	Fabaceae	Shrub	10
Veronica persica	Scrophulariaceae	Annual	10
Parthenocissus quinquefolia	Vitaceae	Woody vine	9
Amaranthus retroflexus	Amaranthaceae	Annual	8
Juncus tenuis	Juncaceae	Perennial	8
Matricaria discoidea	Asteraceae	Annual	8
Pinus strobus	Pinaceae	Tree	8
Reynoutria japonica	Polygonaceae	Perennial	7
Bunias orientalis	Brassicaceae	Perennial	5
Rumex thyrsiflorus	Polygonaceae	Perennial	4
Aster novi-belgii agg.	Asteraceae	Perennial	4
Digitalis purpurea	Scrophulariaceae	Monocarpic	4
Populus ×canadensis	Salicaceae	Tree	4
Virga strigosa	Dipsacaceae	Monocarpic	4
Ailanthus altissima	Simaroubaceae	Tree	3
Telekia speciosa	Asteraceae	Perennial	3
Aster lanceolatus	Asteraceae	Perennial	2
Elodea canadensis	Hydrocharitaceae	Aquatic	2
Helianthus tuberosus	Asteraceae	Perennial	2
Impatiens glandulifera	Balsaminaceae	Annual	2
Oenothera biennis	Onagraceae	Monocarpic	2
Rhus hirta	Anacardiaceae	Shrub	2

Species	Family	Life form	Number of reserves invaded
Amorpha fruticosa	Fabaceae	Shrub	1
Aster ×salignus	Asteraceae	Perennial	1
Lupinus polyphyllus	Fabaceae	Perennial	1
Sedum hispanicum	Crassulaceae	Perennial	1
Veronica filiformis	Scrophulariaceae	Perennial	1