

## Catalogue of expansive plants of the Czech Republic

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**Abstract:** Alien plant invasions have been systematically studied for more than half a century and we already have extensive scientific evidence of their negative role in the current biodiversity decline. Here we aim to draw attention to expansive plants, i.e. native plant species that exhibit similar ecological behaviour to invasive alien plants, being promoted by recent environmental changes. Some of them can also have various negative impacts on native plant communities and ecosystems. However, they have been much less studied than alien species. Our goal was to create an up-to-date catalogue of expansive species (including aggregates or subspecies where needed) in the Czech Republic, compare their functional traits and ecological strategies with non-expansive native species and provide a list of regions and habitats where they spread. We conducted a questionnaire survey, asking local experts to evaluate the expansive character of preselected species in 17 regions and 27 broadly defined habitat types (66 regional assessments). We critically revised these data and verified the distribution patterns. In total, we identified 126 expansive taxa (116 species, eight species aggregates and two subspecies, for

simplicity referred to as species) from 43 families. The most represented were *Poaceae* (27 species, i.e. 21%, while only 7% in the native flora), *Asteraceae* (10 species; 8%) and *Rosaceae* (10; 8%). Our list comprises a heterogeneous group of plants, which tend to be taller and are more frequently polycarpic perennials than the non-expansive native species of the Czech flora. The highest numbers of expansive species were reported at middle elevations. Thirteen species were considered expansive in all regions: *Aegopodium podagraria*, *Alopecurus pratensis*, *Anthriscus sylvestris*, *Artemisia vulgaris*, *Betula pendula*, *Calamagrostis epigejos*, *Dactylis glomerata*, *Elymus repens*, *Phalaris arundinacea*, *Poa trivialis*, *Rumex obtusifolius*, *Trifolium pratense* and *Urtica dioica*. Expansive species were most frequently found in anthropogenic habitats, both non-forest (99 species) and woodlands (including plantations and clearings; 73), as well as in mesophilic meadows and pastures (64) and wet meadows (60). We hope that the presented list of expansive plants will trigger further research on them and their potential impacts on plant communities and other biota.

**Keywords:** checklist, Czech Republic, expansive plants, geographical distribution, habitat, invasions, phytogeographical regions, vascular plants

## Introduction

Distributions and abundances of plants reflect their ability to overcome environmental barriers, disperse effectively and sustain biotic interactions (e.g. D’Amen et al. 2018, Funk 2021). This is particularly relevant for alien (non-native) species, which have been introduced by humans into new areas (e.g. Gallien et al. 2015, Pyšek et al. 2020). In contrast, native plants have had the advantage of long time to adapt to local conditions and increase their ability to survive in local plant communities. Although environmental changes have occurred naturally in history, most of them happened slowly and native plants reacted by gradual expansions or contractions of their distribution ranges and changes in their local abundances (e.g. Magyari et al. 2010, Feurdean et al. 2013).

Recent human-induced environmental changes, namely climate change, changes in land use (including the transformation of agricultural policies, intensification or abandonment of disturbances) and eutrophication represent processes of a comparable magnitude as the past natural changes, but they occur within much shorter time spans (IPBES 2019, dos Santos et al. 2021, Jandt et al. 2022). While some species are promoted by these environmental changes, many others are not (e.g. Klinkovská et al. 2024a). A group of species often reported to be particularly negatively affected are habitat specialists (e.g. Alexander et al. 2015, Hilpold et al. 2018, Klinkovská et al. 2024b) and their local extinctions contribute to global biodiversity decline (IPBES 2019, Isbell et al. 2023). Conversely, many alien plants and invasive species in particular (Richardson et al. 2000, 2011, Blackburn et al. 2011), take advantage of recent environmental changes, establish vital populations, spread across landscapes and often become dominant in local plant communities. Since many invasive species have a direct impact on the diversity of native species (e.g. Hejda et al. 2009, Vilà et al. 2010), they have received considerable attention in recent decades, which is reflected in a large number of studies (Pyšek & Richardson 2010, Pyšek et al. 2020), national and global databases (e.g. van Kleunen et al. 2019) and implementation of legal measures (IPBES 2019, Diagne et al. 2021). However, such a biased focus on invasive species might lead us to overlook important pieces of the puzzle

in the plant biodiversity decline. Some native species exhibit similar patterns, being promoted by recent environmental changes, and are becoming increasingly more frequent and widespread. Here, we refer to them as expansive plants.

Expansive plants is one of the terms used for native species with increasing frequency in the landscape and growing local abundances (e.g. Prach & Wade 1992, Pyšek et al. 2004), although these are also inconsistently (and erroneously) referred to as invasive natives (Valéry et al. 2009, but see Wilson et al. 2009), native invaders (Carey et al. 2012, Nackley et al. 2017), partly also apophytes (Zajac & Zajac 2009) or super-abundant natives (Pivello et al. 2018). Some of the above terms assume that such species potentially negatively affect other species in local communities, while other definitions are broader, without directly considering negative impacts, similarly to different classifications of alien plants (Richardson et al. 2000, 2011, Blackburn et al. 2011). Consequently, there is no broad consensus on the concept so far. Expansions of native species have been discussed especially for animals (Carey et al. 2012), while knowledge on expanding native plants is rather limited to a few species, often grasses (e.g. Holub et al. 2012, Pruchniewicz & Żolnierczak 2017, Těšitel et al. 2017, Roberts et al. 2018). The specific case of shrub and tree encroachment into grasslands has received more attention as it leads to significant ecosystem changes and its extent is relatively easy to assess, for example, by remote sensing (Eldridge et al. 2011, Nackley et al. 2017, Wiczkowski & Lehmann 2022). Although several studies have pointed to the likely underestimated importance of expansive species in the current biodiversity crisis (e.g. Carey et al. 2012, Chytrý et al. 2019), their role is not yet sufficiently studied by experiments or robust data analyses.

Only a few studies emphasized the parallels in the behaviour of invasive alien and expansive plant species and compared these two groups (e.g. Thompson et al. 1995, Májková & Zaliberová 2008, Sabat-Tomala et al. 2020). Direct comparisons of the impacts between native and alien dominant species concluded that both groups can exhibit similar negative impacts on the diversity of local plant communities (Czarnecka-Wiera et al. 2019, Hejda et al. 2021, Pergl et al. 2023). However, there remains a significant knowledge gap that limits generalizations, predictions and, consequently, mitigation strategies against possible negative effects of expansive plants. To initiate research on expansive species and their ecology, species with expansive behaviour in particular regions must first be identified. However, to the best of our knowledge, there is no list of such species in Europe.

In this study, we aim to compile a list of expansive plant species in the Czech Republic. By ‘expansive plants’, we understand native species that have shown a steady increase in their abundance in the landscape or in local communities, both within and outside their natural habitats, over the specified time period, without explicitly considering their negative impact on local plant communities. We adopted an approach similar to that used by plant ecologists for invasive alien species, where the definition of this category is based on the ecology, spread and growth of populations (Richardson et al. 2000, 2011, Blackburn et al. 2011). This definition differs from those that consider impacts on invaded communities (IUCN 2020). We believe it is more appropriate to use the broader ecological definition, which allows us to identify a pool of species with various expansion triggers, while identifying their impacts will be the subject of further research.

The Czech Republic has a long tradition of botanical research (Daníhelka et al. 2017), which has resulted in comprehensive national databases of flora and vegetation (Chytrý & Rafajová 2003, Wild et al. 2019, Chytrý et al. 2021). Although such databases seem to be an excellent source of data for identifying expansive species, there are several aspects that limit their use. First, a large part of the data comes from surveys that have avoided atypical or transitional vegetation types, leading to under-representation of expansive species. Second, the intensity of botanical research has changed over time, with significantly higher effort in the last two decades, which could make a false impression of the recent spread of certain species. Therefore, a different approach must be applied. We took advantage of a network of regional experts and involved them in the compilation of a list of expansive species using a questionnaire survey and follow-up discussions. We also build upon a well-established tradition of research on alien plants in the Czech Republic (Hejný et al. 1973, Pyšek et al. 2002, 2012, 2022).

In this article, we aim to (i) compile the list of expansive plant taxa at the level of species and species aggregates for the Czech Republic, based on expert knowledge and a critical discussion; (ii) characterize the listed expansive species based on their taxonomy, ecological strategies and functional traits and compare them with non-expansive native flora; (iii) describe the geographical pattern of each species' expansion; and (iv) identify habitats in which these species expand.

## Methods

### *Definition of expansive plants*

By expansive plants, we understand native taxa that have increased in abundance at the landscape or community scale since 1990, both within and outside their natural habitat and have achieved dominance in plant communities, while negative impact on other plants is not a condition for being considered expansive. The expansion process is not necessarily caused by changes in biological traits but by the recent environmental changes. The time period was selected to reflect recent changes in the environment and to utilize personal experience of the respondents. We have also included those cases, where there is a possibility that the expanding plants are of different genotypes. We also wanted to draw attention to them, as they are not treated in the alien species list (Pyšek et al. 2022). We focus on the level of species and species aggregates, only in exceptional cases we consider also intraspecific level. Still, we refer to all taxa as to expansive 'species' in the discussion for simplicity.

