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RESEARCH

Vegetation patterns, functional traits and invasion dynamics across railway microhabitats in Slovenia

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Abstract

Purpose Railways are anthropogenic habitats shaped by various disturbances and management practices. Consequently, many studies report on significant plant diversity and vegetation heterogeneity in railway environments. We present results of the first systematic study of railway flora in Slovenia, focusing on microecological differentiation of railway zones and the role of railways as corridors for non-native species.

Methods At 92 locations across 15 segments of the Slovenian railway network, we conducted floristic sampling by transect method, studying four distinctive railway zones – Sleeper Zone (SZ), Ballast Shoulder (BS), Ballast Toe (BT) and Intertrack Area (IA) separately. We compared taxonomic and functional diversity, ecological indicator values and vegetation cover among zones using generalised linear mixed models and multivariate analyses.

Results We recorded 312 taxa from 67 families. Zone type significantly influenced species richness, vegetation cover and community composition. The BT supported the highest richness and densest vegetation, while the SZ and IA harboured thermophilous, heliophytic annuals adapted to the most extreme conditions. Hemicryptophytes and competitive species prevailed in outer zones; therophytes and ruderal species dominated inner zones. Ecological indicator values confirmed clear gradients of light, temperature and moisture across zones. Non-native species (13% of flora) were nearly ubiquitous, with invasive aliens present at 99% of sites, underscoring railways as invasion corridors.

Conclusions Our results confirm the considerable diversity of Slovenian railway flora, microecological specificity of railway zones, and the importance of railways in the spread of non-native species – findings, which have previously been overlooked in Slovenia.

Keywords Ecological corridors · Functional and taxonomic diversity · Invasive species · Microecological differentiation · Railway flora · Vegetation ecology

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Introduction

Railway tracks and embankments are ruderal habitats that are created and maintained under constant and strong anthropogenic influences (Topalić-Trivunović and Pavlović-Muratspahić 2008). Regardless of geographic location or climate zone, they constitute a linear urban infrastructure with many shared ecological characteristics (Májeková et al. 2025). According to Rashid et al. (2021), there are two main ways that railways alter the environment: (a) they cause an initial, severe disturbance of local natural landscapes, and (b) they continuously alter the habitat due to the traffic and railway maintenance. They function as modified land corridors (Jakobsson and Ågren 2014; Krause et al. 2015), serving as pathways for plant migration across natural barriers, including the dispersal of diaspores from distant regions (Tret'yakova 2010). By cutting through the railway landscapes, railway tracks and embankments fragment local ecosystems and create open environments (Gontier et al. 2006; Westermann et al. 2011; Popova 2020). Railway habitats are highly heterogeneous, shaped by both human activities and natural processes (Májeková et al. 2021). Although anthropogenic factors play a major role in determining the diversity of urban plants, climate and habitat type also affect urban vegetation to a certain extent, including in railway habitats (Vakhlamova et al. 2022; Slezák et al. 2025; Aronson et al. 2014; Kalusová et al. 2019). For instance, annual precipitation (Vakhlamova et al. 2022) and mean annual temperature were found to have an impact on railway vegetation (Májeková et al. 2025). The otherwise distinct environmental conditions of railway habitats, including permeable and sometimes calcareous substrates (Whitney 1985), low soil moisture and nitrogen levels (Dziuba et al. 2022), and a warmer and thus drier microclimate due to open spaces with high sun exposure compared to surrounding areas (Jehlík, 1986; Rakotoson et al. 2025), significantly influence the vegetation they support (Wrzesień et al. 2016b). These extreme conditions create a challenging environment for plant establishment and growth (Topalić-Trivunović and Pavlović-Muratspahić 2008). Despite this, ruderal communities along railway habitats worldwide often exhibit unique floristic compositions adapted to these harsh conditions (Whitney 1985).

Due to a great number of transport links within urban areas (Ricotta et al. 2014) and frequent disruption (Popova 2020), these habitats provide plenty of open niches for the introduction and naturalization of non-native and potentially invasive species (Ricotta et al. 2014; Popova 2020). For instance, alien species populations are often more abundant along railway habitats than in the surrounding native habitats (Wrzesień et al. 2016b; Heneidy et al. 2021; Raycheva et al. 2021) and can significantly reduce local biodiversity (Dziuba et al. 2022). Another contributing factor to the impoverishment of flora along active railway habitats are disturbances – not only by train traffic, but also by vegetation management practices, such as herbicide applications, mowing of grass stands, clearing of trees and shrub undergrowth, occasionally also burning (Popova 2020). To insure and maintain safe railway operation, vegetation on railway tracks and embankments must be regularly managed (Hoerbinger et al. 2020). As a result, native flora often becomes impoverished (Tret'yakova 2010), leading to a decrease in species diversity, density and biological productivity (Popova 2020).

Nevertheless, railway habitats may also function as new habitats and distribution corridors for local native species (Dziuba et al. 2022), as they retain a link with the floristic composition of the plant communities of their biogeographic contexts (Jasprica et al. 2017) and may contain up to 50% of all the plant species found in the surrounding regions (Stottele 1994). Therefore, railway habitats are often species-rich, with an important role in maintenance of urban biodiversity (Wrzesień et al. 2016b; Heneidy et al. 2021) and are sometimes even inhabited by rare or endangered species (Májeková et al. 2014; Heneidy et al. 2021).

Studies on railway vegetation in Europe date back to the 1920s, with reports on Ukrainian railway flora by Kotov from 1927 (Májeková et al. 2021), followed by studies carried out in Germany in the 1930s (Brandes 1983). However, scientific analyses of such vegetation have only become more frequent and available in recent years (Tret'yakova 2010), as vegetation in man-made habitats in European urban areas started receiving more attention (Cilliers and Bredenkamp 1998). Extensive floristic research of railway habitats has been conducted across Europe, especially after 2000 (Topalić-Trivunović and Pavlović-Muratspahić 2008; Tret'yakova 2010; Fornal-Pieniak and Wysocki 2011; Westermann et al. 2011; Filibeck et al. 2012; Altay et al. 2015; Galera et al. 2014; Májeková et al. 2014, 2021; Alessandrini 2016; Wrzesień et al. 2016a, b; Denisow et al. 2017; Jasprica et al. 2017; Vanneste et al. 2020; Hoerbinger et al. 2020; Raycheva et al. 2021; Dubyna et al. 2022; Dziuba et al. 2022;). Ecological studies are relatively newer (Hutniczak et al. 2022; Májeková et al. 2025; Rakotoson et al. 2025) and provide general insight into ecological traits which shape vegetation development in these ecosystems.

In this context, our study addresses three questions: (1) How does plant species composition and functional trait distribution vary among distinct railway microhabitats? (2) Do ecological indicator values reveal consistent environmental gradients across these zones? (3) What is the extent and spatial pattern of invasive species colonization along Slovenian railways? By documenting vegetation patterns immediately following the 2021 ban on herbicide use in Slovenian public infrastructure, this study also establishes a baseline for monitoring post-management vegetation dynamics—providing data relevant not only to Slovenia but to ongoing European debates about balancing railway safety with biodiversity conservation.

