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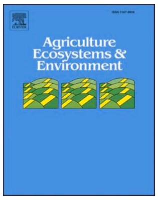

Ninety years of alien plant species accumulation across regional and local scales in central European fields

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ABSTRACT

Alien species are increasingly prevalent worldwide, leading to economic and biodiversity losses. We examined how the spread of non-crop alien plant species (i.e., archaeophytes and neophytes) has evolved in arable fields across ten countries in central Europe from 1930 to 2019. Specifically, we analyzed how regional and local trajectories of alien plant species have changed over the last ninety years. We used a dataset of 21,747 vegetation

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plots from the AgriWeedClim database and applied generalized linear mixed-effect models. We analyzed the percentage of plots containing neophytes to characterize regional scale dynamics, as well as the proportional number and relative abundance of alien species per plot, offering insights into the local scale dynamics of alien species spread in arable fields. The dynamics of species populations in the study area revealed significant contrasts between neophytes and archaeophytes over time. The percentage of plots containing neophytes strongly increased from 34.2 % in 1930 to 70.1 % in 2019. The proportion of neophytes, in plots nearly doubled from 5.5 % in 1930 to 10.2 % in 2019. The relative abundance, meaning their biomass relative to the total biomass of all species in the plot, of neophytes followed a similar upward trend increasing from 4.1 % to 9.9 %. This highlights not only the spatial spread of neophytes in arable vegetation but also their increasing cover on the local scale. Archaeophyte species displayed a different trajectory. Their proportion exhibited only a modest increase from 23.2 % to 25.3 % over the ninety-year period, while their relative abundance slightly decreased from 21.2 % to 19.5 %. A sensitivity analysis of our data further revealed that the temporal increase in the percentage of plots containing neophytes is mainly driven by a few common species, such as *Veronica persica* and *Erigeron annuus*, which had a high number of records during the study period. We anticipate an increasing occurrence of neophytes in local communities in the future, which may contribute to the homogenization of regional arable plant communities.

1. Introduction

Alien species are accumulating in regions worldwide (Seebens et al., 2017), a phenomenon increasingly recognized as one of the consequences of the global expansion of trade and transport, which facilitates their spread and establishment in new environments (Pyšek et al., 2020). This trend is contributing to the emergence of biological invasions as a primary cause of biodiversity loss across the globe (Brondízio et al., 2019; IPBES, 2023; Pyšek et al., 2020, 2012; Seebens et al., 2021), with substantial and growing impacts on human well-being and the economy (Diagne et al., 2021; IPBES, 2023).

Despite the strong increase of alien species in regional species pools (Seebens et al., 2017), this phenomenon is not fully reflected at the local scale. Field data, such as plot-based records, indicate that the contribution of alien species to local community composition remains rather small (Liu et al., 2023). This disparity between the regional accumulation of alien species and their representation in local communities could be attributed to factors such as unsuitable local conditions, native species preventing the establishment of alien species, or time lags before newly arrived alien species become established in local ecosystems (Pagad et al., 2022). While the regional accumulation of alien species is well-documented (Juozaitienė et al., 2023; Seebens et al., 2017), the local-scale dynamics have been less explored.

For vascular plants, the level of invasion in vegetation plots has been shown to depend on the habitat type, with arable fields in Europe being particularly susceptible to invasion due to heavy human impact and the facilitation of propagule dispersal by machinery and attached soils (Chytrý et al., 2009; Richardson and Pyšek, 2006). Over the last century, the transformation of these arable fields through modern agricultural practices has brought about significant consequences for the flora and fauna associated with these habitats (Poschlod, 2016). This period saw not only a reduction in arable land driven by the conversion of less profitable fields into urban areas, forests, or grasslands (with many arable fields converted into pastures or left abandoned), but also the extensive sprawl of cities into all types of land (Fuchs et al., 2015; Klein Goldewijk et al., 2011). These processes were associated with an intensification of agriculture on the remaining land, characterized by increased mechanization and the escalated use of synthetic fertilizers and pesticides. Recent studies indicate that such intensification of human land use has contributed to an increased spread of alien plant species, underlining the interconnected nature of agricultural practices and species invasions (Liu et al., 2023; Scherrer et al., 2022).

In Europe, alien plant species are classified into neophytes (i.e. alien plant species introduced after c. 1492) and archaeophytes (i.e., alien plant species introduced before c. 1492) (Essl et al., 2018; Pyšek et al., 2004). The spread of archaeophyte species was facilitated by early agricultural practices, whereas modern agricultural practices have facilitated the spread of neophytes. Findings from Pyšek et al. (2005) indicated that from 1955 to 2000, neophyte species in European arable plant communities increased in number and proportion, whereas native plant species (i.e., species historically present in the region and not introduced by humans) and archaeophytes declined.

Major changes in weed species composition in central Europe are influenced by a variety of factors, including soil type, crop type, climate, human population density, precipitation, temperature, and soil base status. For example, the number of hemicryptophytes (plants that have their perennating buds at the soil surface) has increased, while therophytes (plants that complete their life cycle within a single year) have decreased (Lososová et al. 2004). Seasonal dynamics play a crucial role as well, with more neophytes, overall higher species richness, and greater beta-diversity observed in summer arable plant communities compared to those in spring. Long-term trends reveal an increase in the number of hemicryptophytes and neophytes, while therophytes, archaeophytes, and overall species richness have declined. Crop-specific management practices influence weed vegetation, with less disturbed crops like cereals harboring fewer neophytes and higher species richness compared to more frequently disturbed crops like root crops (Lososová et al. 2004).

Agricultural fields are known to provide plenty of opportunities for neophyte species to establish. The practices used to sustain crop production inadvertently provide these species with the conditions they need to thrive. Arable fields offer ample sunlight, disturbed soil, and nutrient-rich environments – perfect conditions for neophytic weeds to establish and spread rapidly. An analysis based on over 50’000 vegetation plots from Europe (Chytrý et al., 2008b) showed that arable fields had among the highest levels of invasion by alien plants. As neophytes are often found in habitats also occupied by archaeophytes, it has been suggested that the species richness of archaeophytes can be considered as a good positive predictor for the invasion by neophytes (Chytrý et al., 2008a). A large part of the shift towards more intensified agricultural practices occurred during our study period, which spans from 1930 to 2019.

We asked the following research questions: (i) At the regional scale, how does the percentage of plots containing neophytes change over time? Given the global increase in trade, transport, and agricultural intensification, we expect that the percentage of plots containing neophytes has increased over time; (ii) At the local scale, how does the proportion of alien plant species (neophyte and archaeophyte species) change over time? We expect that the proportion of neophyte species has increased at the local scale, as modern agricultural practices—such as increased mechanization and the use of synthetic fertilizers and pesticides—create favorable conditions for neophytes to establish and spread. In contrast, the proportion of archaeophyte species may have remained stable or decreased due to these same practices; iii) At the local scale, how does the relative abundance of alien plant species (neophyte and archaeophyte species) change over time? We expect the relative abundance of neophyte species to have increased. Modern agricultural practices, such as soil disturbance and fertilizer use, likely promote neophyte growth and competitive advantage, potentially compounded by enemy release, where fewer natural predators and pathogens allow for greater growth. In contrast, the relative abundance of archaeophyte species may have decreased due to competition with neophytes.

