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Railways as a source of alien plants

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Abstract: Railways have served as a pathway in the introduction of many alien species. The majority are introduced mainly as contaminants of commodities or are hitchhikers, but some are ornamentals and utility taxa planted near railway buildings that escape from cultivation. A field survey was carried out along the freight railway corridor Břeclav – Kolín – Praha – Děčín (central Europe, Czech Republic) at 39 localities, such as railway stations, railway yards and important railway junctions, in 2020–2022. Each locality was divided into three zones reflecting the type of management and land use: (i) tracks and embankments, (ii) wider surroundings and (iii) surroundings of buildings. The aim of this study was to produce a list of taxa that occurred in railway stations and yards and their surroundings, determine the incidence in these floras of alien species, and, by comparing historical and recent records, identify species whose distributions have changed over time. A total of 11,139 records belonging to 764 taxa, including 403 (53%) native, 309 (40%) alien species and 85 (11%) Red-Listed taxa of various threat categories were recorded. The tracks and embankments were generally richer in species, including aliens, and the zones and location of railway lines affected the species composition; the effect of zones on both species richness and composition was stronger than that of sections of railway lines. Compared to the historical records, 109 new aliens were recorded, while 112 previously reported were absent. Our results indicate that the tracks and embankments, and close surroundings of buildings constitute a similar habitat with the same alien flora, whereas the wider surroundings host different alien species. Therefore, it can be concluded that for the majority of the alien species the surroundings of railway stations and yards are not a stepping stone for the spread away from railway tracks. One of the reasons why alien species associated with railways do not spread into the wider surroundings is most likely the presence there of many competitively stronger species.

Keywords: alien plants distribution, central Europe, introduction pathways, plant invasion, railway, ruderal assemblages, urban habitats

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Introduction

Globalization and climate change are associated with changes in the distributions of plant species by natural migration (Perrings et al. 2005, Meyerson & Mooney 2007, Walther et al. 2009, Pauchard et al. 2016), as well as plant invasions, involving both deliberate and unintentional human-mediated introductions (Dehnen-Schmutz et al. 2007, Kowarik & von der Lippe 2007, Lehan et al. 2013). Some alien species (sensu Richardson et al. 2000, Blackburn et al. 2011) pose a threat not only to resident plant communities and ecosystems (Hejda et al. 2009, 2017, Vilà et al. 2011, Pyšek et al. 2012, 2020, Kumschick et al. 2015), but also to human health and economy (Schaffner et al. 2020, Diagne et al. 2021, Novoa et al. 2021). The introductions of alien species continue to increase (Seebens et al. 2021), and mitigation of further increase in invasion levels and their effects is a major challenge for nature conservation (Roy et al. 2023). Besides preventing introductions, systematic and coordinated monitoring and effectively applied management are crucial for mitigating the negative impacts of biological invasions (Foxcroft et al. 2013, 2017).

On a continental to global scale, it is known that distribution of alien plants is positively correlated with economic and trade networks (Pyšek et al. 2010, Chapman et al. 2017). At a finer resolution, not only the urban areas (Aronson et al. 2014, Kalusová et al. 2019), but also the presence of linear corridors (e.g. roads, railways and rivers) play a crucial role in the distribution and spread of alien species (Brisson et al. 2010, Jehlík 2013, Medvecká et al. 2018, Jehlík et al. 2019). During the transport of goods, many propagules of alien species are translocated as a stowaway on the vehicles or their wheels (Lonsdale & Lane 1994, von der Lippe & Kowarik 2007) and accumulate in railway stations, yards, transit sheds, etc. Such transport corridors are associated not only with high propagule pressure but also with the permanent or temporary enrichment of otherwise nutrient-poor habitats by passing trains (e.g. the nutrient rich content of toilets on old trains was flushed directly on to the railway track). Moreover, regular disturbances and, hence, low competition in often sparse vegetation create conditions suitable for many newly arriving alien species as well as for low-competitive threatened species that are provided with safe sites for establishment and survival (Vojík et al. 2020). Therefore, these human-made ruderal habitats serve not only as corridors but also as acclimatization areas and reservoirs for the spread of species into the open landscape (Hansen & Clevenger 2005, Májeková et al. 2014, Wrzesień & Denisow 2017); irregular management and transport of soil in these habitats also significantly promote such spread (Jehlík 1998, Wilson et al. 2009, Lemke et al. 2019).

Here, the introduction of plant species along railways (so-called 'ferroviatic introduction'; Jehlík 1998), a disturbed habitat with extreme soil conditions offering a broad spectrum of ecological niches, was studied. Railway habitats are suitable for a wide range of species, namely stress-tolerant, xerophytic and annuals (Chytrý 2009, but see Guo et al. 2018). The different types of substrates that occur there can be colonized by species that prefer well-drained substrates such as screes, while fine-grained, impermeable substrates can be inhabited, for example, by species that can be found on the exposed bottoms of ponds (Jehlík 1986, 1998). Such a mosaic of habitats and different environmental conditions is associated with high biodiversity, a large part of which is often made up of aliens (Procházka & Kovář 1976, Muhlenbach 1979, Raycheva et al. 2021).

The Czech Republic has a dense railway network, which, in addition to passenger transport, is also used for the transport of domestic and transit freight. In previous decades, railways represented an important, well-studied pathway for the spread of alien plants. Three main pathways of introduction were determined for central Europe, called the North Sea, Pannonian, and Oriental pathways (Jehlík & Hejný 1974). Here, the focus is on the former two, the first of which is the East-Medrail freight corridor, according to the European Agreement on Important International Combined Transport Lines and Related Installations (AGTC, https://www.mdcr.cz). The North Sea pathway is the second and is mainly used to transport oil crops, cereals, or soya beans. It played an important role in railway introductions as many North American species arrived in central Europe this way (e.g. *Hordeum jubatum* and some taxa of the genus *Oenothera*; Jehlík 1985). On the other hand, the Pannonian pathway serves as a link to the Mediterranean, a region that is the main donor of alien plants to the Czech Republic, responsible for 31.5% of all introductions (Pyšek et al. 2022); examples of species that arrived via this pathway are *Sisymbrium orientale* and *Ambrosia artemisiifolia* (Jehlík 1985). However, the increasing interconnections of recent transport systems often prevent clear recognition of the pathway by which a species was introduced (Jehlík 1985, 1998). The dynamic change over time in transport volumes, directions and transported material, as well as the confounding effects of other means of transport, such as roads and rivers, makes it difficult to interpret the recorded patterns.