Materials and methods

Time and locations of sampling

We studied the Slovenian railway flora during July, August and September of 2022 and 2023. The timing of the survey is particularly relevant, as the use of plant protection products on public infrastructure, including railways, was prohibited by national legislation in 2021. Prior to this ban, railway tracks in Slovenia were routinely treated with glyphosate-based herbicides once or twice annually over several decades. Our study therefore captures vegetation patterns during the early phase of spontaneous revegetation following the cessation of long-term chemical control, providing insight into initial colonisation dynamics under a newly altered management regime.

This study was carried out at 92 locations (sampling points) distributed along 15 railway segments across the entire country: Celje – Velenje, n.b. (national border) – Dobova – Ljubljana, n.b. – Metlika – Ljubljana, n.b. – Rogatec – Grobelno, Jesenice – Sežana, Ljubljana Šiška – Kamnik Graben, Ljubljana – Jesenice – n.b., Ljubljana – Sežana – n.b., Ljutomer – Gornja Radgona, Maribor – Prevalje – n.b., Ormož – Hodoš – n.b., Ormož – Središče – n.b., Pivka – Ilirska Bistrica – n.b., Prvačina – Ajdovščina and Sevnica – Trebnje (Fig. 1). Chosen railway segments consisted of 68 single-track railway lines and 24 double-track railway lines.

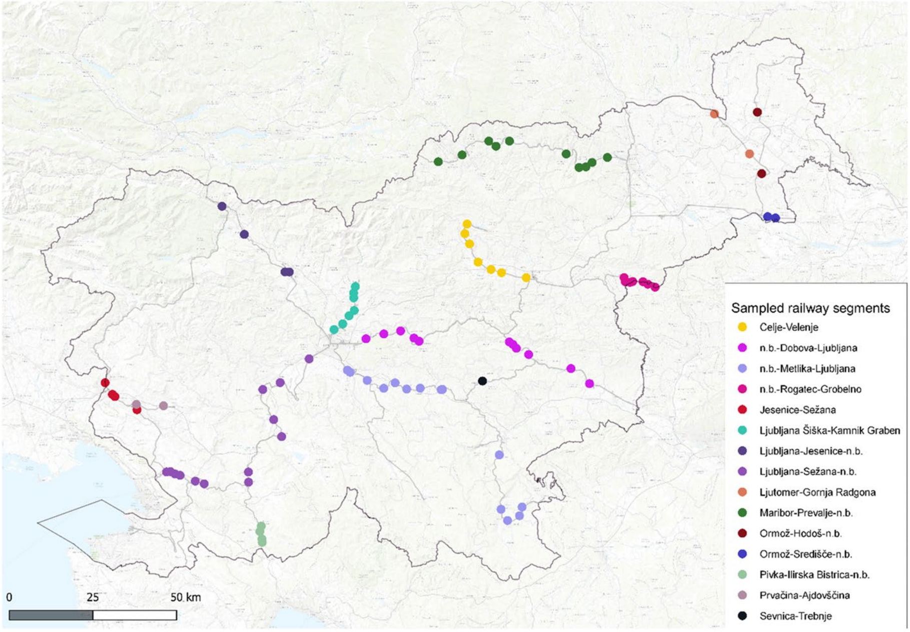

Fig. 1 Locations (sampling points) of the Slovenian railway flora study, denoted with different colours for each railway segment. Each point refers to one transect inventory. Map background: ESRI World Topo (Map Background) (2025), shapefile: Slovenski INSPIRE metapodatkovni portal: INSPIRE železnice WMS (2025)

Sampling points were identified in collaboration with railway personnel, who screened segments using internal inspection videos and field reconnaissance to locate areas with visible and sufficiently developed vegetation. Although the sites were not selected through a fully randomised national design, they were geographically distributed across major railway corridors and encompass a broad range of climatic and topographic contexts. The dataset therefore reflects a wide spectrum of railway microhabitats in Slovenia, while acknowledging that it does not constitute a strictly probabilistic representation of the entire national railway network.

Sampling methodology

We carried out floristic sampling using combined qualitative-quantitative transect method, which was developed specifically for the needs of this study. Hundred meters long transects, set between the two consecutive railway marking stones, were sampled. Along each transect, floristic sampling covered the following zones of the railway (Fig. 2), adapted according to Sadeghi et al. (2016), Alabassi and Hussein (2021) and Guo et al. (2022).

Sleeper Zone (SZ) The top surface of the ballast bed, where the sleepers and tracks are embedded, covering the full width of the sleepers.

Fig. 2 Railway zones as defined in the floristic sampling: SZ (Sleeper Zone), BS (Ballast Shoulder), BT (Ballast Toe) and IA (Intertrack Area), adapted according to Sadeghi et al. (2016), Alabassi and Hussein (2021) and Guo et al. (2022). Two railway marking stones (left bottom and middle of picture) represent the defining starting and finishing points for the 100-m transect length

Ballast Shoulder (BS) The transitional zone at the edge of the ballast bed, where the ballast layer thins out, partially exposes the sub-ballast and merges with adjacent vegetation. This 1–2-m-wide zone represents an intermediate zone between railway infrastructure and the Ballast Toe.

Ballast Toe (BT) The outermost transition zone, located at the edge of the ballast bed, where the ballast meets adjacent vegetation. This ecotone buffer area, 1–2 m wide, serves as a boundary between the railway infrastructure and the surrounding landscape, influencing vegetation dynamics and habitat connectivity.

At each sampling location, we established a 100-m transect between two consecutive railway marking stones, which mark distance from the beginning of the track section in 100-m increments and are positioned in the BT. Left and right sides of the track were defined according to the direction of increasing marker labels. Within each transect, vegetation was surveyed separately in the Ballast Shoulder (BS), Ballast Toe (BT), and Sleeper Zone (SZ). Ballast Shoulder and Ballast Toe were assessed independently on both sides of the track (two observations per zone per transect), whereas the Sleeper Zone was surveyed once per transect in single-track sections, as it represents the central track area. All vascular plant species were recorded within each zone. Species richness was calculated as the total number of species recorded per sampling zone.

For double-track railways, the area between the two tracks was defined as the Intertrack Area (IA) and treated as an additional zone (Fig. 2). In these sections, each track had its own Sleeper Zone, resulting in two SZ observations per transect (left and right track), in addition to the IA. Ballast Shoulder and Ballast Toe were surveyed on the outer sides of each track following the same protocol as described above.

Therefore, each single-track railway line sampling point had 5 subsets of data (left BT and BS, SZ, right BT and BS), whereas sampling positions and transects at the double-track railway lines had 7 subsets of data (left BT, BS and SZ, IA, right SZ, BS and BT). Species' richness was assessed as the total number of present species per sampling zone.

Vegetation cover of evaluated zones was determined in percentages and classified into four categories: minimal (0–10%), sparse (10–30%), moderate (30–60%), and dense (60–100%).

