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Research article

Historic disturbance events overruled climatic factors as drivers of ruderal species distributions in the Scandinavian mountains

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The contemporary interaction of climate and disturbance drives vegetation composition and species distribution shifts, making their respective roles difficult to disentangle. This study describes the long-term ruderal plant species distributions along the 'Rallarvägen' in Abisko, subarctic Sweden. This trail currently serves as a hiking trail but was initially created as a construction road for a railroad from 1898 to 1903 and is paralleled by the E10 Highway since 1982.

Using vegetation and climate data from 1903, 1913, 1983, and 2021, we found that warm-adapted ruderal plant species were common along the Rallarvägen shortly after railroad construction in the early 20th century. Interestingly, many of these native and non-native ruderals with relatively high temperature affinity that were present in 1903 and 1913 have since disappeared and have not reappeared, despite the substantial increase in regional temperature in recent decades.

In addition, the historical disturbances have had long-lasting effects on the current spatial distribution of the ruderal vegetation. Most ruderals still reside close to the railroad tracks and are progressively filtered out with increasing distance from anthropogenically disturbed introductory points, such as train stations, where they peak in species richness – a process we term 'horizontal directional ecological filtering', in parallel to the established concept of 'directional ecological filtering' along elevational gradients.

The historical record of ruderal plant species in the region, influenced by a century-old railroad construction, emphasizes the importance of knowing a system's disturbance history for understanding current vegetation dynamics and anticipating its future in a changing climate.

Keywords: climate change, disturbance, ruderal species, Scandinavia, subarctic

Introduction

Evidence is mounting that human-caused environmental changes, such as climate (e.g. warming temperatures and shifting precipitation patterns) and disturbance, cause substantial species redistributions in mountain areas (Kowarik 2003, Thuiller et al. 2008,

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Elmendorf et al. 2012, Pearson et al. 2013, Hedenås et al. 2016). Climate change is four times the global rate in Arctic regions (Rantanen et al. 2022) and is especially pronounced in cold-climate mountain areas (Callaghan et al. 2013). Signs of the impact of warming on communities are already evident in many of these mountain regions, where migration of species from lower to higher elevations have been well-documented (Frei et al. 2010, Dainese et al. 2017, Rixen and Wipf 2017). The effects of disturbance are usually less profound at higher elevations compared to lower elevations, where the rate of change in communities often lags that of climate (Bertrand et al. 2011). This interchange between predominantly disturbance-driven populations at lower elevations and the largely climate-driven populations along elevational ranges, make mountain areas especially suitable for the study of the synergy between both.

Rising temperatures as a consequence of global change have favored introductions of warm-adapted, non-native species to become established in mountain areas, especially where disturbance was high (Thuiller et al. 2005, Elmendorf et al. 2012, Pearson et al. 2013, Taylor et al. 2017, Heijmans et al. 2022). The vegetation productivity and the length of the growing season have also increased, as a result of both higher temperatures in summer and an on average earlier retreat of snow cover in spring (Elmendorf et al. 2012, Pearson et al. 2013). For some species this leads to increased growth rates or an extended distribution, while other species may experience adverse effects on fitness. The impact of climate change on vegetation communities per se is thus quite difficult to predict, as responses to the changing environment can vary widely in speed and magnitude across species and functional groups (Klanderud and Totland 2005, Parmesan and Hanley 2015).

Mountain regions are becoming increasingly accessible through improved infrastructure. Roads and hiking trails are major conduits for human-mediated dispersal in these regions (Lembrechts et al. 2014, 2016a, Dainese et al. 2017, Liedtke et al. 2020, Wedegärtner et al. 2022), allowing for rapid uphill migration (Hulme 2014). These disturbed sites are often characterized by changes in soil conditions, such as compaction and chemistry, which affect species diversity and composition, by creating an environment that often promotes ruderal species (Frenkel 1977, Guo et al. 2018b, Rendeková et al. 2019). Ruderal species are known for their ability to thrive in areas affected by human activities and changing environmental conditions (Randelovic and Jovanovic 2023). Their opportunistic nature allows them to colonize degraded lands quickly and extensively. With traits such as high seed production, efficient vegetative spread, and rapid nutrient absorption, ruderal species have the capacity to quickly expand into non-native areas in response to these altered environmental conditions (Randelovic and Jovanovic 2023). Roadside dispersion is related to traffic intensity and the size of the road network (Pauchard et al. 2009, Chiuffo et al. 2018), while hiking trails often facilitate ruderal plant dispersal from roads or settlements further into the mountains (Liedtke et al. 2020).

Human-mediated dispersal facilitates non-native plant species influxes from all over the world as tourists are often bringing in hitch-hiking seeds that stick to their clothing, boots, or the tires of cars (Frenkel 1977). Most of these non-native species are ruderals (Kowarik 2003, Alexander et al. 2016, Chiuffo et al. 2018). Consequently, non-native ruderals mostly appear first near train stations (Brandes 2002), parking lots (Frenkel 1977), roadsides (Lembrechts et al. 2014), and other places where human displacement is most abundant (Guo et al. 2018b, Liedtke et al. 2020). The degree of invasion in a community is thus related to the intensity of human activity (Kowarik 2003).

Due to their long, harsh winters, and short, relatively cold summers, subarctic mountain ecosystems were previously believed to be relatively resistant to the influx of non-native species, but climate change and increased disturbance are gradually changing this view (Pauchard et al. 2009, Walther et al. 2009). Many non-native ruderal species are known to be good dispersers that can reach high elevations twice as fast as native species (Dainese et al. 2017), although their climatic tolerance may constrain their survival to the next growing season (Rendeková et al. 2019). Nevertheless, a widespread uphill migration of non-native species has been observed along elevational gradients in response to climate change (Pauchard et al. 2009, Kueffer et al. 2013, Alexander et al. 2016, Dainese et al. 2017). Indeed, introductions tend to take place in the lowlands (Pauchard et al. 2009, Alexander et al. 2010, Guo et al. 2018a, Liedtke et al. 2020), and from these sites species either move through human-mediated dispersal or spread out on their own.

Directional ecological filtering (DEF) describes the unidirectional uphill expansion of non-native species (Alexander et al. 2010). Non-native species richness gradually declines with increasing elevation. With their lower elevational limit consistently in the lowlands, non-native species spread over an elevational range until they reach their upper elevational limit. As a result of this directional movement starting in the lowlands, only climatic generalists are likely to reach high elevations. Non-native species are thus gradually filtered out along the elevational gradient, probably due to increasing climatic harshness (Alexander et al. 2010). However, longer residence times have also been associated with extending elevational limits (Pyšek et al. 2011).

Testing the interactive effects of climate change and disturbances on native and non-native ruderal species expansion requires detailed knowledge on the history of disturbance events and climate data, as well as long-term data on ruderal species distributions. Such data is available for a mountain region in the north of Sweden, around Abisko – a small village known for its hiking trails and the Abisko Scientific Research Station (Andersson et al. 1996). The local climate is defined as subarctic with cool summers and relatively mild winters with extensive snow cover. The Scandes mountain range to the west, creates a rain shadow effect directly over Abisko, making it the sunniest area in northern Sweden (Callaghan et al. 2010, 2013). However, Abisko has been subject to climate warming since the 1980s (Callaghan et al.

2013), in combination with major disturbance events in the early 1900s. This makes it an ideal study area to test the interaction of these drivers, specifically on the temporal dynamics in ruderal species compositions.

In 1903, a railroad was completed from Kiruna to Narvik, soon followed by the first tourist hotel in Abisko (Callaghan et al. 2013). The Rallarvägen trail – the focus of the present study – runs parallel to the railroad. The accessibility of the Abisko region was further improved with the opening of the E10 highway from Kiruna to Riksgränsen in 1982, which followed the existing Rallarvägen and the railroad line. Additionally, over the past decades, the annual air temperature in the region has gradually increased from an average of 0 to 1 °C (ANS 2019, see also Callaghan et al. 2010). These rising temperatures already resulted in significant upward shifts in the treeline and the distribution range of plant species, as well as substantial changes in phenology (Rundqvist et al. 2011, MacDougall et al. 2021).