2. Material and methods

2.1. Study area and data sources

Data on local arable plant communities was obtained from the AgriWeedClim database (Glaser et al., 2022) covering a study area of around 900,000 km^2, across ten central European countries (Austria, Croatia, Czech Republic, Germany, Hungary, Liechtenstein, Northern Italy, Slovakia, Slovenia, Switzerland) (Fig. 1). It compiles data from large repositories (e.g., European Vegetation Archive), specialized regional databases, colleagues, and the literature.

The database was filtered to include only vegetation plots from arable fields, excluding orchards, vineyards, and fallows. The filtered data included only vegetation plots with species abundance measures, geographical coordinates, and the time of sampling. Species within the AgriWeedClim database are categorized based on their biogeographic status as native, archaeophyte, or neophyte, based on national lists of alien species (Glaser et al., 2022). The AgriWeedClim database version 1.0 contains 32,889 vegetation plots sampled from 1916 to 2019 across central European arable habitats. The data was collected opportunistically, and biases, such as spatial unevenness, are inherent due to variations in sampling intensity and focus across regions. Alien species were further categorized as archaeophytes (introduced before c. 1492 CE) or neophytes (introduced after c. 1492 CE), see Pyšek et al. (2004) for details on the terminology. In cases where species were classified differently across countries, the classification was standardized in the AgriWeedClim database. Specifically, we applied the following criteria: if a species was categorized as a native in any country within the study

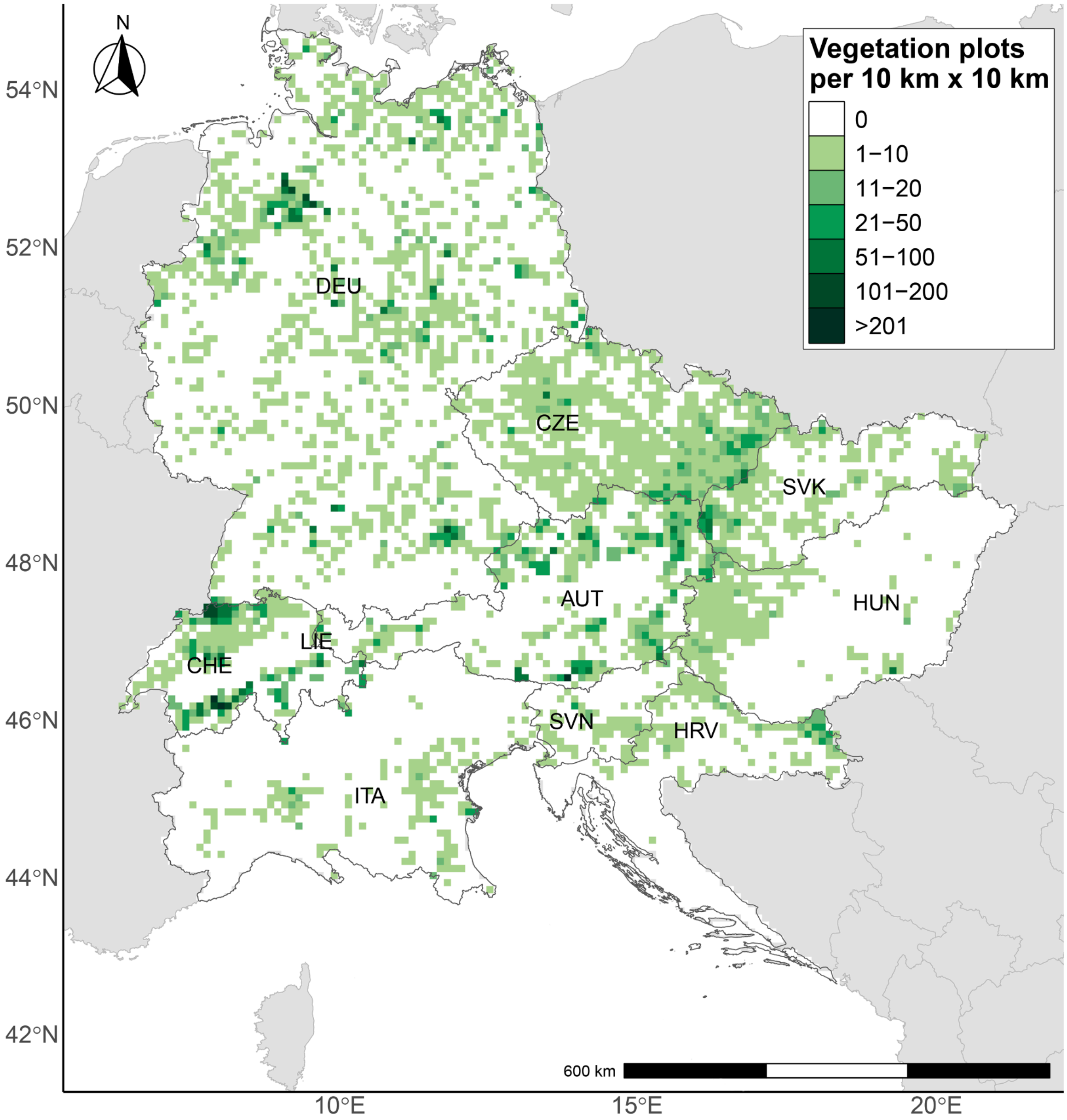

Fig. 1. Density of vegetation plots from 1930 to 2019 (n = 21,747) in arable fields in the AgriWeedClim database on a 10 km × 10 km raster. Regions outside the study area are shown in gray.

area, it was classified as a native across the entire region. If not, and it was categorized as an archaeophyte in any country, it was classified as an archaeophyte in the study region; otherwise if it's native range was outside the study region, it was classified as neophyte. The biogeographic status of each species was determined according to minimum residence time, following the guidelines of (Pyšek et al., 2004). Species with native ranges overlapping the study area were labeled as native, while those without such overlap were considered alien. Native range data was sourced from the World Checklist of Selected Plant Families (WCSP, 2024) and the Germplasm Resources Information Network (GRIN, 2024).

In total, we extracted 21,747 vegetation plots from arable fields, with a total of 413,145 individual species records of vascular plants. Given that more than 100 studies have been incorporated in AgriWeedClim, it is unsurprising that plots differ in size, sampling date (e.g., the time when the records were sampled), and level of completeness of information (e.g., plot size was only available for 60 % of the plots). Despite this, we included all plots in our analysis, regardless of whether plot size information was available, in order to utilize the full extent of the data. To test the effect of plot size, we ran an additional model, using only the subset of plots with reported plot sizes, including the effect of log-transformed plot area (see appendix). Furthermore, information on whether the plot was recorded at the field edge or in the field interior, which is generally poorer in species (Bürger et al., 2022, Wietzke et al., 2020), was not available for the majority of plots. This lack of information is a well-known issue in vegetation science. A review of 172 studies published between 1927 and 2022 (Bürger and Küzmič, 2023) found that many publications lacked detailed methodological reporting, especially in phytosociological studies. For example, the review noted significant variability in reported plot sizes and inconsistencies in specifying study methodologies.