Statistical analysis

Species trait data and descriptive statistics

Descriptive statistical analysis for all recorded species considered data on plant family, life form, lifespan, nativeness status, reproduction mechanism, dispersal strategy, CSR (competitor-stress tolerator-ruderal) life strategy, chorology, syntaxonomic optimum, ecological indicator values, disturbance indices, and ecological specialization. Nomenclature, taxonomy and nativeness status (native, crop – non-native to any of the Slovenian phytogeographic regions, casual, naturalized, invasive), and plant life forms follow Martinčič et al. (2007), Pladias database (Chytrý et al. 2021) and Plants of the World Online (POWO 2025). Data on CSR life strategies (Grime 1977) and ability on vegetative reproduction were gathered from Pladias database (Chytrý et al. 2021). If species had a single life strategy ascribed, we defined it as a specialist, whereas species with multiple strategies were defined as generalists (following Ricotta et al. 2023). Dispersal strategies were determined according to Sádlo et al. (2018). Chorological traits (floristic elements) were defined by Horváth et al. (1995) and Sonkoly et al. (2022). Values of ecological specialization were determined according to Zelený and Chytrý (2019), while disturbance frequency and severity indices were calculated according to Midolo et al. (2023). Syntaxonomic optimum follows Mucina et al. (2016). Ecological indicator values (EIV) for light, temperature, moisture, nutrients, continentality and soil reaction were calculated according to Tichý et al. (2023).

Analysis of species composition

All statistical analyses were conducted in R version 4.5.1 (R Core Team 2025) and maps were produced using QGIS version 3.40 (QGIS Development Team 2025). Vegetation patterns were analyzed using mixed-effects models with locations nested within track sections as random effects [(1|track_section/location)], separating variance attributable to different spatial scales while controlling for non-independence among observations from the same location or section. Count-based responses (species richness, number of species per trait category) were modelled with Poisson generalized linear mixed models (GLMMs); a negative binomial distribution was used when overdispersion was detected. Where residual diagnostics indicated significant zero-inflation, a zero-inflated Poisson (ZIP) model was fitted instead (glmmTMB; Brooks et al. 2017). Proportional data (e.g., proportion of competitor species per zone) were modelled with binomial GLMMs using a logit link, with the number of species possessing a given trait modelled relative to total species count per zone. Ecological indicator values were summarized per zone as unweighted community means (arithmetic mean across all recorded species; Ostrowski et al. 2025) and analysed with Gaussian linear mixed models. Vegetation cover was classified into four ordinal categories (0–10%, 11–30%, 31–60%, 61–100%) and analysed using cumulative link mixed models (CLMM; Christensen 2019).

Model fit was assessed with marginal and conditional R^2 (Nakagawa and Schielzeth 2013), representing variance explained by fixed effects alone and by fixed plus random effects, respectively. Model assumptions were checked with DHARMa residual diagnostics (Hartig 2022); post-hoc pairwise comparisons used Tukey-adjusted tests via *emmeans* (Lenth and Piaskowski 2024). Models for rare life-form categories (phanerophytes, geophytes, chamaephytes) yielded singular fits due to sparse counts (e.g., chamaephytes < 0.15 species/zone). To account for multiple testing, Benjamini–Hochberg false discovery rate correction was applied (Benjamini and Hochberg 1995); all reported significant results remained significant after correction (all $q < 0.05$). All mixed-effects models were fitted using *lme4* (Bates et al. 2015) unless otherwise noted.

Differences in species composition among railway zones and segments were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on Jaccard dissimilarity matrices computed from presence–absence data. For zone-level analyses, permutations were stratified by location to account for non-independence of zones sampled at the same site. Sensitivity analyses excluding intertrack-area zones (present only at double-track locations, 21 of 92) and restricting to double-track locations confirmed that zone effects were robust to this structural imbalance. Compositional heterogeneity was assessed using PERMDISP (Anderson 2006); one segment represented by a single location was excluded, as the test requires within-group replication. Multivariate analyses used the *vegan* package (Oksanen et al. 2025).

Results

Taxonomy

Across 92 survey locations we recorded 6331 individual plant observations, documenting 312 plant taxa from 215 genera and 67 families. Twenty of the most abundant and frequent species, as well as the most species-rich genera and families are shown in Table 1. For species, abundance refers to the total number of occurrences across the individual railway zones at all sampling points, whereas frequency refers to the number of sampling locations (out of 92) where the given species was recorded. For genera and families, values represent the number of species belonging to each taxon recorded across all sampling locations.

Four percent of the taxa were found at over 50% of the sampling locations, whereas 13% of the taxa were found at over 25% of the sampling locations. Fifty-eight percent of the species were considered rare, found at five or fewer of the studied locations.

Non-native species

We recorded 40 non-native and horticultural species, comprising 13% of all taxa. These were predominantly of New World origin, with 58% native to North America and 12% to Central and/or South America, whereas 12% are native to Asia, and 18% to Middle Eastern and Mediterranean regions (the latter dominantly crops). The most widespread non-native species were *Erigeron annuus* (found at 77 locations, 191 observations), *Erigeron canadensis* (found at 60 locations, 120 observations), and *Robinia pseudoacacia* (found at 39 locations, 91 observations). Details on the non-native species origin and status can be found in the Supplementary material 1 (sheet Traits, columns Nativeness status and Native to, whereas details on their occurrences are found in the columns Abundance and Frequency).

Table 1 Twenty of the most common species, genera and families found at Slovenian railways

Species	Abundance (total number of occurences across all railway zones at all sampling points)	Frequency (number of sampling points where the species was present)	Genus	Number of species from the given genus in the entire dataset	Family	Number of plant species from the given family in the entire dataset
Equisetum arvense L.	285	70	*Acer*	7	*Asteraceae*	50
Convolvulus arvensis L.	210	76	*Geranium*	5	*Poaceae*	33
Setaria pumila (Poir.) Roem. & Schult.	204	69	*Campanula*	4	*Fabaceae*	20
Erigeron annuus (L.) Desf.	191	77	*Euphorbia*	4	*Lamiaceae*	18
Lactuca serriola L.	186	69	*Lolium*	4	*Rosaceae*	14
Vicia cracca L.	173	71	*Salix*	4	*Apiaceae*	13
Galium mollugo L.	159	67	*Avena*	3	*Caryophyllaceae*	13
Setaria viridis (L.) P.Beauv.	146	52	*Cirsium*	3	*Brassicaceae*	10
Geranium robertianum L.	132	65	*Crepis*	3	*Scrophulariaceae*	10
Euonymus europaea L.	131	57	*Epilobium*	3	*Aceraceae*	7
Taraxacum sect. *Taraxacum* F.H.Wigg.	128	68	*Galium*	3	*Polygonaceae*	7
Clematis vitalba L.	122	52	*Medicago*	3	*Onagraceae*	6
Erigeron canadensis L.	120	60	*Polygonum*	3	*Salicaceae*	6
Rubus caesius L.	115	54	*Setaria*	3	*Geraniaceae*	5
Robinia pseudoacacia L.	91	39	*Silene*	3	*Boraginaceae*	4
Artemisia vulgaris L.	90	46	*Solidago*	3	*Campanulaceae*	4
Picris hieracioides L.	89	43	*Trifolium*	3	*Dipsacaceae*	4
Oxalis stricta L.	80	43	*Verbascum*	3	*Euphorbiaceae*	4
Ambrosia artemisiifolia L.	79	37	*Vicia*	3	*Primulaceae*	4
Solidago canadensis L.	78	33	*Viola*	3	*Rubiaceae*	4