### *Questionnaire survey and dataset compilation*

To compile a list of expansive species for the Czech Republic, we performed (i) initial assessment, i.e. a questionnaire survey among Czech botanists, followed by (ii) feedback assessment, i.e. a review of the gathered data and additional queries and (iii) final assessment based on the review and a thorough discussion among a smaller group of people.

(i) Initial assessment. During the initial assessment, we distributed the questionnaire (Supplementary Table S1) by email to botanists associated with the Czech Botanical Society, the Nature Conservation Agency of the Czech Republic, national park administrations and universities (around 650 botanists). This survey consisted of a two-layer

assessment (within regions and habitat types) on whether a particular species is expansive or not. For the regional assessment, we defined regions mainly based on the phytogeographical division of the Czech Republic (Skalický 1988, see also Kaplan 2017), consisting of 99 phytogeographical districts which we aggregated into 17 larger regions, taking into account their biogeographical similarities. The habitat-level assessment focused on 27 broadly defined habitat types established by aggregating finer habitat units delimited for the national project of Natura 2000 habitat mapping (Chytrý et al. 2010, crosswalk in Supplementary Table S2A). This initial assessment yielded 66 completed questionnaires from 45 botanists. A single questionnaire always referred to one region only, hence respondents who assessed multiple regions filled in multiple questionnaires. For regions with a small number of questionnaires returned after the first email request, we asked local experts directly in order to achieve a more balanced coverage over the whole Czech Republic. The total number of questionnaires per region is given in Supplementary Fig. S1.

The questionnaire (Supplementary Table S1) initially included 163 native taxa (mostly species or species aggregates) that often dominate local plant communities or are relatively frequent, based on data from the Czech National Phytosociological Database (CNPD, Chytrý & Rafajová 2003). This first selection was refined by a group of senior botanists with significant field experience. However, during the questionnaire survey, we also encouraged respondents to think about additional species that may be included. During this initial assessment, we asked for positive assessments only, i.e. assessments of species that the respondents considered expansive. Species not explicitly mentioned by respondents as expansive were not given any value. Respondents proposed 83 taxa to be added to the original list. Therefore, a total of 246 taxa were considered in the further assessment. The taxonomic concepts and nomenclature of plant taxa follow Kaplan et al. (2019a).

(ii) Feedback assessment. We analysed the data obtained with a focus on the regions where the species was reported as expansive. Taxa for which the distribution patterns based on the initial assessment were unconvincing (e.g. inconsistent assessments between neighbouring regions, large discrepancy compared to distribution patterns based on floristic data) were combined in region-specific feedback questionnaires to obtain a feedback assessment, which we sent to two to seven experts involved in the initial assessment for that region. The feedback assessment also included all newly proposed taxa not included in the preselected group of 163 taxa but relevant to that region. In this assessment, we asked for both positive (expansive) and negative (not expansive in the region) assessments, as well as for comments and justifications.

(iii) Final assessment. After reviewing the data from the feedback assessment, we prepared maps indicating regions where individual taxa were considered to be expansive and validated and discussed these further with a smaller group of experts (co-authors of this article) to obtain the final assessment. During the discussion, we also checked distribution ranges and new records in specific regions of the Czech Republic in the Pladias database (Wild et al. 2019, Chytrý et al. 2021) or contacted experts for specific taxonomic groups to get their opinions. In the final assessment, we classified 126 taxa as expansive (mostly species). When compiling the final assessment, we discussed reasons behind the expansion processes among co-authors and assigned one or more reasons to each taxon, using a standardized list of possible drivers.

During the final assessment, we also reviewed the assignment of all selected expansive taxa to individual broadly defined habitats (see their list in the Supplementary Table S2A) and contacted experts if necessary. For further analyses and comparisons, we calculated the total area of each habitat based on values estimated by Pechanec et al. (2018) based on habitat mapping and compiled habitat species pools considering all vascular plant taxa listed by Sádlo et al. (2007, all categories 1–4). For a crosswalk between the habitat classifications of Sádlo et al. (2007) and Chytrý et al. (2010), see Supplementary Table S2B.

### *Distribution patterns and phytogeography*

Based on the revised region-specific assessments, we prepared maps indicating regions where individual taxa were considered expansive. If a taxon was considered expansive only in a certain part of the given region (e.g. due to environmental heterogeneity), we mapped expansion for the whole region. We also assessed separately if the taxon was expansive in six broad phytogeographical regions defined with respect to elevation, climate, bedrock and biogeographical history (Skalický 1988, see also Kaplan 2017). Following this approach, the area of the Czech Republic is divided into Bohemian-Moravian (Hercynian), Carpathian and Pannonian parts, which are further separated according to prevailing climate into relatively warm lowlands with low precipitation (Thermophyticum), regions with intermediate temperatures and precipitation (Mesophyticum) and mountainous regions with low temperatures and relatively high precipitation (Oreophyticum). The six phytogeographical regions were Bohemian Thermophyticum, Pannonian Thermophyticum, Bohemian-Moravian Mesophyticum, Carpathian Mesophyticum, Bohemian-Moravian Oreophyticum and Carpathian Oreophyticum (see Supplementary Table S3).

### *Plant characteristics*

To characterize expansive plants by their traits, we used data on life form (Kaplan et al. 2019a) and life span (Klotz et al. 2002, our categories perennial monocarpic and perennial polycarpic correspond to pluriennial-hapaxanthic and pluriennial-pollakanthic in the original source). To estimate competitive ability, we used plant height (Kaplan et al. 2019a) and Grime's life strategy categories (Grime 1974, 1979) determined according to Pierce et al. (2017, values adapted for the Czech flora by Guo & Pierce 2019). Based on analysis of large trait dataset, the authors proposed that C, S or R strategies reflect the trade-offs in resource investment between three key leaf traits: leaf area (LA; high in competitive taxa), leaf dry matter content (LDMC; high in stress-tolerant taxa) and specific leaf area (SLA; high in ruderal taxa). For each taxon, the values are standardized to a sum of 100%. To further characterize ecological demands of expansive species we used indicator values for disturbance frequency, disturbance severity (Herben et al. 2016) and Ellenberg-type indicator values for nutrients (Chytrý et al. 2018). To account for phylogenetic patterns, we assigned all taxa to their families. All data on plant characteristics were extracted from the Pladias database (Chytrý et al. 2021).



### *Comparison of expansive species with the non-expansive native species*

We compared expansive plants with the non-expansive native flora of the Czech Republic in terms of plant families, life forms, life span, life strategies, plant height and indicator values. We considered only taxa at the species level (disregarding subspecies) and merged some large and taxonomically complicated groups into aggregates (e.g. *Rubus fruticosus* agg.), following the concept used in the Key to the Flora of the Czech Republic (Kaplan et al. 2019a). Species with no data available were removed from the comparisons. Differences among groups were tested with Mann-Whitney tests. Differences in plant heights were tested within each life-form category, as an overall comparison would be strongly biased by the proportions of taller (trees) vs. shorter life forms.

The data were handled in PyCharm 2023.2.3 Community Edition using R language software version 4.3.0. In particular, we used the tidyverse packages (Wickham et al. 2019) for data handling and visualization. The entire project, including the data, is available in the Zenodo repository (<https://doi.org/10.5281/zenodo.14232471>). The version corresponding to the data presented in this article is tagged as release v1.

## Results

The list of 126 vascular plant taxa that we consider expansive in at least one habitat type and at least one region of the Czech Republic is presented in Table 1. The selected expansive species belong to 43 families. The most numerous are *Poaceae* (27 species; 21.4%), *Asteraceae* (10 species; 7.9%), *Rosaceae* (10 species incl. one subspecies; 7.9%) and *Cyperaceae* (eight species; 6.3%). These families also belong to the most represented families in the native flora, although *Poaceae* have a much higher relative share in the expansive flora (21% in expansive vs. 7% in the non-expansive native flora). Other families that are relatively more represented in the expansive flora include *Salicaceae* (5.6% vs. 1.1%) and *Polygonaceae* (5.4% vs. 1%). In contrast, some species-rich families of the native flora are under-represented among expansive plants, especially *Fabaceae* (0.8% vs. 4.9%), *Lamiaceae* (0.8% vs. 3.4%), *Brassicaceae* (1.6% vs. 3.4%) and *Plantaginaceae* (0% vs. 2.7%) (Fig. 1). The most represented genera are *Salix* (five species) and *Cirsium* (four), followed by *Acer*, *Cerastium*, *Calamagrostis*, *Rubus* (three species each) and *Prunus* (two species, one subspecies).