Using the precise timelines of the disturbance events (railroad and E10 highway construction), in combination with continuous climate data since 1913, vegetation surveys along the Rallarvägen trail dating back to 1903 (Sylvén 1904, 1913–15, Lewenjohann and Lorenzen 1983, ANS 2019), our own recent resurvey of the Rallarvägen from 2021, and additional vegetation data from along two hiking trails leading from the Rallarvägen into the mountains (Wedegärtner et al. 2022), we set out to answer three key research questions about the history of ruderal species along the Rallarvägen and uphill into the surrounding mountains:

1. Was there a continuous increase in the number of native and non-native ruderal species following railroad (1903) and E10 highway (1982) construction, and the manifestation of climate change since the 1980s?
2. Did more warm-adapted native and non-native ruderal species get introduced in the Abisko region since climate change has manifested in the 1980s?
3. Is there evidence for human-mediated dispersal in the spatial expansion of native and non-native ruderal species along the Rallarvägen and uphill into the surrounding mountains?

We hypothesized that railroad building would have facilitated the establishment of a significant number of ruderal species along the Rallarvägen trail. Subsequently, we expected that later disturbance events, i.e. the development of the E10 highway, would have introduced a new influx of largely non-native ruderals, albeit to a much lesser extent. This was primarily because the Rallarvägen was not employed for the E10 highway construction. With the confluence of climate change and disturbance, we foresaw another significant increase in the presence of warm-adapted ruderal species in recent decades.

We hypothesized ruderal species to be concentrated around points of introduction with continuous disturbance, such as the main train stations, with a progressive decline in richness with increasing distance to these introductory points. Additionally, more recent introductions and warm-adapted ruderals were expected to be restricted to lower elevations.

Methods

Study site

Our study focused on a 40-km stretch of the Rallarvägen trail starting in Abisko (68°21′N, 18°49′ E) at the Abisko Östra train station, and ending in Riksgränsen, the Swedish settlement near the Norwegian border (Fig. 1). The Rallarvägen was built to serve as a transport road for the construction of the railroad connecting Kiruna (Sweden) with Narvik (Norway) and since then has been used as a hiking trail. The trail follows the railroad line through the mountain valley, with a minor elevational gradient ranging from approximately 368 m a.s.l. near Abisko till 522 m a.s.l. near Vassijaure. Along the Rallarvägen are small settlements, some with train stations: Abisko (with the Abisko Tourist Station), Björkliden, Låktatjåkka, Kopparåsen, Vassijaure, and Riksgränsen. The E10 highway between Kiruna and Narvik parallels the Rallarvägen and the railroad (Fig. 1).

Not every part of the Rallarvägen trail is equally popular with hikers. Some parts near Koppåråsen are overgrown and in bad condition, while other parts, such as the stretch between Abisko and Björkliden, are easily accessible and extensively used. Between Abisko and Björkliden lies the Abisko National Park (since 1909), which attracts many tourists in both summer and winter. Most summer tourism is focused on hiking, resulting in extensive use of hiking trails. Especially through this park, many hiking trails follow the Rallarvägen before diverging to different parts of the area.

Vegetation data

We combined 1) historical vegetation data (1903, 1913, and 1983) from settlements and train stations along the Rallarvägen with 2) a resurvey of the same area in 2021 and 3) additional surveys performed in 2016 by the Mountain Invasion Research Network (MIREN; Haider et al. 2022) along two hiking trails leading from the Rallarvägen into the mountains: the Björkliden and Låktatjåkka trail (Wedegärtner et al. 2022).

The vegetation surveys in 1903 and 1913 focused on the establishment of ruderal species after the railroad construction (Sylvén 1904, 1915–17). During its construction, the surrounding vegetation was destroyed, leaving bare soil whereupon construction materials were transported and assembled. Near the end of the railroad construction in 1903, Sylvén observed new ruderal species to have emerged in the Abisko region. Along the Rallarvägen, and most notably near the settlements of Abisko, Björkliden, and Vassijaure, construction efforts led to various dump piles of horse manure and rubbish, which compelled him to survey the vegetation near here (Sylvén 1904). In July, he compiled a list of all present species within and around the specified settlements, with a particular focus on ruderal species. In his report, Sylvén elaborated that the highest diversity of ruderal species was observed near horse stables, strategically positioned at every settlement during construction, with an especially high prevalence of members

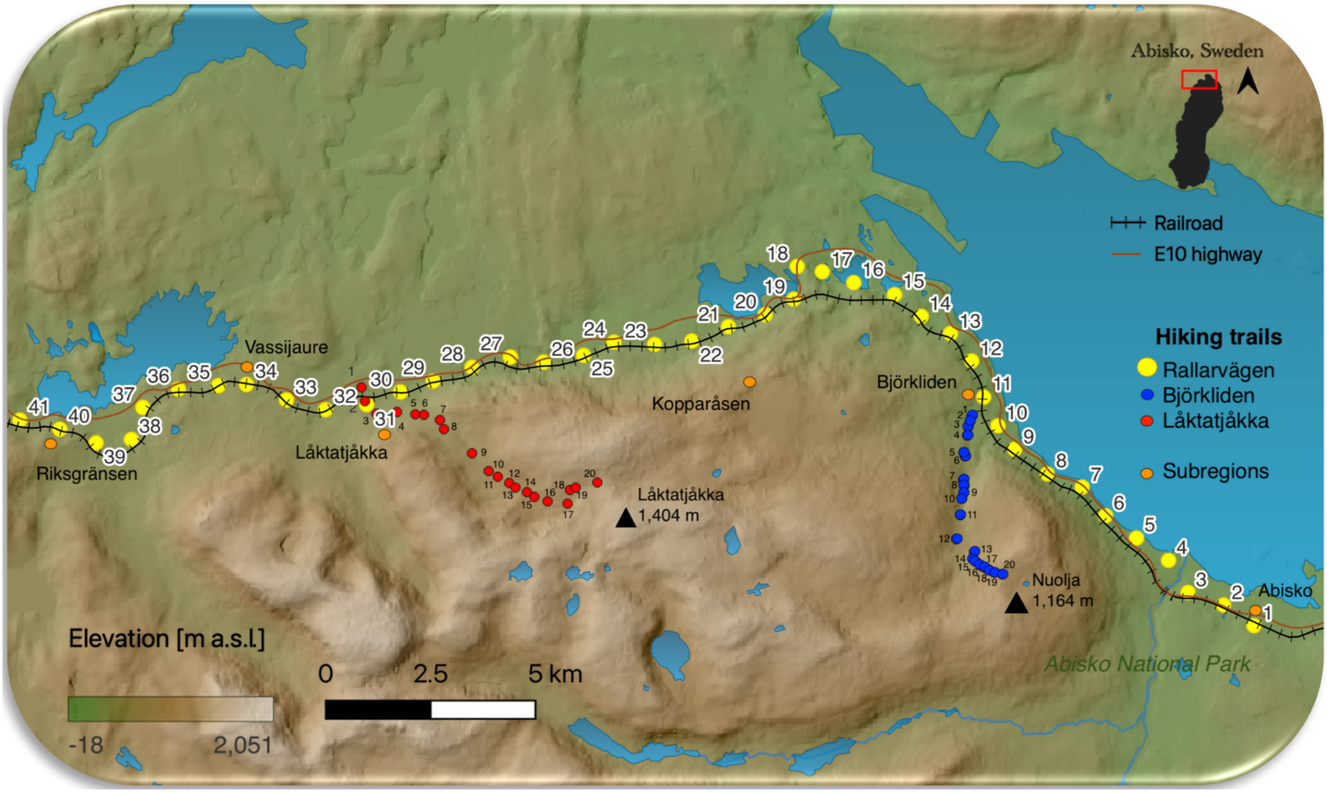

Figure 1. Map of the study region between Riksgränsen and Abisko in subarctic Sweden, on a digital elevation model, with transects along hiking trails Rallarvägen (yellow dots), Björkliden (blue), and Låktatjåkka (red). Each Rallarvägen transect number indicates the start of each transect, from where it reaches till the consecutive number. Number 41 indicates the end of transect 40. The transect numbers along the Låktatjåkka and Björkliden trail indicate the start of a T-transect (below), situated perpendicular to the trail and stretching into the vegetation.

of the Poaceae family (e.g. *Poa annua, Poa pratensis, Poa trivalis, and Phleum pratense, which are all non-native to the region*). Consequently, he surmised that the majority of these ruderals had likely been introduced through the transportation of horse feed. Ruderals that were omnipresent throughout the area were members from the Fabaceae and Brassicaceae family. Most of the ruderal species observed were annuals of a primitive (i.e. very small and vegetative) type and only few individuals were flowering, contrasting our observations in July 2021 (where, e.g. members of the Fabaceae family were at times very abundant, large in size, and already flowering in early July). Sylvén's report is rather descriptive and lacks specific methods for assessing abundance, precise locations, areas, and specific dates of the survey remain undisclosed. Even so, he does share his observations to be concentrated around the settlements of Abisko, Björkliden, and Vassijaure, and that he carried it out in the immediate vicinity of the railroad construction sites (i.e. the Rallarvägen and train stations), settlements, and the horse stables.