Non-native plant species were nearly ubiquitous, occurring at 91 of 92 locations (99%) and averaging 4.9 ± 2.3 species per location (median = 5, range = 0–12). At the zone level ($n=482$), non-native richness differed significantly among railway zones (Poisson GLMM: $\chi^2=26.4$, $p<0.001$; R^2 marginal = 0.052, R^2 conditional = 0.329). Sleeper Zones (SZ) supported the highest richness of non-native species (mean = 2.16 species, 95% CI = 1.75–2.68), followed by BT zones (1.96, CI = 1.61–2.39) and BS (1.55, CI = 1.27–1.91), whereas IA showed consistently low richness of non-native species (0.91, CI = 0.56–1.49). The model accounted for substantial geographic variation among track segments (28% of variance), with railway zone type explaining an additional 5% of variance. Distance-based redundancy analysis (dbRDA) found no significant spatial gradient in non-native species composition along track sections when controlling for between-section variation ($F=0.80$, $p=0.70$, explaining < 1% of variance).

Invasive alien species – subset of 16 non-native species dominated the non-native flora, occurring at 99% of locations and accounting for approximately 81% of non-native richness at the typical site (mean = 4.0 ± 1.9 species per location). Invasive species showed substantially higher dispersal success than other non-native categories, averaging 24.6 occurrences per species. Invasive richness varied significantly among zones (Poisson GLMM: $\chi^2=17.4$, $p<0.001$; R^2 marginal = 0.040, R^2 conditional = 0.294), peaking in BT (1.78 species/zone, CI = 1.46–2.16) and SZ (1.64, CI = 1.31–2.04) and declining sharply in IA (0.78, CI = 0.46–1.32), where invasives occurred in only 52% of locations. Similarly to non-native species dbRDA, the invasive species subset showed no spatial pattern ($F=0.76$, $p=0.68$).

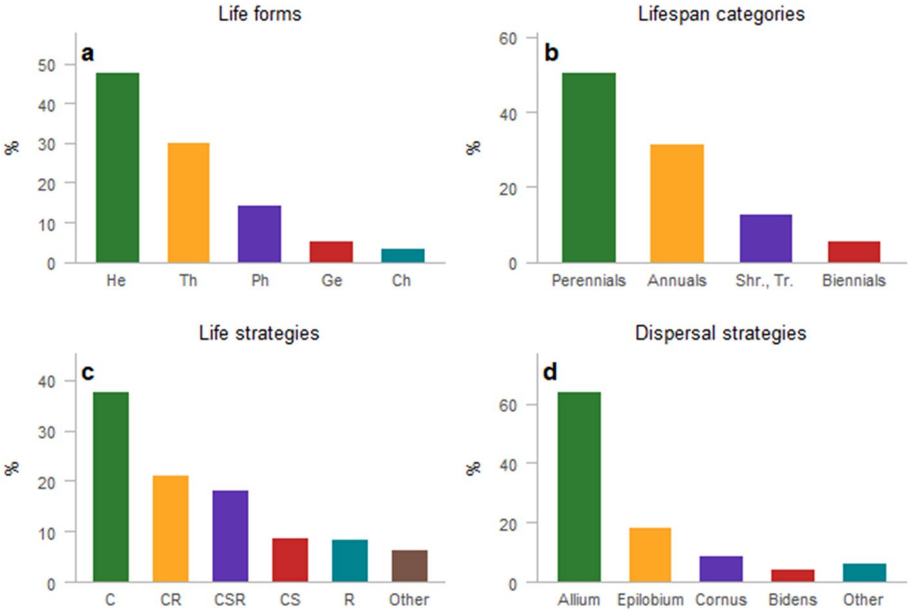

Fig. 3 Graphical representation of life forms (**a**), lifespan categories (**b**), life strategies (**c**) and dispersal strategies (**d**) of the Slovenian railway flora. Y-axis represents percentage shares, whereas individual categories are shown on x-axis. Abbreviations: He – hemicryptophytes, Th – therophytes, Ph – phanerophytes, Ge – geophytes, Ch – chamaephytes (**a**); Shr., Tr. – shrubs and trees (**b**); C – competitors, CR – competitive ruderals, CSR – competitor-stress tolerant-ruderals, CS – competitive stress tolerators, R – ruderals (**c**)

Plant life forms and lifespan categories

In general, the most dominant plant forms (Fig. 3a) were hemicryptophytes (47%), followed by therophytes (27%), phanerophytes (14%), geophytes (5%) and chamaephytes (3%). The most dominant plant lifespan categories (Fig. 3b) were herbaceous perennials (51%), followed by annuals (26%), shrubs and trees (13%), and herbaceous biennials (5%).

Zone-level analysis revealed significant variation for all five life forms (Poisson GLMMs, all $p \leq 0.008$). Outer ballast zones were dominated by hemicryptophytes (BT: 6.39 species/zone; BS: 4.10), which were also accompanied by phanerophytes (BT: 1.77; BS: 1.75) and geophytes (BS: 1.48; BT: 1.17). The SZ was characterized by therophyte dominance (SZ: 6.44), the highest value of any life form in any zone. The IA supported the lowest richness across all life forms, with therophytes (3.77) being the most represented group. Chamaephytes were rare throughout (all zones < 0.15 species/zone). The strongest zone effects were found for hemicryptophytes ($\chi^2 = 213.3$, df = 3, $p < 0.001$; $R^2m = 0.215$, $R^2c = 0.721$) and therophytes (zero-inflated Poisson GLMM: $\chi^2 = 69.5$, $p < 0.001$; $R^2m = 0.074$, $R^2c = 0.522$), followed by phanerophytes ($\chi^2 = 37.3$, $p < 0.001$; $R^2m = 0.118$), geophytes ($\chi^2 = 15.5$, $p = 0.001$; $R^2m = 0.032$), and chamaephytes ($\chi^2 = 11.9$, $p = 0.008$; $R^2m = 0.029$).

Lifespan categories showed significant zone-level variation (Poisson GLMMs, all $p < 0.001$). Outer ballast zones were dominated by herbaceous perennials (BT: 7.35, CI: 6.05–8.92; BS: 5.48, CI: 4.50–6.67), accompanied by shrubs and trees (BS: 1.74; BT: 1.67). In the SZ, annuals were the dominant category (SZ: 6.01, CI: 5.06–7.14), significantly exceeding all other zones (BS: 3.94; BT: 3.80; IA: 3.44). The IA supported the lowest richness across all lifespan categories, with perennials reduced to 1.98 species/zone (CI: 1.34–2.94). Herbaceous biennials ($\chi^2 = 46.2$, df = 3, $p < 0.001$; $R^2m = 0.084$) and shrubs/trees ($\chi^2 = 34.9$, $p < 0.001$; $R^2m = 0.111$) also declined sharply in inner zones, following the same outer-to-inner gradient as perennials ($\chi^2 = 137.7$, $p < 0.001$; $R^2m = 0.177$) and annuals ($\chi^2 = 85.9$, $p < 0.001$; $R^2m = 0.079$).

