

Participation of the Czech flora in succession at disturbed sites: quantifying species' colonization ability

Účast druhů české flóry v sukcesi – kvantifikace kolonizační schopnosti druhů

Karel Prach^{1,2}, Lubomír Tichý³, Kamila Vítovcová¹ & Klára Řehounková¹

¹*Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 1760, CZ-370 05 České Budějovice, Czech Republic, e-mail: prach@prf.jcu.cz, lencova.kamila@seznam.cz, klara.rehounkova@gmail.com;* ²*Institute of Botany, The Czech Academy of Sciences, Dukelská 135, CZ-379 82 Třeboň, Czech Republic;* ³*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: tichy@sci.muni.cz*

Prach K., Tichý L., Vítovcová K. & Řehounková K. (2017): Participation of the Czech flora in succession at disturbed sites: quantifying species' colonization ability. – *Preslia* 89: 87–100.

The colonization of newly created sites by plants is determined by the characteristics of the species and their frequency in the surrounding landscape (mass effect). We used species frequencies from the Database of Successional Series of various disturbed sites across the Czech Republic (DaSS, 2817 phytosociological relevés, 1013 species of vascular plants) to calculate two indices of species colonization ability. One index (index of colonization potential – ICP) was corrected using occurrence data in the Czech National Phytosociological Database (CNPd) and the other (index of colonization success – ICS) was used without correction. We also evaluated the participation of species in successional stages of different ages and assessed their maximum cover. Then we asked, species of which habitat types are the most successful in colonizing disturbed sites and how their participation changes over the course of succession. Species characteristic of the following habitat types were statistically over-represented in the successional series compared to in the CNPD: synanthropic habitats; cliffs, scree and walls; acidophilous grassland; dry grassland; and sandy grassland. Species characterizing particular types of habitat exhibited significant trends in their participation in different successional stages: those of dry grassland, heathland, scrub land and forest increased during succession whereas species of synanthropic acidophilous grassland, mesic grassland and wetland decreased. Species with high values of both indices are more likely to spread in landscapes continuously disturbed by human activity. Thus, these indices can help to predict future changes in vegetation in central-European landscapes and be used in ecological restoration projects.

Key words: colonization ability, Czech Republic, disturbances, succession, vascular plants, habitat types

Introduction

The colonization ability of plants has to date been inferred indirectly from their life history strategies (Noble & Slatyer 1980, Grime 2002) or their ability to disperse (Klotz et al. 2002, Consens et al. 2008). A more exact colonization ability has only been assessed for limited sets of species at particular localities and in certain habitats (e.g. Eriksson 1996, Kirmer et al. 2008), but such results can hardly be applied in different types of vegetation. The colonization ability of species can only be directly evaluated from their

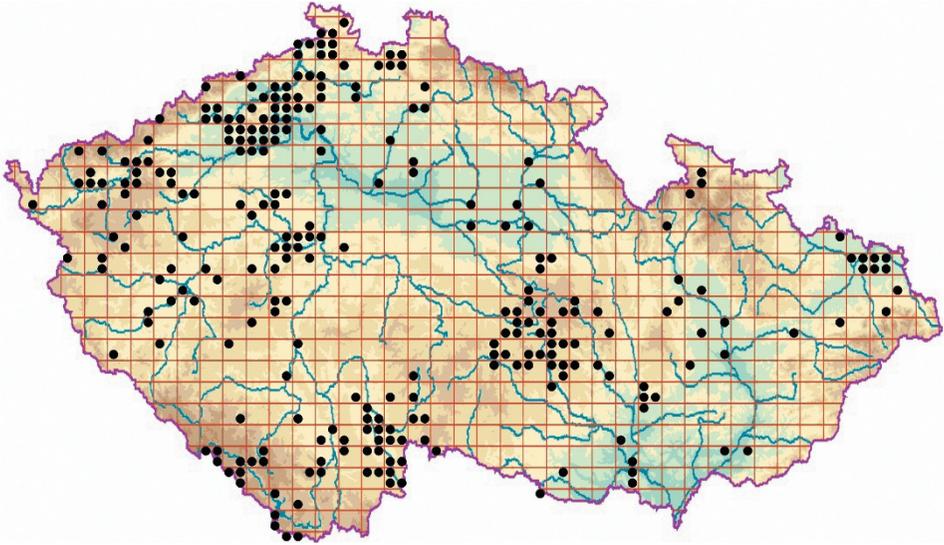


Fig. 1. – Location of the relevés included in the Database of Successional Series (DaSS; based on occupied quadrats).

occurrence at a high number of disturbed sites in areas that differ widely in their environmental conditions.

Therefore, we gathered data on the occurrence of particular species at various seral stages in differently disturbed sites throughout the Czech Republic (Fig. 1). This data set (Database of Successional Series – DaSS; Prach et al. 2014, 2016) includes nearly 3000 phytosociological relevés from seral stages aged 1 to > 150 years, for a high number of successional series (hereafter seres), both primary and secondary, and in terms of the encountered species it includes more than half of the Czech flora (Prach et al. 2014, 2016). This extensive material therefore is sufficiently representative and suitable for evaluating the ability of the Czech flora to colonize disturbed sites, based on real quantitative data.

