

# Historic disturbance events may overrule climatic factors as drivers of ruderal species distributions in the Scandinavian mountains

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## Abstract

The contemporary interaction of climate and land use change drives vegetation composition and species distribution shifts, making their respective roles difficult to disentangle. In this study, we investigated long-term ruderal plant species distributions along the ‘Rallarvagen’ trail in Abisko, subarctic Sweden – a trail established for railroad construction in 1903 and 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 already common along the Rallarvägen at its initial creation at the start of the 20th century. Interestingly, however, many of these native and non-native ruderals with relatively high temperature affinity that were present in 1903 and 1913, disappeared since then and did not return, despite the substantial rise in temperature in the region over the last decades. The historical disturbances also 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 richness – a process we coined Horizontal Directional Ecological Filtering, in parallel to the established concept of Directional Ecological Filtering along elevational gradients. We conclude that it is important to know the disturbance history of a system to get a good understanding of the long-term dynamics in the vegetation community, and thus its possible future in a changing climate.

## Introduction

Evidence is mounting that rapid human-caused environmental changes, such as climate (e.g., temperature warming and shifting precipitation patterns) and land use change, cause substantial species redistributions in mountain areas (Elmendorf et al. 2012; Hedenås et al. 2016; Kowarik, 2003; Pearson et al. 2013; Thuiller et al. 2008). 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 (Dainese et al. 2017; Frei et al. 2010; Rixen & Wipf, 2017). The effects of land use changes are usually less profound at higher elevations compared to lower elevations, 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, makes 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 (Elmendorf et al. 2012; Heijmans et al. 2022; Pearson et al. 2013; Taylor et al. 2017; Thuiller et al. 2005). The vegetation productivity and the length of the growing season have also increased, as a result of both higher temperatures

in summer and on average a decrease in snow cover in winter (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 have 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 & Totland, 2005; Parmesan & 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 (Dainese et al. 2017; Lembrechts et al. 2014 and 2016a, Liedtke et al. 2020; Wedegartner 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. 2018; Rendekova et al. 2019). Roadside dispersion is related to traffic intensity and the size of the road network (Chiuffo et al. 2018; Pauchard et al. 2009), 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 have a ruderal growth strategy (Alexander et al. 2016; Chiuffo et al. 2018; Kowarik, 2003). 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. 2018; 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 (Pauchard et al. 2009), but climate change and increased anthropogenic 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 (Rendekova et al. 2019). Nevertheless, a widespread uphill migration of non-native species has been observed along elevational gradients in response to climate change (Alexander et al. 2016; Dainese et al. 2017; Kueffer et al. 2013; Pauchard et al. 2009). Indeed, introductions tend to take place in the lowlands (Alexander et al. 2010; Guo et al. 2018; Liedtke et al. 2020; Pauchard et al. 2009), and from these sites species either move through human-mediated dispersal or spread out on their own.

The Directional Ecological Filtering (DEF) process 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), although evidence shows that a longer residence time also inevitably results in higher elevational limits (Pyšek et al. 2011).

Testing the interactive effects of climate change and anthropogenic disturbances on native and non-native ruderal species expansion requires detailed knowledge on the history of disturbance events, 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 and 2013). However, similar to other high latitude regions, Abisko has been subject to increasingly severe climate warming in combination with substantial anthropogenic disturbance since the early 1900s (Callaghan et al.

2013). This makes it an ideal study area to test the interaction of these global change drivers, specifically on the introduction and changes in ruderal species compositions over time.

In 1903, a railroad was completed from Kiruna to Narvik, soon followed by the first tourist hotel in Abisko (Callaghan et al. 2013). The Rallarvagen trail - the focus of the underlying study - runs parallel to the railroad and served as a transport road during construction. The accessibility of the Abisko region was further improved with the opening of the first paved road (the E10 highway) from Kiruna to Riksgränsen in 1982, which followed the existing Rallarvagen and the railroad line. The effects of the E10 on roadside vegetation were studied in 1989 (Back & Jonasson, 1998). Yet, in contrast to other studies that have examined the role of roads on the influx of non-native species (e.g. Lembrechts et al. 2014 and 2016a), the effects of the E10 construction were very limited (Back & 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 road may have become noticeable only now. Additionally, over the past decades, the average annual air temperature in the region has gradually increased from 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 of a range of plant species, as well as substantial changes in their phenology (MacDougall et al. 2021). The effects of the railroad in combination with the E10, tourism, and climate change may have caused a steady increase in ruderal species in the vegetation and dynamic changes in the ruderal composition over the past 120 years.