Life strategies, ecological specialization and disturbance indices

The most dominant life strategies (Fig. 3; c) were competitors (C) (37%), followed by competitive ruderals – CR (21%), competitor-stress tolerant-ruderals – CSR (18%) and competitive-stress tolerators – CS (9%). They are followed by ruderals (R) (8%), whereas other strategies (SR, S, C/CR, SR/CSR, CS/CSR, CR/CSR and R/CR) had individual presences of 2% or lower, resulting in a total of 6%. Fifty-three percent of all taxa are generalists, 47% are specialists. Specialization index of the entire dataset (ESI_w) reflects these results, with the overall ecological specialization average value of 4.5 (SD ± 0.7), which falls in the middle range of the value (Zelený and Chytrý, 2019). Abundance and ecological specialization index were statistically significantly negatively correlated (Spearman's rho = −0.21, $p < 0.01$). Average value of the disturbance frequency was 1.28 (SD ± 0.70), whereas the average for disturbance severity was 0.47 (SD ± 0.20).

Life strategies showed clear zone-level differentiation. In BT, competitors (C) were the dominant strategy (44.8%, 95% CI: 41.1–48.6%), followed by competitor-ruderals (CR, 22.4%), and ruderals (R, 8.8%). BS showed a similar pattern with strategy C (38.1%, CI: 34.5–41.9%), followed by CR (27.0%) and R (12.0%). In contrast, the inner zones were characterized by competitor-ruderal dominance: IA was dominated by CR (37.0%, CI:

27.8–47.3%), followed by C (20.1%) and R (18.4%). SZ showed an intermediate pattern with CR most common (32.0%, CI: 28.4–35.8%), followed by C (26.8%) and R (17.3%). The proportion of competitors differed significantly among zones (binomial GLMM: $\chi^2 = 117.5$, df = 3, $p < 0.001$; $R^2m = 0.218$), as did competitor-ruderals ($\chi^2 = 44.2$, $p < 0.001$; $R^2m = 0.119$) and ruderals ($\chi^2 = 53.9$, $p < 0.001$; $R^2m = 0.138$).

Dispersal strategy and reproductive type

Fifty-eight percent of taxa have *Allium* dispersal strategy (generalistic autochory), followed by *Epilobium* (predominant anemochory) found in 16% (57% of those are from family Asteraceae). The third most abundant dispersal strategy was *Cornus* (predominant endozoochory), found in 8% of all taxa, typically in shrubs and trees with fleshy fruits (e.g. *Euonymus europaea*, *Rubus caesius* and *Cornus sanguinea* L.*)*. Four percent of all plant taxa have *Bidens* type of dispersal strategy (epizoochory). Most abundant taxa with this dispersal strategy were bristlegrasses (*Setaria* sp. pl.) and wild carrot (*Daucus carota* L.). We recorded presence of 4 other dispersal strategies – *Sparganium*, *Phragmites*, *Lycopodium* and *Zea* – sharing 5% of the contribution to the main dataset (Fig. 3d). Thirty-nine percent of all present taxa can reproduce asexually, 9 of those primarily. The most common species with primary vegetative reproduction is field bindweed (*Convolvulus arvensis*).

Wind-dispersed species (*Epilobium*- and *Phragmites*- types) showed small but significant zone-level differences in relative abundance (binomial GLMM: $\chi^2 = 17.1$, df = 3, $p < 0.001$). Their proportion was highest in IA (28%, 95% CI: 19–38%) and SZ (25%, CI: 22–29%), and lower in BT (24%, CI: 21–26%) and BS (20%, CI: 18–23%).

Floristic elements and syntaxonomic optimum

We confirmed presence of 13 floristic elements, with dominance of Eurasian (34%), followed by adventive (16%) and cosmopolitan (15%). The species found are diagnostic of 42 higher syntaxa. Generally, most of them were assigned to various vegetation classes of semi-natural or anthropogenic ecosystems, predominantly to mesic grasslands of the class *Molinio-Arrhenatheretea* Tx. 1937 (21%); semi-natural perennial vegetation on disturbed forest-edges, riparian fringes and forest clearings *Epilobietea angustifolii* Tx. et Preising ex von Rochow 1951 (15%); perennial (sub)-xerophilous ruderal vegetation of the class *Artemisietea vulgaris* Lohmeyer et al. in Tx. ex von Rochow 1951 (12%); riparian vegetation of the class *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968 (11%) and annual weed segetal vegetation of arable ecosystems *Papaveretea rhoeadis* S. Brullo et al. 2001 (11%).

Vegetation composition differed significantly but explained a modest proportion of variance compared to geographic identity, with grassland, ruderal, and riparian syntaxonomic classes all showing strong zone-level differentiation (Poisson GLMMs, all $p \leq 0.010$). Mesic grassland species (*Molinio-Arrhenatheretea*) were most frequent in BT (3.04 species per zone, 95% CI: 2.35–3.95), followed by BS (1.95, CI: 1.49–2.54) and SZ (1.53, CI: 1.14–2.04), and were scarce in IA (0.37, CI: 0.16–0.86; $R^2m = 0.197$). Ruderal species (*Artemisietea*) showed a similar pattern, peaking in BT (3.15, CI: 2.58–3.86), with comparable richness in BS (2.03, CI: 1.65–2.50) and SZ (1.91, CI: 1.52–2.40), and lowest values in IA (1.02, CI: 0.65–1.61; $R^2m = 0.117$). Riparian species (*Alno glutinosae–Populetea albae*) were most frequent in ballast-associated zones, with similar richness in BS (1.70, CI: 1.37–2.10) and BT (1.60, CI: 1.30–1.99), declining in SZ (0.95, CI: 0.73–1.23) and reaching lowest values in IA (0.43, CI: 0.21–0.88; $R^2m = 0.121$). In contrast, annual ruderal species (*Sisymbrietea* Gutte et Hilbig 1975) and weed species (*Papaveretea rhoeadis*) showed the opposite pattern, with highest richness in SZ. *Sisymbrietea* species were significantly more frequent in SZ (2.45, CI: 2.05–2.92) than BT (1.90, CI: 1.61–2.24; Tukey $p = 0.012$; $\chi^2 = 11.44$, $df = 3$, $p = 0.010$; $R^2m = 0.020$). Similarly, *Papaveretea* species peaked in SZ (1.41, CI: 1.14–1.75), significantly exceeding BT (1.00, CI: 0.82–1.22; Tukey $p = 0.009$; $\chi^2 = 14.20$, $df = 3$, $p = 0.003$; $R^2m = 0.028$).

Ecological indicator values

Light

Average indicator value for light in the entire dataset was 7.09 (SD ± 1.01). Sixty-eight percent of the species had indicator values of 7–9 and are described as heliophytes. Light requirements differed significantly among railway zones ($\chi^2 = 43.57$, $df = 3$, $p < 0.001$), with communities in inner zones (IA, SZ) showing higher light preferences and supporting the most heliophytic communities (community means 7.36 and 7.32, respectively), followed by BT (7.21), whereas BS had the lowest value (7.13).