The composition of species inhabiting a disturbed site generally depends on their ability to survive the disturbance or to colonize disturbed sites (Fenner & Thompson 2005). Since nearly all of the seres we investigated started on bare ground, it can be assumed that colonization from the surroundings was decisive in determining the successional vegetation despite the presence of initial seed banks in some cases of secondary succession. The colonization of disturbed sites depends on the influx of propagules and the ability of species to establish and persist (Lõhmus et al. 2014). Propagule arrival at a site is determined by its intrinsic dispersal characteristics, type and effectiveness of transport vectors (Consens et al. 2008), composition of the local flora (i.e. species pool; Zobel 1997) and the frequency of species occurring in the surroundings, i.e. mass effect (Pärtel et al. 1998). Even though disturbed sites provide species with very different opportunities for becoming established during the process of succession (Walker & del Moral 2003), a general ability to colonize various disturbed sites has not yet been quantified for central-European plants.

By analysing the DaSS database, we aimed to answer the following questions: (i) What is the ability of the Czech flora to colonize disturbed sites, i.e. to participate in succession? (ii) How do species participate in different successional stages and what dominance can they reach? (iii) What are the habitat affiliations of the species that are most successful at colonizing disturbed sites and how does their participation change over the course of succession? To answer these questions, we introduce two indices of species' colonization ability: (i) 'index of colonization success', which reflects the actual realized colonization of a disturbed site by a species, and (ii) 'index of colonization potential', which is a measure of a species' potential colonization ability, based on its frequency of occurrence in seral stages corrected by its commonness in the country (as recorded in the Czech National Phytosociological Database; Chytrý & Rafajová 2003).

Methods

Database of successional series (DaSS)

We sampled 39 different seres including 21 main types of succession (for example, there were four particular seres recorded after coal mining in four different parts of this country.) We also extracted some data from published and unpublished records (see Prach et al. 2014). We considered all seres, which we identified in a sufficient number of representative successional stages in the Czech Republic over the past four decades (1975–2015). The seres included successional stages on various spoil heaps from brown coal, black coal and uranium mining, sand and sand-gravel pits, limestone quarries, acidic rock quarries, basalt quarries, extracted peatlands, road verges, ploughed and then abandoned strips along the state border (the former “iron curtain”), river gravel bars, artificial islands and barriers in fishponds, the bottom of a former water reservoir, sedimentary basins, ruderal urban sites, abandoned fields, bulldozed sites of forests damaged by air pollution, forest clearings and burnt forests. Most of the seres are described in separate studies or summarized in papers (Prach et al. 2013, 2014, 2016). In these references, there are details of the seres, including determination of successional age, which was based on rather precise records provided by mining companies, land owners and our own observations. In some cases, when woody species established immediately at the start of the succession, we used a tree-ring analysis.

The particular seres differed in number of samples, number of sites, location and successional age, but they were all sampled in a comparable way (Prach et al. 2014). All but one of the seres (river gravel bars) were initiated by human activity. All the seres thereafter developed without any additional significant disturbances, so are examples of spontaneous succession (Prach et al. 2001).

In total, 2817 phytosociological relevés are available in DaSS, in which 1013 species of vascular plants are recorded. The abundance or cover of each species was visually estimated by using the values of the semi-quantitative Braun-Blanquet scale transformed to percentages, or by directly estimating percentages in the field (van der Maarel 1979, Kent & Coker 1992). We had to make certain adjustments to the list of species before we could compare the DaSS with the checklist of vascular plants in the Czech Republic, which contains 3601 species, not including cultivars and hybrids (Daníhelka et al. 2012). First, we left out all alpine species (43 species), halophytic species (11 species) and aquatic

macrophytes (47 species; distinguished according to Ellenberg et al. 1991), except those present in DaSS, because we did not sample any seres in alpine, saline or aquatic habitats. We also excluded extinct and currently missing species (155 species of the categories A1, A2 and A3 in the Red List of the Czech Republic – Grulich 2012). Furthermore, all neophytes evaluated as casuals (834 species) according to the checklist of vascular plants (Danihelka et al. 2012) and the catalogue of alien plants (Pyšek et al. 2012) were excluded because they often occur only temporarily and are not permanent components of the Czech flora. Groups of species and subspecies difficult to distinguish were merged (*Rubus* spp., *Alchemilla* spp., *Taraxacum* spp. and some others), which further reduced the list by excluding 810 species. The resulting list (hereafter termed ‘adjusted Czech flora’) comprised 1701 species. The final list of species in DaSS, based on this adjusted list, was 958.

Index of colonization success (ICS)

This index estimates the realized colonization success. Generally rare species do not have a very high realized success, even if their potential to colonize newly established sites is high. To define this index, species frequency data (i.e. the numbers of occurrences in 2817 phytosociological relevés in the database; SF) were divided between 21 types of seres. Each sere was then geographically stratified (within a grid of 0.75' × 1.25' or ≈ 1.4 × 1.3 km), thus obtaining the total number of grid cells with a sere for each species (i.e. ecologically and geographically stratified species frequency; EGSSF). In this way, the effect of replicated occurrence of species in permanent plots or at closely located sites is completely removed. However, we believe that repeated observations at the same location may also contain some additional information about a species' success. Therefore, we defined the ICS index as a combination of both frequencies:

$$ICS^* = \log ((SF + EGSSF)/2) + 1$$

The ICS^* index was then rescaled and rounded to integer numbers in the range of 1 to 9 (or 2 to 9, if the value 1 was reserved for all species not found in the seral stages):

$$ICS = 1.5 + 8 \times ICS^*/ICS^*_{\max}$$

Index of colonization potential (ICP)