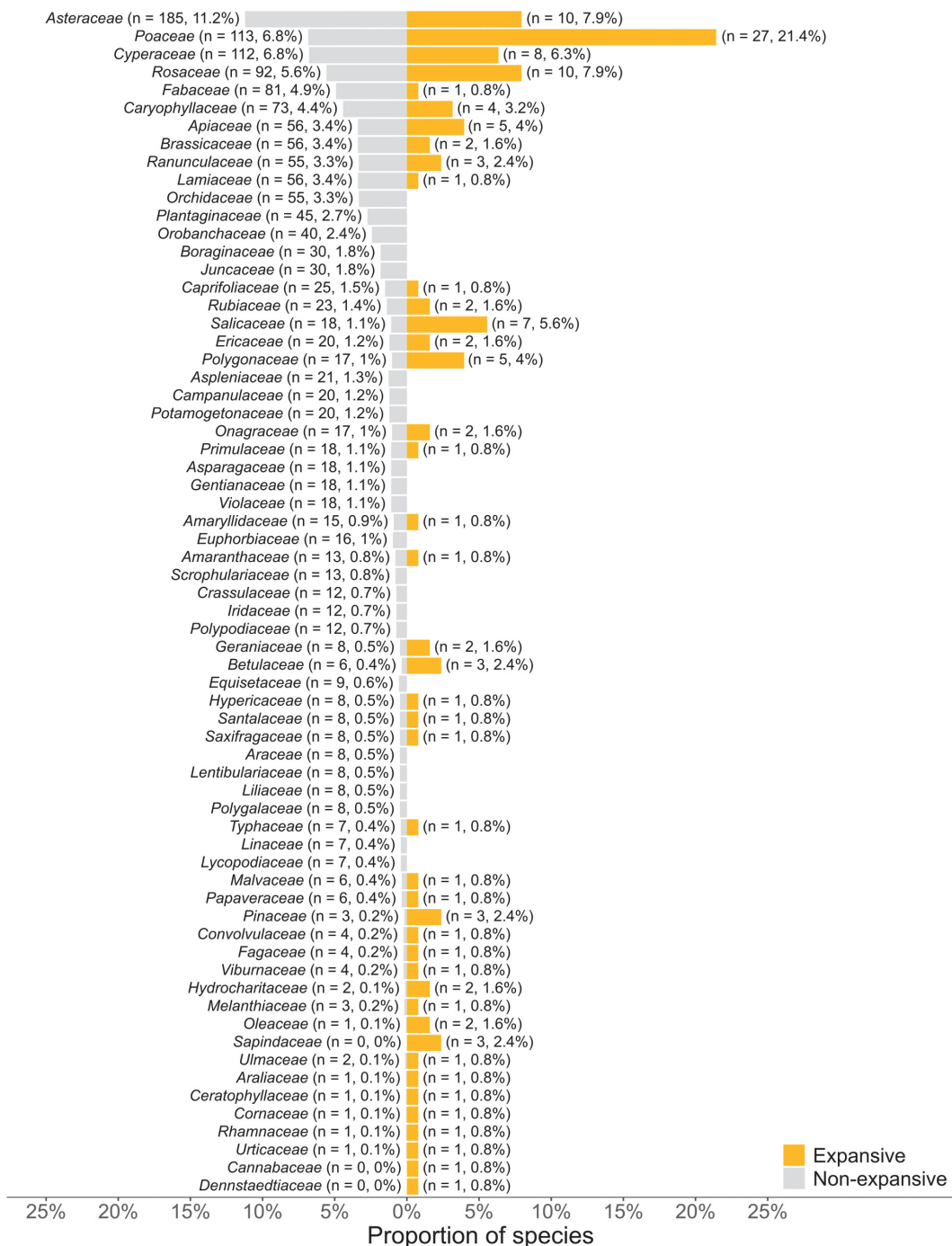
We see a similar pattern in the distribution of life-form categories between the expansive and non-expansive native flora (Fig. 2A). In both groups, hemicryptophytes are most represented, although less so in the expansive than in the non-expansive flora (46% and 60%, respectively). They are followed by therophytes (13% and 14%). In contrast, there is a higher proportion of trees (16% vs. 2%) and shrubs (12% vs. 4%) in the expansive flora than in the non-expansive flora. Consistent with the distribution of life-form categories, the pattern for life span (Fig. 2B) shows a clear prevalence of perennial, polycarpic plants over categories of short-lived strategies in both the expansive and non-expansive flora, with a higher proportion in the former group (81% vs. 68%).

The distributions of life strategies show a significantly higher proportion of competitors (C;  $P = 0.004$ ), a higher proportion of stress tolerators (S;  $P = 0.007$ ) and a much lower proportion of species with ruderal strategy (R;  $P < 0.001$ ) in the expansive flora than in the non-expansive flora (Fig. 3A). A comparison of disturbance indicators reveals

**Table 1.** List of expansive plant taxa of the Czech Republic. Taxa considered expansive in 15–17 regions (of 17) are in bold, Reg refers to the number of regions, Hab to the number of habitats (of 27), asterisks indicate taxa classified as threatened in the Red List of the Czech Flora (Grulich 2017, categories CR, EN, VU, NT, see the text).

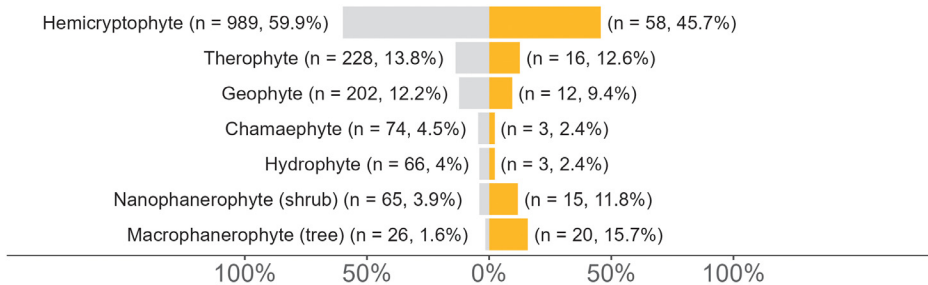
Taxon	Reg	Hab	Taxon	Reg	Hab	Taxon	Reg	Hab
<i>Acer campestre</i>	10	9	<i>Clematis vitalba</i>	11	5	<b><i>Phragmites australis</i></b>	16	11
<b><i>Acer platanoides</i></b>	16	10	<i>Cornus sanguinea</i>	13	10	<i>Picea abies</i>	12	12
<b><i>Acer pseudoplatanus</i></b>	16	10	<b><i>Crataegus sp. div.</i></b>	15	9	<i>Pinus mugo</i>	2	3
<b><i>Aegopodium podagraria</i></b>	17	12	<i>Crepis biennis</i>	5	4	<i>Pinus sylvestris</i>	13	9
<i>Agrostis canina</i>	7	3	<b><i>Dactylis glomerata</i></b>	17	9	<i>Poa chaixii</i>	4	3
<i>Agrostis capillaris</i>	14	8	<i>Deschampsia cespitosa</i>	13	9	<b><i>Poa trivialis</i></b>	17	10
<b><i>Alliaria petiolata</i></b>	15	11	<i>Draba muralis</i> *	6	1	<b><i>Polygonum aviculare agg.</i></b>	16	4
<i>Allium ursinum</i>	3	2	<i>Elymus caninus</i>	8	7	<i>Populus alba</i>	5	4
<b><i>Alnus glutinosa</i></b>	16	9	<b><i>Elymus repens</i></b>	17	10	<b><i>Populus tremula</i></b>	16	8
<b><i>Alopecurus pratensis</i></b>	17	3	<b><i>Epilobium angustifolium</i></b>	16	4	<i>Prunus mahaleb</i> *	5	6
<b><i>Anthriscus sylvestris</i></b>	17	13	<i>Epilobium lamyi</i>	10	1	<i>Prunus padus</i> subsp. <i>padus</i>	6	5
<b><i>Artemisia vulgaris</i></b>	17	3	<i>Eupatorium cannabinum</i>	6	8	<b><i>Prunus spinosa</i></b>	16	8
<i>Avenella flexuosa</i>	11	8	<i>Fagus sylvatica</i>	14	7	<i>Pteridium aquilinum</i>	13	8
<b><i>Betula pendula</i></b>	17	14	<i>Fallopia dumetorum</i>	5	2	<b><i>Puccinellia distans</i></b> *	15	1
<i>Bolboschoenus laticarpus</i>	3	2	<b><i>Festuca arundinacea</i></b>	16	4	<b><i>Ranunculus repens</i></b>	16	8
<i>Bolboschoenus planiculmis</i> *	4	2	<b><i>Filipendula ulmaria</i></b>	16	6	<i>Ranunculus rionii</i> *	3	1
<i>Brachypodium sylvaticum</i>	8	8	<i>Frangula alnus</i>	12	14	<b><i>Rosa canina agg.</i></b>	16	9
<i>Bromus erectus</i>	6	2	<b><i>Fraxinus excelsior</i></b>	16	15	<b><i>Rubus caesius</i></b>	15	14
<i>Bromus inermis</i>	12	5	<b><i>Galeopsis tetrahit agg.</i></b>	16	14	<b><i>Rubus fruticosus agg.</i></b>	16	22
<i>Calamagrostis canescens</i>	9	6	<b><i>Galium aparine</i></b>	16	19	<b><i>Rubus idaeus</i></b>	15	17
<b><i>Calamagrostis epigejos</i></b>	17	21	<i>Galium saxatile</i>	7	5	<b><i>Rumex obtusifolius</i></b>	17	3
<i>Calamagrostis villosa</i>	11	10	<i>Geranium pratense</i>	12	3	<i>Salix alba</i>	3	4
<i>Calluna vulgaris</i>	1	1	<b><i>Geranium robertianum</i></b>	16	9	<i>Salix aurita</i>	7	6
<b><i>Calystegia sepium</i></b>	15	7	<b><i>Geum urbanum</i></b>	16	9	<b><i>Salix caprea</i></b>	16	9
<i>Carex acutiformis</i>	6	3	<i>Glyceria maxima</i>	14	5	<b><i>Salix cinerea</i></b>	16	9
<i>Carex brizoides</i>	13	13	<i>Hedera helix</i>	14	7	<b><i>Salix euxina</i></b>	15	9
<i>Carex buekii</i>	3	2	<i>Holcus lanatus</i>	14	5	<b><i>Sambucus nigra</i></b>	16	13
<b><i>Carex hirta</i></b>	16	10	<b><i>Holcus mollis</i></b>	15	11	<b><i>Saxifraga tridactylites</i></b> *	15	1
<i>Carex rostrata</i>	4	4	<b><i>Humulus lupulus</i></b>	15	7	<b><i>Scirpus sylvaticus</i></b>	16	9
<i>Carpinus betulus</i>	10	9	<i>Hypericum maculatum</i>	12	4	<b><i>Senecio nemorensis agg.</i></b>	15	15
<i>Cerastium glomeratum</i>	11	3	<i>Ligustrum vulgare</i>	8	8	<b><i>Spergularia marina</i></b> *	16	1
<i>Cerastium glutinosum</i>	12	1	<b><i>Lolium perenne</i></b>	16	2	<i>Tilia cordata</i>	5	5
<i>Cerastium semidecandrum</i>	9	2	<i>Lysimachia vulgaris</i>	13	9	<b><i>Torilis japonica</i></b>	16	9
<i>Ceratophyllum submersum</i>	4	1	<i>Melica uniflora</i>	2	4	<b><i>Trifolium pratense</i></b>	17	2
<b><i>Chaerophyllum aromaticum</i></b>	16	5	<i>Molinia caerulea agg.</i>	12	10	<b><i>Tussilago farfara</i></b>	15	2
<i>Chaerophyllum aureum</i>	3	3	<i>Najas marina</i> *	5	1	<b><i>Typha latifolia</i></b>	15	7
<i>Chelidonium majus</i>	12	7	<i>Najas minor</i> *	2	1	<i>Ulmus minor</i>	5	6
<b><i>Chenopodium album agg.</i></b>	15	4	<i>Nardus stricta</i>	5	4	<b><i>Urtica dioica</i></b>	17	22
<i>Cirsium eriophorum</i>	1	1	<b><i>Persicaria hydropiper</i></b>	15	3	<i>Vaccinium myrtillus</i>	11	12
<i>Cirsium heterophyllum</i>	3	3	<b><i>Persicaria lapathifolia</i></b>	15	3	<i>Valerianella locusta</i>	12	3
<b><i>Cirsium oleraceum</i></b>	15	5	<i>Petasites hybridus</i>	11	6	<i>Veratrum album</i> subsp. <i>lobelianum</i>	2	3
<b><i>Cirsium vulgare</i></b>	16	2	<b><i>Phalaris arundinacea</i></b>	17	11	<i>Viscum album</i>	11	7