Temperature

Average indicator value for temperature in the entire dataset was 5.83 (SD ± 0.95). Seventy-eight percent of the species had indicator values of 5 and 6, with a preference to moderate heat. Temperature preferences varied markedly among zones ($\chi^2 = 115.30$, $df = 3$, $p < 0.001$), showing the strongest differentiation of all ecological indicator values. Intertrack areas (IA) supported the most thermophilic communities (6.63), differing significantly from all other zones. The ballast toe (BT) harboured the coolest-adapted assemblages (5.70), followed by BS (5.82) and SZ (6.17).

Moisture

Average indicator value for moisture was 5.14 (SD ± 1.50). Half of the species (50%) are xerophytes adapted to drier conditions, with indicator values of 2–4. Thirty-four percent are adapted to averagely moist conditions, with indicator values of 5–6, whereas 16% are moderately hydrophilic to hydrophilic, with indicator values of 7–10. Moisture preferences differed significantly among zones ($\chi^2 = 26.98$, $df = 3$, $p < 0.001$). Outer ballast zones (BT: 4.94; BS: 4.87) had the highest community means, indicating preference for mesic conditions, whereas inner railway zones (SZ: 4.70; IA: 4.63) supported more xerophytic assemblages adapted to drier conditions.

Reaction

Average indicator value for pH reaction was 6.59 (SD ± 0.79). It was the most consistent value, with 80% of the taxa indicating neutral pH reaction, with values of 6 or 7. pH preferences showed significant zone-level variation ($\chi^2 = 41.26$, $df = 3$, $p < 0.001$), with outer ballast zones supporting communities adapted to more neutral to slightly basic conditions. Ballast shoulder (6.57) and BT (6.54) had the highest community means, followed by SZ (6.44), whereas IA (6.35) supported the most acidophilic assemblages.

Nutrients

Average indicator value of the entire dataset for nutrients was 5.69 (SD ± 1.58). Fifty-nine percent of the taxa are indicators of moderately nutrient-rich sites, with indicator values of 4–6, whereas 25% are indicators of nutrient-rich sites with indicator values of 7–9. Nutrient preferences showed weaker zone differentiation compared to other EIV, but still significant ($\chi^2 = 12.10$, df = 3, p = 0.007), indicating more homogeneous nutrient availability across most railway zones. Ballast toe (BT) (5.92), BS (5.89), and SZ (5.86) supported similar communities of moderately nitrophilic species, whereas IA (5.55) harboured slightly fewer nitrogen-demanding taxa.

Diversity and vegetation cover analysis

Vegetation cover varied significantly among the railway zones (Ordinal CLMM: $\chi^2 = 269.85$, df = 3, p < 0.001; Fig. 4). The BT showed the highest cover, with 72.7% of zones classified as densely covered (60–100%). In contrast, the IA and SZ were predominantly sparsely vegetated, with 66.7% and 42.5% of zones in the minimal cover category (0–10%), respectively. The BS showed intermediate cover patterns, with most zones falling into the moderate (34.7%) or dense (21.0%) categories.

Species richness also varied significantly among zones (Fig. 5a; negative binomial GLMM: $\chi^2 = 49.94$, df = 3, $p < 0.001$). BT showed the highest species' richness (14.8 ± 1.00), followed by BS (12.5 ± 0.85) and Sleeper Zone (12.2 ± 0.91), while the Intertrack Area had significantly lower richness (6.3 ± 0.91). Tukey's HSD post-hoc test confirmed that IA differed from all other zones and BT from BS and SZ (all $p < 0.01$), whereas BS and SZ did not differ significantly ($p = 0.97$).

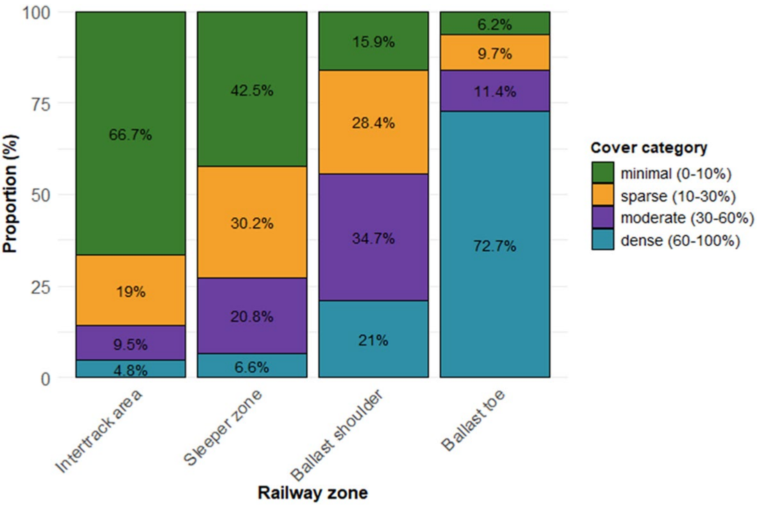

Fig. 4 Results of the comparative analysis of vegetation cover between the four railway zones: Sleeper Zone, Ballast Shoulder and Ballast Toe

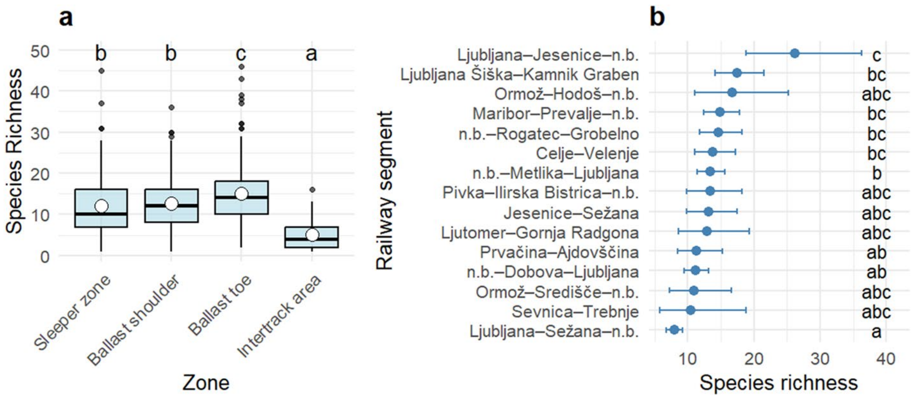

Fig. 5 Results of the species richness analysis by railway zones (**a**) and 15 railway segments (**b**). Small letters a–c indicate statistically significant differences ($p < 0.001$) in species richness between railway zones (**a**) and railway segments (**b**), confirmed by Tukey HSD post-hoc test

Significant differences in species richness were also found between the railway segments (Fig. 5b; negative binomial GLMM: $\chi^2 = 74.00$, df = 14, $p < 0.001$). Tukey's HSD post-hoc test identified the segment Ljubljana–Jesenice as the segment that is significantly the richest in species (26.1 ± 4.37), whereas the segment Ljubljana–Sežana was identified as the least species-rich (7.9 ± 0.63). Several segments, including Prvačina–Ajdovščina, n.b.–Dobova–Ljubljana, Ormož–Središče, and Sevnica–Trebnje, showed intermediate species richness patterns.