This index estimates the relative ability of species to colonize disturbed sites, i.e. it indicates the relative success of species establishment at disturbed sites in comparison with its relative frequency in all types of Czech vegetation (except alpine, saline and aquatic – see above). Therefore, it takes into account the ratio between relative ecologically and geographically stratified species frequencies (relEGSSF) in the DaSS database and its relative frequency in the geographically stratified data set in the Czech National Phytosociological Database (relCNPd; Chytrý & Rafajová 2003) comprised of 20,467 relevés and 2027 species (Knollová et al. 2005). Relative species frequencies from both data sets were standardized to the same median value. The index was calculated as:

$$ICP = 0.5 + \arctg (\text{relEGSSF}/\text{relCNPd}) / 10$$

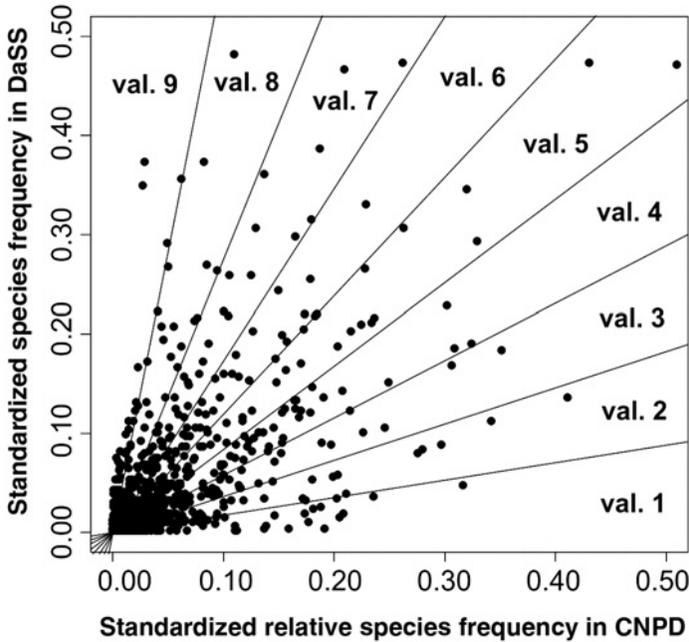


Fig. 2. – The index of colonization potential (ICP) takes into account ratios between relative standardized species frequencies in the DaSS and CNPD databases. The species were divided into nine categories. Both axes were standardized to the same median value of relative frequencies.

The ICP index was then rounded to integer numbers in the range of 1 to 9 (Fig. 2). Each index value was evaluated by means of a bootstrap model. The preciseness of the estimated ICP value was categorized into three levels, i.e. good, sufficient and weak, if the range of the bootstrapped confidence interval ICP index ($Q_{95}-Q_5$) estimated from 10,000 bootstrapped selections was smaller than 1.5, between 1.5 and 3.0 or higher than 3.0, respectively. We assigned the value X to generally rare species present in less than 20 relevés in the CNPD, i.e. the index was not assessed. Other more frequent species not found in the DaSS were considered as poor colonizers (ICP index value 1).

Species minimum, optimum and maximum stages, and maximum cover attained

The minimum, optimum and maximum stages were assessed for each species occurring in the DaSS using the minimum, median and maximum successional age (expressed as the number of years from the start of succession) in which they occurred. The preciseness of each median was defined by the bootstrap confidence interval of age medians ($Q_{95}-Q_5$) estimated from 10,000 bootstrapped selections. Values higher than 50 years were included into one category (> 50) as imprecisely estimated when some late successional stages were not properly dated and the seres differed in duration. To reduce possible subjective bias in estimating the cover of species, we transformed all percentage values into values on the Braun-Blanquet scale: r, +, 1–5 (van der Maarel 1979).

Affiliations of colonizing species with particular types of habitat

We compared the relative frequencies of species included in the CNPD and the DaSS with their affiliations to the main habitats occurring in the Czech Republic. We used the database elaborated by Sádlo et al. (2007) based on CNPD and expert knowledge, to affiliate each species to 10 broad habitats in which it frequently occurs: cliffs, screes and walls; springs and mires; other wetlands; meadows and mesic pastures; acidophilous grasslands; dry grasslands; sandy grasslands and rocky outcrops; heathlands and scrub land; forests and synanthropic habitats (for more information about the methods see Sádlo et al. 2007). To reduce the heterogeneity in the data (different alpha- and beta diversity of plots) in both databases, medians of species frequencies in both datasets were standardized to the same value. Therefore, all relative species frequencies in the dataset with successional series (DaSS) were multiplied by the ratio of the medians from both datasets. Modified relative species frequencies from the CNPD and DaSS for species typical of a particular habitat were compared, and their differences tested using a non-parametric Wilcoxon test (R Core Team 2015).

Results

Colonization ability of species

The frequency distribution of both indices in the adjusted Czech flora is presented in Fig. 3. Values of both indices for the adjusted Czech flora are listed in Electronic Appendix 1 together with other characteristics of species occurring in various successional stages. In the adjusted Czech flora, 43% of the species were not recorded as occurring in any of the successional stages studied.