When Sylvén returned to the Abisko region in 1913, he noticed significant transformations in the local vegetation due to human influences. Houses had greatly expanded in numbers and size, often with lawns and gardens, around the Abisko Tourist Station and the train stations. In Riksgränsen, where no outstanding developments in the vegetation had been observed in 1903, large areas now had to be considered ruderal-dominated vegetation. Only in Vassijaure, the vegetation structure had remained in the same state as in 1903. Sylvén suspected this shift in the environment to be driven by 1) the first attempts at kitchen gardening; including *Pastinaca sativa*, *Pisum sativum*, *Solanum tuberosum*, and *Matricaria chamomilla*, 2) the ongoing annual (re-)introduction of numerous ruderal species through horse and cattle feed (e.g. *Trifolium sp.* might have been used in cattle feed), and 3) the sowing of bags of plant seeds from the Cyperaceae family on the embankments surrounding the railroad, train stations, and Abisko Tourist Station – however, no ruderal members of the Cyperaceae family were found along the Rallarvägen in 1913. Additionally, one might expect species such as *Trifolium sp.* or *Achillea millefolium* to have escaped from garden lawns or semi-natural grasslands or entered as seeds in foreign soils used for the construction of the railroad.

These new findings led Sylvén to conduct a follow-up survey, which now included the area in and around Riksgränsen (Sylvén 1915–17). He carried out his survey from 16 July to 4 August, 1913, and documented the presence and absence of species in both 1903 and 1913. His research revealed the introduction of 55 new species and the disappearance of 23 species since 1903 and indicated that most ruderal species (74.5%) were concentrated in various scrap heaps, around residential areas, and along the old construction road known as the Rallarvägen.

Almost 70 years later the Abisko area gained its first paved road (the E10 highway). Expecting possible changes in the vegetation composition due to the building of the E10 in 1982, Lewejohann and Lorenzen (1983) surveyed the vegetation in the month of July in 1983 and documented all present vascular plant species in the broader Abisko region (20 areas of unspecified size), using Flora Europaea vol. I (Tutin et al. 1980). Additionally, they compiled plant records from manuscripts and lists from an unknown number of unmentioned visitors. Although there is mention of the use of these lists, there are no specifics given on how many were used, which locations they comprise, whom the authors were, and what survey methods were used. There is a short reference list of manuscripts given, ranging from 1950 till 1983, but none contain the locations we use in the present study. It is also unknown to what extent they surveyed the vegetation themselves, which locations they surveyed, what survey methods were used, and the exact dates they carried out the survey. Nevertheless, Lewejohann and Lorenzen (1983) described certain areas within the region, using the settlements as points of interest, which allows us to delineate with rough confidence the areas that were surveyed in each period. In this study, we included the following areas intersecting the Rallarvägen: **Björkliden** – which included the nearby settlement Tornehamn that is also situated along the Rallarvägen, **Kopparåsen** – surveyed from Kopparåsen to Vadvetjåkka (at a distance of 8.3 km from the Rallarvägen), **Låktatjåkka** – from Låktatjåkka to Kärketjårro (at a distance of 3.2 km), **Vassijaure** – which includes Vassitjåkka (at a distance of 5.4 km) and Kärkevagge (at a distance of 4.2 km), and **Riksgränsen** – which includes Råtjuvare (at a distance of 4.7 km), Katteråive (at a distance of 2.2 km), and Katterjaure (at a distance of 5.0 km). The listed Abisko area, although including the Abisko settlement and train station, was not included in our investigation as the covered survey area lay at too great a distance from the Rallarvägen: from Abiskojåkka to Tjuonavaggejåkka – about 25 km distance from the Rallarvägen – which includes other hiking trails and encompasses the Abisko National Park.

In 1989, the effects of the E10-highway construction on roadside vegetation were studied by Bäck and Jonasson (1998) – who were particularly concerned about the potential colonization of non-native species. However, the impact of non-native species was considerably limited, in contrast to other studies that have examined the role of roads on the influx of non-native species (Lembrechts et al. 2014, 2016a). Due to the design of road cutting, there were still areas that exhibited incomplete vegetation cover, which were intentionally structured to allow the wind to sweep away snow during winter. This design choice significantly affected plant succession since snow cover plays a crucial role in the local flora, providing protection against frost heaving and desiccation for both plants and soil (Bäck and Jonasson 1998). Since its opening, the upgraded infrastructure has contributed to an increase in tourism in the region, so it is possible that changes in vegetation composition resulting from the E10 may have become noticeable only now. There is no data available on this study, only a report exists. Nevertheless, our emphasis is on the Rallarvägen rather than the vegetation along the E10 highway and therefore there is no justification of its conclusion.

2021 Rallarvägen resurvey

Between 5 July and 6 August, 2021, we documented all vascular plant species present in 1 km transects, within 1.5 m distance from the edge of the trail, along the 40-km stretch of the Rallarvägen, following the taxonomic reference 'Den nya nordiska floran' (Mossberg and Stenberg 2003) (Fig. 1). Our survey team comprised four individuals who worked in pairs, with each pair completing three to four transects per day. On average, each transect took approximately 2 to 3 hours to complete. However, some transects located near train stations and settlements required more time, while those in less frequented areas contained more monotone vegetation and demanded less attention. To mitigate potential observer bias and account for seasonal variations, we conducted the survey twice, with the transects being alternated between the two groups.

To be able to make comparisons with the historical data, transects were merged to represent nearby subregions as delineated in the historical surveys: Abisko = transect 1–5, Björkliden = transect 6–15, Kopparåsen = transect 16–25, Låktatjåkka = transect 26–30, Vassijaure = transect 31–35, Riksgränsen = transect 36–40. Because human settlements and plant introduction points in each of these subregions have remained remarkably consistent since Sylvén's time, we can say with relative confidence that these subregions overlap at least regarding their most critical point (i.e. points of introduction for ruderal species) with the subregions that were surveyed by Sylvén and Lewejohann and Lorenzen.

The 2021-resurvey was additionally used to investigate the current spatial distribution of ruderal species in detail. For these analyses, we calculated a species' abundance along the trail using the Z-score transformation for population abundance (Clark-Carter 2005), defined as: $Z = [X - \mu]/s$, where X is the abundance of species x (between 1 and 40 transects), μ is the mean abundance of the entire set of ruderal species, and s is the standard deviation of the mean abundance of the entire set of ruderal species. This 'trail-level' abundance is thus related to the number of transects in which a species was found along the Rallarvägen. Rescaling to Z-scores is done with a linear transformation whereby s and μ are constants, and the result can thus be used in linear models. Using this transformation, it is possible to determine how rare or common a particular species is relative to the whole group of ruderals (Supporting information).

Combining all surveys (1903, 1913, 1983, 2021) resulted in a total of 401 documented species. As Sylvén focused on ruderal species only, we filtered the species based on ruderality (below). For an overview of the differences and similarities between the surveys, we refer to table 17 in the appendix.

MIREN T-trail survey

A third dataset from 2016 was obtained from the Mountain Invasion Research Network (MIREN), comprising vegetation survey data from along elevational gradients on the

Björkliden and Låktatjåkka mountain trails that are leading from the Rallarvägen into the mountains (Wedegärtner et al. 2022). For further description on both trails, we refer to the Supporting information. Along both mountain trails, presence of all plant species was documented in 20 T-shaped transects (T-transects) at fixed distance intervals, each consisting of three plots of 2 × 10 m; one parallel and two perpendicular to the hiking trail into the vegetation (Supporting information). For every plant species we calculated the 95th percentile of its highest elevational occurrence (elevational maximum) using the *quantile* function in R (www.r-project.org).