Importantly, a unique historical time series is now available for the region: we know the exact timing of major disturbance events (railroad and road building), we have a clear view of the changes in climate in the region (weather data has been continuously measured by the Abisko Scientific Research Station) since 1913 (ANS, 2019), and we have vegetation surveys along the Rallarvägen dating back till 1903 (Lewejohann & Lorenzen, 1983; Sylvén, 1904 and 1913-15). With these datasets in hand, augmented with a recent resurvey of the Rallarvägen trail and additional vegetation monitoring along trails leading from the Rallarvägen into the mountains, we set out to answer three key research questions about the history of ruderal species along the Rallarvägen and in the broader Abisko region:

- What are the temporal dynamics of ruderal species introductions along the Rallarvägen over the last century?
- Do these dynamics correlate most strongly with climate or land use change?
- What drives the spatial expansion of ruderal species in the Abisko region?

We hypothesized that railroad building at the beginning of the 20<sup>th</sup> century would have facilitated the establishment of significant amounts of ruderal species – both native and non-native – along the Rallarvägen trail. Additionally, we expected later disturbance events, such as the building of the E10 in the early 1980s, to have created a new influx of largely non-native ruderals, with in the last decades an influx of mostly warm-adapted ruderal species as a result of climate change.

We expected these 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 low-elevation and/or warmer environments.

## Methods

### Study site

Our study focused on a 40-km stretch of the Rallarvagen trail starting in Abisko (68°21'N, 18°49' E) at the Abisko Ostra train station, and ending in Riksgränsen, the Swedish settlement near the Norwegian border (Fig. 1). The Rallarvagen 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 track 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 Rallarvagen are numerous small settlements,

some with train stations: Abisko (with the Abisko Tourist Station), Björkliden, Låktatjåkka, Kopparåsen, Vassijaure, Katterjokk, and Riksgränsen. The E10 highway between Kiruna (Sweden) and Narvik (Norway) parallels the Rallarvagen and the railroad (Fig. 1).

Not every part of the Rallarvagen trail is equally popular. Some parts near Kopparåsen 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 (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 Rallarvagen before diverging to different parts of the area.

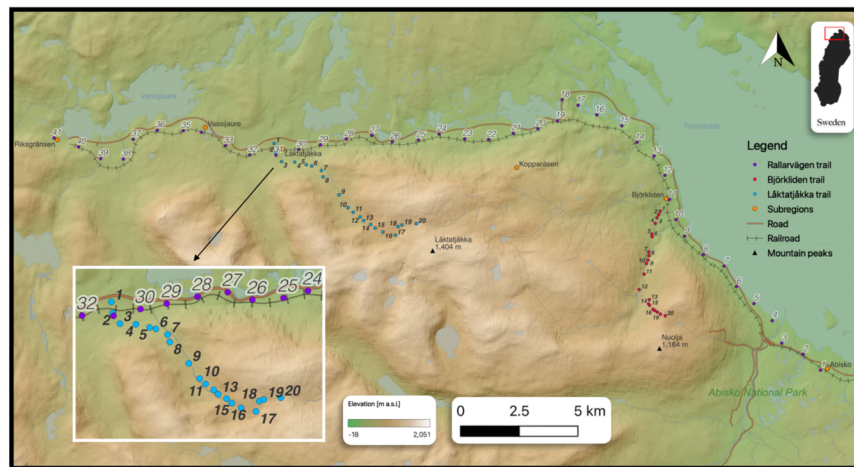


Figure 1. Map of the study region between Riksgränsen and Abisko in subarctic Sweden, on a Digital Elevation Model, with transects along hiking trails Rallarvagen (purple dots), Björkliden (red), and Låktatjåkka (blue). Each transect number along the Rallarvagen indicates the start of each transect, 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 the T-transect (see below), situated perpendicular to the trail into the vegetation. Inset shows the Låktatjåkka trail.

## Vegetation data

Here we combined 1) historical vegetation data (1903, 1913, and 1983) from along the Rallarvagen with 2) a new resurvey of the Rallarvagen in 2021 and 3) an additional survey performed in 2016 by the Mountain Invasion Research Network (MIREN; Haider et al. 2022) along two hiking trails leading from the Rallarvagen into the mountains: the Björkliden and Låktatjåkka trail (Wedegärtner et al. 2022).

The vegetation surveys by Sylvén in 1903 and 1913 focused on the establishment of ruderal species after the railroad construction (Sylvén, 1904 and 1915-17). During its construction, the surrounding vegetation was destroyed, leaving bare soil whereupon construction materials were transported and assembled. Near the end of railroad construction in 1903, Sylvén's observation of an influx of ruderal species along the Rallarvagen, most notably near the settlements of Abisko, Björkliden, and Vassijaure where construction efforts led to various dump piles of horse manure and rubbish, compelled him to survey the vegetation (Sylvén, 1904). Upon his return to the Abisko region in 1913, Sylvén observed remarkable changes in human influences on vegetation composition. 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. These new observations led him to perform a follow-up survey, this time including Riksgränsen (Sylvén 1915-17). Both publications did not specify their survey methods.