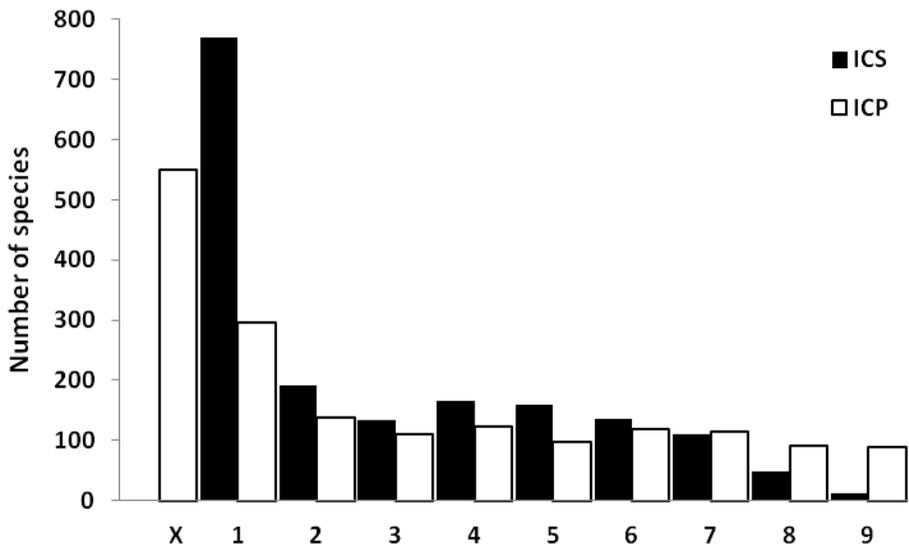


Fig. 3. – Frequency distributions of both indices (ICS and ICP), i.e. frequencies in the successional database and colonization ability, respectively, based on the adjusted Czech flora: X – species occurring in less than 20 relevés in CNPD and not in DaSS; ICP 1 – species more frequent in CNPD but not recorded, or very poorly so in DaSS; ICS 1 – species not recorded in the DaSS.

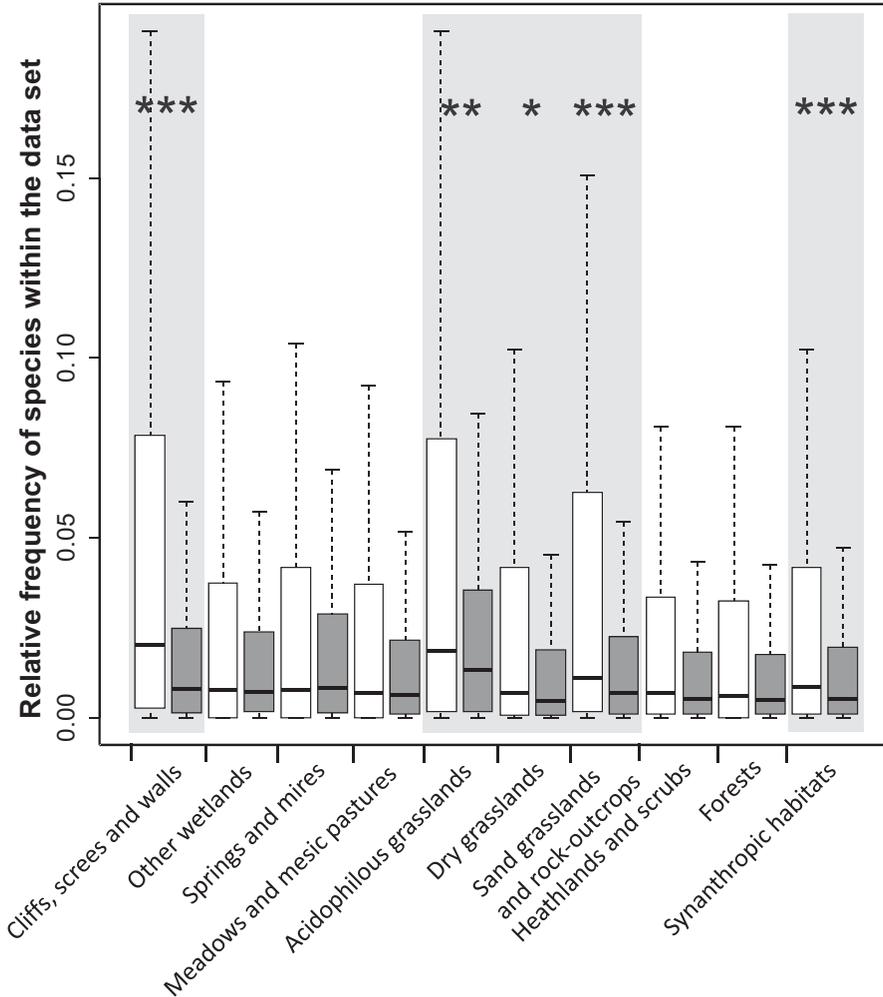


Fig. 4. – Relative frequencies of species in the successional series (DaSS, white boxplots) and relative frequencies of species in the Czech National Phytosociological Database (CNPd, dark grey boxplots). Both species frequencies were standardized with the database median (see the text). Differences in relative species frequencies in both datasets for each type of habitat were statistically tested using the Wilcoxon test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Habitat types for which the ratio of frequently occurring species in DaSS is significantly higher than in CNPD are highlighted by a light grey background.

The following 12 taxa were the most frequent (highest ICS index 9, in decreasing order) and are therefore the most successful colonizers of seral stages: *Betula pendula*, *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Achillea millefolium* agg., *Taraxacum* spp., *Salix caprea*, *Rosa canina* agg., *Pinus sylvestris*, *Hypericum perforatum*, *Rubus* spp., *Artemisia vulgaris* and *Cirsium arvense*. These species usually occurred also in the highest number of seres (see Electronic Appendix 1).