The study's geographical scope extends in latitude from 43.92°N to 54.8°N, and in longitude from 6.02°E to of 22.56°E (Fig. 1). This extensive spatial coverage encompasses regions with diverse topographical features and climatic gradients. These range from oceanic influences in the western parts of Germany to more continental and sub-Mediterranean climates in the east and south, respectively. The selection of such a geographically varied region allowed for a comprehensive investigation of alien plant species' occurrences across different landscapes within central Europe. To describe the environmental conditions of each plot, we used climate data, specifically mean monthly temperatures, and total precipitation, from the CRU database (Harris et al., 2020). The mean annual temperatures in the lowlands were approximately 7–10 °C.

2.2. Statistical analysis

To study the temporal trends in alien plant species accumulation, we used the following metrics: the percentage of plots containing at least one neophyte species (archaeophytes were not considered as they were present in nearly all plots), the proportion of neophytes or archaeophytes per plot (expressed as the ratio between the number of neophytes or archaeophytes and the total number of plant species recorded in a given plot), and the relative abundance of neophytes or archaeophytes per plot (expressed as the ratio between the abundance of neophytes or archaeophytes and the total abundance of all plant species in a given plot). These metrics were selected because they capture different aspects of invasion dynamics at two distinct scales. The percentage of plots containing neophytes provides a large-scale measure of the spread of neophytes across the study region. The proportion and relative abundance of alien species per plot reflect the community composition at the plot level. We used these relative measures because they offer a better assessment than absolute species counts or total abundance, which are influenced by plot size, species richness, and sampling conditions. Relative metrics reduce biases related to location and sampling time, offering a more robust measure of the composition of neophytes, archaeophytes, and native species.

To study the differences in alien plant species accumulation across regional and local scales, we define the regional scale as the presence of alien plant species across plots and the local scale as their presence in terms of abundance and species composition within plots. While archaeophytes are already widely established across plots, neophytes are not, making it important to investigate their spread across both scales, whereas changes in archaeophytes are analyzed within plots, at local scale.

We employed generalized linear mixed-effect models (Bolker et al., 2009) to investigate the probability of neophyte presence, along with the proportion and relative abundance of alien plant species within plots. To determine the percentage of plots containing neophytes (i.e., those containing at least one neophyte species), we used a binary logistic model with random effects, using a logit link function. Our primary focus was on examining the temporal trend. To ensure our observations accurately reflected this trend over time, we controlled for confounding effects by considering other fixed and random effects. Our fixed effects included the year of record for each plot to analyze temporal trends, the geographical coordinates (latitude and longitude) to account for spatial heterogeneity in sampling effort, and climatic variables (annual temperature and annual precipitation) to adjust for potential spatio-climatic sampling bias. The number of species were also included in the regional model to account for the potentially higher detection rate of neophytes when more species were present. Since the percentage and relative abundance are calculated based on the number of species, we didn't include it as a predictor in the plot-level models, as these measures inherently reflect a proportion of alien species within the total species count in each plot. Due to the high correlation between temperature and precipitation ($r = 0.80$ for all plots or $r = 0.81$ for plots containing neophytes), only temperature was included in each model to prevent variance inflation of regression coefficients (see Fig. S1 in supplementary material). We added random effects to control for potential biases, which included the month of sampling to account for seasonal variation, crop type because the cultivated crop species and associated management practices could influence plot invasibility and the study (indicated by bibliographic reference; for complete reference list see Table S6, supplementary material) to account for variability caused by different methodologies. A detailed outline of the fixed and random effects used in our models is given in Table 1.

In the following we give a detailed description of the response variables and the fixed and random effects used in the model.

2.2.1. Response variables

To determine the percentage of plots containing neophytes, we used a binary response variable indicating whether a plot contained at least one neophyte species. For the proportion of neophytes and archaeophytes per plot, we divided the number of neophyte and respectively

Table 1
Set of fixed and random effects used to model i) percentage of plots containing neophytes, ii) proportion of neophyte and archaeophyte species and iii) relative abundance of neophyte and archaeophyte species. Responses indicated by * were arcsine transformed.

Response	Fixed effects	Random effects	Model family
Percentage of plots containing neophyte species	Year, Number of Species, Latitude, Longitude, Temperature	Month of sampling, Crop type, Study	Binary logistic
Proportion of neophyte and archaeophyte species*	Year, Latitude, Longitude, Temperature	Month of sampling, Crop type, Study	Gaussian
Relative abundance of neophyte and archaeophyte species*	Year, Latitude, Longitude, Temperature	Month of sampling, Crop type, Study	Gaussian

archaeophyte species in a plot by the total number of species. Similarly, for the analysis of the relative abundance of neophytes and respectively archaeophytes per plot, we calculated the cumulative abundance of both types of alien species, divided by the total cumulative abundance. We only included plots that had at least one neophyte or archaeophyte present, as our focus was on the changes in these variables over time in plots where alien species were already present, rather than on the binary presence of absence of these species. An arcsine square root transformation was applied to the response variables to homogenize variance. Subsequently, the transformed responses were analyzed using linear mixed effects models with Gaussian error distribution.

2.2.2. *Fixed effects*

To analyze the relationship between time and the dependent variables, we used the year when each plot was recorded. To mitigate the effect of extreme weather in single years on response variables, we computed the mean temperature of 10 years before the year of the record. This approach provided a representative characterization of long-term climate conditions. To control for geographical effects, we included latitude and longitude as fixed effects in every model to account for spatial heterogeneity and mitigate sampling biases in the spatial distribution of plots. This approach helps separate location-based influences from other variables, resulting in less biased estimates of the effects of primary explanatory variables. In the analysis of the percentage of plots containing neophytes, we used the total number of species per plot as a proxy for the combination of plot size, sampling effort and detection rate. We did not directly include information about the plot size as it was only available for about two thirds of the plots.

2.2.3. *Random effects*

A total of 396 bibliographic references called hereafter ‘studies’ were added to the analyses as a random effect to account for potential biases from varying study methodologies and designs. One plot did not have a study assigned to it and was excluded from the analysis. To take into account the influence of climatic seasons on arable plant communities, we used the month of sampling as a random effect. The 1142 plots for which the sampling month remains unknown were treated as an additional group (i.e., “unknown”). Most plots were recorded during the peak growing season, with June (3840 plots) and July (5233 plots) having the highest number of records, followed by May (3698 plots) and August (3169 plots). Sampling was least frequent during the winter months, with February (5 plots) and December (47 plots) having the fewest records. January had a surprisingly high count of 1191 plots, likely due to database errors or unknown dates. Since we could not differentiate between true records from January (which are expected to be few) and database errors, we treated January as a separate group in the random effect. This accounts for the variability by allowing the model to estimate a separate variance for the plots from this month, enabling it to handle the additional uncertainty and potential anomalies in the January data without biasing the overall results. To consider potential variations in species composition, crop type information was also used as a random effect. The breakdown of the study plots by crop type is as follows: cereals (9934 plots), root crops (7358), oil crops (2310), fodder and fertilizer crops (731), vegetable crops (564), and other types of crops (849).