Expecting possible changes in the vegetation composition due to the building of the E10 in 1982, Lewejohann and Lorenzen (1983) re-surveyed the trail following an earlier publication from the 1950s (Asplund, 1950). They documented all vascular plant species in 20 areas of unspecified size in the broader Abisko region, using Flora Europaea vol. I (Tutin et al. 1980). We include the following surveyed areas intersecting the Rallarvägen: Björkliden, Kopparåsen, Låktatjåkka, Vassijaure, and Riksgränsen. From this publication, the Abisko area, although including the Abisko settlement and train station, was not included in our investigation as the covered survey area lay outside our area of interest: from Abiskojakka to Tjuonavaggejakka – about 25 km distance from the Rallarvägen – which includes other hiking trails and encompasses the Abisko National Park.

## 2021 Rallarvägen resurvey

In 2021, we documented all vascular plant species present in 1-km transects, within 1.5 m of the edge of the trail, along the 40-km stretch, following the taxonomic reference ‘Den nya nordiska Floran’ (Mossberg & Stenberg, 2003) (Fig. 1). The trail was surveyed twice during the growing season (July and early August) to reduce survey bias due to seasonal patterns in species presence. 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.

The 2021 survey 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),  $\mu$  is the mean abundance of the entire set of ruderal species along the Rallarvägen, and  $s$  is the standard deviation of the mean abundance of the entire set of ruderal species along the Rallarvägen. Rescaling to  $Z$ -scores is done with a linear transformation whereby  $s$  and  $\mu$  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 ruderal species is relative to the whole group of ruderals.

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 (see below).

## MIREN T-trail survey

A third dataset was obtained from the Mountain Invasion Research Network (MIREN), comprising vegetation survey data from along elevational gradients of the Björkliden and Låktatjåkka mountain trails that are leading from the Rallarvägen into the mountains (Wedegartner et al. 2022). For further description on both trails, we refer to the supplementary methods. 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 x 10 m; one parallel and two perpendicular to the hiking trail into the vegetation (supplementary Fig. 1). For every plant species we calculated the 95<sup>th</sup> percentile of its highest elevational occurrence (elevational maximum) using the *quantile* function in R (R core Team, 2021).

## Dataset compilation

For all datasets, all plant species names were standardized using the canonical name from the Catalogue of Life using the taxize package in R (Chamberlain & Szocs, 2013). Additionally, for approximately 80% of the plant 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 and databases on introduced species in Nordic areas). 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, 240 were identified as ruderal and 100 were identified as non-native ruderals. The Rallarvagen 2021 resurvey 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

We combined the Rallarvagen 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 km<sup>2</sup> for 0-5 cm depth (SoilTemp; Lembrechts et al. 2021). These maps were constructed by calculating differences (i.e., offsets) between *in situ* soil temperature time series from over 1,200 1-km<sup>2</sup> pixels, summarized from 8,500 unique temperature sensors across all the world’s major terrestrial biomes, and coarse-grained air temperature estimates from ERA5-Land (Lembrechts et al. 2020). ERA5-Land provides a reanalysis dataset with monthly free-air temperatures at a spatial resolution of 0.1 x 0.1 degrees (Copernicus Climate Change Service (C3S), 2019). We used the mean annual soil temperature (SBIO1), mean soil temperature of the warmest quarter (SBIO10; hereafter named Mean Summer Soil Temperature (MSST)), and mean soil temperature of the coldest quarter (SBIO11). 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 Rallarvagen 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 (in meters) using the measuring line and the Basemap ESRI 102113 – WGS 1984 from the QuickMapServices plugin in the QGIS software 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 version 4.1.3 (R Core Team, 2021). Every analysis was carried out for two groups: for the total ruderals and for the non-native ruderals. Using the historical Rallarvagen surveys, we analyzed 1) region-wide species richness as a function of the observational year, and 2) the mean EIV-T as a function of the observational year and first year of observation. Using the 2021 Rallarvagen survey, we analyzed 3) species richness as a function of distance to the railroad, distance to the E10, and soil temperature variables and 4) the *Z*-score abundances as a function of the ruderal species richness. Finally, using the MIREN trail survey, we modeled 5) species richness as a function of elevation and 6) the elevational maximum as a function of the first year of observation.