Among the species with the highest ICP (= 9), i.e. those with a distinctly higher relative occurrence in the successional database DaSS than in the CNPD, several groups of

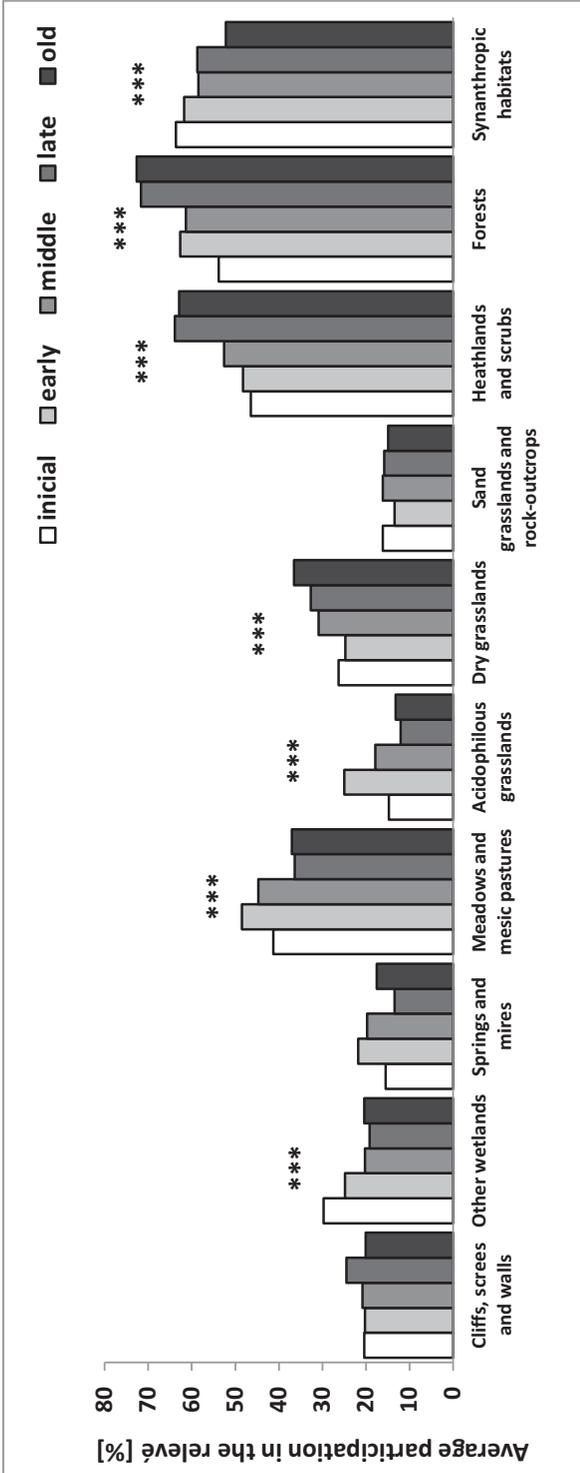


Fig. 5. — Participation of species characterizing different types of habitats in differently aged seral stages (based on numbers of species): initial (1–3 years) – 353 relevés, young (4–10 years) – 660 relevés, middle (11–25 years) – 695 relevés, late (26–40 years) – 518 relevés and old (> 40 years) 591 relevés. The categories roughly corresponded to the general experience that pioneer annuals usually prevail at the initial stages, followed by perennial herbaceous plants, grasses and woody species, later accompanied by species typical of the natural vegetation of the respective geographical region. The sums of values exceed 100% because species can belong to many types of habitats (Sádlo et al. 2007). Trends in the participation of species characterizing different habitats during succession were statistically tested using GLM (family: Gaussian; link: identity) with absolute values of successional age.

species can be distinguished: (i) generally common species that easily colonize seral stages (e.g. *Salix caprea*, *Rosa canina* agg., *Populus tremula*, *Epilobium angustifolium*), with a high ICS; (b) species, often synanthropic and/or alien neophytes, less common but also colonizing seral stages if they occur in the surroundings (e.g. *Acer negundo*, *Pinus strobus*, *Quercus rubra*, *Lupinus polyphyllus*); (iii) some rare species in both databases, which usually produce a high number of easily dispersed seeds, that are able to establish in seral stages with a higher frequency than expected from their occurrence in CNPD (e.g. *Pyrola minor* and *Epilobium dodonaei*), including some less common neophytes such as *Hordeum jubatum*, *Erucastrum gallicum* and *Senecio vernalis*.

Species common in the CNPD but not (ICS = 1) or only rarely (ICS = 2) occurring in seral stages and therefore exhibiting a low intrinsic colonization ability, include e.g. *Caltha palustris*, *Cirsium oleraceum*, *Crepis paludosa*, *Filipendula ulmaria*, *Sanguisorba officinalis* and *Abies alba*, typical of wet meadows or occasionally woodlands.

Affiliation of colonizing species with particular habitats

Species typical of cliffs, screes and walls, acidophilous grasslands, dry grasslands, sandy grasslands and rocky outcrops, heathlands and scrub land, and synanthropic vegetation were significantly over-represented in the seral stages compared to CNPD (Fig. 4). There was no significant over-representation of any particular species groups in CNPD compared to the DaSS.

The participation of species characteristic of different types of vegetation in the five successional stages distinguished is shown in Fig. 5. Species typical of dry grasslands and woody vegetation clearly increased during succession, while synanthropic and wetland species markedly decreased. Only species typical of spring and mires, cliffs, screes and walls, and sandy habitats did not exhibit statistically significant trends. Species typical of woody vegetation and synanthropic species were the most common in seral stages, being followed by species typical of mesic and dry grasslands. Species of acidophilous grasslands, sandy grasslands, springs and mires, and rocky-outcrop vegetation were least frequent.

Discussion

Colonization of disturbed sites by the Czech flora

More than half of the species in the Czech flora colonized seral stages at disturbed sites. The seral stages were scattered across the Czech Republic, so our dataset is representative of the whole country and comparable on the basis of the entire Czech flora. Because seral stages of different ages were similarly frequent in our database (Fig. 5 and Prach et al. 2016), we do not expect any bias towards over-representation of species typical of young seral stages, which is usually the case in human-altered landscapes (Walker et al. 2007). It should also be mentioned that late-successional species may also occur in early successional stages (Egler 1954) and thus reduce the importance of some differences in frequencies between differently aged seral stages. We found many rare and a low number of very common species in the seral stages studied. This is in accordance with the usual frequency distribution of species in floras as a whole (Preston 1948, Preston et al. 2002).