2.2.4. *Sensitivity analysis*

To determine the species most influential in the observed trend of neophyte species accumulation over time, we conducted a sequential sensitivity analysis by systematically excluding each neophyte species one at a time from the dataset for all three response variables. Upon excluding each species, we reanalyzed the data before excluding the next one. This iterative process continued until we had individually processed all neophyte species. By calculating the percentage decrease in the year effect size with each exclusion, we were able to identify key species that influenced the temporal trend. Archaeophytes were already widely established in almost every vegetation plot, making it impossible to analyze their spread using this method, as the trend line would remain at 100 %.

We performed data extraction, modeling, and the analysis of results using *R* (R Core Team, 2023) with the packages ’lme4’ (Bates et al., 2015), ’lmerTest’ (Kuznetsova et al., 2017), ’corrplot’ (Wei et al., 2017), ’tidyverse’ (Wickham, Averick, et al., 2019). All programming was done in the IDE RStudio (Posit team, 2024).

3. Results

3.1. *Percentage of plots containing neophytes*

The percentage of plots containing neophytes increased from 34.3 % (1930) to 70.1 % (2019) (Fig. 2a). The number of species per plot had a significant positive effect, adjusting for the increased probability of detecting neophytes as species richness increases. Latitude showed a significant negative effect and longitude a positive one, capturing spatial structure potentially tied to regional distribution or sampling variation (Table 2). Including plot size information (available for 60 % of the plots) as log-transformed area did not change the results (see Fig. A.1 and Table A.1 in appendix). The sensitivity analysis showed that the temporal increase of detecting at least one neophyte in a plot is mainly driven by a few common neophyte species, like *Veronica persica*, *Matricaria matricarioides* or *Galinsoga quadriradiata* with a high number of records in the study period (Fig. 2b; Table S3, supplementary material) indicating that these species had recently spread rapidly in the study region.

3.2. *Proportion of neophytes and archaeophytes in plots*

The proportion of neophytes nearly doubled from 5.5 % to 10.2 % in the period from 1930 to 2019 (Fig. 3a) whereas the proportion of archaeophyte species showed only a slight increase from 23.2 % to 25.3 % (Fig. 3c). Latitude and longitude had significant negative effects on both neophyte and archaeophyte species, capturing spatial structure potentially tied to regional distribution or sampling variation. Additionally, temperature had a significant positive effect on the proportion of alien plant species (Table 3). When plot size information (available for 60 % of plots) was included as log-transformed area, the results showed similar trends as for the whole dataset for both neophytes and archaeophytes (see Fig A.2a,c and Table A.2 in appendix).

The sensitivity analysis revealed that the proportion of neophytes at the plot level is influenced by species with a high number of records in the study region, with significant differences in their influences. Specifically, the neophyte species that are driving the effect size of time on the proportion of neophytes at the plot level were identified (Fig. 4a; Table S4, supplementary material). *Veronica persica* emerges as a leading contributor, showing an increase substantially above the average trend. Similarly, *Amaranthus powellii*, *Amaranthus retroflexus*, *Erigeron annuus*, and *Galinsoga quadriradiata* had a high influence. In contrast, species such as *Amaranthus albus*, *Bromus diandrus*, *Erigeron canadensis*, and *Galinsoga parviflora* increased below the average trend, indicating a lesser influence on the overall upward trend of neophyte proportions.

3.3. *Relative abundance of neophytes and archaeophytes*

We found a significant increase in the relative abundance of neophyte species in plots from 4.1 % to 9.9 % (Fig. 3b) between 1930 and 2019 and a slight decrease in the relative abundance of archaeophyte species from 21.2 % to 19.5 % (Fig. 3d). The relative abundance of both neophyte and archaeophyte species decreased toward the north, as indicated by a significant negative effect of latitude, which is also correlated with decreasing mean temperature. Similarly, archaeophyte abundance declined toward the east, shown by a significant negative effect of longitude, accounting for spatial heterogeneity related to

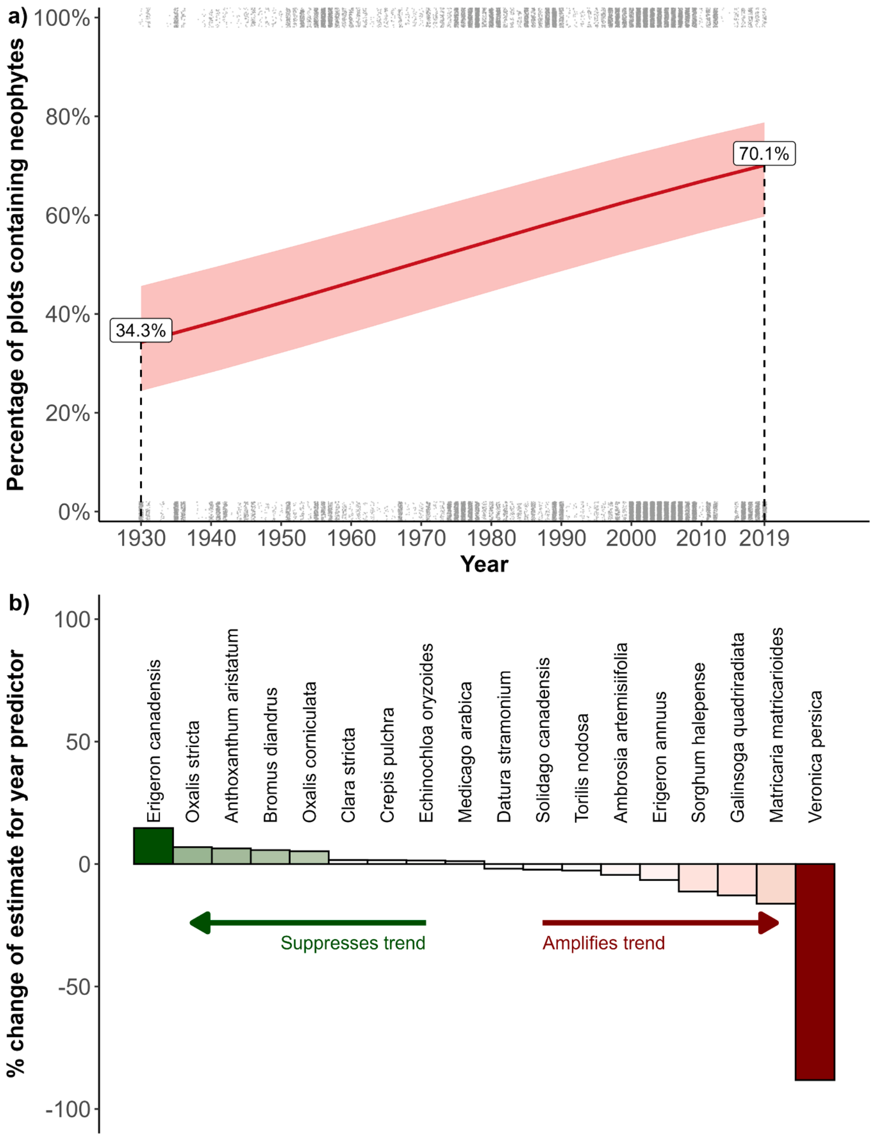

Fig. 2. (a) Partial regression plot for the percentage of plots containing neophyte species (red line) over time. The shading shows the 95 % confidence interval. The dots above and below the regression line show the invasion status of a plot (bottom: uninvaded, top: invaded) over time. The model parameters are described in Table 2. (b) Percentage of change of the year effect size of the regression model by removing individual neophytes from analysis. From left to right, species shown in green are those whose removal from the analysis increases the year effect size, indicating that their presence suppresses the trend. Conversely, species depicted in red are those whose removal decreases the year effect size, suggesting that their presence amplifies the trend. Only species with a change in effect size larger than 1 % are depicted.

regional distribution or sampling variation (Table 4). Including plot size information (available for 60 % of plots) as log-transformed area produced similar trends as the whole dataset in the relative abundance for both neophytes and archaeophytes (see Fig. A.2b,d and Table A.3 in appendix).