Multivariate analysis of species composition

At the location level, species composition differed significantly among railway segments (PERMANOVA: F = 2.29, df = 14, p = 0.001, $R^2 = 0.294$). Segments also differed in compositional heterogeneity (PERMDISP: F = 14.65, df = 14, $p < 0.001$), with dispersion values ranging from 0.24 to 0.55.

At the zone level, species composition differed significantly among zone types (PERMANOVA: F = 4.57, df = 3, p = 0.001, $R^2 = 0.028$, permutations stratified by location). Zone types did not differ in compositional heterogeneity (PERMDISP: F = 1.75, df = 3, p = 0.141), with all zones showing similar dispersion (0.62–0.64). Variance partitioning indicated that location identity explained 38.3% of compositional variance (F = 2.76, df = 91), while zone type explained 2.4% (F = 5.26, df = 3). Zone effects remained significant when excluding intertrack area zones (F = 4.93, p = 0.001, n = 461) and when restricting analysis to double-track locations only (F = 2.92, p = 0.001, $n = 161$).

Discussion

In general, results of our taxonomic analysis of Slovenian railway flora (Table 1) align with those published in other similar studies (Filibeck et al. 2012; Galera et al. 2014; Alessandrini 2016; Jasprica et al. 2017; Raycheva et al. 2021). In most of these, Asteraceae are noted as the most abundant family (Topalić-Trivunović and Pavlović-Muratspahić 2008; Tret'yakova 2010; Filibeck et al. 2012; Altay et al. 2015; Denisow et al. 2017; Májeková et al. 2021; Raycheva et al. 2021) and are usually followed by either Poaceae (Topalić-Trivunović and Pavlović-Muratspahić 2008; Tret'yakova 2010; Denisow et al. 2017; Raycheva et al. 2021; Májeková et al. 2021) – as seen in our results; or by Fabaceae (Filibeck et al. 2012; Altay et al. 2015). However, dominance of these plant families is not surprising, since both families are considered as one of the globally species-richest, and have a cosmopolitan distribution (Hodkinson 2018; Fu et al. 2023).

Studies of railway flora are generally carried out in urban areas and at railway stations. Consequently, railways are usually represented as hotspots of synanthropic and adventive vegetation, which was meticulously studied by Brandes (1983) in the previous century and repeatedly confirmed in more recent works (e.g. Fornal-Pieniak and Wysocki 2011; Filibeck et al. 2012; Jasprica et al. 2017; Dziuba et al. 2022). Most of the most abundant species we found were indeed representatives of typical urban ruderal and weed vegetation, and we confirmed the presence of species defined as diagnostic for railways by Brandes (1983): *Amaranthus albus* L., *A. retroflexus* L., *Arenaria serpyllifolia* L., *Artemisia vulgaris*, *Chaenorhinum minus* (L.) Lange, *Diplotaxis tenuifolia* (L.) DC., *Erigeron canadensis, Linaria vulgaris* Mill., *Polygonum aviculare* aggr. and *Festuca myuros* L. However, since our study did not focus on urban areas and railway stations, we also registered presence of species diagnostic of various other vegetation types which surround the railway segments (agricultural—*Papaveretea rhoeadis*, forest—*Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968, shrub and fringe vegetation—*Epilobietea angustifolii*, *Trifolio-Geranietea sanguinei* T. Müller 1962, riparian—*Alno glutinosae-Populetea albae*, grassland—*Molinio-Arrhenatheretea*, *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947). Even though railways can serve as a refugia for natural vegetation (Tikka et al. 2000; Oldén et al. 2021), we hypothesize that this isn't the case in Slovenia, but rather a consequence of sampling in different areas, which were surrounded by different natural vegetation types. This is also reflected in the heterogeneity of floristic elements and species composition, among railway segments (PERMANOVA), where location identity explained 38% of compositional variance compared to only 2.4% explained by zone type. Since Slovenia consists of six phytogeographical areas: pre-Alpine, Alpine, pre-Dinaric, Dinaric, sub-Pannonian and sub-Mediterranean area (Wraber 1969) and represents a biodiversity junction in Europe, the presence of 13 floristic elements, with a prevalence of Eurasian floristic elements is expected. Our results coincide with the previous findings by Wrzesień et al. (2016b) and Heneidy et al. (2021), which confirm species richness and heterogeneity of railway flora. However, we have also found concerningly high occurrence of adventive floristic elements (non-native and invasive species), what additionally confirms a well-documented role of railways in biological invasions, which was previously reported in other studies (Jehlík and Dostálek 2008; Raycheva et al. 2021; Kutlvašr et al. 2024). This also raises conservational concerns: non-native species were nearly ubiquitous across both sampled locations (91 of 92) and all railway zones, with high mean richness per location and no significant spatial gradient in their composition, suggesting multiple independent introduction points rather than diffusion from a single source. Notably, non-native species richness was highest in the Sleeper Zone rather than in the more species-rich Ballast Toe, indicating that disturbed, open inner-track substrates may facilitate alien establishment. Invasive alien species, although a subset of 16 taxa, accounted for approximately 81% of non-native richness at typical sites and were present at 99% of sampled locations. These findings underscore the need for continued monitoring of invasive species on railways, particularly in the context of the 2021 herbicide ban, as the cessation of chemical control may accelerate their spread in zones that were previously managed most intensively. Additionally, we recorded the presence of non-native horticultural species – such as *Acer rubrum* L. and *A. saccharum*

Marshall, which are not included in the Slovenian plant determination key (Martinčič et al. 2007) but are available in local garden centres. These findings represent potential beginnings of naturalization of these non-native horticultural species, whose invasiveness potential in Slovenia is highly overlooked.