Dataset compilation

For all datasets, plant species names were standardized using the canonical name from the Catalogue of Life using the 'taxize' package in R (Chamberlain and Szocs 2013). Additionally, for approximately 80% of the species, we obtained their evolutionary strategy (Grime 1979), Landolt's ecological indicator value for temperature (EIV-T; Landolt et al. 2010), and their native status (Weidema 2000, a compilation of information on different literature studies and databases on introduced species in Nordic areas – including Sweden. All authors have reviewed the suggestions made by Weidema). EIV-Ts are useful indices to reflect the environmental temperature where a plant species is most likely to sustain a population. They range from 1 to 5 (1 = cold-loving and 5 = warm-adapted; Landolt et al. 2010), therefore providing a one-dimensional broad-scale temperature niche for each species. A species was identified as at least partially ruderal when its Grime's CSR strategy classification (C: Competitive, S: Stress-tolerant, R: Ruderal) contained an R, e.g. CRS, CRR, or RRR (Grime 1979).

Of the 401 observed species in the combined historical dataset (1903, 1913, 1983, and 2021), 240 were identified as ruderal and 100 were identified as non-native ruderals. There were five observations (that may or may not contain one or more species) that could not be identified to species level. Given that there are 121 genera in this dataset, this implies that 6% of the genera contain species not identified at species level. The Rallarvägen 2021 dataset contained 268 species of which 94 were identified as ruderal and 36 were identified as non-native ruderals. The MIREN T-trails dataset contained 128 species of which 39 were identified as ruderal and 12 were identified as non-native ruderals. We managed to obtain the EIV-T for every identified ruderal species.

Temperature data

Although a quantitative analysis to evaluate species richness over time in relation to climate change is not feasible due to the nonlinear nature of climate change, the methodological differences between the different surveys, and the limited number of time steps in our dataset, we were able to assess the spatial effect of temperature. We thus combined the Rallarvägen 2021 dataset with soil temperature estimates from the 'Global maps of soil temperature', which provides global modeled soil temperatures averaged for the period 1979–2013 at a spatial resolution of 1 km² for 0–5 cm depth (SoilTemp; Lembrechts et al. 2022). For each transect, we used the mean annual soil temperature (SBIO1) – ranging from −3.8 to 3.4 °C, the mean soil temperature of the warmest quarter (SBIO10; hereafter named mean summer soil temperature (MSST)) – ranging from 8.7 to 10.4 °C, and the mean soil temperature of the coldest quarter (SBIO11) – ranging from −13.8 to −1.2 °C. We extracted temperatures for each transect using the *extract* function from the 'raster' package in R (Hijmans 2021).

Maps and measurements

For the start and end of every transect in the Rallarvägen 2021 dataset, we obtained the geographical coordinates with a handheld GPS system. Geographical coordinates for train stations were obtained through Google Maps (maps.google.com). Since species monitoring began at the starting point of each transect – and thus most species occurrences were documented here – we used this location to measure the perpendicular distance to the railroad and the E10 highway (in meters) using the measuring line and the Basemap ESRI 102113 – WGS 1984 from the QuickMapServices plugin in the QGIS software ver. 3.22.0 (QGIS Development Team 2021). The elevational gradient in the map of the study region (Fig. 1) was produced using Copernicus data and information funded by the European Union – EU-DEM layers (WGS 4258) (© European Union, Copernicus Land Monitoring Service 2022, European Environment Agency (EEA)). The EU-DEM is a 3D raster dataset with elevations captured approximately every 30 m. Other aspects of the map (i.e. lakes and waterways, subregions, roads, and railroad) were produced using the Sweden shapefile map layers that were obtained from the global community-owned project OpenStreetMap and downloaded from the MapCruzin website (Meuser 2019).

Data analysis

All data manipulations and statistical analyses were performed in R ver. 4.1.3. The ruderal community was split into two groups and every analysis was carried out for both: the total ruderal group (natives and non-natives) and the non-native ruderal group. To answer research question 1 and 2, we used the Rallarvägen historical surveys and our 2021-resurvey to analyze 1) region-wide species richness as a function of the observational year, and 2) the mean EIV-T as a function of subregion and the observational year and first year of observation. To answer research question 3, we used the 2021-resurvey to analyze spatial patterns in 3) species richness as a function of distance to the railroad, distance to the E10 highway, and soil temperature variables and 4) the Z-score abundances as a function of the ruderal species richness and distance to the railroad. Finally, to further answer research question 3, we used the MIREN trail surveys in combination with the Rallarvägen historical surveys and the 2021-resurvey, to analyze 5) species richness as a function of elevation and mountain trail, 6) the elevational maximum as a function of the first year of observation and mountain trail, and 7) mean EIV-T as a function of the elevational maximum, the first year of observation and mountain trail.

Models consisting of a dependent variable with count data (number of species) were analyzed using generalized linear models (function *glm*, *poisson* or *quasipoisson* distribution), otherwise linear models were used (function *lm*). To compare different possible models and to determine which one was best fitting in analyses 3, 5, 6 and 7 (as numbered in the previous paragraph), we used the Akaike information criterion with a correction for smaller sample sizes (AICc) from the 'AICcmodavg' package (Mazerolle 2020). For significant interactions consisting of two continuous variables (analysis 3), we centered one independent variable to make statistical interpretation and visualization easier (Schielzeth 2010). We plotted trends across one variable while keeping the other variable constant at its mean, as well as at one standard deviation above and below the mean. In multiple regression analysis (analyses 3 and 4), we checked for possible multicollinearity of independent variables by calculating the variance inflation factor (vif) using the *vif* function from the 'car' package (Fox and Weisberg 2011). We considered results to be significant when $p \leq 0.05$ and marginally significant when $p < 0.10$.

To visualize differences in ruderal vegetation composition between subregions and observational years, we performed a principal coordinates analysis (PCoA), also known as multidimensional scaling (MDS) – with similar compositions lying closer together in the plot. Distances were calculated with the function *vegdist* from the 'Vegan' package (Oksanen 2022), and from this distance matrix the principal coordinate scaling was computed with the *pcoa* function from the 'ape' package (Paradis 2022). For this, we used the Jaccard distance which is defined as: Jaccard distance $= 2B/(1+B)$, where B is the Bray–Curtis dissimilarity. Bray–Curtis dissimilarity usually focuses on the dissimilarity of abundance, but by specifying *binary = TRUE* in the function it calculates distances based on presence-absence data.

Results

Number of species in the total ruderal community and non-native ruderal community over time

The total number of ruderal species differed significantly between 1983 and other observational years (Table 1, Supporting information), with the highest richness in 1913, followed by 2021, and 1903. The number of non-native ruderal species decreased significantly since the early 20th century, with most non-natives present in 1913 and least in 1983 (Table 1, Supporting information). Finally, it was evident that the dissimilarity among ruderal communities was greater between observational years than different subregions (Supporting information), indicating substantial species turnover between observational years.

Table 1. Differences in ruderal richness between observational years along the Rallarvägen. Total number of ruderal species (left) and the number of non-native ruderal species (right) as a function of the observational year, based on the number of species across subregions of all present total ruderals ($n = 239$) and non-native ruderals ($n = 100$). All model coefficients and p-values are shown in Supporting information.

Total ruderal count		Non-native ruderal count	
Observational year	Number of species	Observational year	Number of species
1903	82	1903	56
1913	104	1913	69
1983	57	1983	14
2021	94	2021	36
One-way ANOVA			
Predictor	p-value	Predictor	p-value
Observational year	< 0.001	Observational year	< 0.001
Tukey HSD			
Observational year	p adj.	Observational year	p adj.
1913–1903	0.5	1913–1903	0.6
1983–1903	< 0.001	1983–1903	< 0.001
2021–1903	1	2021–1903	0.004
1983–1913	< 0.001	1983–1913	< 0.001
2021–1913	0.6	2021–1913	< 0.001
2021–1983	< 0.001	2021–1983	< 0.001

Temperature affinity over time

The mean ruderal community temperature index (expressed as mean EIV-T per subregion per time step) was higher in historical records than in recent times. For the total ruderal community, there was a significant interactive effect of the observational year and subregion (Fig. 2a, Supporting information), with mostly lowest EIV-Ts in general observed in 1983 (2.2 ± 0.2) and highest in 1903 (3.3 ± 0.1) and 1913 (3.3 ± 0.1). Mean EIV-Ts were constant within subregions between observational years, except for 1983, which showed the most variation in these values. The mean EIV-T for the non-native ruderal community decreased gradually through time, without an interactive effect of subregion (Fig. 2b, Supporting information). Similar negative trends occurred for the mean EIV-T as a function of the first year of observation in a subregion (Fig. 2c–d, Supporting information). In combination with the high degree of heterogeneity that existed between communities (Supporting information), this shows that newly introduced species (in 1983 and 2021) were less warm-adapted than in 1903–13.