The number of research papers on the introduction of plants along railways is increasing (Galera et al. 2014, Jasprica et al. 2017, Kotenko et al. 2022, Galkina et al. 2023). However, botanists are often more interested in recording rare, endangered or newly introduced species linked to the railway system (Májeková et al. 2014, Denisow et al. 2017); only the floras of large railway stations, yards and cities are published (Rutkovska et al. 2013, Heneidy et al. 2021, Májeková et al. 2021, Dziuba et al. 2022). The current study combines historical and recent data collected along long corridors with detailed sampling of railway stops and focuses on various habitats. Similar studies are uncommon, and comparisons of historical and recent data in the context of central Europe are lacking. The aims of this study are (i) to compile a complete list of taxa occurring in railway environments in the Czech Republic and (ii) to explore the distribution patterns of alien species and their traits in the localities studied. In addition, (iii) by comparing recent and historical alien species recorded along railways, (iv) species whose distribution has changed over time will be identified.

Methods

Study area

This study was based on data collected in the Czech Republic along the First Transit Railway Corridor from Břeclav to Děčín (Fig. 1). This includes two routes of the Eastern and Eastern-Mediterranean Rail Freight Corridor (RFC), the Baltic-Adriatic RFC from Břeclav to Ústí nad Orlicí, the Rhine-Danube RFC from Česká Třebová to Prague and the section from Prague to the north-west that complements the North Sea-Baltic RFC (https://www.spravazeleznic.cz/documents/50007830/51603382/2018-m03-rfc.pdf).

1. Břeclav
2. Zaječí
3. Hrušovany u Brna
4. Brno dolní nádraží
5. Brno-Maloměřice
6. Skalice nad Svitavou
7. Svitavy
8. Česká Třebová
9. Ústí nad Orlicí
10. Choceň
11. Pardubice
12. Přelouč
13. Kolín
14. Tišnov
15. Křižanov
16. Žďár nad Sázavou
17. Havlíčkův Brod
18. Světlá nad Sázavou
19. Čáslav
20. Kutná Hora
21. Velký Osek
22. Nymburk
23. Lysá nad Labem
24. Praha-Horní Měcholupy
25. Praha-Malešice
26. Praha-Libeň
27. Praha-Modřany
28. Praha-Bubny
29. Kralupy nad Vltavou
30. Všetaty
31. Mělník
32. Roudnice nad Labem
33. Lovosice
34. Velké Žernoseky
35. Ústí nad Labem západ
36. Ústí nad Labem-Střekov
37. Děčín
38. Děčín-Prostřední Žleb
39. Děčín východ

Fig. 1. Map showing the locations of the railway stations studied along with assignment to stretches (I.–V., see Supplementary Table S2). The phytogeographic division of the Czech Republic (according to Skalický 1988) is shown in the background.

The climate in the Czech Republic is transitional between temperate oceanic in the west and temperate continental in the east (Rivas-Martínez et al. 2004). The mean annual temperature is 7.1–8.9 °C, and mean annual precipitation is 650–720 mm (Tolasz et al. 2007). The transit railway corridor connects, via areas suitable for mesophytic plants in the Czech-Moravian highlands, two areas suitable for thermophilous species, the Pannonian area in the south-east and Elbe canyon in the north-west of the Czech Republic.

Sampling

A complete inventory with a rough estimate of the abundance of vascular plant taxa (including cultivated ornamentals) recorded at 39 railway stations, railway yards and their vicinities during the summer vegetation period (June–August) of 2020–2022 was compiled (Fig. 1). The most important stops and stations were selected based on the number of passengers and volume of freight transported (hence forth referred to as 'stations'). Each station was sampled only once, and if spring geophytes were recorded, they were removed from the analyses because, for logistic reasons, it was not possible to sample this group consistently.

Each station was divided into three zones according to the use and type of management: (i) track and embankment (referred to as 'track zone'), (ii) surroundings of station buildings ('building zone'), and (iii) wider surroundings of the station ('surrounding zone') (Fig. 2). Track zone was defined as areas where vegetation is affected by the passage of trains, high and frequent use of herbicides and trampling. The building zone was subject to management that differed from that applied in the track zone. The surroundings zone included the area around the station with mainly seminatural stands, which are extensively managed (pruning of trees encroaching on the railway, etc.), or there is no management. Outer borders of the surrounding zone were defined by private areas or by a significant land-use change (e.g. forest, abandoned field). Ornamental species are often planted, the frequency of mowing is higher, the use of herbicide is limited and the species pool is generally not directly connected with ferroviatic transport. The abundance of plants was recorded for each zone separately by using a semiquantitative scale: 1 = sporadic occurrence (1–2 individuals), 2 = rare occurrence, 3 = scattered over most of the area, 4 = abundant but not dominant, 5 = abundant and dominant (Fig. 2). Taxa were determined to subspecies in order to make the comparison with the historical dataset as precise as possible.

Data selection

Due to the variation in the quality and amount of data in historical records for the stations sampled and increase in the robustness of analyses based on recent data, the stations were grouped into five clusters (corresponding to particular stretches of railway; Fig. 1). The stations in individual stretches were selected according to the biogeographic provinces of the vegetation of the Czech Republic (Skalický 1988) and, at the same time, the direction of transport along the corridor and the main intersections was considered.

The first stretch included stations belonging to the Pannonian thermophytic area (five stations, 71.5 km long; Fig. 1, https://www.spravazeleznic.cz/documents/50007830/ 51603382/ 2018-m03-rfc.pdf). The second stretch runs along the upper corridor, which includes the railway stations on the eastern line of the Czech-Moravian Mesophyticum, and continues to Pardubice and Přelouč, which are in the Czech Thermophyticum (seven stations, 184.5 km long). The third stretch runs through the western course of the Czech-Moravian Mesophyticum (seven stations, 186.0 km long). The fourth stretch is located mainly in the Czech Thermophyticum (11 stations, 146.5 km long). The fifth stretch extends the range of the Czech Thermophyticum and Czech-Moravian Mesophyticum (nine stations, 153.5 km long).

The historical dataset was obtained from the Pladias database (Wild et al. 2019, Chytrý et al. 2021) based on a search using the following keywords: nádraží (*nádr*), železniční (*železn*), Bahn (*Bahn*), rail (*rail*) a ferroviae (*ferr*). The data was divided into records before 1959 and then at 20-year intervals: 1960–1979, 1980–1999 and 2000–2019. To compare the historical and recent distributions of species, historical records were organized according to the above-defined stretches of railway track instead of using data collected from individual stations that was of varying quality and completeness. This approach allowed the inclusion of the distribution of species that were rarely recorded in the past, reduced the effect of station size, increased the robustness of historical data, and tracked the distributions of species over a longer period of time. The data remains very sparse, even when the historical data is pooled for stretches and long periods.