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*). We identified the best fitting models using 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, we centered one independent variable at its sample mean to make

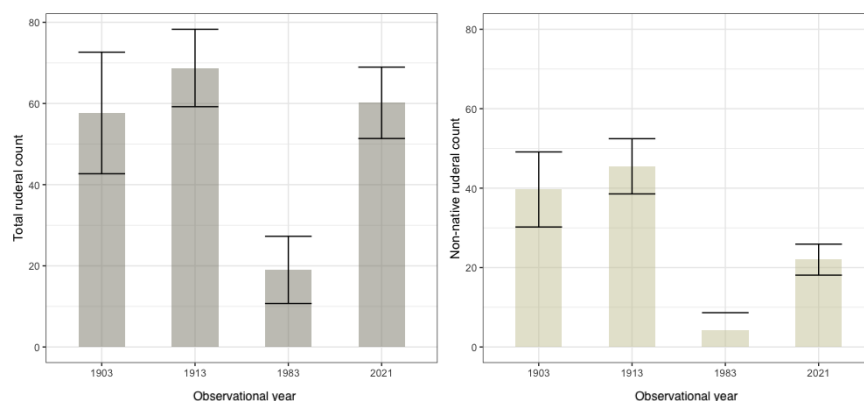
interpretation easier (Schielzeth, 2010). In multiple regression analyses, we checked for possible multicollinearity of independent variables by calculating the variance inflation factor (vif) using the *vif* function from the *car* package (Fox & Weisberg, 2011). We considered results to be significant when  $p \leq .05$  and marginally significant when  $p < .10$ .

To visualize the dissimilarities in vegetation composition between subregions and observational years, we conducted a Principal Coordinates Analysis (PCoA, = Multidimensional scaling, MDS). PCoA is an ordination technique to explore and visualize dissimilarities in species composition data by focusing on distances. The more similar the compositions are, the closer together they occur 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). 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. The obtained dissimilarity is a number between 0 and 1 – this value is 0 when two communities share all the same species, and 1 when they do not share any species.

## Results

### Number of native and non-native ruderal species over time

The total number of ruderal species did not increase significantly over time from 1903 until 2021 (Fig. 2, supplementary Table 1), with highest richness in 1913 (69  $\pm$  10 species) and the lowest in 1983 (19  $\pm$  8 species). The number of non-native ruderal species decreased significantly over that 120-year period from 69 in 1913 to 36 in 2021 (Fig. 2, supplementary Table 2). For both the total and non-native ruderals, 1983 showed the lowest species richness. Finally, ruderal communities were more dissimilar between the different surveys than subregions (supplementary Fig. 4), except for 1983 which had higher variation between subregions.

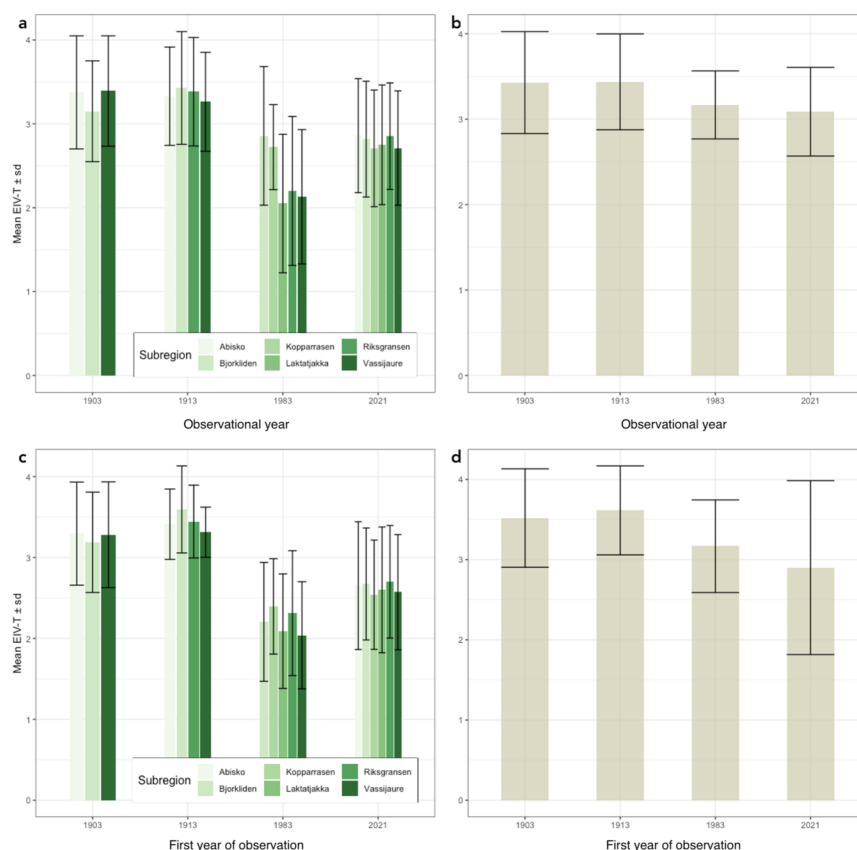


*Figure 2. Average ruderal species richness over time along the Rallarvägen. Total number of ruderal species (left) and the number of non-native ruderal species (right) as a function of the observational year, based on the number of species across subregions of all present total ruderals ( $n = 239$ ) and non-native ruderals ( $n = 100$ ) in the historical dataset. Error bars denote  $\pm$  s.d. Model coefficients and  $p$ -values are shown in supplementary Table 1-2.*