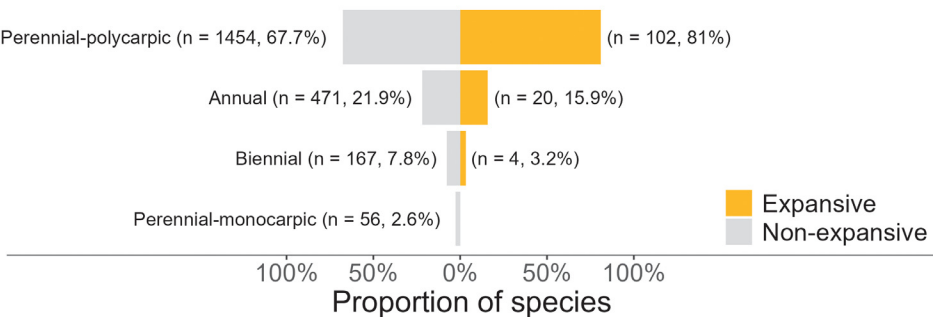


**Fig. 1.** Absolute numbers (n) and proportions (%) of species (including selected species aggregates) belonging to different families for the native non-expansive and expansive Czech flora. Only families with more than five species or those with at least one expansive species are shown.

A



B

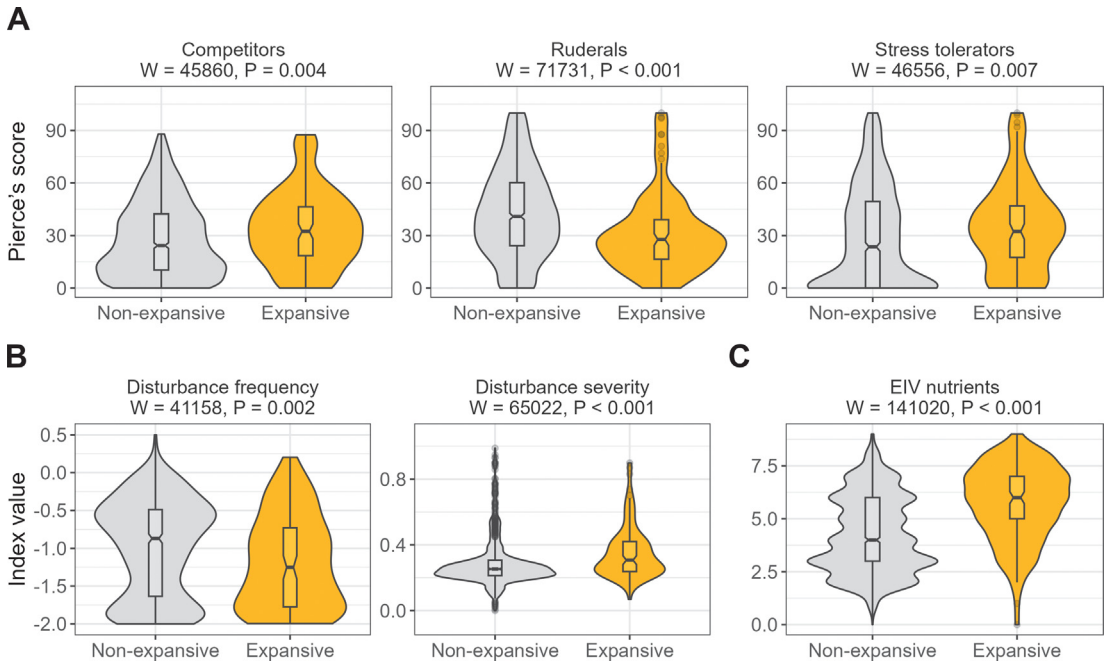


**Fig. 2.** Absolute numbers (n) and proportions (%) of species (including selected species aggregates) belonging to different (A) life-form and (B) life-span categories in the non-expansive and expansive native Czech flora. The categories are sorted by their proportion in the native Czech flora.

a tendency to lower disturbance frequency ( $P = 0.002$ ) but higher disturbance severity ( $P < 0.001$ ) in the expansive than in the non-expansive flora (Fig. 3B). Expansive species show higher Ellenberg indicator values for nutrients ( $P < 0.001$ , Fig. 3C).

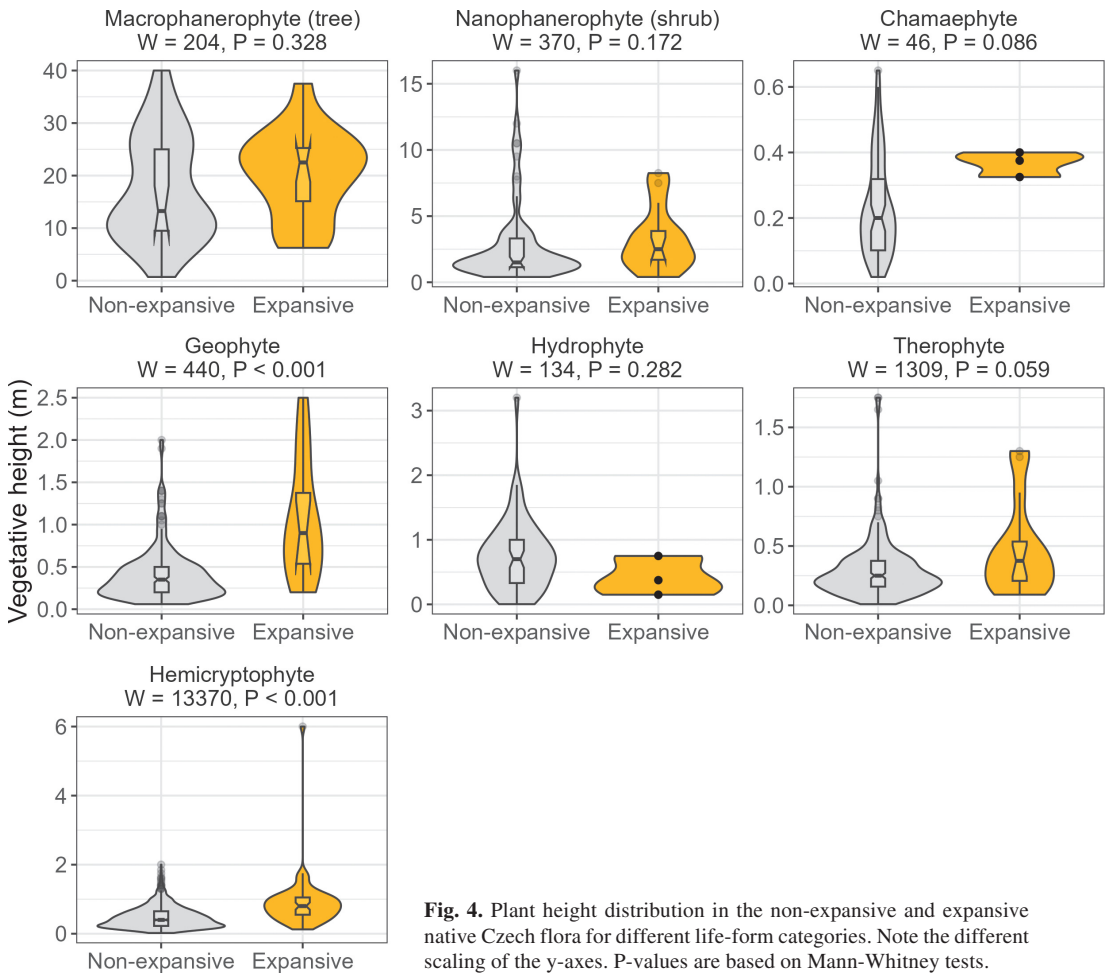
A comparison of plant heights (Fig. 4) reveals that hemicryptophytes ( $P < 0.001$ ) and geophytes ( $P < 0.001$ ) are significantly taller in the group of expansive species than in the native non-expansive flora. Such a tendency is also visible within therophytes or chamaephytes, but the differences are not significant in these and other life-form categories.