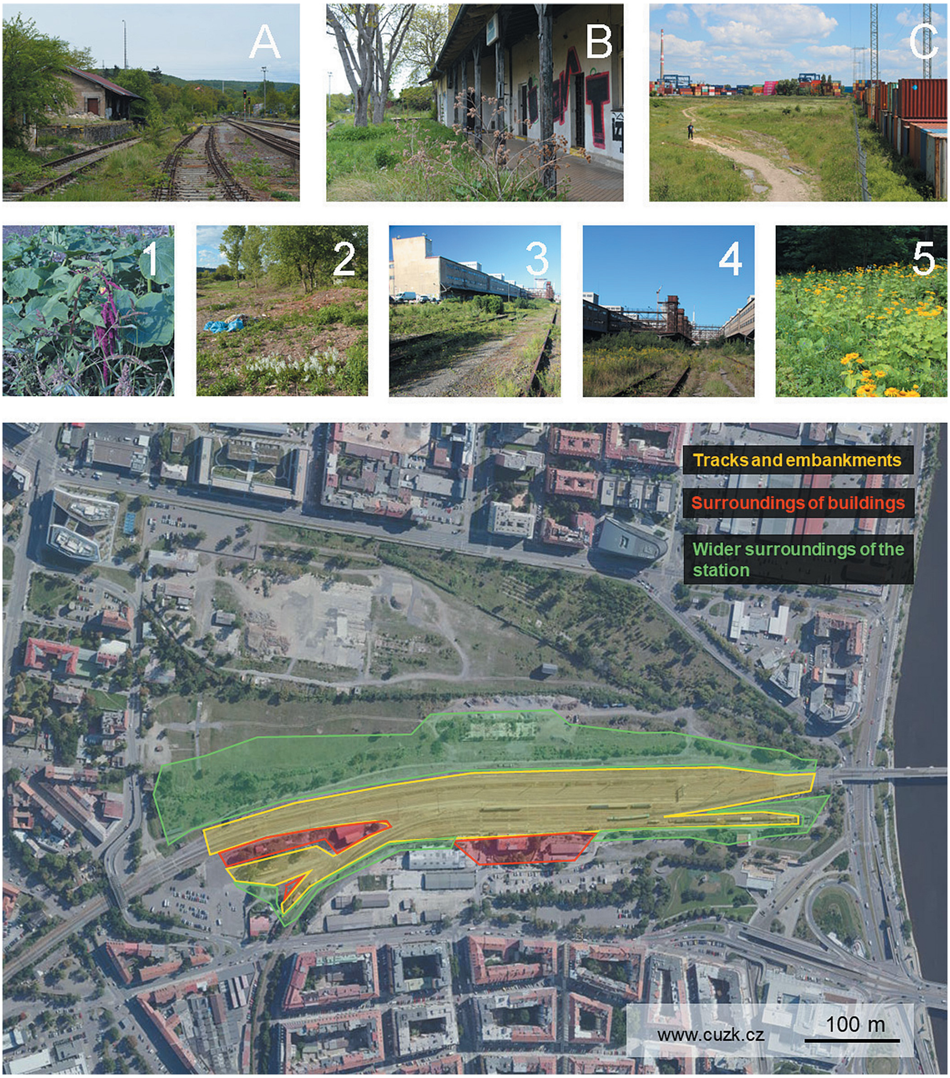

Fig. 2. Zones distinguished in the railway stations studied. (A) Track zone, comprising tracks and embankments, (B) building zone, defined as the surroundings of station buildings (C) and surroundings zone, referring to the wider surroundings of the railway station. The categories of abundance used in sampling along with photographs of the plants: (1) Sporadic occurrence of *Amaranthus caudatus* and *Cucurbita pepo* found only in one place at a station, (2) rare occurrence of a few plants of *Ornithogalum nutans* in the wider surroundings of a station, (3) scattered occurrence of *Senecio inaequidens* in most of the area, (4) abundant but not dominant *Solidago canadensis*, (5) abundant and dominant *Telekia speciosa*. Photo: Josef Kutlvašr (A, B, C, 1, 5) and Jan Pergl (2–4). A schematic map of railroad station Praha-Bubny (N50.103°, E14.439°) with the delimitation of the zones is shown at the bottom: (i) tracks and embankments – yellow, (ii) wider surroundings of the station – green, and (iii) surroundings of buildings – red. Source of orthophoto map: https://ags.cuzk.cz/geoprohlizec.

Therefore, the data was not statistically analysed and the comparison with recent data is only descriptive.

For alien taxa (including both archaeophytes and neophytes), their invasion status was assigned as casual, naturalized, or invasive in the Czech Republic (Pyšek et al. 2022). The Red List of the Czech vascular flora and Czech legal protection status was used to obtain threat categories (Ministry of Environment of the Czech Republic 1992, Grulich 2017). These are similar to, but not equivalent to those used in the IUCN Red List (IUCN 2014). The main category A includes taxa that are extinct or missing and category C includes taxa that are threatened, including rare taxa requiring attention and unclear cases. Plant dispersal strategies were taken from Sádlo et al. (2018). For the assignment of life forms, the Raunkiaer scheme (Raunkiaer 1934, Kaplan et al. 2019) was used. Nomenclature follows that used in the Pladias database (Kaplan et al. 2019, Chytrý et al. 2021).

Statistical analysis

All statistical analyses were applied to (i) all recorded species pooled, (ii) all alien species, (iii) naturalized alien species (including invasive ones that could not be tested as a separate category due to the low number of species) and (iv) casual alien species.

The differences in species richness, represented by the numbers of recorded species, were analysed using mixed-effect models (LMM). The identity of the station was set as a random effect, while the ‘zone’ and ‘stretch’ were set as fixed effects. A square-root and logarithmic transformation of the input data was used to improve their normality, and the data tested using the Shapiro-Wilk test. The quality of the models was inspected by testing the normality of residuals using the Shapiro-Wilk test and by visual inspection of normal probability plots.

In the case of casual alien species, normality could not be achieved by transformation and the data resembled Poisson rather than Gaussian distribution due to generally low numbers and zeros. Therefore, GLMM models with Poisson errors and identical structure of random and fixed effects were used in the case of the richness of casual aliens.

The data with species richness as a response was analysed using a two-stage process: First, a mixed-effect model with species richness as the response and area as a predictor was developed, with stations as a random effect. Then, another mixed-effect model was used, with the zones and stretches as predictors and residuals of the model on the effect of area as a response. This was done to account for the effect of the different areas of zones because the aim of the analysis was to test the effect of zones beyond that given by their different areas. All univariate models were developed in R software (Crawley 2007, R Core Team 2023), using the packages nlme in the case of LMM and lme4 in the case of GLMM models (Pinheiro et al. 2021). The differences between zones were tested by the Tukey HSD method, using the package emmeans.