### Temperature affinity over time

The mean ruderal community temperature index (expressed as mean EIV-T value per subregion per time step) was higher in historical records than in recent times. For total ruderal species, there was a significant interactive effect of the observational year and subregion (Fig. 3a, supplementary Table 3), with mostly

lowest EIV-Ts in general observed in 1983 ( $2.2 \pm 0.2$ ) and highest in 1903 ( $3.3 \pm 0.1$ ) and 1913 ( $3.3 \pm 0.1$ ). Mean EIV-Ts were constant within subregions between observational years, except for 1983, which showed the most variation in these values. The mean community temperature index for non-native ruderal species decreased gradually through time, without an interactive effect of subregion (Fig. 3b, supplementary Table 4). Similar negative trends occurred for the mean community temperature indices as a function of the first year of observation in a subregion (Fig. 3c-d, supplementary Tables 5-6). In combination with the high degree of heterogeneity that existed between communities (supplementary Fig. 4), this suggests that newly introduced species (in 1983 and 2021) were less warm adapted than in 1903-13.



*Figure 3. Ecological Indicator Values (EIV-T) of all (left) or only non-native (right) ruderal species observed over time (top) and as a function of 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 in the historical dataset. Error bars denote  $\pm$  s.d. Model coefficients and p-values are shown in supplementary Tables 3-6.*

#### Ruderal richness and abundance with distance to introductory points and temperature

The number of total ruderal species and non-native ruderal species 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. 4, supplementary Tables 7-8). No additional variation was explained by distance to the E10, the mean soil temperature of the coldest quarter, or mean annual soil temperature.



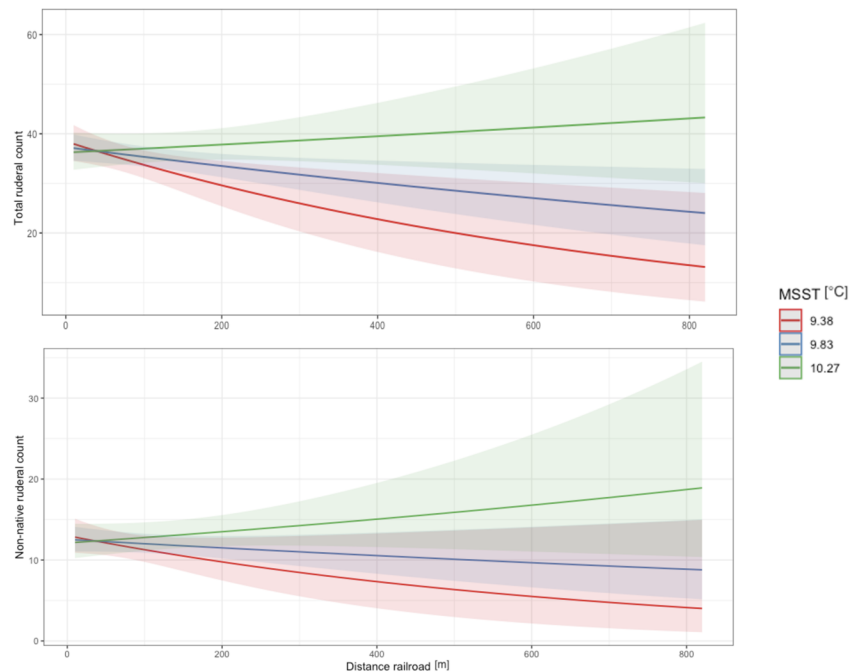


Figure 4. Effects of Mean Summer Soil Temperature (MSST, in °C) and distance of the Rallarvågen trail to the railroad (x-axis, in m) on the total number of ruderal species (top) and the number of non-native ruderal species (bottom) per 1-km transect along the Rallarvågen. To make interpretation easier we centered the covariate MSST at its sample mean (see methods). Graphs are prediction plots with the estimated marginal effects. Lines show the model means (blue) with standard deviation (green and red); shading indicates at which chi-squared value a significant p-value is reached. Raw data points are not shown for clarity. Model coefficients and p-values are shown in supplementary Tables 7-8.

Importantly, transects with lower ruderal species richness had a higher  $Z$ -score (Fig. 5, supplementary Table 9), indicating that the few species present in these transects were common throughout the region. Transects with higher ruderal species richness – especially those nearest to the railway stations – hosted more and on average rarer ruderal species that only occurred in these few transects.