Ruderal richness and trail-level abundance with distance to introductory points and temperature

The number of species in the total ruderal community and non-native ruderal community declined with distance to the railroad in all but the warmest parts of the gradient, where these numbers increased slightly with distance to the railroad (Fig. 3, Supporting information). According to the variance of inflation factor (vif), there was no evidence of collinearity between the distance to the railroad and the distance to the E10 highway. However, there was no additional variation

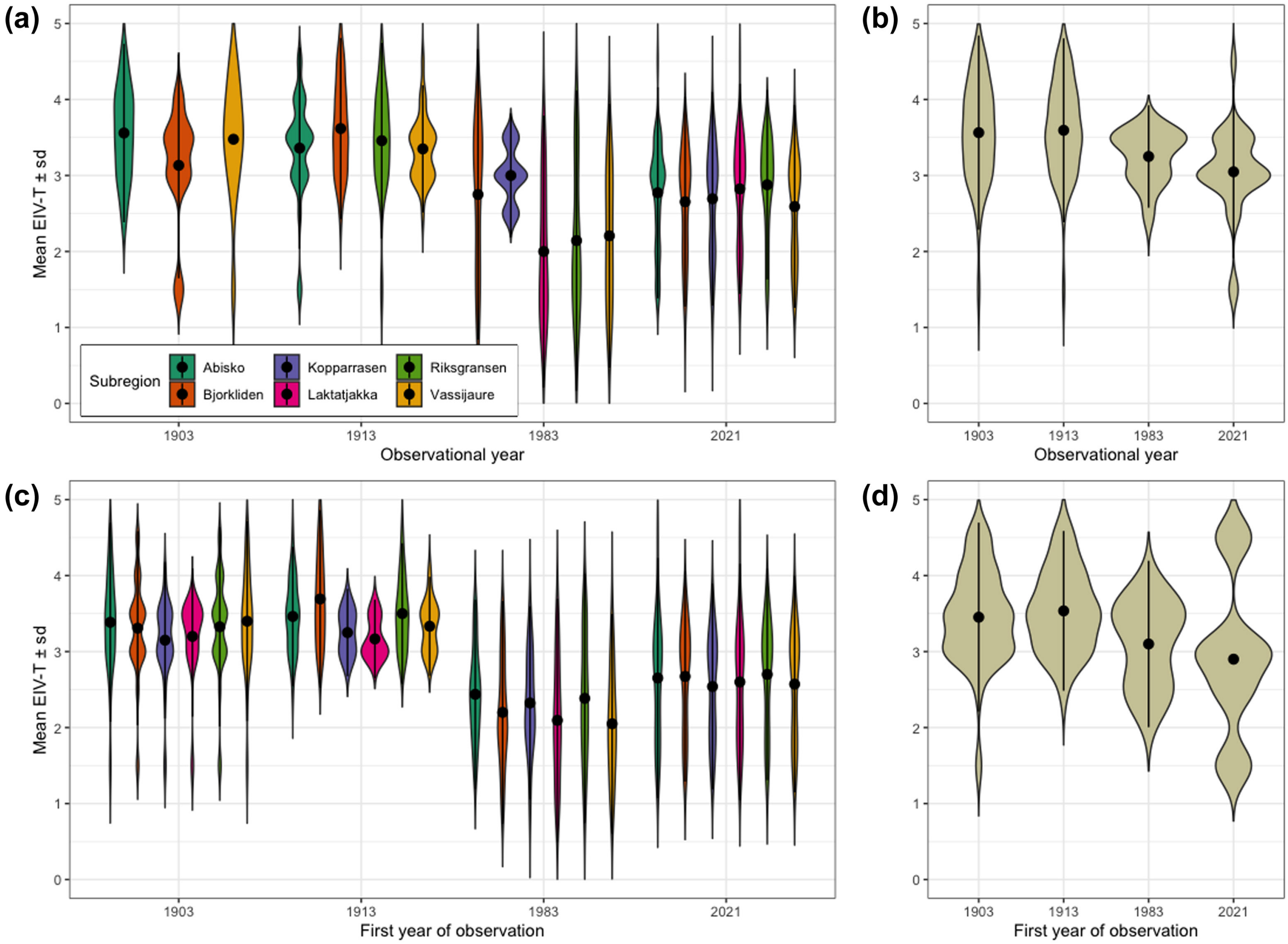

Figure 2. Ecological Indicator Values (EIV-T) of all ruderal species (on the left) or non-native ruderal species (on the right) observed over time (top) and as a function of the first year of observation (bottom). In a and c, numbers are shown as a function of the observational year and subregion, as in this case subregion was significant in the model. Data are averages over all present total number of ruderals (n = 239) and non-native ruderals (n = 100) per subregion. Model coefficients and p-values are shown in Supporting information.

explained by the E10, the mean soil temperature of the coldest quarter nor the mean annual soil temperature.

Unsurprisingly, rare ruderal species resided closer to the train stations, as these transects had the lowest average trail-level abundance (Fig. 4, Supporting information). According to the vif, the distance to the railroad and number of ruderal species were highly correlated and therefore the railroad was excluded from further analysis.

Elevational limits

Along the two trails leading from the Rallarvägen into the mountains, we found a significant negative association between species richness in the total ruderal community and elevation (Fig. 5a). A similar negative, but less pronounced, relationship was found for the non-native ruderal richness (Fig. 5b, Supporting information). There were no significant differences in these relationships between mountain trails for both groups.

For the total ruderal community, the elevational maximum of a species showed an unexpected positive association with the first year of observation in the whole region for the Björkliden trail, yet not so for the Låktatjåkka trail (Fig. 5c, Supporting information). For the non-native ruderal community as well, a marginally significant positive association was found between the elevational maximum and the first year of observation to the whole region, but was not different between trails (Fig. 5d, Supporting information). No trends were observed in the mean EIV-T as a function of the elevational maximum, the first year of observation and mountain trail for the total ruderal community (R^2 adj. = 0.26, AICcwt = 1, 2nd best model Delta_AIcc = 15.88) and in the mean EIV-T as a function of the elevational maximum for the non-native ruderal community (R^2 adj. = −0.05, AICcwt = 0.9, 2nd best model Delta_AIcc = 4.33).

Discussion

Temporal patterns

The temporal dynamics of the ruderal community deviated surprisingly much from our initial hypothesis (Table 1).