The compositional differences between zones and stretches were tested by multivariate direct gradient ordination analyses. The linear vs unimodal method (RDA and CCA, respectively) was chosen based on the length of the compositional gradient within the data. The significance of the differences was tested using Monte Carlo permutation tests with 499 permutations. The data was permuted using a split-plot scheme, with the stations representing whole plots and zones (within the stations) representing the split-plot level. This arrangement reflected the hierarchical arrangement of the data. First, we tested the marginal effects of (i) zones (split-plot level) and (ii) stretches (whole-plot level). Then, we tested the partial (conditional) effects of zones and stretches by adding stretches as a covariable when testing the partial effect of zones and by adding zones as a covariable when testing the partial effect of stretches. The area of zones was used as a covariable in all multivariate analyses to account for possible sampling effects given by their different size. All multivariate analyses were performed in CANOCO 5 (ter Braak & Šmilauer 2012). The frequency of representation of life forms across zones was tested by count data and analysed in row × column contingency tables, with GLM with log-link function and Poisson distribution of errors (Crawley 2007). Differences between the groups were tested using G-tests. Differences in the origins of aliens in stretches were tested using the chi-squared test (Řehák & Řeháková 1986).

Results

General pattern

The field sampling yielded 11,139 records belonging to 764 taxa, with more native species (403; 53%) than alien species (309; 40%). For 52 taxa (7%), it was not possible to determine the area of origin (anecophytes). The complete list of species with their invasion status, distribution and threat category is shown in Supplementary Table S1. The numbers of archaeophytes (153) and neophytes (155) were almost balanced. The majority of alien species were naturalized (239, i.e. 77%), 53 (17%) of them were invasive and 70 (23%) were casual. Neophytes (36 species) were more represented among invasives than archaeophytes (17). Most alien species came from the Mediterranean (130), the rest of Europe (55), North America (54) and Asia (53). The most frequent invasive archaeophytes were *Lactuca serriola* (102), *Arrhenatherum elatius* (97), *Cirsium arvense* (77), *Digitaria sanguinalis* (76) and *Portulaca oleracea* (65). The most frequent invasive neophytes were *Conyza canadensis* (90), *Solidago canadensis* (90), *Erigeron annuus* (86), *Robinia pseudacacia* (58) and *Sisymbrium loeselii* (58).

During the inventory, 85 taxa of various threat categories were recorded, of which four are critically endangered (C1; *Crepis setosa*, *Filago germanica*, *Polycnemum majus*) and 10 are strongly endangered (C2; *Anthriscus caucalis*, *Centaurea montana*, *Equisetum ramosissimum*, *Euphorbia seguieriana*, *Geranium molle*, *Malva pusilla*, *Misopates orontium*, *Myosotis discolor* subsp. *discolor*, *Salsola tragus* subsp. *tragus*, *Torilis arvensis*). Another 33 taxa are in the category threatened (C3; see Supplementary Table S1). Some of these taxa may be escapes from cultivation or cultural relicts.

The highest diversity of alien and invasive species was recorded at the stations of Nymburk (124 alien; 39 invasive; area 63 ha), Ústí nad Labem západ (113; 34; 59 ha) and Česká Třebová (110; 28; 88 ha). These railway stations are among the largest in the Czech Republic. Other large stations include Kolín and Brno-Maloměřice (Supplementary Table S2). A high diversity of alien and invasive species (99; 28) was also recorded at Kolín, a little less so at Brno-Maloměřice (92; 21). An interesting finding is the high numbers of invasive species in the localities Děčín východ (34) and Velký Osek (29), which are not as large as the other localities studied. There was a significant relationship between alien species richness and station area (linear regression: $R^2_{adj} = 0.28$, $F_{1,36} = 15.48$, $P < 0.001$; Fig. 3, Supplementary Table S2).

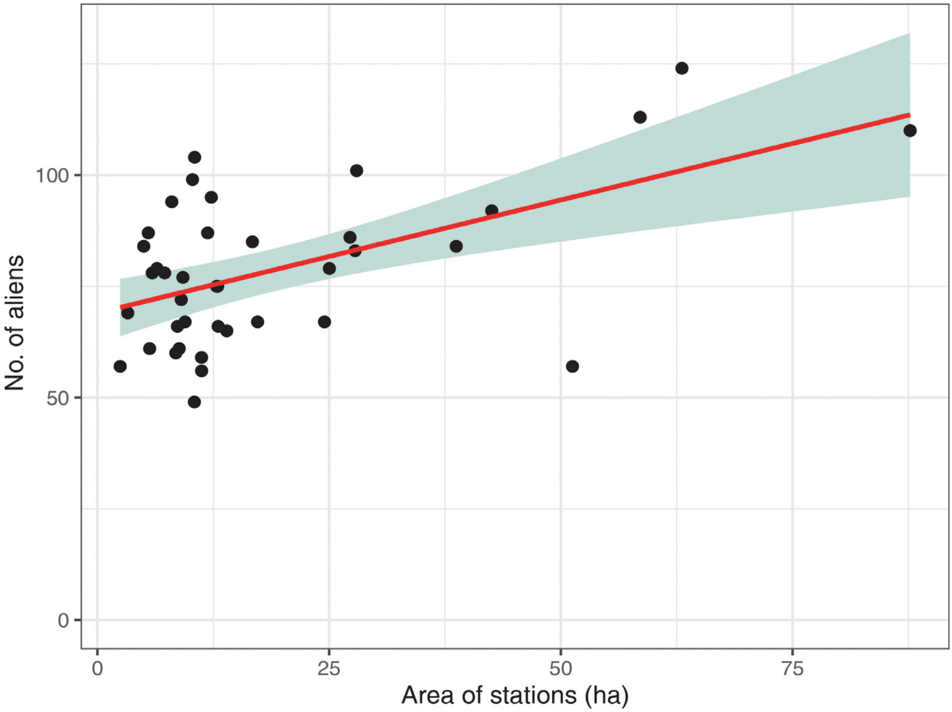

Fig. 3. Relationship between the number of alien species and the area of the railway station (untransformed data). Estimate of the number of aliens per area: 69.31 + 0.51 × area (ha); $R^2 = 0.28$, $P < 0.001$; 95% confidence interval varies between 68.3 and 70.3.

Effect of stretches and zones on species numbers and composition: the role of alien species

The numbers of species in all groups except casual aliens significantly ($P < 0.05$) differed between the zones within individual stations. The multiple comparisons revealed that the track zone was significantly richer in species than the buildings and surroundings zones, and the latter two did not differ. The numbers of all species taken together also differed between individual stretches ($P = 0.022$; see Supplementary Table S3 for the detailed results of LMM and GLMM models on species richness). Based on the total number of species recorded, the first three stretches host almost the same number of alien species (158, 171, 173), whereas the third and fourth hosted more (229 and 207 alien species, respectively; Table 1).

Table 1. The mean numbers of taxa in the different species groups analysed for particular stretches and zones of railway network. Note that for casual aliens nonparametric methods were used therefore the median numbers are given. SD – standard deviation, Q – quantile.