The index of colonization success (ICS) is not an intrinsic characteristic of a species, as it is substantially influenced by the rarity or commonness of the species in the surrounding landscape. In other words, the more common a species is in a region, the more likely it is to colonize new sites (Pärtel et al. 1998). This is better reflected in the other suggested index of colonization potential (ICP), which better characterizes the real colonization ability of a species. However, it was not possible to calculate this index for many species due to their low frequency or absence in both databases. It should also be mentioned that the ability to colonize disturbed sites is not only based on propagule quantity and dispersibility, but also largely on the tolerance of species of environmental conditions, so it also includes establishment capacity. The broader this capacity is, the greater the chance of a species becoming established elsewhere (Grime 2002). Moreover, competition codetermines the species composition of seral stages (Walker & del Moral 2003). Considering all these aspects, we expect that the actual frequency of species in seral stages, and thus their ICS, says more about the probabilities with which different species colonize new sites in the contemporary Czech landscape than their ICP. Correlation coefficient between these indices is not high ($r = 0.33$), which justifies using both. Only species with the highest ICS categories also had a high ICP, in the other categories the correlation was low.

Looking at particular species, distortions may occur caused by the fact that some of the seral stages were concentrated in areas where certain otherwise rare species are common and vice versa. They may, therefore, be over- or under-represented to some degree in our successional database compared to the CNPD, resulting in similarly high or low values of both indices, especially the ICP. Thus, differences between regional species pools (Zobel 1997) throughout this country influenced the participation of species in seral stages.

We preferred the metric scale rounded to integer numbers for both indices, which corresponds to the widely used Ellenberg's indicator values (Ellenberg et al. 1991). Both values are obviously influenced by our sampling design, occurrence of seral stages and possibly by various random factors. Decimal values would have been misleading, because decimal digits are not significant due to insufficient internal reliability. Both indices, as well as the median of successional age of species occurrence (which may be called the "successional status of species"), are potentially useful in ecological studies, at least in the context of central Europe. The advantage of our indices is that they are based on real quantitative data, which reduces their subjectivity (Zelený & Schaffers 2012, Herben et al. 2016).

Our indices can be used in ecological restoration, for example, for predicting species composition at a restored site based on the list of local flora. For this, we consider the ICS to be more convenient because it only considers the actual presence of a species in seral stages, i.e. the "realized successional niche". On the other hand, its use should be restricted to the Czech Republic. The ICP can be more convenient for various theoretical ecological studies dealing, for example, with species traits. It may also have a broader application and not only in the area studied. It will be possible to compare our indices with the disturbance indices recently proposed by Herben et al. (2016), who partly address similar issues but from the opposite direction, i.e. going from vegetation to particular species, while our approach goes from particular species to vegetation. Moreover, their approach is not based on real field data. However, our indices, like all other similar indices, must be used and interpreted with some caution. Besides the above-mentioned

limitations, certain undisclosed factors could have biased the values. However, such discrepancies should be balanced out by using larger sets of species in particular studies (Diekmann 2003).

Successional age, i.e. the time that has elapsed since the last disturbance, can be seen as a factor to which species respond in a way similar to other environmental conditions. The response of a species to such factors is usually expected to be unimodal, so the extent of the response indicates a species' tolerance, which also applies to successional age (see minimum, maximum and median age values over the course of succession in the Electronic Appendix 1). Tolerance is usually a missing parameter in the cases of indicator values (ter Braak & Gremmen 1987). It should be mentioned that the "tolerance" of species to successional age is summarized here across all the seres, disregarding sere identity. This is justified by our earlier finding (Prach et al. 2014) that sere identity is not a statistically significant factor determining the species composition of seral stages; successions over a large geographical area and across environmental factors form a continuum in space. This validates our decision to consider all the seral stages together and disregard their identity.

Differences between groups of species in their ability to colonize different seral stages

Species characterizing five of the 10 main habitat types (based on Sádlo et al. 2007) are over-represented in the seral stages studied (Fig. 4) and all of them are well interpretable. Species typical of synanthropic vegetation are naturally frequent at human-disturbed sites, which constitute nearly the whole database. Species typical of the vegetation on cliffs, screes and walls are obviously over-represented due to the presence of many stone quarries in our database (Novák & Prach 2003, Trnková et al. 2010). Especially sand and sand-gravel pits, sampled across the whole country (Řehouňková & Prach 2006), and some acidic spoil heaps support the presence of species typical of sandy and other acidophilous grasslands. Species typical of dry grasslands are present in many seral stages if they occur in warmer and dry parts of this country, e.g. in limestone and basalt quarries, some abandoned fields (Prach et al. 2016) and on some coal mining spoil heaps (Prach 1987).

Species characteristic of woodlands, scrubland, synanthropic vegetation and mesic grasslands are the most common in the seral stages (Fig. 5), which is in accordance with the prevalence of these vegetation types in the entire Czech landscape (Chytrý & Rafajová 2003). Also, the trends of changing participation during succession of species with different affiliations to different habitats are mostly in accordance with common ecological expectations, both in the literature (Walker & del Moral 2003, Prach et al. 2014) and based on field experience (Fig. 5 and Electronic Appendix 1). During succession, synanthropic species continuously decreased, while species typical of scrub and woodland vegetation increased, which is quite typical of successions in human-altered temperate landscapes (Glenn-Lewin et al. 1992, Walker & del Moral 2003). In the geographical area considered, succession usually proceeds towards potential natural vegetation, which in most cases is some kind of woodland, as documented by Prach et al. (2016). In non-synanthropic heliophilous vegetation in open habitats, only species typical of dry grasslands increased while others decreased or did not exhibit any significant trend. This can be explained by the fact that at very dry sites, woody species develop

slowly or not at all, so succession may eventually lead to vegetation resembling steppes (Prach et al. 2016). The decrease in heliophilous wetland species can be explained by gradual silting of some wet depressions due to sedimentary processes, especially at mining sites, and by increasing transpiration and shading accompanying the development of woody species (Bazzaz 1996).