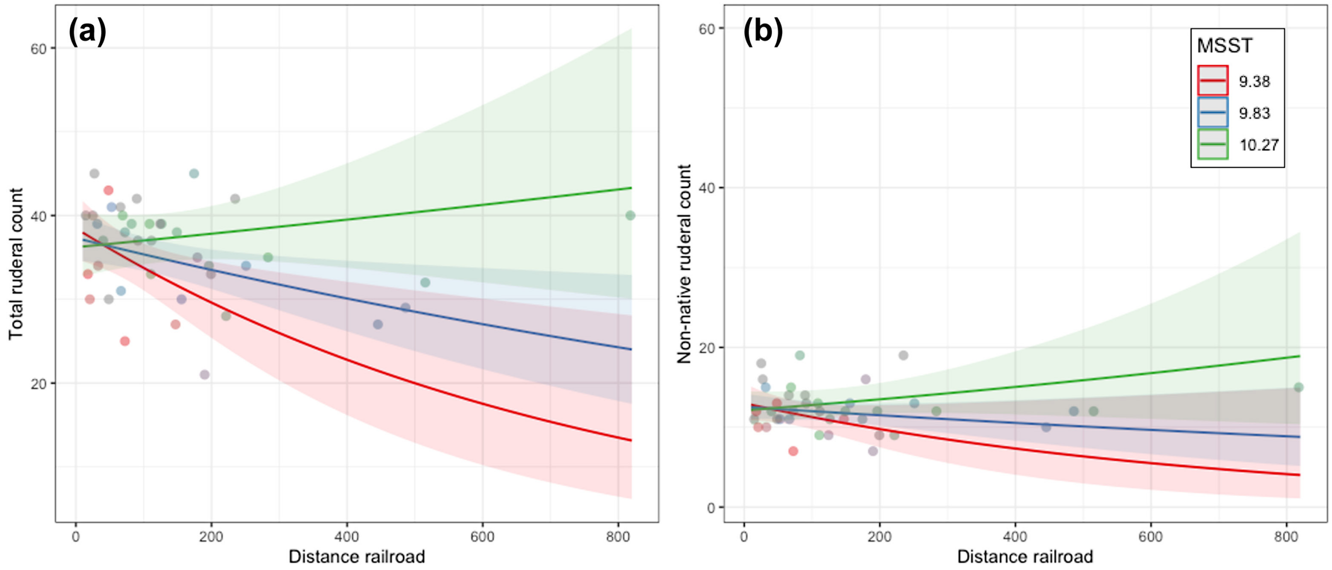

Figure 3. Effects of mean summer soil temperature (MSST, in °C) and distance from the Rallarvägen trail to the railroad (x-axis, in m) on a) the number of species in the total ruderal community, R^2 adj. = 0.23, AICcwt = 55%, 2nd best model Delta_AICc = 2.72 and b) the number of species in the non-native ruderal community, R2 adj. = 0.05, AICcwt = 42%, 2nd best model Delta_AICc = 2.35, per 1-km transects along the Rallarvägen. Graphs are prediction plots with the estimated marginal effects. To make interpretation easier, we plotted the ruderal count as a function of distance to the railroad for three values of MSST (methods): the mean MSST (blue), as well as one standard deviation above (green) and below (red) the mean; shading indicates the standard deviation of each MSST line. Dots show raw data. Model coefficients and p-values are shown in Supporting information.

Although ruderals are known to respond to disturbance and changing environments (Randelovic and Jovanovic 2023), we had anticipated an increase in the number of ruderal species over time as a result of the joint impact of local disturbance and climate change (Thuiller et al. 2005, Chiuffo et al. 2018, Guo et al. 2018a).

Aside from Sylvén's noted observation that a significant portion of ruderal species in the region arrived via the transportation of horse and cattle feed, we also believe that the introduction of foreign soils and materials have played a role, albeit to a lesser degree, in facilitating colonization. Surprisingly, our findings indicate that the construction of the railroad and settlement expansion in 1903 and 1913 has had a somewhat bigger impact on the introduction of ruderal species along the Rallarvägen than the construction and utilization of the E10 highway (since 1982), increased tourism, and the influence of climate change combined. However, it's essential to note that apart from transect 18 (Fig. 1), we have not examined the ruderal vegetation adjacent to the E10, and the vegetation here might harbor recently (re)introduced non-native ruderals that are yet to colonize the Rallarvägen.

The significant drop in 1983 must be attributed to a methodological anomaly, but even then, we must consider that the total number of ruderal species has remained relatively stable over time, with even a decrease in the number of non-native ruderals (limitations).

While the above mentioned patterns in species richness could in theory be the result of differences in monitoring intensity, patterns in the community temperature index (expressed as the ecological indicator values for temperature; EIV-T) revealed that most relatively warm-adapted ruderal species were already present in the early 20th century, right after the building of the railroad, with little evidence of an influx of relatively warm-adapted species due to climate change in recent years (Fig. 2). In fact, we even observed a steady decline in mean EIV-T of the non-native ruderals in

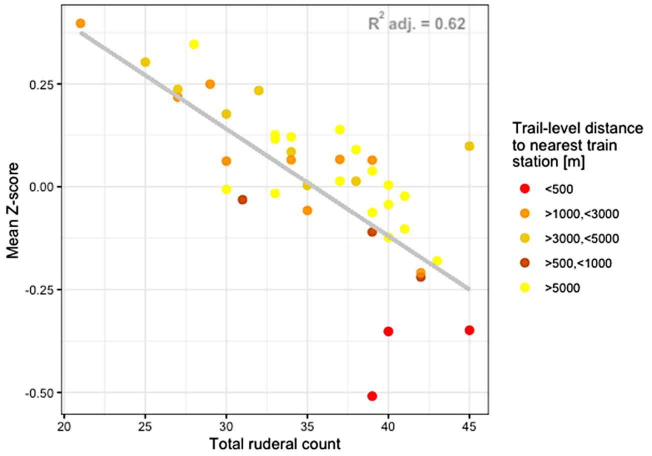

Figure 4. Relationship between the average trail-level abundance of all ruderal species in a transect (expressed as mean Z-scores of all species in a transect, with a higher Z-score indicating that a transect hosts on average more common species) and the total number of ruderal species (in counts) along the Rallarvägen. Colors indicate the distance to the nearest train stations (either Abisko Östra, Björkliden or Riksgränsen). Model coefficients and p-values are shown in Supporting information.