		Stretch					Zone		
Species group		I.	II.	III.	IV.	V.	Track	Building	Surroundings
Alien	mean±SD	40.1±13.1	40.4±14.3	40.1±15.8	41.9±17.0	47.8±18.1	54.2±16.8	35.5±12.1	36.3±11.7
Naturalized	mean±SD	38.7±12.6	38.9±13.4	37.7±15.4	39.1±16.2	45.2±17.5	52.2±15.9	33.0±11.2	34.9±11.1
Casual	median±Q	1.0±1.5	1.0±1.8	2.0±2.0	1.0±2.3	2.0±2.3	2.0±2.0	2.0±2.0	1.0±1.8
All species	mean±SD	120.9±41.9	140.9±47.2	141.5±41.5	126.8±46.7	152.7±48.5	169.7±48.6	115.3±38.4	124.2±30.8

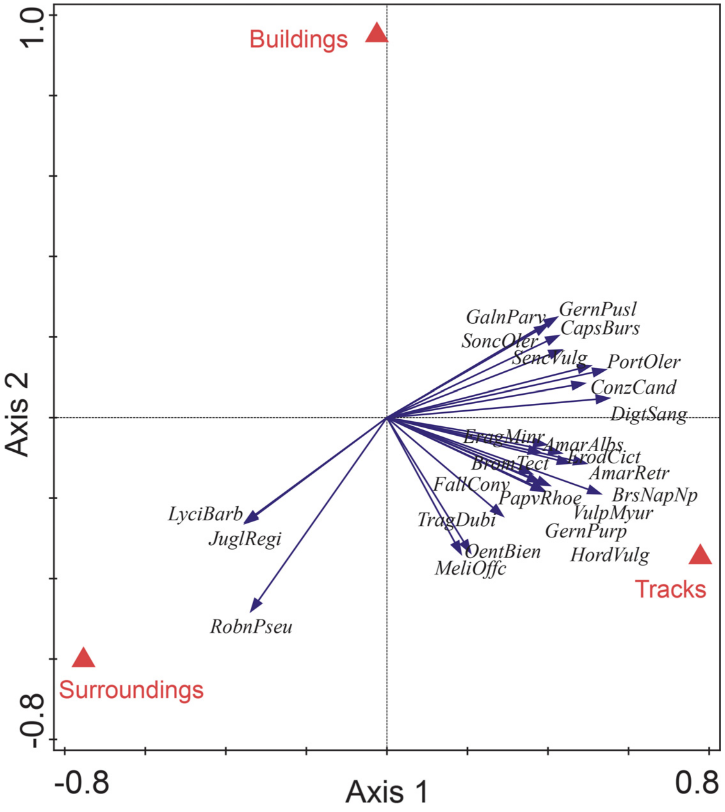

Fig. 4. A plot of the ordination analysis (RDA), displaying the affinity of alien species to the three zones within stations: tracks, buildings and surroundings (P = 0.002, with 499 permutations). The plot shows a marginal effect of zones (without accounting for stretches); however, the area of zones is included as a covariable. The first ordination axis accounts for 7.4% of the total variation and the second axis 2.8%. All canonical (constrained) axes together account for 10.1% of the variation. Only 25 species with the highest fit are displayed. Abbreviations: AmarAlbs = *Amaranthus albus*, AmrRetr = *Amaranthus retroflexus*, BrsNapNp = *Brassica napus*, BromTect = *Bromus tectorum*, CapsBurs = *Capsella bursa-pastoris*, ConzCand = *Conyza canadensis*, DigtSang = *Digitaria sanguinalis*, EragMinr = *Eragrostis minor*, ErodCict = *Erodium cicutarium*, FallConv = *Fallopia convolvulus*, GalnParv = *Galinsoga parviflora*, GernPurp = *Geranium purpureum*, GernPusl = *Geranium pusillum*, HordVulg = *Hordeum vulgare*, JuglRegi = *Juglans regia*, LyciBarb = *Lycium barbarum*, MeliOffc = *Melilotus officinalis*, OentBien = *Oenothera biennis*, PaprRhoe = *Papaver rhoeas*, PortOler = *Portulaca oleracea*, RobnPseu = *Robinia pseudacacia*, SencVulg = *Senecio vulgaris*, SoncOler = *Sonchus oleraceus*, TragDubi = *Tragopogon dubius*, VulpMyur = *Vulpia myuros*.

Multivariate ordination analyses (RDA, Fig. 4–7) revealed that the species composition of all groups (all recorded species, all alien species, naturalized alien species including invasive), except for casuals, significantly differed between zones and stretches. This concerns both their marginal and conditional effects when the zone was set as a covariable for testing the conditional effect of the stretch and, vice versa, when the stretch was set as a covariable for testing the conditional effect of the zones. When considering both the variance accounted for and significance, zone was a stronger predictor than stretch for all groups of species, i.e. naturalized aliens, including invasive aliens, and all casuals (see Table 2 for detailed results of multivariate ordination models).

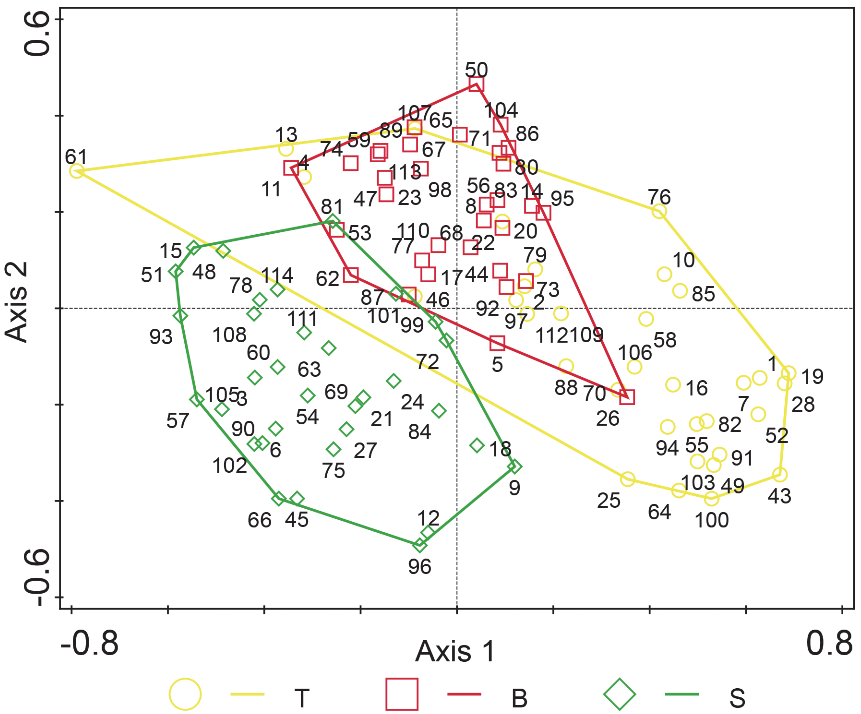

Fig. 5. Ordination diagrams displaying the two first axes of RDA, calculated for all alien plants. The enclosing polygons separate plots belonging to the zones of interest: T = track zone, B = buildings zone, S = surroundings zone, indicated by different colours. The plot shows the marginal effects of zones without accounting for stretches. The area of zones was included as a covariable.