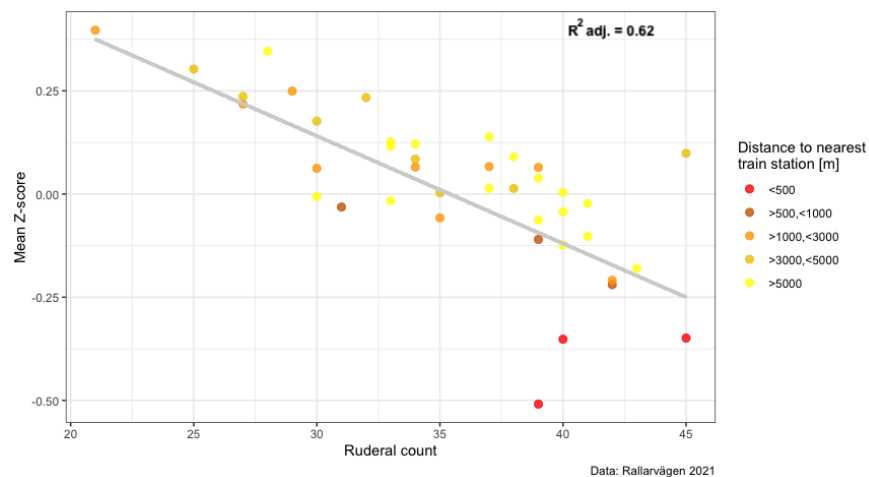


Figure 5. Relationship between ruderal species abundance (expressed as mean Z-scores of all species per transect, with a higher Z-score indicating more common species) and the total number of ruderal species (in counts) along the Rallarvågen. Colors indicate the distance to the nearest train stations (either Abisko Östra, Björkliden or Riksgränsen). Model coefficients and p-values are shown in supplementary Table 9.

## Elevational limits

Along the two trails leading from the Rallarvågen into the mountains, we found a significant negative association between total ruderal species richness and elevation. A similar negative, but less pronounced, relationship was found for non-native ruderals (Fig. 6, supplementary

Tables 10-11). There were no significant differences in these relationships between mountain trails for both total ruderals and non-native ruderals.

For total ruderal species, the elevational maximum 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. 7, supplementary Tables 12-14). For non-native ruderals as well, a marginally significant positive association was found between the elevational maximum and the first year of observation to the whole region, for both trails (Fig. 7, supplementary Table 15). There was no additional variation explained by EIV-T for both total ruderals and non-native ruderals.

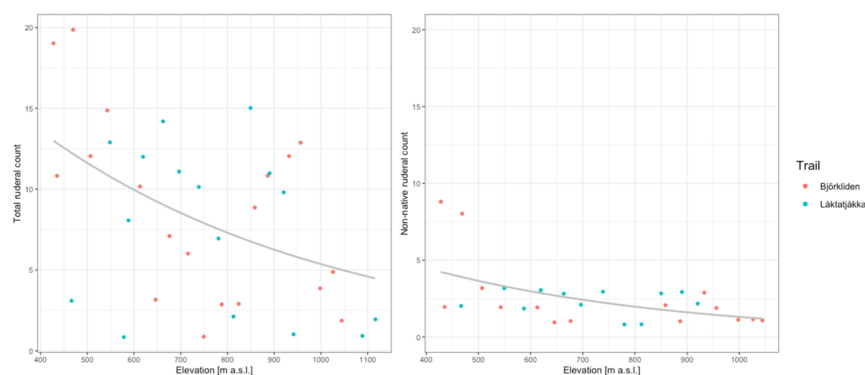


Figure 6. Relationship between ruderal species richness (left: total, right: non-native only) and elevation on two mountain trails. Left  $n = 39$ , right  $n = 12$ ). Björkliden (in red) and Låktatjåkka (in blue) mountain trails, trendline in gray as no significant difference between both trails was observed. One dot is the species count at a certain elevation and hiking trail. Model coefficients are shown in supplementary Tables 10-11.