The sensitivity analysis conducted on the abundance of neophytes in plots showed that, despite its high record count and widespread distribution, *Veronica persica* did not significantly influence effect size (Fig. 4b; Table S5 supplementary material). This finding diverges from the results of the proportion analysis, where a clear correlation was observed: species with a high number of records substantially influenced the proportion of neophytes at the plot level (Fig. 4a). In contrast, the most significant impacts on neophyte abundance were attributed to species such as *Galinsoga quadriradiata*, *Amaranthus retroflexus*, *Amaranthus powellii*, and *Galinsoga parviflora*. Meanwhile, *Erigeron canadensis, Veronica persica*, and *Amaranthus albus* had a lesser influence, contributing below the average trend (Fig. 4b).

4. Discussion

4.1. The role of time in alien species accumulation

Our temporal analysis, spanning from 1930 to 2019, offers an in-depth view of alien species dynamics in arable fields. Unlike previous studies conducted at regional or national scales, such as those by Májeková et al. (2021), Lososová et al. (2004), and Pyšek et al. (2005) which compared invasion levels across different habitats, including a 70-year study in Moldavia (Sîrbu et al., 2012), our study traces the temporal trend of alien species in arable fields. We addressed the sampling biases in our dataset by employing generalized linear mixed-effect models with random effects to analyze the temporal trend of neophyte invasion. This approach allowed us to effectively handle variability across different time points and locations. The observed increase in neophytes indicates a shift in species composition within agricultural ecosystems, likely driven by agricultural intensification. These changes

Table 2
Results of the model for the percentage of plots containing neophyte plant species. Note that all predictors were scaled for analysis. Significance codes: $p < 0.0001$ = '****', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'.

Parameter	Estimate	Std. Error	Z-value	P-value	Significance
(Intercept)	0.300	0.212	1.416	0.157	n.s.
Year (scaled)	0.387	0.0586	6.602	4.05e−11	****
Number of species (scaled)	0.964	0.0299	32.218	< 1e−12	****
Latitude (scaled)	−0.512	0.0598	−8.562	< 1e−12	****
Longitude (scaled)	0.398	0.0583	6.822	8.99e−12	****
Temperature (scaled)	−3.54e−03	0.0206	−0.172	0.863	n.s
Random effect	Variance	Std. Dev.	Groups		
Study	1.825	1.351	352$^{\#}$		
Crop type	6.34e−02	0.252	6		
Month	0.216	0.465	12		

may have created more suitable conditions for neophytes, such as increased nutrient availability or more frequent soil disturbances, which facilitate their establishment. Our findings are consistent with previous research indicating a rise in neophyte occurrence at a regional scales (Seebens et al., 2018; Šilc, 2015), while we also observed an increase at the local scale (Sîrbu et al., 2012).

4.2. What different metrics of plot-level invasions tell us

By using different metrics of changes in neophyte occurrence, we found diverging trends between the percentage of plots containing neophytes and the proportion and relative abundance of neophytes. At the regional level, we found that approximately 70 % of vegetation plots contained one or more neophytes at the end of our study period in 2019, reflecting a substantial spread, which is in alignment with the findings of Sîrbu et al. (2012). At the start of our study period in the 1930s, about a third of vegetation plots had already been occupied by at least one neophyte species, indicating that the spread of neophytes in the study region is not a recent phenomenon. One possible reason for the continued spread of neophytes in modern times could be contamination from flowering strips or the deliberate introduction of species, which may subsequently establish in the seed bank. However, this potential

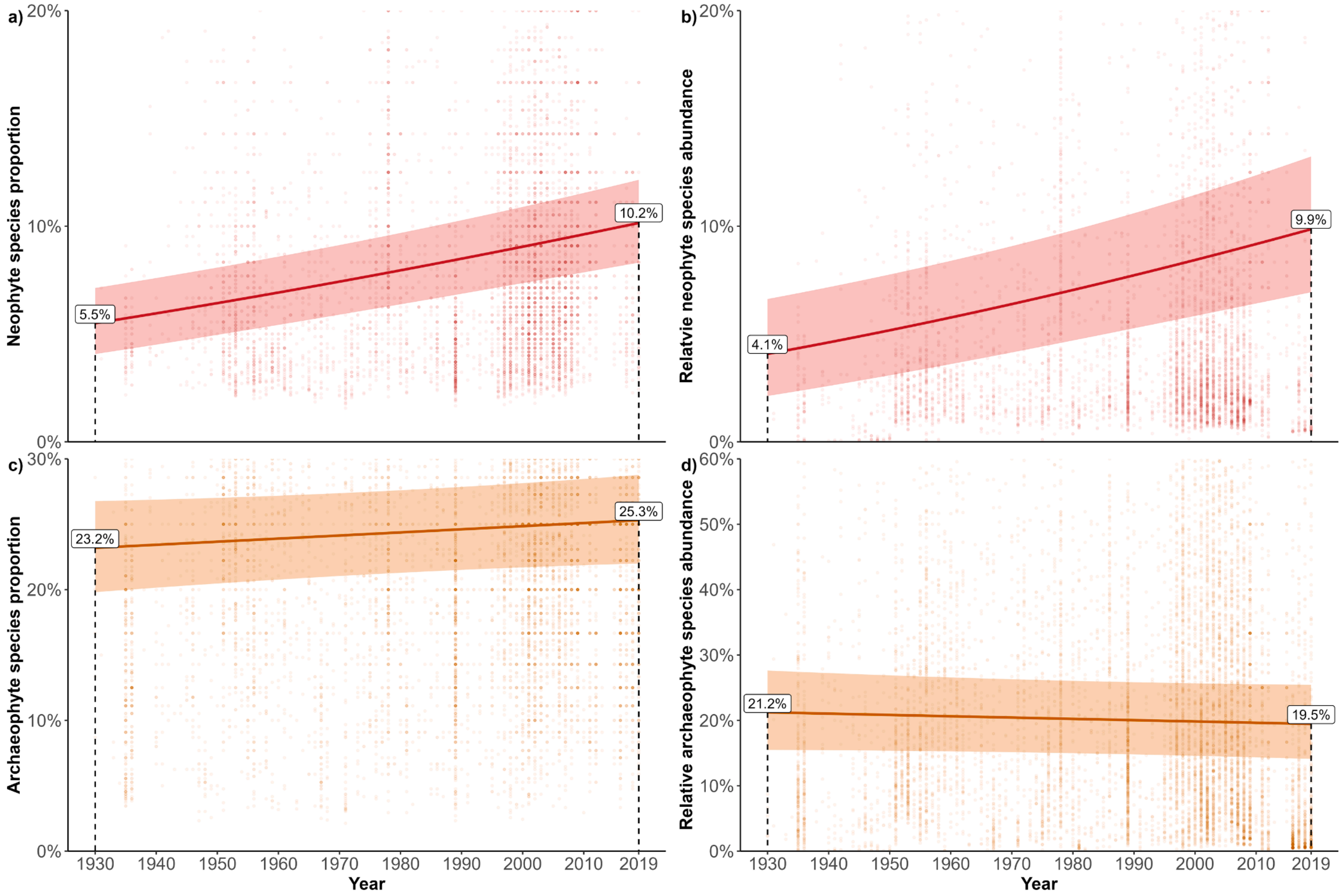

Fig. 3. Partial regression plots showing (a) neophyte species proportion, (b) relative neophyte species abundance, (c) archaeophyte species proportion, and (d) relative archaeophyte species abundance, each plotted against time. The shaded areas show the 95 % confidence interval. The response variable is depicted as small dots, outliers were omitted from the plot. The model parameters are depicted in Tables 3 and 4. Random effects for the month when the vegetation plot was surveyed, study (indicated by bibliographic reference), and crop type are incorporated for all models.