Table 2. Results of the multivariate tests for individual species groups. Adjusted variation accounted for is shown in brackets in the explained variation column.

Subgroup	Predictor	Effect	Covariable	Analysis	Pseudo-F	Explained variation	P-value
All species	area	marginal	–	RDA	5.6	9.2 (7.6)	0.002
All species	area	partial	stretch	RDA	5.9	10.1 (8.4)	0.002
All species	stretch	marginal	–	RDA	2.2	7.6 (4.2)	0.002
All species	stretch	partial	area	RDA	2.5	8.5 (5.0)	0.002
All aliens	area	marginal	–	RDA	6.2	10.1 (8.5)	0.002
All aliens	area	partial	stretch	RDA	6.6	11.1 (9.3)	0.002
All aliens	stretch	marginal	–	RDA	2.1	7.2 (3.8)	0.002
All aliens	stretch	partial	area	RDA	2.3	8.1 (4.6)	0.004
Naturalized aliens	area	marginal	–	RDA	4.6	12.4 (9.7)	0.002
Naturalized aliens	area	partial	stretch	RDA	4.5	12.9 (10.0)	0.002
Naturalized aliens	stretch	marginal	–	RDA	1.7	9.6 (3.8)	0.002
Naturalized aliens	stretch	partial	area	RDA	1.7	10.1 (4.2)	0.002
Casuals	area	marginal	–	CCA	1.7	10.3 (4.2)	0.006
Casuals	area	partial	stretch	CCA	1.6	10.6 (4.0)	0.004
Casuals	stretch	marginal	–	CCA	0.4	2.8 (0.0)	0.556
Casuals	stretch	partial	area	CCA	0.4	3.0 (0.0)	0.626

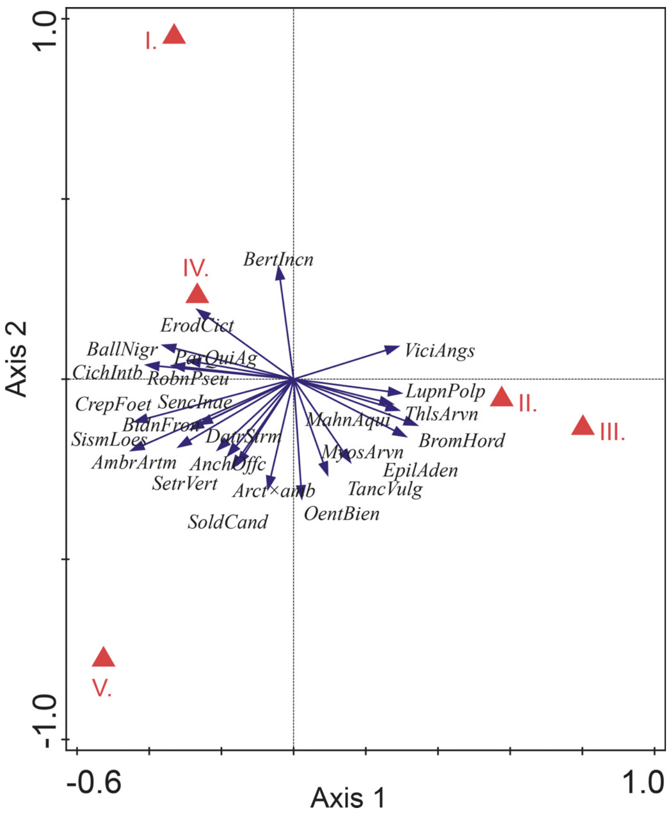

Fig. 6. A plot of the ordination analysis (RDA), displaying the affinity of alien species to five stretches of the railroad corridors (P = 0.002, with 499 permutations). The plot shows a marginal effect of stretches (without accounting for zones); however, the area of zones is included as a covariable. The first ordination axis accounted for 2.8% of the total variation and the second for 1.7%. All canonical (constrained) axes together account for 7.2% of the variation. Only 25 species with the highest fit are displayed. Abbreviations: AmbrArtm = *Ambrosia artemisiifolia*, AnchOffc = *Anchusa officinalis*, Arct×amb = *Arctium ×ambiguum*, BallNigr = *Ballota nigra*, BertIncn = *Berteroa incana*, BidnFron = *Bidens frondosa*, BromHord = *Bromus hordeaceus*, CichIntb = *Cichorium intybus*, CrepFoet = *Crepis foetida*, DatrStrm = *Datura stramonium*, EpilAden = *Epilobium adenocaulon*, ErodCict = *Erodium cicutarium*, LupnPolp = *Lupinus polyphyllus*, MahnAqui = *Mahonia aquifolium*, MyosArvn = *Myosotis arvensis*, OentBien = *Oenothera biennis*, ParQuinAg = *Parthenocissus quinquefolia* agg., SencInae = *Senecio inaequidens*, SetrVert = *Setaria verticillata*, SismLoes = *Sisymbrium loeselii*, SoldCand = *Solidago canadensis*, RobnPseu = *Robinia pseudacacia*, TancVulg = *Tanacetum vulgare*, ThlsArvn = *Thlaspi arvense*, ViciAngs = *Vicia angustifolia*.

Comparison of recent and historical records

Due to a lack of historical data, the recent and historical datasets were not compared statistically. Overall, the number of alien species tended to increase and was highest in all stretches in 2020–2022 (Fig. 8, Supplementary Fig. S1).

A total of 109 alien species were recently recorded that were not present in the historical dataset, and 112 previously recorded were not recorded recently. For endangered species, the corresponding figures are 50 and 73, respectively (Supplementary Table S4).