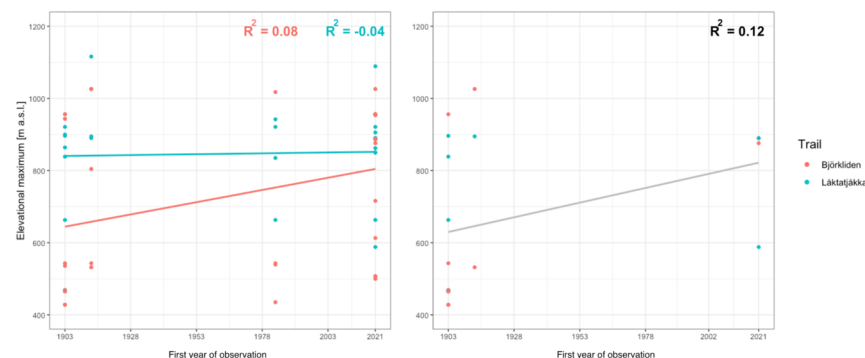


Figure 7. Relationship between ruderal species' elevational maximum (left: total, right: non-native only) and the first year of observation in the whole region on two mountain trails. Left  $n = 39$ , right  $n = 12$ . Björkliden (in red) and Låktatjåkka (in blue) mountain trails, trendline on the right in gray as no significant difference was observed between both trails. The elevational maximum was defined for each species as the 95th percentile of its elevational occurrences. One dot is the species count at a certain elevation and hiking trail. Model coefficients and  $p$ -values are shown in supplementary Tables 12-14.

## Discussion

### Temporal patterns

Native and non-native ruderal species temporal dynamics deviated surprisingly much from our hypotheses. Indeed, we expected to find an increase in ruderal species over time as a result of the joint impact of climate and land use change on the vegetation composition along the Rallarvägen, since both have been shown to be advantageous for ruderal species (Chiuffo et al. 2018; Guo et al. 2018; Thuiller et al. 2005). Following this hypothesis, we can indeed assume that already shortly after the building of the railroad at the beginning of the 20th century substantial numbers of ruderal species were already present along the Rallarvägen trail - both native and non-native to the region, as the bare ground that remained accommodated up to 82 ruderal species, of which 44 were non-native, according to the first survey in 1903 (Fig. 2). Contrary to expectations, however, ruderal species (both the total and the non-native ruderals separately) were most numerous along the trail during the time of the railroad building and settlement expansion (1903-1913). The building of the E10 road (completed in 1983) did not result in an additional influx of ruderal species, nor did the substantial climate warming since the late 1980s. In 2021, total ruderal species richness was just below the levels of 1913, while non-native ruderal richness was only half of the numbers in 1903 and 1913. The drop in 1983 must be at least partially a methodological anomaly, but even then, we must consider the total number of ruderal species to have remained roughly constant through time, and the number of non-native ruderals to be decreasing (see 'limitations' below).

What is more, patterns in the community temperature index (expressed as the Ecological

Indicator Values for Temperature; EIV-T) revealed that most warm-adapted ruderal species were already present in the early 20<sup>th</sup> century, after the building of the railroad, with little evidence of an influx of warm-adapted species due to climate change in recent years (Fig. 3). In fact, we even observed a steady decline in mean EIV-T of the non-native ruderals up until 2021. Our data showed that 36 (mostly 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 on average lower EIV-T values. It is likely that those warm-adapted ruderal species were introduced along the Rallarvägen with its initial construction (and likely the addition of non-native soil introduced into gardens in settlement areas). After this initial introduction, however, these species did not manage to sustain a stable population, potentially due to a combination of harsh winters and the lack of continuous disturbance after 1913 (Lembrechts et al. 2016b; Niittynen & Luoto, 2017; Rendekova et al. 2019). Interestingly, the lack of additional significant disturbance events along the trail in recent years, seems also to have prevented these species from re-establishing now that the climate has warmed to an average 1.0degC (ANS, 2019; Lembrechts et al. 2016b). 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. 4 and 5). 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 degC) and below

average (9.4 degC) 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). However, our findings also showed a climatic response on ruderal species distributions as the predicted number of both the total ruderals and non-native ruderals increased with distance to the railroad in transects where summer soil temperatures (MSST) reached above average values (10.3 degC; Fig. 4). This could indicate a potential role for climate change: if climate warms, the current climatic limitations might decrease, allowing for non-natives to expand further away from disturbed sites (Lembrechts et al. 2018).

Interestingly, average ruderal species abundances were negatively correlated with the total number of ruderal species per transect (Fig. 5), revealing a gradient from sites that accommodated relatively few and predominantly common ruderal species to sites that accommodated relatively many and often rare ruderals. Transects with train stations, such as Bjorkliden, Abisko Ostra and Riksgransen, experience continuous disturbance and appear to be the sites where rare ruderals reside and are thus (re)introduced (Brandes, 2002). From here they must spread out through local human-mediated dispersal (e.g., hiking) or through self-dispersal. In less disturbed transects along the Rallarvagen, only fewer and more common ruderal species still reside. Those sites were sometimes not easily accessible, lay further away from train stations, and were places where significant disturbance (outside of occasional hiking) only happened once (i.e., during railroad building in the early 20<sup>th</sup> century) (Rendekova et al. 2019). Exact drivers for this relationship are difficult to determine from observational data only, but we can assume a link with the degree of disturbance intensity. Distance to the E10 highway, railroad, and train station, and hiking-intensity were all interconnected and sum-up to a certain degree of disturbance intensity that facilitates species dispersal (Kowarik, 2003; Pauchard et al. 2009).