Table 3
Model results for the relative abundance of alien plant species, a) neophytes and b) results for the archaeophytes. Significance codes: $p < 0.0001$ = '****', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'.

a) Neophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	−0.690	0.262	1305	−2.636	8.48e−03	**
Year	9.83e−04	1.31e−04	1691	7.525	< 1e−12	****
Latitude	−0.0191	1.43e−03	642	−13.330	< 1e−12	****
Longitude	−3.49e−03	8.12e−04	1735	−4.299	1.81e−05	****
Temperature	1.5e−04	3.56e−05	5830	4.223	2.45e−05	****
Random effect	Variance	Std. Dev.	Groups			
Study	4.17e−03	0.0645	268$^{\#}$			
Crop type	3.99e−04	0.02	6			
Month	1.42e−03	0.0377	10			
Residual	5.57e−03	0.0746				

b) Archaeophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	0.279	0.376	1850	0.742	0.458	ns
Year	2.77e−04	1.82e−04	2679	1.523	0.128	ns
Latitude	−5.34e−03	2.13e−03	923	−2.503	0.0125	*
Longitude	−4.32e−03	1.17e−03	2757	−3.682	2.36e−04	***
Temperature	1.57e−04	4.86e−05	9356	3.233	1.23e−03	**
Random effect	Variance	Std. Dev.	Groups			
Study	0.0114	0.107	301$^{\#}$			
Crop type	5.87e−04	0.0242	6			
Month	1.84e−03	0.0429	11			
Residual	0.0161	0.127				

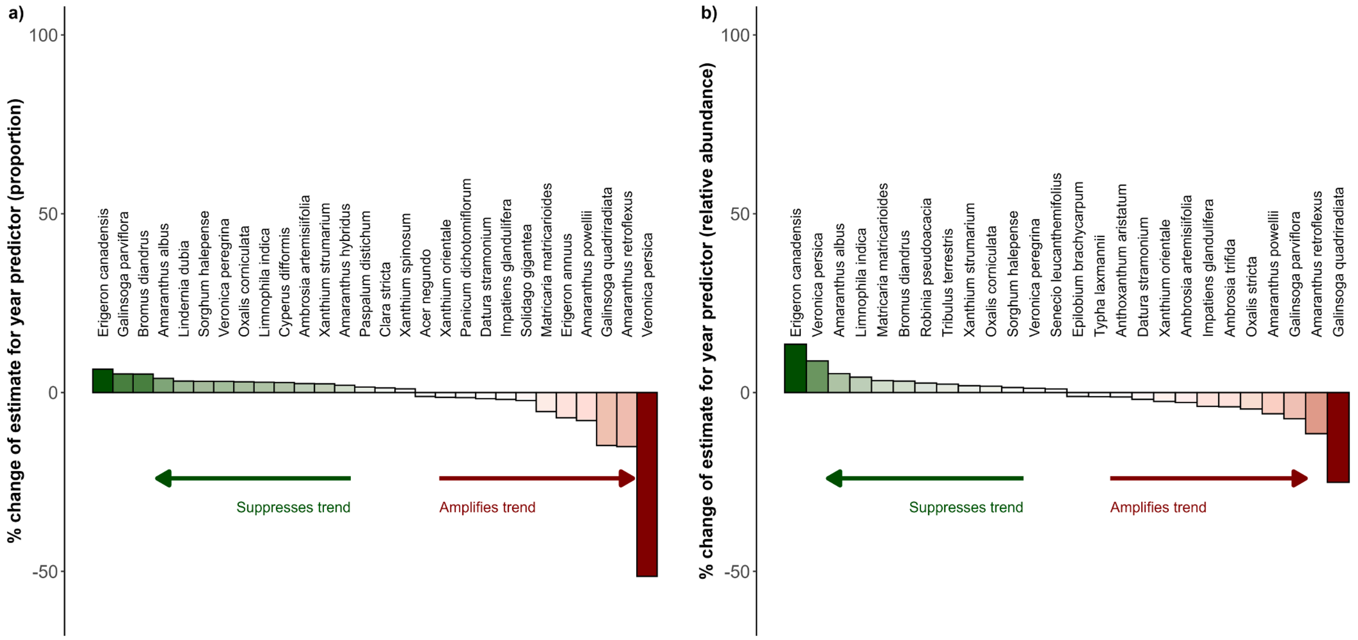

Fig. 4. Percentage decrease in the year effect size (excluding the intercept) for (a) the proportion of neophyte species and (b) the relative abundance of neophyte species, obtained by sequentially excluding individual neophytes from the analysis. Species are arranged according to their influence on the temporal trend, with the highest decrease on the left, and the highest increases on the right.

source of entry would need further investigation. A study by Seebens et al. (2017) predicted that the accumulation of new neophytes worldwide will not reach saturation, as the rate of first records shows no decline on a regional scale. Additionally, in another study by Seebens et al. (2021) they have projected an increase in the total number of neophyte species across Europe, continuing until the end of the modeling period in 2050. Future trends are likely to see neophyte species expanding at the plot level, with increasing proportions and relative abundances. This is expected as a consequence of ongoing agricultural intensification (Fried et al., 2008; Storkey et al., 2012) and climate change (Walther et al., 2009), which may further enhance the conditions favoring neophyte establishment and spread. As the proportion and relative abundance of neophyte and archaeophyte species increase, native plant species logically decline in both relative richness

Table 4

Model results for the relative abundance of neophyte and archaeophyte species. Significance codes: $p < 0.0001$ = '****', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'.

a) Neophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	−1.506	0.508	813	−2.964	3.13e−03	**
Year	1.3e−03	2.56e−04	1001	5.096	4.15e−07	****
Latitude	−0.0164	2.71e−03	467	−6.054	2.91e−09	****
Longitude	−8.29e−04	1.59e−03	1027	−0.521	0.603	ns
Temperature	2.75e−05	7.4e−05	5862	0.372	0.710	ns
Random effect	Variance	Std. Dev.	Groups			
Study	0.0115	0.107	268$^{\#}$			
Crop type	1.65e−03	0.0406	6			
Month	2.66e−03	0.0516	10			
Residual	0.0242	0.155				

b) Archaeophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	1.389	0.552	1312	2.515	0.012	*
Year	−2.48e−04	2.7e−04	1848	−0.919	0.358	ns
Latitude	−7.07e−03	3.07e−03	696	−2.302	0.0216	*
Longitude	−6.1e−03	1.74e−03	1830	−3.510	4.58e−04	***
Temperature	2.68e−05	7.49e−05	9375	0.357	0.721	ns
Random effect	Variance	Std. Dev.	Groups			
Study	0.0195	0.140	301$^{\#}$			
Crop type	6.29e−03	0.0793	6			
Month	7.44e−04	0.0273	11			
Residual	0.0383	0.196				

and abundance. This pattern is likely driven by increased competition for resources such as light and space, with neophytes particularly advantaged by conditions associated with modern agricultural practices, where higher nutrient availability can favor a few dominant species, indirectly suppressing less competitive species (Pyšek et al., 2005). Neophyte species, which have increased under recent agricultural practices, often compete for resources and might lead to declines in native species richness and relative abundance. Archaeophyte species, on the other hand, have been part of the ecosystem for millenia, and their impact on native species tends to be more stable, but their interactions with native species might vary depending on ecological and environmental conditions (Lososová et al., 2004)

The regional increase in plots containing neophytes is often driven by the presence of a single additional neophyte species in a previously unoccupied plot. However, at the plot level, the overall proportion of neophytes remains much lower due to the more complex dynamics of neophyte occurrence and abundance. Unlike regional accumulation, which can be influenced by the continuous addition of new species to the regional species pool, an increase in the proportion of neophytes per plot can either be due to an accumulation of different neophyte species or a decline of native and archaeophyte species.

The increase in the relative abundance of neophytes is likely influenced by individual species traits, including their competitive ability against native and archaeophyte species (Pyšek et al., 2005). Factors such as growth rate, nutrient uptake efficiency, and adaptability to disturbances may determine which neophyte species become more dominant in plots over time. For example, if a highly competitive neophyte like *Amaranthus retroflexus* arrives in a plot and displaces other neophytes with smaller cover, such as *Erigeron canadensis*, the overall effect on relative abundance is significant. The presence of species such as *Robinia spp.* and *Impatiens glandulifera* in our dataset was initially surprising, as their occurrence in arable fields is uncommon. However, we think it is plausible given their adaptability and tendency to invade disturbed environments. *Robinia*, particularly *Robinia pseudoacacia* or black locust, is known for its fast growth rate and its resilience, often establishing as a resprouting individual from adjacent areas or as a seedling (Vítková et al., 2020). Similarly, *Impatiens glandulifera* could find suitable conditions along the moist edges of fields, extending beyond its typical riparian habitats.

The discrepancy between regional and local scale is not unique to our findings; similar trends have been observed in previous studies. For instance, Chytrý et al. (2005) noted that while a high percentage of neophytes were found at a country level (27 %) in Europe, only 2.3 % of the species were determined as neophytes in individual vegetation plots. The study considered various habitats, including arable fields, trampled areas, urban environments, and anthropogenic tall-forb stands, highlighting how neophytes are more concentrated in these specific habitats. This observation aligns with the recent findings by Liu et al. (2023), where a pronounced increase in alien plant species was noted in regional species pools of arable fields, yet this surge was not mirrored at the plot level, underscoring the complexity and varied nature of biological invasions across different scales. Preferential sampling may also play a role. Some studies might have been oriented towards alien plant species such as *Sorghum halepense* and *Cyperus esculentus* due to their prominence or diagnostic value for certain plant associations or environmental characteristics. However, in some cases, stands dominated by alien plant species may have been avoided to focus on classification or conservation objectives, leading to an a priori exclusion of plots heavily influenced by alien species. The discrepancy between the regional and local levels could also be partially attributed to the time lags in colonization (Essl et al., 2024). Such time lags, which represent the delay between initial introduction and the successful spread to all suitable habitats, may explain the lower proportion and abundance of neophytes at the plot level compared to the regional rate of invasion.

While an increase in the proportion of alien species is generally expected to also increase their relative abundance, we analyzed these variables independently to ascertain that any differences among these aspects of alien plant species spread could be observed. Our results revealed that the ratio and the relative abundance of neophyte species in plots containing neophytes have both increased over time, with similar trends. The analysis of proportion and relative abundance changes offers valuable insights, but these measures alone cannot fully capture the underlying mechanisms and identifying the specifics needs further inquiry. Neophyte species can migrate to surveyed plots from sources either within or outside the study region. The proportion of alien plant species could potentially increase due to a decrease in native plant species or an increase in alien plant species. Moreover, an increase in abundance within a plot might be due to an increase in alien plant richness, a reduction in native plant species richness, or shifts in the respective abundances of both groups (Fig. S2, supplementary material). Detailed understanding of these dynamics would ideally require monitoring individual plots over extended periods, enabling a more nuanced exploration of potential shifts and influences.

By examining the geographical effects across all models, we accounted for spatial heterogeneity by including latitude and longitude as control variables to capture structural variation. Temperature effects are challenging to interpret in general; while temperature significantly influenced species composition, suggesting neophyte preference for warmer climates (consistent with prior studies: Anačkov et al., 2013; Polce et al., 2011; Scherrer et al., 2022), it did not significantly affect relative abundance. This may be because agriculture is practiced in areas with temperatures suitable for cultivation, where irrigation mitigates the effects of insufficient rainfall. Additionally, factors such as soil conditions, land management, and species interactions may more directly influence relative abundance.

4.3. *Neophytes vs archaeophytes*

In our study, neophyte species exhibited a significant increase in both proportion and relative abundance within plots, reflecting their ongoing and successful colonization. In contrast, archaeophyte species showed only a modest rise in their proportion and even a minor decrease in abundance, indicating a relative stability in their populations. This stability might suggest that archaeophytes, as a group, are neither particularly advantaged nor disadvantaged by recent changes in agricultural practices. Archaeophytes historically accompanied the spread of traditional agriculture and are better adapted to earlier agricultural practices, which contrasts with the conditions created by modern management. Intensified management practices, including mechanization, the extensive use of fertilizers and pesticides, and deep plowing, may challenge some archaeophytes and many native plant species. In contrast, many neophytes and some archaeophytes thrive under these modern practices, benefiting from changes such as the introduction of high-yield crop varieties and mechanized cultivation techniques. Richner et al. (2015) found that plant species preferring nutrient-rich sites, neophytes, and monocotyledons generally increased since 1980, while characteristic or threatened species of arable plant communities further declined. This suggests that current agricultural practices may favor neophytes and other nutrient-demanding species. These adaptations include evolved resistance to herbicides, high nitrogen preferences, and in some cases, the C4 assimilation pathway - particularly prevalent among panicoid grasses (Fanfarillo et al., 2019). Additionally, the increase in cultivation of wide-row root crops such as maize, soybean, and sunflower, which are nutrient-demanding, has further facilitated the spread of neophytes (Lososová and Cimalová 2009; Fried et al., 2019). European agriculture has seen dramatic changes since 1960s, with trends towards increased productivity, specialization, and structural changes across regions (Einarsson et al., 2021). Some regions have intensified agricultural practices, incorporating more synthetic fertilizers, manure, and symbiotic nitrogen fixation, while others have extensified or abandoned agricultural land (Fayet et al., 2022). These changes in nitrogen management practices have significantly influenced crop production patterns and had a notable environmental impact, including biodiversity loss in European cropland, further accelerating the ongoing spread of neophyte species in arable fields. Pyšek et al. (2005) identified key drivers determining the number of native and alien plant species on arable land in central Europe, such as soil type, crop type, climatic variables, altitude, and human population density. Their study demonstrated that these factors influenced species richness differently for native species, archaeophytes, and neophytes. Archaeophytes were common in traditionally cultivated crops like cereals but less prevalent in newer crops like maize and oilseed rape, where neophytes thrived. This reflects the historical patterns of plant invasions, with Neolithic agriculture introducing archaeophyte species and more recent agricultural practices supporting the spread of neophyte species, primarily invaders from overseas.