At the level of regions, we consider 13 species to be expansive in all 17 regions, namely *Aegopodium podagraria*, *Alopecurus pratensis*, *Anthriscus sylvestris*, *Artemisia vulgaris*, *Betula pendula*, *Calamagrostis epigejos*, *Dactylis glomerata*, *Elymus repens*, *Phalaris arundinacea*, *Poa trivialis*, *Rumex obtusifolius*, *Trifolium pratense* and *Urtica dioica*. The geographical patterns mostly reflect the climatic preferences of the species. For example, *Bromus erectus*, *Ligustrum vulgare* and *Populus alba* only spread in warm lowlands and middle elevations, whereas *Calluna vulgaris* or *Poa chaixii* only spread at high elevations. However, the regions in which we consider a particular species to be expansive are only a subset of all the regions where the plant actually grows. Distinct geographical patterns can be found for species restricted to specific habitats, e.g. *Allium ursinum*, *Bolboschoenus planiculmis* and *Galium saxatile* (Fig. 5, Supplementary Fig. S2, Supplementary Table S3).



**Fig. 3.** Distribution of (A) Grime's life strategies, (B) disturbance and (C) Ellenberg indicator values in the non-expansive and expansive native Czech flora. The proportions of CRS strategies for each species are calculated based on trade-offs in resource investment between three key leaf traits in the multidimensional space: leaf area (high in C strategy), leaf dry matter content (S) and specific leaf area (R); standardized to the total of 100% following Pierce et al. (2017). Indicator values for disturbance frequency reflect inverse disturbance return time at a logarithmic scale (higher values, higher frequency), while disturbance severity is expressed on an arbitrary scale between 0 (low severity) and 1 (high severity) (Herben et al. 2016). Ellenberg indicator values reflect nutrient demands from low (1) to high (9) at an ordinal scale (Chytrý et al. 2018). P-values are based on Mann-Whitney tests.

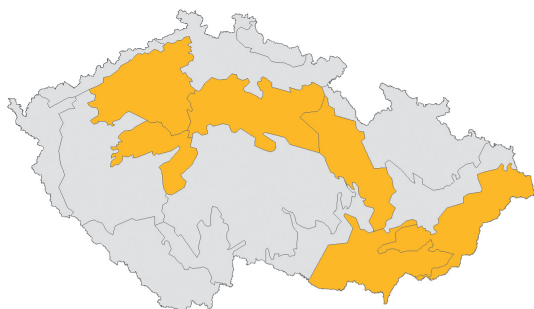
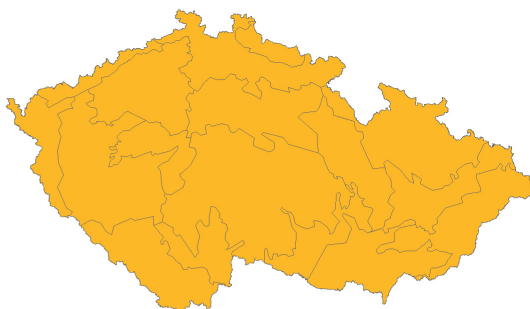
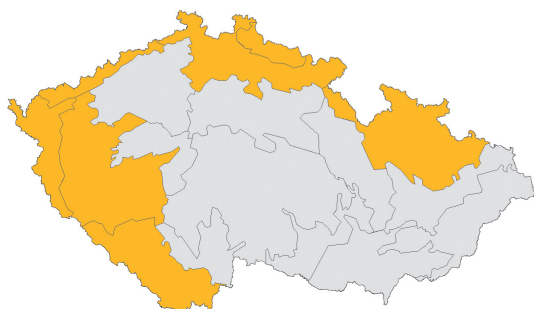
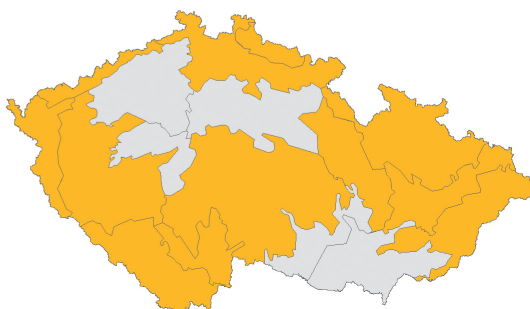
At the level of broad phytogeographical regions, the patterns in the Hercynian part of the Czech Republic are very similar to those in the Carpathian and Pannonian parts (Supplementary Table S3). The highest number of expansive plants are associated with the Bohemian-Moravian (110 taxa) and Carpathian Mesophyticum (109), i.e. middle elevations with typical central-European temperate flora and vegetation (90% of expansive taxa in total). This region is followed by the two Thermophyticum regions, i.e. warm areas with thermophilous flora and vegetation (91 taxa, i.e. 72%, in the Bohemian and 80 taxa, i.e. 63%, in the Pannonian Thermophyticum). A much lower number of taxa behave as expansive in the Oreophyticum regions, i.e. mountain regions with cold-tolerant species (49 taxa, i.e. 39%, in the Bohemian-Moravian and 44 taxa, i.e. 35%, in the Carpathian Oreophyticum). Most of the expansive taxa are considered expansive in more than one phytogeographical region and 24 taxa in all regions. In contrast, only 20 taxa are exclusively associated with Thermophyticum (e.g. *Fallopia dumetorum*, *Prunus mahaleb*), Mesophyticum (e.g. *Cirsium eriophorum*, *Carex rostrata*) or Oreophyticum (e.g. *Veratrum album* subsp. *lobelianum*, *Pinus mugo*) with no overlap with neighbouring regions (Supplementary Table S3).



**Fig. 4.** Plant height distribution in the non-expansive and expansive native Czech flora for different life-form categories. Note the different scaling of the y-axes. P-values are based on Mann-Whitney tests.

The habitats with the highest representation of expansive plants are anthropogenic non-forest habitats (99 species, corresponding to 8.1% of all species in the habitat species pool according to Sádlo et al. 2007, e.g. *Bromus inermis*, *Cerastium glomeratum*, *Chaerophyllum aromaticum*) and anthropogenic types of woodlands and clearings (73 species, 7.3%, e.g. *Alliaria petiolata*, *Brachypodium sylvaticum*, *Melica uniflora*), followed by mesic meadows and pastures (64 species, 7.6%, e.g. *Acer* spp., *Calamagrostis epigejos*, *Holcus lanatus*) and wet meadows (60 species, 7.9%, e.g. *Carex brizoides*, *Deschampsia cespitosa*, *Filipendula ulmaria*). The species with the broadest ecological range estimated by the number of habitats are *Rubus fruticosus* agg. (22 habitats), *Urtica dioica* (22), *Calamagrostis epigejos* (21), *Galium aparine* (19), *Rubus idaeus* (17), *Fraxinus excelsior* (15) and *Senecio nemorensis* agg. (15).