We conclude that species with high values of our two indices are more likely to spread over landscapes continuously disturbed by human activity. The quantification of species occurrence in differently aged successional stages presented here also allows the prediction of which stage in succession particular species may participate, or possibly dominate. Thus, the results presented may help predict future successional patterns in the central-European landscape and might prove useful in various restoration and landscape management projects.

See www.preslia.cz for Electronic Appendix 1

Acknowledgements

This study was supported by the Czech Science Foundation, project no. 17-09979S and project CZ.1.07/2.3.00/20.0289 under the Education for Competitiveness Operational Programme. LT was supported by the PLADIAS Centre of Excellence (Czech Science Foundation; 14-36079G). We thank all our colleagues and students who agreed to include their data into our database, namely Martin Adámek, Alena Bartošová, Marek Bastl, Helena Dvořáková, Darina Hodačová, Alena Jírová, Alexandra Klaudivová, Petra Konvalinková, Petr Košťel, Tomáš Koutecký, Ondřej Mudrák, Jan Novák, Petr Petřík, Petr Pyšek, Jiří Sádlo, Petr Šmilauer, Zdeněk Špringar, Vojtěch Študent, Romana Trnková and Zdeněk Vaněček. We also thank Milan Chytrý for providing the stratified dataset of the Czech National Phytosociological Database. We are indebted to Tomáš Herben, Péter Török, Jitka Klimešová, Petr Pyšek and anonymous reviewers for their valuable comments on earlier versions of the manuscript, Frederick Rooks and Jan W. Jongepier for their linguistic improvements, Tony Dixon for editing English of the accepted manuscript, and Petr Šmilauer for his advice on statistics. We also thank Alena Jírová and Lenka Šebelíková for their help in completing the database.

Souhrn

Využili jsme rozsáhlou databázi fytoecologických snímků z různých narušených míst v České republice (DaSS), pořízených v rozmanitých, různě starých sukcesních stádiích (2817 snímků) a obsahujících 1013 druhů cévnatých rostlin, k vyhodnocení kolonizační schopnosti druhů české flóry. Počet výskytů jednotlivých druhů v této databázi se stal základem výpočtu indexu vycházejícího z prosté frekvence výskytu jednotlivých druhů v sukcesních stádiích (ICS – index kolonizační úspěšnosti v sukcesních stádiích) v rozsahu 1 (žádný výskyt), až 9 (vysoká frekvence v sukcesních stádiích). Protože je ale výskyt druhů v sukcesních stádiích ovlivněn vedle vlastností druhů i jejich hojností v krajině, byl výskyt v sukcesních stádiích korigován frekvencí příslušných druhů v České národní fytoecologické databázi (ČNFD). Takto upravený index (ICP – index kolonizačního potenciálu) vyjadřuje lépe vlastní kolonizační potenciál jednotlivých druhů stanovený opět v rozsahu 1 (nízký) až 9 (vysoký kolonizační potenciál). Hodnotili jsme rovněž výskyt druhů v různě starých sukcesních stádiích s označením prvního a posledního výskytu a mediánu sukcesního stáří. Zároveň je udána i maximální zaznamenaná pokryvnost (v sedmičlenné Braun-Blanquetově stupnici). Tyto základní informace o uplatnění druhů české flóry v sukcesi jsou shrnuty v příložené tabulce (Electronic Appendix 1). Dále jsme se ptali, jak se liší zastoupení druhů charakterizujících 10 základních typů stanovišť v DaSS a v ČNFD. Statisticky významně byly v sukcesních sériích více než v ČNFD zastoupeny druhy synantropní, druhy skalních štěrbin, sutí a zdí, druhy psamofytní a druhy typické pro acidofilní a suché trávníky. Statisticky významně se měnilo zastoupení následujících cenotických skupin druhů během sukcese: vzrůstalo zastoupení lesních druhů, druhů typických pro keřová společenstva a suché trávníky, naopak klesalo zastoupení synantropních druhů, mokřadních druhů, psamofytních druhů a druhů typických pro mezické trávníky. Předpokládáme, že zde navržené indexy mohou být úspěšně využity v řadě navazujících studií podobně jako Ellenbergovy indikační hodnoty a pomocí nich by

bylo možné s určitou pravděpodobností předpovídat sukcesní změny v člověkem narušovaných krajinách střední Evropy. Indexy (hlavně ICS) mohou být rovněž využity v různých praktických projektech ekologické obnovy.