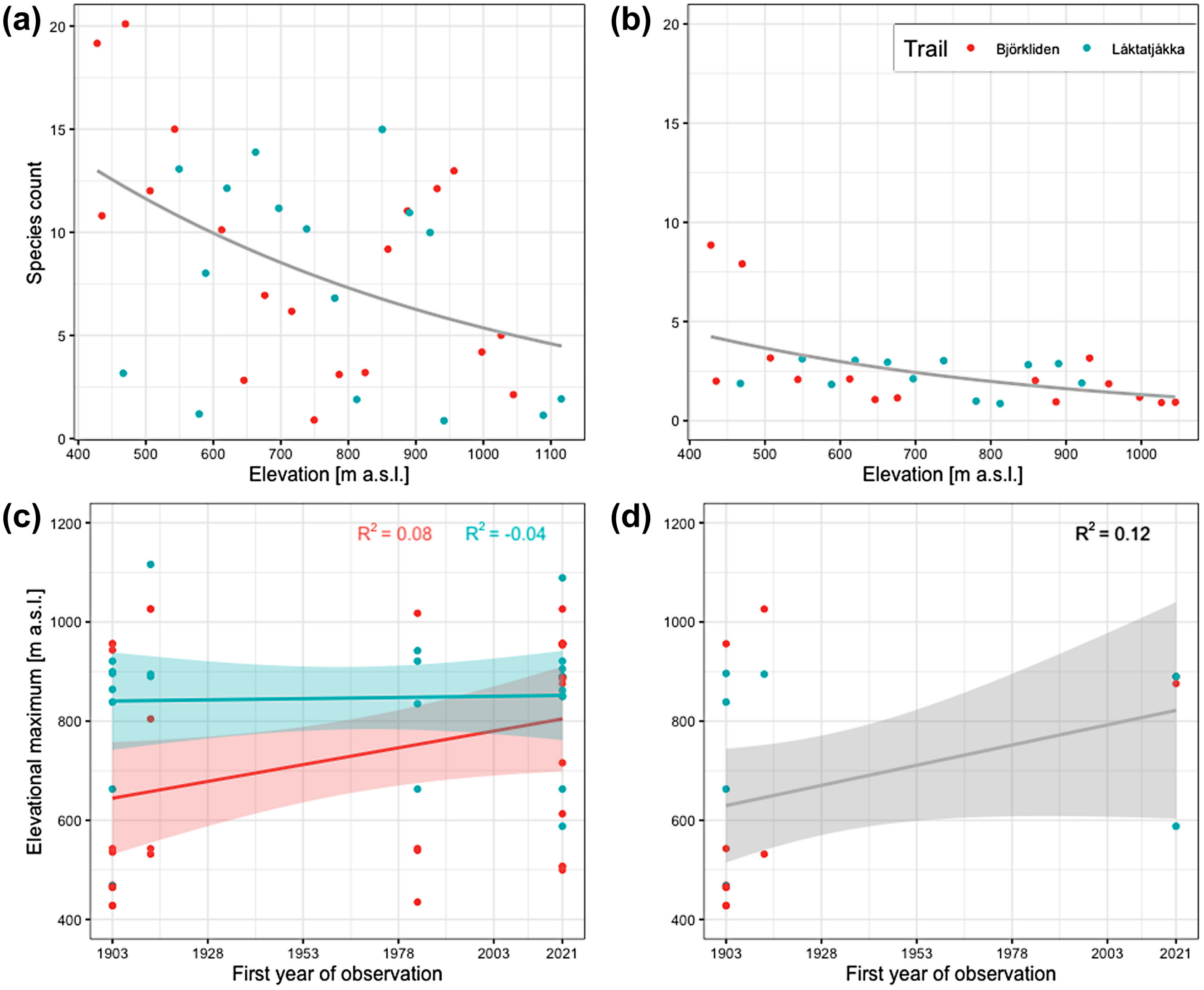

Figure 5. In the top two graphs, the relationship between ruderal species richness and elevation (dots are species counts) along two trails perpendicular to the Rallarvägen and leading into the mountains (Björkliden, red, and Låktatjåkka, blue), with a) Total ruderal community (n = 39), R^2 adj. = 0.14, AICcwt = 0.83, 2nd best model Delta_AICc = 3.2, and b) non-native ruderal community (n = 12), R^2 adj. = 0.28, AICcwt = 0.82, 2nd best model Delta_AICc = 3.1. In the bottom two graphs, the relationship between ruderal species' elevational maximum along these trails and the first year of observation in the whole region (one dot is a species), with c) Total ruderal community (n = 39), R^2 adj. = 0.10, AICcwt = 0.76, 2nd best model Delta_AICc = 2.27, and d) Non-native ruderal community (n = 12), R^2 adj. = 0.10, AICcwt = 0.58, 2nd best model Delta_AICc = 3.4. Trendlines in gray indicate no significant difference between both trails. The elevational maximum was defined for each species as the 95th percentile of its elevational occurrences. Model coefficients are shown in Supporting information.

2021. Our data showed that 36 (mostly annual non-native) ruderal species with high EIV-Ts (≥ 4) in the historical years, had disappeared by 1983, and did not reappear in 2021, while species observed for the first time more recently had lower EIV-T values (≤ 3; Supporting information). These species with high EIV-Ts did not manage to sustain a stable population, likely due to a combination of the local weather conditions and the lack of continuous or new significant disturbance after 1913 (Lembrechts et al. 2016b, Niittynen and Luoto 2017, Rendeková et al. 2019). Such disturbance events may not only be critical for ruderal species in general to establish, they also likely create beneficial microclimatic conditions that might have been a prerequisite for these relatively warm-adapted ruderal species to establish (Lembrechts et al. 2018). The lack of such disturbance events seems to have prevented these species from re-establishing even now that the climate has warmed to an average 1.0 °C and the length of the growing season in 2021 was approximately 13 days longer compared to 1913 (Supporting information, Lembrechts et al. 2016b, ANS 2019). In time, many of the ruderal species along the trail were thus again outcompeted by the native species that thrive in subarctic mountain environments – demonstrating community resilience. Nevertheless, as climate change progresses, we expect that warmer temperatures might still tip the scale, allowing subsequently introduced warm-adapted non-native species to gradually establish successfully in areas where disturbance is prominent (Dainese et al. 2017).

Spatial patterns along the Rallarvägen

As expected, ruderal species were concentrated around points of introduction with continuous disturbance, with a progressive decline in ruderal species richness with increasing distance to these introductory points (Fig. 3, 4). Historic disturbance was the strongest driver – especially for the total ruderal community – since the number of ruderals decreased significantly with distance to the railroad at average (9.8 °C) and below average (9.4 °C) mean summer soil temperature (MSST). This supports other studies that illustrate the key role of disturbance for new plant species introductions (Alexander et al. 2010, Lembrechts et al. 2016b). Although the E10 highway lies often closer to the Rallarvägen than the railroad does, the construction of the railroad still marks its imprint on the ruderal vegetation. What is more, our findings showed a climatic response on ruderal species distributions as the predicted number of species for both the total ruderal community and the non-native ruderal community increased with distance to the railroad in transects where MSST reached above average values (10.3 °C; Fig. 3). This could indicate a potential role for climate change: if climate warms, the current climatic limitations might decrease, allowing for ruderals to expand further away from disturbed sites (Lembrechts et al. 2018).

As anticipated, the most visited train stations, i.e. Björkliden, Abisko Östra, and Riksgränsen accommodate rarer ruderal species compared to other train stations and transects along the Rallarvägen (Fig. 4). These locations, including the trail segments around and between Abisko and Björkliden, are widely recognized as among the most frequented, although precise quantitative data is unavailable. Continuous disturbance is prevalent in these areas, facilitating the continuous (re)introduction of (rare) ruderals (Brandes 2002). Subsequently, these species must disperse through either human-mediated dispersal or self-dispersal. In less disturbed trail segments along the Rallarvägen, only fewer and more common ruderal species still reside that were first observed in 1903 (e.g. *Achillea millefolium*, *Cirsium heterophyllum*, *Equisetum arvense*, *Rumex acetosa*, and *Poa pratensis*). Those sites were sometimes not easily accessible, often lay further away from train stations, and were places where major disturbance only happened once (i.e. during railroad building in the early 20th century) (Rendeková et al. 2019). Pinpointing the exact drivers for this relationship remains challenging when solely relying on observational data. However, it is reasonable to infer a link with the degree of disturbance intensity. Distance to settlements, the E10 highway, the railroad, and train stations, and the level of hiking activity are all interconnected factors that contribute to a certain degree of disturbance intensity, which facilitates species dispersal (Kowarik 2003, Pauchard et al. 2009). While human activities are increasingly important in plant dispersal, we do acknowledge that self-dispersal also plays a part in our system.

We propose that the correlation between human impact and ruderal species distributions demonstrates horizontal directional ecological filtering (HDEF; Fig. 4). The term directional ecological filtering (DEF) was first coined by Alexander et al. (2010) for elevational (climatic) gradients, but here we show that the concept is applicable to a horizontal anthropogenic disturbance intensity gradient – within the same climatic band – as well. The original DEF hypothesis states that non-native species migrations happen from anthropogenically disturbed sites in the lowlands to higher elevations in the mountains, and that their richness declines with elevation but their elevational range increases with their maximum elevation (Alexander et al. 2010). Non-native species thus progressively drop out with increasing elevation. Unlike in DEF, where climate harshness is considered the most likely filter, albeit often correlated with gradients in disturbance and propagule pressure (Pauchard et al. 2009, McDougall et al. 2018), native and non-native ruderal species originating at the train stations were here thus progressively filtered out with increasing distance to these introductory points as the degree of disturbance intensity declined, showing that such directional filters can still be strong when climatic gradients are minimal. Such a strong relationship with disturbance lies of course at the very core of the definition of ruderal species, yet the directionality of the observed filter carries important implications, including a strong nestedness in the community. It is important to recognize that disturbance has multiple effects on ecosystems, including changes in propagule pressure, microclimate and soil conditions, and biotic interactions. These effects are hard to disentangle based on observational studies like this (Lembrechts et al. 2016b).

Spatial patterns along the secondary trails

In support of the original DEF hypothesis along elevational gradients (Alexander et al. 2010), we observed declining ruderal species richness with increasing elevation on the trails branching off the Rallarvägen (Fig. 5) (Alexander et al. 2010, Lembrechts et al. 2014, Dainese et al. 2017, Liedtke et al. 2020, Wedegärtner et al. 2022). Interestingly, only few non-native ruderals were observed along these trails, especially above 500 m a.s.l., rendering the decline in non-native richness less obvious.