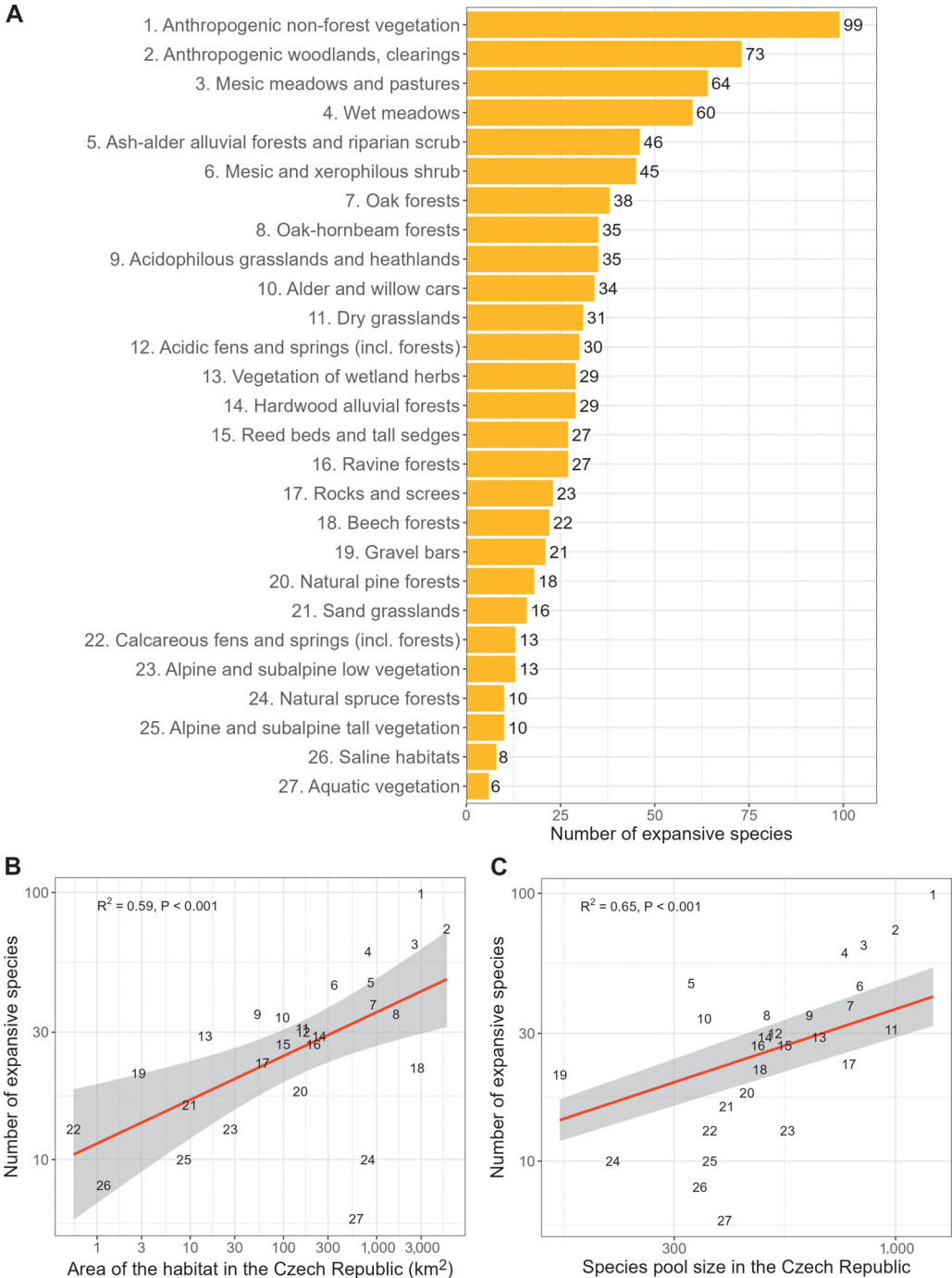
By contrast, the habitats with the lowest numbers of expansive plants include aquatic vegetation (six species, corresponding to 1.5% of all species in the habitat species pool, e.g. *Najas marina*), saline vegetation (eight species, 2.3%, e.g. *Bolboschoenus planiculmis*),

*Bromus erectus**Calamagrostis epigejos**Galium saxatile**Hypericum maculatum*

**Fig. 5.** Examples of different regional patterns of selected expansive plants. Regions were defined by aggregation of phytogeographical districts (Skalický 1988, Kaplan 2017) to a higher level, considering their biogeographical similarities. Maps for all taxa are in the Supplementary Fig. S2.

alpine and subalpine tall-forb vegetation (10 species, including one subspecies, 2.7%, e.g. *Pinus mugo*), natural spruce forests (10 species, 4.7%, e.g. *Avenella flexuosa*), alpine and subalpine low vegetation (13 species, 2.3%, e.g. *Poa chaixii*), calcareous fens and springs (13 species, 3.6%, e.g. *Scirpus sylvaticus*), sandy grasslands (16 species, 4%, e.g. *Cerastium semidecandrum*) and natural pine forests (18 species, 4%, e.g. *Pteridium aquilinum*) (Fig. 6A, Supplementary Table S4). Species exclusively associated with one habitat are aquatic plants, such as *Najas marina* and *Ranunculus rionii*, and species of specific anthropogenic non-forest habitats, such as *Draba muralis*, *Saxifraga tridactylites* and *Spergularia marina*, all threatened in their natural habitats (for more details see Supplementary Table S4).

Interestingly, some species we considered expansive are classified in the Czech Red List of vascular plants according to IUCN classification criteria (Grulich 2017) as CR – critically endangered: *Puccinellia distans*, *Spergularia marina*; EN – endangered: *Draba muralis*, VU – vulnerable: *Najas minor*, *Ranunculus rionii*; and NT – near threatened: *Bolboschoenus planiculmis*, *Najas marina*, *Prunus mahaleb*, *Saxifraga tridactylites*.



**Fig. 6.** (A) Counts of expansive species per habitat and (B) the relationship between the number of expansive species and the total area of individual habitats or (C) their overall species pool. For details see Methods and Supplementary Table S2.



## Discussion

### *Expansive versus invasive plants*

We considered 126 taxa (mostly species, 0.05% of the Czech native flora) as expansive, while the recent overview of the alien flora of the Czech Republic identified 75 species as invasive aliens (18 archaeophytes and 57 neophytes; Pyšek et al. 2022). More than half of the expansive species (72) belonged to only seven families. While *Asteraceae*, *Poaceae*, *Cyperaceae*, *Rosaceae* and *Apiaceae* are among the 10 most diverse families in the Czech flora and also globally (Hassler 2023), the other two, *Polygonaceae* and *Salicaceae*, comprised only 17 and 18 species of the Czech native non-expansive flora, respectively. A similar pattern was also found within the Czech alien flora, where *Asteraceae* and *Poaceae* were among the most represented families, followed by *Amaranthaceae*, *Brassicaceae* and *Polygonaceae* (Pyšek et al. 2022). At the same time, both expansive and invasive species were under-represented in some families that are species-rich both in the Czech flora and globally (Hassler 2023), such as *Fabaceae* (81 non-expansive species, one expansive and two invasive in the Czech flora) and *Lamiaceae* (56 non-expansive species, one expansive, no invasive). We can therefore expect that expansive plants seem to be recruited from families/genera with certain trait combinations, similarly to invasive plants (e.g. Divíšek et al. 2018). In general, selected expansive species tended to be taller and were more frequently polycarpic perennials than the non-expansive native Czech flora. These traits have also been reported for successful invasive plants in the Czech Republic (e.g. Divíšek et al. 2018). In contrast, only a relatively small group of expansive plants displayed a ruderal strategy (producing many seeds rather than investing in vegetative tissues and competitive ability), such as the tiny monocarpic species *Cerastium semidecandrum* and *Saxifraga tridactylites*, which spread in specific habitats, including road verges, sand grasslands and railways.

Interestingly, some species considered expansive in the Czech Republic show invasive behaviour outside Europe. For example, alien species checklists for the Canary Islands (Acebes et al. 2004, Expósito et al. 2018) and Madeira (Vieira 2002) reported 19 and 11 alien species, respectively, that we considered expansive in the Czech Republic. Of these, species listed in both regions are trees (*Acer campestre*, *A. pseudoplatanus* and *Populus alba*) and grasses (*Holcus lanatus* and *Lolium perenne*), reflecting the high proportion of woody plants (27%) and grasses (more than 21%) on our list. Examples of species with large invaded ranges are the grasses *Calamagrostis epigejos* (e.g. Aiken et al. 1989) and *Bromus inermis* with an invaded range across the Americas, South Africa and Australia (Vinton & Goergen 2006). Similarly, some woody species and forbs are also strongly invasive, such as *Salix alba* and *Galeopsis tetrahit* in North America, or *Cirsium vulgare* and *Galium aparine* in the Americas, South Africa and Australia (POWO, <https://powo.science.kew.org>; GloNAF database, van Kleunen et al. 2019).

### *Geographical and ecological patterns of native plant expansions*

Looking at the regional expansion patterns, the main differences were revealed along the elevation gradient, while the differences between the Hercynian, Carpathian and Pannonian parts of the country were negligible. The strong decrease in the expansive species number towards the highest elevations resembles the distribution of native flora, as the

highest native species richness is mostly associated with middle and low elevations and the overall pattern is driven by additional factors, such as bedrock type and soil pH, habitat diversity, historical continuity of forest and grassland areas and human population density (Wild et al. 2019). On the other hand, the highest numbers of alien species in the Czech Republic occur in the lowlands (Chytrý et al. 2009, Pyšek et al. 2022), where most of them are first introduced and from where they spread to higher elevations if they have suitable adaptations (Pyšek et al. 2011). This pattern has also been confirmed in other European regions and across different habitats (e.g. Wagner et al. 2017, Axmanová et al. 2021).

The higher relative numbers of expansive than invasive plants at middle elevations can also be explained by other factors. The lowlands have experienced most of the anthropogenic environmental changes (intensification of agriculture and associated land-use changes and eutrophication) since the mid-20th century (Le Moal et al. 2019) and we assume that many expansions already occurred in that time and were therefore not considered in our study. Moreover, the ongoing climate change enables the spread of thermophilous species (e.g. *Najas minor* and *Ranunculus rionii*) from lowlands to middle elevations (upward shifts of the species optimum, e.g. Lenoir et al. 2008, Gottfried et al. 2012). Finally, at middle and high elevations, nutrient availability seems to be lower than in the lowlands (see maps based on Ellenberg indicator values, Chytrý et al. 2021); therefore, the current anthropogenic supply of nutrients may further support the expansion of lowland species.