References

- Bazzaz F. A. (1996): Plants in changing environments: linking physiological, population, and community ecology. – Cambridge Univ. Press, Cambridge.
- Chytrý M. & Rafajová M. (2003): Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – *Preslia* 75: 1–15.
- Consens R., Dytham C. & Law R. (2008): Dispersal in plants: a population perspective. – Oxford Univ. Press, Oxford.
- Danihelka J., Chrtěk J. jr. & Kaplan Z. (2012): Checklist of vascular plants of the Czech Republic. – *Preslia* 84: 647–811.
- Diekmann M. (2003): Species indicator values as an important tool in applied plant ecology: a review. – *Basic Appl. Ecol.* 4: 493–506.
- Egler F. E. (1954): Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. – *Vegetatio* 4: 412–417.
- Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulissen D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. – *Scr. Geobot.* 18: 1–248.
- Eriksson O. (1996): Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. – *Oikos* 77: 248–258.
- Fenner M. & Thompson K. (2005): The ecology of seeds. – Cambridge Univ. Press, Cambridge.
- Glenn-Lewin D. C., Peet R. K. & Veblen T. T. (eds) (1992): Plant succession: theory and prediction. – Chapman & Hall, London.
- Grime J. P. (2002): Plant strategies, vegetation processes, and ecosystem properties. Ed. 2. – J. Wiley and Sons, Chichester.
- Grulich V. (2012): Red List of vascular plants of the Czech Republic: 3rd edition. – *Preslia* 84: 63–645.
- Herben T., Chytrý M. & Klimešová J. (2016): A quest for species-level indicator values for disturbance. – *J. Veg. Sci.* 27: 628–636.
- Kent M. & Coker P. (1992): Vegetation description and analysis. – Belhaven Press, London.
- Kirmer A., Tischew S., Ozinga W. A., von Lampe M., Baasch A. & van Groenendael J. M. (2008): Importance of regional species pools and functional traits in colonization processes: predicting re-colonization after large-scale destruction of ecosystems. – *J. Appl. Ecol.* 45: 1523–1530.
- Klotz S., Kühn I. & Durka W. (ed.) (2002): BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. – Schriftenrh. Vegetationsk. 38, Bundesamt für Naturschutz, Bonn.
- Knollová I., Chytrý M., Tichý L. & Hájek O. (2005): Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. – *J. Veg. Sci.* 16: 479–86.
- Lõhmus K., Paal T. & Liira J. (2014): Long-term colonization ecology of forest-dwelling species in a fragmented rural landscape: dispersal versus establishment. – *Ecol. Evol.* 4: 3113–3126.
- Noble I. R. & Slatyer R. O. (1980): The use of vital attributes to predict successional changes in plant-communities subject to recurrent disturbances. – *Vegetatio* 43: 5–21.
- Novák J. & Prach K. (2003): Vegetation succession in basalt quarries: pattern over a landscape scale. – *Appl. Veg. Sci.* 6: 111–116.
- Pärtel M., Kalamees R., Zobel M. & Rosen E. (1998): Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. – *Ecol. Engin.* 10: 275–286.
- Prach K. (1987): Succession of vegetation on dumps from strip coal mining, N.W. Bohemia, Czechoslovakia. – *Folia Geobot. Phytotax.* 22: 339–354.
- Prach K., Lencová K., Řehouňková K., Dvořáková H., Jírová A., Konvalinková P., Mudrák O., Novák J. & Trnková R. (2013): Spontaneous vegetation succession at different central European mining sites: a comparison across seres. – *Environ. Sci. Pollut. Res.* 20: 7680–7685.
- Prach K., Pyšek P. & Bastl M. (2001): Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. – *Appl. Veg. Sci.* 4: 83–88.

- Prach K., Řehouňková K., Lencová K., Jírová A., Konvalinková P., Mudrák O., Študent V., Vaněček Z., Tichý L., Petřík P., Šmilauer P. & Pyšek P. (2014): Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. – *Appl. Veg. Sci.* 17: 193–200.
- Prach K., Tichý L., Lencová K., Adámek M., Koutecký T., Sádlo J., Bartošová A., Novák J., Kovář P., Jírová A., Šmilauer P. & Řehouňková K. (2016): Does succession run towards potential natural vegetation? An analysis across seres. – *J. Veg. Sci.* 27: 515–523.
- Preston C. D., Pearman D. A. & Dines T. D. (2002): *New atlas of the British and Irish Flora.* – Oxford Univ. Press, Oxford.
- Preston F. W. (1948): The commonness and rarity of species. – *Ecology* 29: 254–283.
- Pyšek P., Danihelka J., Sádlo J., Chrtěk J. jr., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. (2012): *Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns.* – *Preslia* 84: 155–256.
- R Core Team (2015): *R: A language and environment for statistical computing.* – R Foundation for Statistical Computing, Vienna, URL: <http://www.R-project.org/>.
- Řehouňková K. & Prach K. (2006): Spontaneous vegetation succession in disused gravel-sand pits: role of local site and landscape factors. – *J. Veg. Sci.* 17: 583–590.
- Sádlo J., Chytrý M. & Pyšek P. (2007): Regional species pools of vascular plants in habitats of the Czech Republic. – *Preslia* 79: 303–321.
- ter Braak C. J. F. & Gremmen N. J. M. (1987): Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. – *Vegetatio* 69: 79–87.
- Trnková R., Řehouňková K. & Prach K. (2010): Spontaneous succession of vegetation on acidic bedrock in quarries in the Czech Republic. – *Preslia* 82: 333–343.
- van der Maarel E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – *Vegetatio* 39: 9–14.
- Walker L. R. & del Moral R. (2003): *Primary succession and ecosystem rehabilitation.* – Cambridge Univ. Press, Cambridge.
- Walker L. R., Walker J. & Hobbs R. J. (eds) (2007): *Linking restoration and ecological succession.* – Springer, New York.
- Zelený D. & Schaffers A. P. (2012): Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. – *J. Veg. Sci.* 23: 419–431.
- Zobel M. (1997): The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? – *Trends Ecol. Evol.* 12: 266–269.

Received 22 September 2016

Revision received 2 February 2017

Accepted 22 February 2017