In the traditional view of the DEF-hypothesis, high anthropogenically disturbed sites in the lowlands ensure quick and repeated introductions of non-native ruderals, from where they move uphill until they reach their (current and species-specific) elevational limits. This results in decreasing richness with elevation. However, our results showed that, in our system, a species' elevational maximum for neither the non-native nor total ruderal community were correlated with their climatic affinity (EIV-T). Instead, elevational limits unexpectedly related positively with their first year of observation in the whole region (Fig. 5): newest introductions were residing on average farther uphill. These patterns evoke two possible interpretations. First, there has not been incremental, linear uphill migration over time. This incremental migration might here be overruled by human-mediated long-range dispersal, which usually results in faster uphill migration than by climate change (Hulme 2014). This is in accordance with what we said earlier and suggests that the DEF is often as much disturbance-driven as it is climate-driven. These higher elevation populations might, however, not be stable as climatic conditions may not allow interannual survival, and long-term monitoring is thus needed to verify these patterns (Lembrechts et al. 2016a). Second, our analysis could be missing key variables responsible for the elevational distribution. The goodness-of-fit for these regression analyses was very low (Fig. 5), substantiating the fact that the first year of observation to the whole region does not fit the elevational maximum very well.

Limitations

The primary difficulty in this research lies in the reliability and comparability of historical surveys. The comparison of historical data always involves a level of uncertainty. However, we took precautions to base our conclusions on trends and patterns that are largely unaffected by such issues. For instance, recognizing the susceptibility of simple species richness metrics to methodological choices, we focused our conclusions on temporal trends, such as changes in temperature affinity across the recorded species.

While acknowledging the theoretical possibility of bias in the observed species' identity and temperature affinity, the evident trend, specifically the decline in non-native ruderal species, particularly those with a high temperature affinity, appears unlikely to be a random event. What is more, Sylvén's detailed descriptions provide confidence in the accurate identification of these species. Our comprehensive survey of the entire Rallarvägen stretch in 2021, conducted twice during the season, reduced the probability of overlooking ruderal species. While we acknowledge the potential oversight of rare and small species, the absence of several species in 2021 in comparison to Sylvén's surveys (such as *Agrostemma githago* in 1903, *Barbarea vulgaris* in 1903 and 1913, and *Matricaria chamomilla* in 1903 and 1913) – all easily identifiable and difficult to overlook flowering plants – leads us to conclude that, within a reasonable margin of error, the observed trends are not a result of observer error.

The deviation in numbers of ruderal species in the 1983-survey is at least partially the result of methodological differences. These methodological differences can be interpreted when considering the following aspects: 1) monitoring differences, 2) weather conditions, and 3) disturbance intensity.

While the vegetation survey of Lewejohann and Lorenzon in 1983 took place during the same month (July) as Sylvén's surveys in 1903 and 1913 and our own in 2021, the covered study area was substantially larger, encompassing 20 areas. Additionally, the number and the extent of contributors involved in their survey remain unknown. This has likely resulted in two issues: 1) the possibility that they surveyed areas they personally covered only once, potentially overlooking ruderal species that emerge later in the season, and 2) a high degree of observer bias as only they were focusing on monitoring changes in the vegetation due to the E10 highway. Their data missed perennial species such as *Trifolium pratense*, *Trifolium repens*, and *Vicia cracca*, which were present in 1903 and 1913 and are currently very abundant in each settlement and train station, and along the rest of the Rallarvägen trail. Even when these ruderal species are not flowering, they are easily identified, suggesting some selectivity in documenting species. An unexpected discovery, as Lewejohann and Lorenzon (1983) set out to survey vegetation changes following the disturbance caused by the building of the E10 highway, and thus should have shown particular interest in ruderal species (Lembrechts et al. 2014). We did learn that tourism in the area declined substantially in the early 1980s due to a temporarily reduced availability of tourist accommodation during that time. Consequently, we cannot exclude a recovery period from ruderal dominance in the vegetation. Nevertheless, the train stations would have seen continuous disturbance even in those days, and we thus deem it unlikely that these common ruderals would have disappeared entirely.

Importantly, 1983 was also an anomalous year in terms of weather conditions (Supporting information). Summer temperatures were on average 1 °C lower than in 1913, and summer precipitation was exceptionally high (238.8 mm). Snow cover and snowmelt timing are among the most important drivers of structuring subarctic community composition and distribution (Wipf 2010). Depending on the thickness, snow cover insulates species from the harsh winter conditions as it decouples the soil surface temperature from the air temperature (Niittynen and Luoto 2017). If the snow layer disappears too early, the species underneath will be exposed to the spring frost. Snowmelt timing determines the growing season length (Wipf 2010, Niittynen and Luoto 2017). Moderate rainfall can speed-up the snow-melting process, expediting the onset of the growing season. In contrast, heavy rainfall leads to even earlier snowmelt, but subsequent cold spells could potentially kill off ruderals, or reduce the surviving species' ability to exploit the whole growing season. Such negative effects are especially disadvantageous for annual species as they do not get the chance to adapt their physiology or morphology in similar ways to perennial plants (Li et al. 2019). While we do not have information on the spring snow cover in 1983, the anomalous precipitation value could suggest that such a scenario of early snowmelt followed by spring forest events might have happened. Annual species are rare in tundra ecosystems (Weidema 2000), but their distribution in 1983 is rather noteworthy. Seven of 57 (about 13%) of the observed ruderal species in 1983 had an annual life cycle, which was substantially lower than in earlier observational years: 54% in 1903, 49% in 1913 (and 16% in 2021). Five out of those seven occurred only at Björkliden. Interestingly, this was also the subregion in 1983 that accommodated species with highest average EIV-Ts (Fig. 2). This, in addition to the observed degree of heterogeneity between the subregions in 1983 (Supporting information), is probably caused by the timing of observation, which seems of particular importance during that summer.

Another aspect that could have contributed to the low number of ruderal observations in 1983 was the low disturbance intensity during the E10 highway building between 1976 and 1982 (methods, Bäck and Jonasson 1998). We found that ruderal species distributions along the Rallarvägen were in 2021 still clearly correlated to the railroad, rather than the E10 (Fig. 3). In contrast to the railroad construction, the E10 was not built using the Rallarvägen as a transport road, and hence its direct impact was substantially smaller. Since then, the E10 highway facilitated easier movement in and around the area by cyclists, cars, and trucks, while parking lots now enable hikers to enter the trail at numerous locations, which were less accessible in the past (e.g. *Cynoglossum officinale* seeds are known hitchhikers that is found in the area; Frenkel 1977, Bäck and Jonasson 1998, Lembrechts et al. 2014). The number of ruderal species has increased again since 1983. Whether this was simply methodological, disturbance, or climate related we cannot know for certain, but the proportionally rising number of non-native ruderal species (1903: 66%, 1913: 66%, 1983: 25%, 2021: 38%) is potentially an indication of a delayed response, yet the above discussion should make clear that caution regarding species patterns in 1983 is warranted.

Conclusions

We found that the current composition and distributions of ruderal species along the Rallarvägen were primarily associated with the initial disturbance event that occurred at the start of the 20th century, and to continuous gradients in disturbance intensity. Contrastingly, the influence of climate change did not appear to be significant at this point in time. Different parts of our investigation support this conclusion: 1) the number of ruderal species that has remained stable over time and the higher influx of non-native ruderals during railroad building back in 1903 and settlement expansion in 1913, 2) the lower EIV-T-values of recent ruderal observations, 3) the higher abundance of ruderals closer to the railroad and train stations in 2021, and 4) the upward migration of ruderals that was not related to the species' climatic constraints (EIV-T), but rather (positively) to their first year of observation. Most importantly, these findings demonstrate that historic disturbances, not climate change, have resulted in an influx of warm-adapted species into this subarctic region. We therefore conclude that these findings warrant for discretion when we make conclusions about the precise effects of climate change on ecosystems, especially in situations where significant historic disturbances have occurred. These events can leave long-lasting effects on vegetation, therefore potentially overruling climatic factors as drivers of vegetation composition and species distribution shifts (Lenoir et al. 2022).

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Author contributions

Dymphna Wiegmans: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (lead). **Keith Larson**: Conceptualization (equal); Investigation (supporting); Methodology (equal); Resources (equal); Supervision (supporting); Writing – review and editing (supporting). **Jan Clavel**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Lore Hostens**: Investigation (supporting); Writing – review and editing (supporting). **Jasmine Spreeuwers**: Investigation (supporting); Writing – review and editing (supporting). **Amber Pirée**: Writing – review and editing (supporting). **Ivan Nijs**: Writing – review and editing (supporting). **Jonas J. Lembrechts**: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (lead); Resources (equal); Supervision (lead); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (supporting).

Data availability statement

Data are available from the Zenodo Digital Repository: https://zenodo.org/records/11102224 (Wiegmans et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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