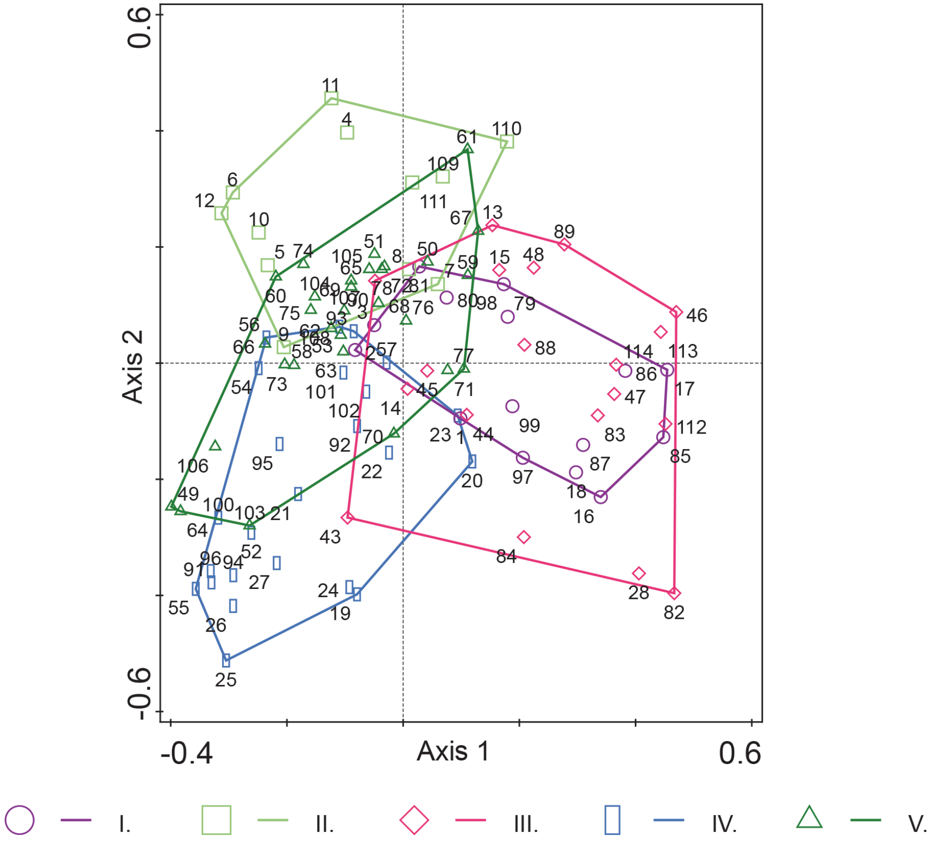

Fig. 7. Ordination diagrams displaying the two first axes of RDA, calculated for all alien species recorded. The enclosing polygons separate plots belonging to the individual stretches, indicated by different colours. The plot shows the marginal effects of stretches without accounting for zones. The area of zones was included as a covariable.

Most of the alien species were therophytes (historical = 190, recent = 137) and hemicryptophytes (historical = 79, recent = 87); the other life forms occurred only in small proportions (Supplementary Table S3). In recent observations, a significant difference was found among the life forms in the individual zones (P < 0.001). In the track zone, fewer nanophanerophytes and more therophytes than expected were recorded (both P = 0.05). On the other hand, marginally significantly more chamaephytes and fewer therophytes were recorded in the surrounding zone (P = 0.1). Considering the dispersal strategy, the *Allium* type was the most common among alien species (mainly autochory, historical = 223, recent = 185); the other strategies occurred only occasionally (Supplementary Table S3). No significant difference was found among individual zones in the recent observation (P = 0.43).

The main donor region of alien species was the Mediterranean (historical = 127, recent = 142, Supplementary Table S3), followed by North America (historical = 55, recent = 44), Asia (historical = 47, recent = 31) and the rest of Europe (historical = 32, recent = 44). A large part of the species pool consisted of anecophytes (historical = 34, recent = 29). However, the origins of the alien species did not differ significantly among the different stretches (P = 0.65).

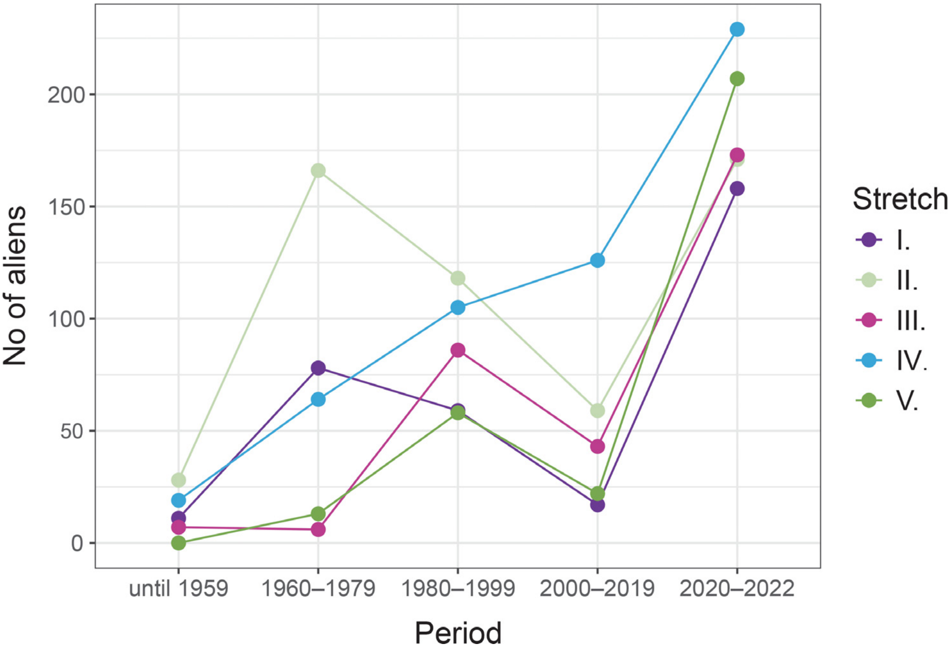

Fig. 8. The number of alien plant taxa recorded over time for the stretches of track studied (see Fig. 1 for the location of stretches).

Discussion

During the sampling of railway areas, we recorded 764 plant taxa, confirming that railways and surrounding areas are among the habitats richest in plant species; if the historical records are included, the total species pool increases to 1054. These numbers are comparable to those recorded by other European studies on this habitat (Brandes 2005, Vinogradova et al. 2017). The percentage of alien species was rather high (40%), which also corresponds to that reported from Europe (Wrzesień & Denisow 2017, Májeková et al. 2021) and other parts of the world (Özaslan et al. 2016) and is comparable with the percentage of alien taxa in the Czech Republic (37.8%; Pyšek et al. 2022). This makes the railway flora an important component of the alien species pool in the Czech Republic.

Ruderal habitats are important for invasions, as for the majority of alien plants they serve as the starting point for further spread (Lososová et al. 2012, Jehlík et al. 2019). The area around railways is a specific type of ruderal vegetation (Jehlík 1998). It is noteworthy that the connection between track and embankment and ruderal habitats in their vicinity is essential for the spread of alien plants (Wrzesień & Denisow 2017). We hypothesize here that species introduced by railway vehicles initially become established along the railway tracks and later spread to the wider surroundings and into the landscape. However, the results reveal that the tracks and embankments and the surroundings of the buildings are, in terms of the occurrence of aliens, closely connected habitats, whereas the wider surroundings differ significantly and host different species. Therefore, they do not confirm that the surroundings of railway stations and yards are a stepping stone for the further spread of alien species along the tracks. However, there may be exceptions that this study did not cover. Such cases might include the spread of *Buddleja davidii*, *Senecio inaequidens* and *Ailanthus altissima* in warmer regions.