Compared to the relatively small differences among regions, there were large differences in the numbers of expansive species among habitats, which correspond to a high importance of the habitat type for alien plant invasions (e.g. Chytrý et al. 2008a, b, Kalusová et al. 2015). The highest numbers of expansive plants were associated with anthropogenic habitats, mesic meadows and pastures, wet meadows and alluvial forests. All of these habitats are affected by disturbances and have fluctuating nutrient levels, suggesting the importance of similar drivers as those supporting alien plant invasions (Davis et al. 2000, Chytrý et al. 2008a, b). However, in the case of natural or seminatural habitats, the expansion process often starts with a decrease in the intensity or frequency of disturbances due to the abandonment of traditional management, which triggers ecological succession of strong dominants (Prach et al. 2014). The habitats with the lowest numbers of expansive plants included saline and sandy habitats, natural pine and spruce forests and alpine vegetation, all of which are characterized by limited nutrient availability and high environmental stress requiring strong adaptations of plants. The number of species tolerating such conditions is generally limited (Grime 1979), which is reflected in low numbers of expansive species (see also the comparison of habitat species pools and numbers of expansive species in Fig. 6C). However, such plants can be locally very abundant and spreading, e.g. *Bolboschoenus planiculmis* in slightly saline habitats on wet arable land, or *Calamagrostis villosa* in alpine vegetation.

The numbers of expansive species in individual habitats can also be partly affected by the area of individual habitats in the Czech Republic (log-transformed regression  $R^2 = 0.34$ , Fig. 6B). While anthropogenic habitats are among the most represented in terms of both area and numbers of expansive species, alpine habitats, sand grasslands, gravel bars, saline habitats and calcareous fens are rare in this country and have low numbers of expansive plants. There are some exceptions to this trend, such as beech forests with a relatively large total area (2,722 km<sup>2</sup>, according to Pechanec et al. 2018) but few expansive

species (22). In contrast, wet meadows have a relatively small total area (809 km<sup>2</sup>) but many expansive species (60).

The expansion process is always connected to specific environmental conditions and their changes over time. Therefore, it is important to note that the regions and habitats in which we consider individual species to be expansive are usually only subsets of all the regions and habitats in which the species occurs. In extreme cases, there are regions and habitats where a species can be rare or even threatened and other regions where it is expansive. A pronounced example is *Nardus stricta*, which we only consider expansive at the highest elevations, where the originally species-rich grasslands are becoming overgrown by this grass. While *N. stricta* was reported to decrease in mountainous areas in the early 1990s (Klimešová 1992), recently an increasing frequency was observed (S. Březina, M. Vymazalová, personal communication). In contrast, at lower elevations, *Nardus* grasslands (*Violion caninae* alliance) are mostly disappearing due to higher nutrient inputs or management cessation (see also Palaj et al. 2024).

#### *Potential drivers of native plant expansions*

We assume that the expansion process is influenced by different drivers that are closely related to habitat type:

(i) Planting. The most obvious factor is the intentional sowing and planting of native species, which then become increasingly abundant in the landscape and continue to spread from the source populations. These plants include the grassland species *Alopecurus pratensis*, *Dactylis glomerata*, *Festuca arundinacea*, *Lolium perenne* and *Trifolium pratense* and some shrubs and trees, such as *Ligustrum vulgare*, *Picea abies* and *Pinus mugo*. Although these species are considered native, some of the expansions may only concern a specific genotype that may have originated outside the country, as in *Festuca arundinacea* (Gibson & Newman 2001).

(ii) Increasing area of suitable habitats. Another important factor behind expansions is the establishment of new habitats or the extension of existing ones, which mostly concerns anthropogenic habitats. A group of plants supported by the extensions of anthropogenic habitats includes various growth forms, from short-lived therophytes with ruderal strategy, such as *Cerastium glomeratum* and *C. glutinosum*, through hemicryptophytes, such as *Epilobium lamyi* and *Puccinellia distans*, to phanerophytes, such as *Populus alba*. Special habitats in this category are roads and railways, which have unique combinations of environmental conditions and management and facilitate species dispersal. For example, the halophytes *Puccinellia distans* and *Spergularia marina* used to be confined to natural saline habitats in warm areas, where they are considered threatened (Grulich 2017), while recently they have become widespread along roads treated with salt in winter (Kaplan et al. 2016, Danihelka et al. 2022). Similarly, *Draba muralis* and *Saxifraga tridactylites*, formerly rare and threatened species of rocky steppes with shallow soils, have spread along railways during the last two decades (Kaplan et al. 2017, 2021). The difference between expansion and invasion process is not even always clear in these cases, as some of the spreading species might belong to a non-native genotype (e.g. *Puccinellia distans*; Kúr et al. 2023).

(iii) Management changes. Changes in the management in forest, grassland and wetland habitats are indisputably important drivers of expansions. These habitats were traditionally

maintained by anthropogenic disturbances of different types, intensities and frequencies and abandonment of this management supports vegetation succession (Prach et al. 2014).

Czech grasslands were traditionally managed by mowing or grazing, which supported high diversity and evenness of these communities (Chytrý et al. 2019). Abandonment of this management favours woody species spreading from neighbouring habitats and competitive graminoids and forbs creating a large amount of biomass and litter, thus suppressing the growth of other plant species (Eldridge et al. 2011, Klinkovská et al. 2024a). In dry to mesic grasslands, examples of expansive plants include graminoids and forbs, such as *Bromus erectus*, *Calamagrostis epigejos* and *Holcus mollis* or shrubs, such as *Crataegus* spp. and *Prunus spinosa*. As dry grasslands are among the most species-rich habitats in central Europe (Chytrý et al. 2015, Biurrún et al. 2021), they are often protected and subject to research (Merunková et al. 2012, Palpurina et al. 2017, Janišová et al. 2021, Klinkovská et al. 2024b). Therefore, both problematic herbs and shrub encroachment in dry and mesic grasslands have already received significant attention (e.g. Eldridge et al. 2011, Těšitel et al. 2017, Czarniecka-Wiera et al. 2019). Some species on our list of expansive plants are also spreading and becoming increasingly frequent in other European countries, where they may have an even greater impact on dry grassland communities. This is the case of *Bromus erectus*, which is becoming dominant and considered problematic especially in north-western Europe (Poniatowski et al. 2018). This tufted perennial grass is supported by both the abandonment of traditional management and by climate warming, as it can sprout early in the season, produce large amounts of biomass (Moser et al. 2011) and is well-adapted to drought (Sutkowska et al. 2013).

In wet meadows, less frequent or no mowing supports highly competitive tall forbs such as *Cirsium oleraceum* and *Filipendula ulmaria*, graminoids, such as *Carex brizoides*, *C. buekii* and *Phalaris arundinacea* (see also increase reported by Klinkovská et al. 2024a) and woody species, such as *Alnus glutinosa*, *Salix aurita* and *S. cinerea*. However, resuming regular management together with a reduction in nutrient input can reverse the changes in the community and lead to the suppression of expansive plants (Prach 1996, George et al. 2021, Hájková et al. 2022).

In alpine and subalpine grasslands, the abandonment of traditional grazing and mowing is considered one of the most important factors leading to community changes (e.g. Dullinger et al. 2003, Vittoz et al. 2009, Czortek et al. 2018). In Czech mountain areas, the cessation of management in combination with high atmospheric nitrogen depositions favours e.g. *Calamagrostis villosa* (Hejcman et al. 2009), *Vaccinium myrtillus* (Klinkovská et al. 2023), or *Phalaris arundinacea* (Bureš 2022). The role of these expansive plants has already been discussed, especially with regard to the species-rich *Nardus* grasslands (Chytrý et al. 2015), as all the above-mentioned changes are likely to have a negative effect on their species richness (Hejcman et al. 2009, Chytrý et al. 2019).

Wetlands, including fens and mires, are spatially limited and belong to the most endangered habitats in both the Czech Republic (Chytrý et al. 2019) and Europe (Janssen et al. 2016). Here, anthropogenic changes have been even more intense, including drainage, nutrient inputs and abandonment of traditional management (Chytrý et al. 2019). Examples of expansive taxa in wetlands are *Molinia caerulea* agg., *Phragmites australis* and *Scirpus sylvaticus*, as well as woody plants, such as *Salix* spp. and *Frangula alnus*. The spread of these species has already been studied experimentally in the context of changes in management practices (Güsewell et al. 2000, Marrs et al. 2004, Hájková et al.

2009, 2022). A steady increase of *Molinia caerulea* agg. in the landscape was also reported by Klinkovská et al. (2024a), although the expansion is mainly relevant in regions with low availability of nutrients, where drainage or abandonment of management supports overgrowing of mires or nutrient-poor wet meadows. Changes in mires can also support expansions of non-vascular plants, namely of several *Sphagnum* species (Limpens et al. 2003, Singh et al. 2022), but this falls outside the scope of this catalogue.