We propose that the correlation between human impact and ruderal species distributions demonstrates Horizontal Directional Ecological Filtering (HDEF; Fig. 5). The term Directional Ecological Filtering (DEF) was first coined by Alexander et al. (2010) for elevational (climatic) gradients, but here we demonstrate that the concept is applicable to a horizontal anthropogenic disturbance intensity gradient 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 the DEF, where climate harshness is considered the most likely filter, 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. This led to the conclusion that gradients of disturbance intensity coinciding with the elevation gradient should not be ruled out as a critical driver of the DEF either (Pauchard et al. 2009).

### 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 Rallarvagen (Fig. 6) (Alexander et al. 2010; Dainese et al. 2017; Lembrechts et al. 2014; Liedtke et al. 2020; Wedegartner 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 neither the non-native nor all ruderal species' elevational maxima in our system 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. 7): 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 might 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. 7), substantiating the fact that the first year of observation to the whole region does not fit the elevational maximum very well.

## Limitations

The core challenge in this study lies in the quality and comparability of the historical surveys. While we here focused on overarching trends in species richness, these trends mask a substantial turnover in species composition between surveys, which is likely at least partially the result of methodological differences. These methodological differences seem to have been most substantial for the 1983 effort, yet these can be interpreted when considering the following aspects: 1) monitoring differences, 2) weather conditions, and 3) disturbance intensity.

While the vegetation survey of Lewejohann & Lorenzen (in 1983) was conducted during the same month (July) as Sylven's surveys (in 1903 and 1913) and our own in 2021, the covered perimeter (20 areas in total) was much larger. As a result, they presumably had the time to survey all areas only once, therefore likely missing ruderal species that appear later in the season. Additionally, their data missed perennial species such as *Trifolium pratense* L., *Trifolium repens* L., and *Vicia cracca* L., which were present in 1903 and 1913 and are currently very abundant along the Rallarvagen trail. Even when these ruderal species are not flowering, they are easily identified, suggesting some selectivity in documenting species during their survey. An unexpected discovery, as Lewejohann & Lorenzen set out to survey vegetation changes following the disturbance caused by the building of the E10 road, and thus should have shown particular interest in ruderal species (Lewejohann & Lorenzen 1983; 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 mentioned above would have disappeared entirely. We do believe that all survey locations are still comparable as the landmarks in the surveyed villages have remained the same since 1903: the train stations have always been an anchor point for the villages.

Importantly, 1983 was also an anomalous year in terms of weather conditions (supplementary Table 16). Summer temperatures were on average 1degC 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 & 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 (Niittynen & Luoto, 2017; Wipf, 2010). Moderate rainfall can speed-up the snow-melting process, expediting the onset of the growing season. Heavy rainfall, on the other hand, causes earlier snowmelt, yet then 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 the other observational years: 54% in 1903, 49% in 1913, and 16% in 2021. Five out of those seven occurred only at Bjorkliden. Interestingly, this was also the subregion in 1983 that accommodated species with highest average EIV-Ts (Fig. 3). This, in addition to the observed degree of heterogeneity between the

subregions in 1983 (supplementary Fig. 4), 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 (Back & Jonasson, 1998). We found that ruderal species distributions along the Rallarvagen were in the most recent survey still clearly correlated to the railroad, rather than the E10 (Fig. 4). In contrast to the railroad construction, the E10 was not built using the Rallarvagen as a transport road, and hence its direct impact on the Rallarvagen vegetation during that time was substantially smaller. Since then, the 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 (Back & Jonasson, 1998; Frenkel, 1977; Lembrechts et al. 2014). Nevertheless, the resulting influx of ruderals along the Rallarvagen was possibly not yet detectable in 1983. Indeed, ruderal species numbers increased again since then, yet whether this was simply methodological, disturbance, or climate related we do not know. The proportionally rising number of non-native ruderal species 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

In this study, ruderal species composition and distributions along the Rallarvagen showed to be mostly related to the original disturbance event since its inception at the start of the 20<sup>th</sup> century, as well as to continuous gradients in disturbance intensity, while recent climate change effects were not (yet) significant. 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, 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 exact impacts of climate change to ecosystems, especially when historic disturbances have been present. Such significant disturbance events can have long-lasting effects on vegetation compositions and distributions and therefore overrule climatic factors as drivers of species distributions (Lenoir et al. 2022). Most importantly, our results highlight the importance of the knowledge of disturbance history of a system when interpreting species distributions. Nevertheless, the rapid changes in climate observed in the Abisko region suggest that we will likely see the fingerprints of climate change effects on the vegetation communities in the future.

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