There are two most likely scenarios of species' spread from tracks and embankments into the landscape. First, the species must spread along the railway line to a location where the track meets a suitable habitat (see Hansen & Clevenger 2005). Such places can be anthropogenically disturbed areas, for example, after forestry interventions, management measures in a protected area or where the track passes through a city (Rutkovska et al. 2013, Wrzesień et al. 2016, Vinogradova et al. 2017). The second scenario is the spread of propagules by human travellers to a suitable place, e.g. on the soles of their shoes.

One of the reasons why alien species growing along railways do not spread into the wider surroundings is the limited or lack of management outside the railway stations, which has resulted in the presence there of many competitively strong species, such as expansive (*Calamagrostis epigejos*) and invasive archaeophytes and neophytes (*Arrhenatherum elatius*, *Solidago canadensis*); these species prevent the further spread of new species. However, it must be mentioned that this approach cannot be generalized to all species. Some species, such as *Conyza canadensis* and *Sisymbrium loeselii*, can colonize microhabitats in the wider surroundings of the stations. The distance from the tracks also plays a role because some species can only spread a short distance. Transport volumes and frequency are another factor, as air currents caused by a passing train help anemochoric species to spread over longer distances (Wrzesień & Denisow 2017).

In contrast, management in the zone of tracks and embankments is often very intensive, mainly for safety and technical reasons. Herbicides are routinely applied in high volumes in combination with mowing to preserve the quality and safety of the track. However, the effect of herbicides is only partial and relatively short-term (Jehlík 1998), yet it can reduce the occurrence of alien species (Zimmermann et al. 2014).

The influence of railway stretch on the occurrence of alien species was not as significant as that of individual zones representing habitats. The distribution of alien species depends more on assignment to a habitat than on the phytogeographical region that the given stretch passes through (Skalický 1988). A linear model considering the numbers of aliens in individual stretches yielded non-significant results, unlike the ordination analyses with abundances of individual species included. We assume that stretches IV and V differed from the others because they included a higher number of large railway stations and yards, where strong propagule pressure results in higher numbers of aliens.

The east-west orientation of the railway corridor studied allowed geographical patterns related to the origins of alien species to be tested. A reasonable assumption is that North American species would occur in corridors along the Elbe pathway of introduction and Mediterranean species in south-eastern corridors along the Pannonian pathway (Jehlík & Hejný 1974). However, this was not evident in the data, possibly because the mixing of floras typical for particular pathways occurred a long time ago, and also, in order to detect these associations, a more extensive railway transect would be needed.

In addition to analysing recent patterns in species distribution along railway tracks, we aimed to compare the current and historical occurrences of species. This comparison was constrained by incomplete historical floristic data that usually focused on selected species that were considered interesting (e.g. newly introduced, charismatic, popular) and common species were less thoroughly recorded. Complete floristic inventories of railway stations are rare, and the uneven quality of the data is another problem. The active regional botanists (Petřík et al. 2010) working in a given region greatly influence the entire historical dataset; this trend is evident when comparing trends recorded for aliens and endangered taxa. To overcome these constraints, we only compared selected endangered and alien species for which the historical dataset was robust. For example, there is a gap in the record for the years 2000 and 2019; the low number of species recorded in this period is more related to the low intensity of botanical research than to the absence of species (Wild et al. 2019).

Despite the results indicating a limited role of railways in small-scale spread, railway tracks remain one of the main pathways by which alien species spread over long distances. The introductions are rare events occurring in a few suitable localities rather than a frequent and continuous process. Not all alien species can spread from railways into the open landscape in the same way; some depend on unique opportunities to escape and become successful invaders.

Supplementary materials

Fig. S1. Additional figures of the analyses.
Table S1. Presence table for recent and historical records.
Table S2. Characteristics of individual railway stations.
Table S3. Summary tables of the historical and recent data for particular stretches of railway.
Table S4. Tables comparing the presence of alien and threatened species.

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

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Železnice jako zdroj nepůvodních rostlin

Mnoho nepůvodních druhů bylo zavlečeno neúmyslně, ať už v podobě příměsí nebo jako černí pasažéři při dopravě zboží. Zavlékání nepůvodních druhů rostlin podél liniových struktur je jedním z nejčastějších způsobů, jakým se tyto druhy dostávají na nová území. V naší studii jsme se zaměřili na zavlékání podél kolejišť, konkrétně v nákladním koridoru Břeclav – Kolín – Praha – Děčín. V letech 2000–2022 jsme navštívili a inventarizovali 39 železničních nádraží a seřadišť. Jednotlivé lokality byly přiřazeny do úseků podle fytogeografického členění ČR. Každá lokalita byla také rozdělena na tři zóny podle probíhajícího managementu a způsobu využívání: (i) kolejiště a přilehlé náspy, (ii) okolí staničních budov a (iii) širší okolí nádraží. Cílem práce bylo zjistit, jak jsou na zkoumaných lokalitách nepůvodní druhy rozšířeny, porovnat současná data s historickými záznamy a identifikovat druhy, jejichž rozšíření se změnilo. Celkem bylo nalezeno 11 139 záznamů náležících 764 druhům. Z tohoto počtu 53 % (403) tvořily původní druhy. Nepůvodních druhů bylo zjištěno 309 (40 %) a u 52 druhů (7 %) nebylo možné určit spolehlivě původ. Celkem 239 (77 %) nepůvodních druhů bylo naturalizovaných, 53 (17 %) z nich invazních, a 70 (23 %) druhů bylo přechodně zavlečených. Bylo nalezeno také 85 (11 %) druhů spadajících do některé z kategorií červeného seznamu. Nejvíce druhů, včetně nepůvodních, bylo nalezeno v zóně kolejišť. Zóna a úsek železnice ovlivňovaly nejen počet druhů, ale také druhové složení, přičemž vliv zóny byl silnější. Porovnání s historickými nálezy odhalilo nárůst počtu nepůvodních i ohrožených druhů v čase. Složení společenstva nepůvodních druhů v jednotlivých zónách se lišilo; průkazný rozdíl by zjištěn mezi zónou kolejišť a náspů a zónami širšího okolí a okolím staničních budov. Signifikantní rozdíl byl nalezen také mezi jednotlivými úseky, nicméně podíl vysvětlené variability byl nízký. Ukazuje se tedy, že příslušnost společenstva nepůvodních druhů k lokálnímu habitatu je důležitější, než jakým fytogeografickým okrskem daný úsek železnice prochází. Skutečnost, že kolejiště a náspy hostí jiné druhy než zbylé dvě zkoumané zóny, svědčí o tom, že okolí nádraží není odrazovým můstkem pro další šíření zavlečených druhů po kolejích. Jedním z důvodů, proč se nepůvodní druhy na železnici nešíří do širšího okolí, je omezený nebo chybějící management mimo železniční stanice a přítomnost mnoha konkurenčně silných, často expanzních či invazních druhů.

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