In forests, we also expect management to affect expansion processes, especially in the lowlands and at middle elevations. At these elevations, human influence used to be much more intensive and supported an open canopy and thus a high proportion of light-demanding species in the understorey (Becker et al. 2017, Vild et al. 2018, Klinkovská et al. 2024a). However, these forests are continuously changing into more or less closed stands with predominant mesic conditions (Chudomelová et al. 2017, Máliš et al. 2021), which promote the spread of *Brachypodium sylvaticum*, *Melica uniflora* and other shade-tolerant mesophilous species, including tree juveniles. At the same time, high levels of forestry mechanization create disturbed areas which, together with ongoing eutrophication, support the spread of nitrophilous species, e.g. *Aegopodium podagraria*, *Galium aparine* and *Sambucus nigra*.

(iv) Eutrophication. High nutrient inputs from atmospheric nitrogen deposition, excessive fertilizer applications or released as a consequence of water-table decline support competitive dominants at the expense of stress-tolerators (Bobbink et al. 1998, Olde Venterink et al. 2009, Chytrý et al. 2019, IPBES 2019). These processes affect both relatively nutrient-rich habitats such as alluvial forests, meadows or anthropogenic habitats, but also habitats where nutrient scarcity used to be a strongly limiting factor (e.g. mires). For example, increased nutrient input supports the spread of *Calamagrostis villosa* (Hejzman et al. 2009) or *Senecio nemorensis* agg. (Klinkovská et al. 2023) in subalpine grasslands, although we cannot strictly separate it from the effects of the cessation of traditional management.

(v) Climate change. Direct effects of climate change are recognized in the greening of high mountains, which has been shown e.g. in the Alps (Rumpf et al. 2022), where it has been attributed to the spread of species from lower elevations (e.g. *Calluna vulgaris*, *Vaccinium myrtillus*) into the alpine and subnival belts (Pauli et al. 2007). In the Czech Republic, the alpine belt is very limited and even high elevations have a relatively long history of management by humans (Chytrý 2017). Therefore, the increasing abundances of dwarf shrubs and some grasses are rather attributed to encroachment and successional development after the abandonment of traditional management (Klinkovská et al. 2023). In forests at middle and low elevations, climate change affects the vitality of forest stands and increases the probability of the occurrence of various diseases, pathogens (Coker et al. 2019) or insect outbreaks (Hlásny et al. 2021). These processes support expansions of various species groups such as forest ruderals (e.g. *Epilobium angustifolium*). Severe drought events can significantly alter also the structure of grasslands at middle and low elevations (Fischer et al. 2020), supporting shrub encroachment.

In mires, warming and consequently higher evapotranspiration together with drought events have a strong impact on the water table decline, increased mineralization, and N and P availability (Breeuwer et al. 2008, Gerdol et al. 2008). Consequently, the growth of tall forbs (e.g. *Filipendula ulmaria*) and graminoids (e.g. *Phragmites australis*) is facilitated by the increased productivity (Zhaojun et al. 2011). In aquatic habitats, an example



of a species supported by climate change is the threatened *Najas minor*, a rare plant that has spread over southern Bohemia, north-eastern Moravia and Silesia during the past three decades. Such range expansion of this thermophilous annual species may have been supported by exceptionally hot summers, which favoured fast growth, seed production and dispersal (Kaplan et al. 2018). Another previously rare thermophilous aquatic plant, *Ranunculus rionii*, which is classified as endangered (Grulich 2017), also thrives with progressive eutrophication, fertilizing and liming of fishponds and with climate change (Husák et al. 1988). Most occurrences in this country have been recorded since the 1990s (Kaplan et al. 2019b).

#### *Species not included on the list*

We have not included species of seminatural to ruderal anthropogenic habitats that we consider to be generally abundant with little or no recent change, although several respondents selected them due to their high occurrence frequency in the Czech landscape (e.g. *Achillea millefolium* agg., *Festuca rubra*, *Poa annua*, *Plantago lanceolata* and *Stellaria media* agg.). We also did not consider species with highly fluctuating occurrence patterns, such as some forest species, *Sambucus racemosa* or *Sorbus aucuparia* increasing their abundance after the recent bark beetle outbreaks in spruce forests (Hlásny et al. 2021). We assume that their spread is temporary and will soon be followed by a decline in their frequency. Similarly, we did not include species such as *Echium vulgare* and *Verbascum lychnitis*, which were supported by drought events in the past 10 years in the dry grasslands (Fischer et al. 2020), because we have evaluated trends that started earlier during the last 30 years. However, it is possible that these species are just at the beginning of their expansion and as drought events are becoming more frequent, it is very likely that these two species will continue to spread.

Moreover, we have not considered species that had already spread in the past, such as the aquatic plants *Ceratophyllum demersum*, *Potamogeton natans*, *Spirodela polyrhiza* and *Stuckenia pectinata*, whose spread peaked before 1990 due to the eutrophication of still waters (Sand-Jensen et al. 2017, Le Moal et al. 2019).

#### *Impact and use of this catalogue*

We believe that the presented catalogue of expansive plants of the Czech flora is an important step towards establishing new research lines. However, future environmental changes or new combinations of factors can trigger or suppress the expansion process of various species. Therefore, our list cannot be considered final, as we clearly see the need for regular revisions and updates, similar to the list of alien taxa (Pyšek et al. 2002, 2012, 2022). We already see that some species on our list will most probably decline in the future, such as *Fraxinus excelsior*, which suffers from the invasive fungal disease *Hymenoscyphus fraxineus* (ash dieback; Coker et al. 2019). In contrast, some species that have not received enough support to be included in this list may increase in frequency and dominance in the following years (such as *Echium vulgare*).

Our concept of expansive plants is based on the ecology and dynamics of plant populations, which means that we have included some species that do not have a substantial impact on native plant communities. On the other hand, we assume that many of the listed species significantly affect other species and community diversity. Here, we should bear



in mind the context in which we assess the potential negative effects, particularly the habitat and region, but also the overall abundance (cover) of the plants. While many protected areas already employ strategies to control expansive plants, these are limited to the most obvious cases of spread. We would like to emphasise the need to identify potential threats to plant diversity from native expansive plants and to support initiatives to further study their impact.

## Supplementary materials

**Fig S1.** Number of completed questionnaires for different regions of the Czech Republic.

**Fig S2.** Geographical patterns of expansion for each expansive taxon.

**Table S1.** Questionnaire table with preselected list of taxa for evaluation of expansiveness.

**Table S2.** Conversion tables of broad habitats used in this study and habitats delimited according to Chytrý et al. (2010) and Sádlo et al. (2007).

**Table S3.** Assessment for individual regions and broad phytogeographical regions.

**Table S4.** Occurrence of expansive plants in broadly defined habitats.

Supplementary materials are available at <https://www.preslia.cz>

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## Katalog expanzivních druhů české flóry

Již přes půl století se vědci systematicky zabývají rostlinnými invazemi a podařilo se jim shromáždit řadu důkazů o jejich negativním vlivu na biodiverzitu. Ze současných změn prostředí ale profitují i některé původní druhy, které se šíří v krajině. Jejich frekvence v posledních desetiletích stoupá a často významně narůstá i jejich abundance v lokálních rostlinných společenstvech, někdy s významným negativním dopadem na jejich biodiverzitu. Tyto druhy označujeme jako expanzivní nebo expanzní (oba názvy se používají). Naším cílem bylo vytvořit první katalog expanzivních druhů rostlin České republiky, stručně je charakterizovat pomocí základních funkčních vlastností a popsat, v jakých regionech a biotopech se šíří. Při sestavování katalogu jsme nejdříve oslovili botanickou veřejnost prostřednictvím dotazníku, ve kterém jsme žádali o hodnocení vybraných druhů v 17 regionech a 27 široce vymezených vegetačních typech. Získaná data jsme kriticky zhodnotili a ověřili regionální rozšíření. Celkem jsme identifikovali 126 expanzivních druhů ze 43 čeledí, z nichž nejčastější jsou zástupci čeledí *Poaceae* (27 druhů, což odpovídá 21 % všech druhů, zatímco na neexpanzivní české flóře se podílejí 7 %), *Asteraceae* (10 druhů, 8 %) a *Rosaceae* (10 druhů, 8 %). Přestože je skupina expanzivních druhů heterogenní, ve srovnání s neexpanzivní původní flórou jsou tyto druhy často vyššího vzrůstu a zpravidla jsou vytrvalé. Expanzivní druhy jsou nejvíce zastoupeny ve středních nadmořských výškách. Třináct z nich považujeme za expanzivní ve všech regionech, konkrétně *Aegopodium podagraria*, *Alopecurus pratensis*, *Anthriscus sylvestris*, *Artemisia vulgaris*, *Betula pendula*, *Calamagrostis epigejos*, *Dactylis glomerata*, *Elymus repens*, *Phalaris arundinacea*, *Poa trivialis*, *Rumex obtusifolius*, *Trifolium pratense* a *Urtica dioica*. Expanzivní druhy se nejhojněji vyskytují v antropogenních biotopech, ať už nelesních (99 druhů) nebo lesních (73), dále na mezofilních loukách a pastvinách (64) a vlhkých loukách (60). Věříme, že předkládaný seznam expanzivních druhů podnítl další výzkum těchto druhů a jejich potenciálních dopadů na změny v rostlinných společenstvech.

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