According to our results, annual therophytes and perennial hemicryptophytes represent two life forms that are best adapted to railways, as previously reported in various literary sources (Fornal-Pieniak and Wysocki 2011; Filibeck et al. 2012; Altay et al. 2015; Galera et al. 2014; Alessandrini 2016; Wrzesień et al. 2016b; Denisow et al. 2017; Jasprica et al. 2017; Raycheva et al. 2021). Our analysis additionally shows that hemicryptophytes thrive in outer zones of the railways (BS and BT), whereas annual ruderals are more adapted to the inner zones (SZ and IA). Various conditions and differing management practices on railways stimulate development of both groups. Therophytes are usually found in open pioneer habitats, whose harsh conditions they usually overcome by their short life cycles; or at sites that are recovering from anthropogenic disturbance, which do not favour other plant functional types (Galera et al. 2014). On the other hand, regular management practices, such as cleaning and mowing of the railways, stimulate development and persistence of adult hemicryptophytes (Topalić-Trivunović and Pavlović-Muratspahić 2008). Our sampling area included railway segments with differing disturbances, since they are managed differently (by mowing or chemical treatments) and are exposed to differing traffic regimes. These disturbance variations allow for development of specific microecological conditions and (co-)dominance of these two life forms. Additionally, we confirmed substantial presence of phanerophytes (Fig. 3a). However, woody functional types showed weak functional specialization regarding most of the railway zones apart from the outer edges, since we usually registered sporadic presence of juveniles of various native tree and shrub species, found in the proximity of forest and shrub stands, the latter being proven as directly correlated in previous studies of railway vegetation (Hutniczak et al. 2022). Similarly, we confirmed that competitive life strategy – along with ruderal – is the best suited for railways. Rakotoson et al. (2025) reported a general differentiation between railway tracks dominated by ruderal strategies and embankments dominated by competitive perennials. In our study, we detected a similar functional gradient, but at a finer spatial resolution, with ruderal and competitor-ruderal strategies increasing toward inner zones and competitors dominating the outer zones. Species with a ruderal life strategy and weeds are connected to the anthropogenic and urban influence, whereas high presence of C-strategists can correspond with the proximity of grasslands (Šerá, 2008) and lower disturbances in comparison to open areas (Toffolo et al. 2021). This is in line with prevalence of grassland species (*Molinio-Arrhenatheretea*) and hemicryptophytes in BT. In general, railway verges represent open, well-lit habitats that could be well suitable for the species that are well adapted to regular disturbances – particularly hemicryptophyte grassland species, adapted to mowing (Tikka et al. 2000). Our results have directly confirmed this, since we found prevalence of mesic grassland species (*Molinio-Arrhenatheretea*) in marginal railway zones (BT and BS), whereas annual ruderal and segetal species – diagnostic of classes *Papaveretea* and *Sisymbrietea* – were indicators of the inner railway zones (SZ and IA). Results of our EIV analysis additionally confirm this, since they show clear differentiation of thermal and light gradients, with intensity of these conditions increasing from the outer railway zones towards the inner, what supports dominance of thermophilous (Májeková et al. 2025) and heliophytic species (Toffolo et al. 2021) in SZ and IA. Temperature showed the strongest zone-level differentiation of all five indicator values, consistent with the well-documented role of ballast and rail heating (Brandes 1983; Galera et al. 2014; Alessandrini 2016; Dziuba et al. 2022). Contrary to light and temperature, moisture gradient decreased from outer towards the inner zones, supporting xerophilous species in SZ and IA. Some of the most common plant species we found, which epitomize these conditions are *Lactuca serriola*, *Ambrosia artemisiifolia*, *Erigeron annuus* and *Chaenorhinum minus*. Consequently, riparian species (*Alno glutinosae-Populetea albae*) were significantly less common in the inner zones, being primarily confined to ballast zones. Similar results were noted by Rakotoson et al. (2025), who found species adapted to darker, cooler and wetter conditions in the embankments. Ecological specialists such as sciophytes were found only sporadically and mostly include species of forest undergrowth, such as *Oxalis acetosella* L., *Asarum europaeum* L. and *Circaea lutetiana* L., or tree juveniles, like *Fagus sylvatica* L., likewise indicators of lower temperatures, such as *Doronicum austriacum* Jacq. and *Prenanthes purpurea* L., specialists of forest fringes. These findings are in line with the negative correlation between abundance and ecological specialization. Regarding dispersal, particularly interesting are wind-dispersed species, which require highly open areas to successfully spread (Tikka et al. 2000), as reflected in their significantly higher proportions in inner railway zones (SZ and IA). This pattern reflects is consistent with stronger longitudinal airflows and turbulence generated by traffic (Wrzesień et al. 2016a, b).

Analyses of species richness and vegetation cover show that site-specific conditions in different railway zones influence plant establishment differently. The Ballast Toe (BT), positioned at the edge of the railway infrastructure (Fig. 2), appears to provide a more favourable environment for denser and more diverse vegetation growth compared to SZ and BS (Figs. 4 and 5). These results are in line with those of Rakotoson et al. (2025) but are different in comparison to the study carried out in Czechia, where authors found higher diversity along the tracks (Kutlvašr et al. 2024). These findings highlight that railway verges, particularly the BT, can function as ecological corridors, where species from adjacent plant communities spread into the railways. Based on results from Tikka et al. (2000) and Penone et al. (2012), as well as ours, this could particularly be noted in the case of grassland species. On the other hand, the most distant zone – IA, had the lowest values of both species' richness and vegetation cover, confirming the importance of distance on propagule pressure. Additionally, IA supported species, adapted to warm, dry, open, slightly acidic and nutrient-poor niches of the railway, mostly the aforementioned railway specialists (sensu Brandes 1983).

The observed zone-level differences in vegetation are largely reinforced by differential management intensity. The inner zones (SZ, BS and IA) are routinely subjected to ballast sifting and cleaning and were, prior to the 2021 herbicide ban, the primary targets of glyphosate-based herbicide applications. On double-track lines, the IA effectively received a double herbicide dose, as it was sprayed during the treatment of each adjacent track. In contrast, the BT was largely exposed only to spray drift, and its denser vegetation likely provided additional physical protection for smaller and establishing plants. These management differences likely contribute, at least in part, why the IA harbours the most species-poor, disturbance-tolerant vegetation – consistent with the general finding that disturbance intensity reduces railway biodiversity (Sudnik-Wójcikowska and Galera 2005) – and why the BT acts as a refugium for more diverse, competitive assemblages, functioning as a semi-natural verge habitat (Oldén et al. 2021; Penone et al. 2012). Our study captures vegetation patterns during the early phase (1–2 years) of spontaneous revegetation following the cessation of chemical control, and the functional trait patterns we observed – dominance of short-lived ruderals in inner zones versus perennial competitors in outer zones – are consistent with expected successional dynamics under relaxed disturbance.

Several limitations should be acknowledged. Our sampling sites were selected based on the presence of visible vegetation rather than through a fully randomised design, which may introduce bias toward more vegetated locations. Additionally, the absence of pre-ban vegetation data precludes direct before-after comparison. Finally, we did not measure environmental variables (e.g. soil properties, microclimate) directly, and the ecological gradients inferred from indicator values should be validated by future studies incorporating such measurements.

Conclusions

Overall, we have addressed our research questions and confirmed that railway flora in Slovenia is indeed shaped by multiple interacting biotic and abiotic factors. As a vegetation habitat, railways can be microecologically divided into two parts – inner and outer zone, which provide different ecological conditions and carry different functional traits. The outer – ballast zone is significantly more species rich, with higher coverage and prevalence of mesic, competitive species – particularly grassland hemicryptophytes. Dependence on surrounding ecosystems, which act as sources of propagules, is the most pronounced here. On the other hand, inner zones harbour more ecologically specific and extreme conditions, with pronounced dominance of annuals, diagnostic to ruderal flora. These findings highlight the importance of railways as ecological transition zones and dispersal corridors within fragmented landscapes.

A significant part of the Slovenian railway flora consists of non-native and invasive species, which are distributed throughout the entire railway network and across all zones, representing a conservation concern that warrants targeted monitoring – particularly considering the recent herbicide ban. By documenting these patterns immediately following the 2021 cessation of herbicide use, this study provides a baseline for tracking vegetation dynamics under changing management regimes – a question relevant not only to Slovenia but to ongoing European debates about balancing railway safety with biodiversity conservation. To build on these results, future studies should incorporate environmental variables, management intensity and long-term monitoring data to better understand the mechanisms driving vegetation patterns along railways.

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Data availability Dataset containing information on reported species, their traits and sampling locations is available in Supplementary Material 1 and is made publicly available.

Declarations

Competing interests The authors declare no competing interests.

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