4.4. *Temporal trends are influenced by a few common species*

Our sensitivity analysis provides insights into the invasion dynamics across both regional and local scales. Regionally, prevalent and widespread neophyte species such as *Veronica persica*, the most common neophyte in our dataset, have a strong influence on our models; excluding it results in a noticeably reduced increase in the temporal trend for the probability of plots containing at least one neophyte at the regional level and the proportion of neophyte species at the plot level. Conversely, excluding less common alien plant species from the model results in an increase in the effect size of time on both the proportion and the probability of plots containing alien plant species. This suggests that the regional spread of alien plant species, as well as their proportion within plots, is largely driven by the most common plant species in our data set. The importance of widespread plant species in contrast to rare ones may have significant implications for the management of alien plant species in arable fields.

At the local plot level, there is a notable discrepancy in the drivers of invasion. For instance, while *Veronica persica* has a substantial impact on the proportion of neophytes—likely due to its high dispersal capacity—it does not significantly influence the relative abundance of neophytes. *Veronica persica* has a flexible germination period, occurring in autumn, winter, spring, and summer. It produces seeds more than a month after the first flowers open, allowing for a prolonged period of seed dispersal and its seeds do not experience significant mortality until after seedling emergence (Boutin and Harper, 1991). These traits collectively improve its ability to spread.

Interspecific competition may significantly influence the relative abundance among different species, but this must not always be the case. For instance, species like *Veronica persica* and thermophilous species such as *Galinsoga quadriradiata*, *G. parviflora*, *Amaranthus retroflexus*, and *A. powellii* have differing seasonal growth patterns. *Veronica persica* thrives during cooler periods, while the thermophilous species germinate later in the season under warmer conditions. Their greater height may allow them to overshadow smaller plants like *Veronica persica* in specific contexts, such as wide row crops. The low relative abundance of *Veronica persica* may also reflect the timing of sampling, which typically occurs during summer when species like Amaranthus are at peak abundance.

The differing contributions of common versus rare neophyte species to various metrics highlight complex ecological interactions, where even species with a low frequency can exert significant effects if they achieve high local abundance. Understanding these interactions would require considering both species traits and environmental conditions that drive these outcomes. Species with low proportion of the total species list but high relative abundance can still exert significant ecological impact, potentially causing substantial economic damage despite their limited representation. Further exploration through resurveyed data at the plot level, using occupancy modeling as proposed in Glaser et al. (2024), could provide deeper insights into how environmental changes might alter the roles of these neophytes.

4.5. Limitations

While our analysis addresses many potential biases through the use of relative measures and appropriate random effects, and assesses them with a sensitivity analysis, some limitations remain. Like many large databases compiled from diverse sources, this dataset contains inherent biases due to uneven spatial and temporal sampling intensity, with certain regions and time periods over- or underrepresented, which may impact the overall trends observed.

Additionally, while species were standardized as either archaeophytes or neophytes across countries, classification discrepancies may still arise. The distinction between archaeophytes and native species is particularly challenging, as the classification of archaeophytes as ’native’ or ’non-native’ can vary depending on historical and geographical context. This ambiguity in classification could influence our results, especially where archaeophyte presence overlaps significantly with native species distributions.

Some species may have the potential to increase in the future but remain underrepresented in our dataset due to their delayed establishment times. Thus, while increases in neophyte abundance are observed, some species that are currently less prevalent may still pose a significant threat in the future and should not be overlooked. We did not include certain environmental factors, such as local soil conditions or information about the position of the plot (e.g., whether it was located at the field margin or center), as data on these variables were not available at the scale required of this study. Future research could investigate the pathways of introduction and the roles of human-mediated activities or environmental changes (e.g. climate change) in driving these trends.

5. Conclusions

Our study showed that the incidence of neophyte species in arable fields across central Europe has increased. At the regional scale, archaeophyte species are already widespread and well-established. Locally, neophyte species have become more common in arable fields, while archaeophyte species, as a group, have maintained a relatively stable presence with minimal changes. However, within this group, individual species may have experienced differing trends, with some increasing and others decreasing, as shown by Glaser et al. (2024). This trajectory is expected to reduce the regional disparities in alien species composition leading to a biotic homogenization of the central European arable plant communities. Such homogenization processes have been found for other communities such as grasslands in Switzerland (Bühler and Roth, 2011). As this process continues, we anticipate a significant increase in the dominance of neophytes in local communities, which are progressively extending over extensive geographical areas, thereby posing a considerable threat to regional biodiversity (Brondízio et al., 2019). We could also show that the invasion process at the regional level is primarily driven by the most widespread species, suggesting that management measures should target these species. However, our findings also underscore the importance of less widespread but locally abundant neophytes, which can play a significant role at the local scale and should not be neglected in management strategies. Given the trends in globalized and standardized agriculture, there is a potential for certain species within arable plant communities, particularly neophytes with negative ecological and economic impacts, to spread more easily and become more frequent, posing additional challenges for control measures. Our results suggest that the species pool driving the effect of time on neophyte presence at the regional level differs from the pool of neophyte species driving invasion processes at the local plot level. Furthermore, we highlight the ongoing spread of neophyte species, which may act as catalysts for the spread of invasive species with negative ecological and economic impacts into previously unaffected arable fields and surrounding habitats.

CRediT authorship contribution statement

Urban Šilc: Writing – review & editing, Investigation, Data curation. **Stefan Dullinger:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Jana Bürger:** Writing – review & editing, Investigation, Data curation. **Alexander Wietzke:** Writing – review & editing, Investigation, Data curation. **Serge Buholzer:** Writing – review & editing, Investigation, Data curation. **Filip Küzmič:** Writing – review & editing, Investigation, Data curation. **Michaela Kolářová:** Writing – review & editing, Investigation, Data curation. **Matthias Schumacher:** Writing – review & editing, Investigation, Data curation. **Gilles Colling:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Zdeňka Lososová:** Writing – review & editing, Investigation, Data curation. **Emanuele Fanfarillo:** Writing – review & editing, Investigation, Data curation. **Franz Essl:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Milan Chytrý:** Writing – review & editing, Investigation, Data curation. **Florian Jansen:** Writing – review & editing, Investigation, Data curation. **Swen Follak:** Writing – review & editing, Investigation, Data curation. **Michael Glaser:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

Statement: During the preparation of this work, the corresponding author used DeepL Write in order to improve the readability and language of the manuscript. The authors reviewed and edited the content and take full responsibility for the final content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

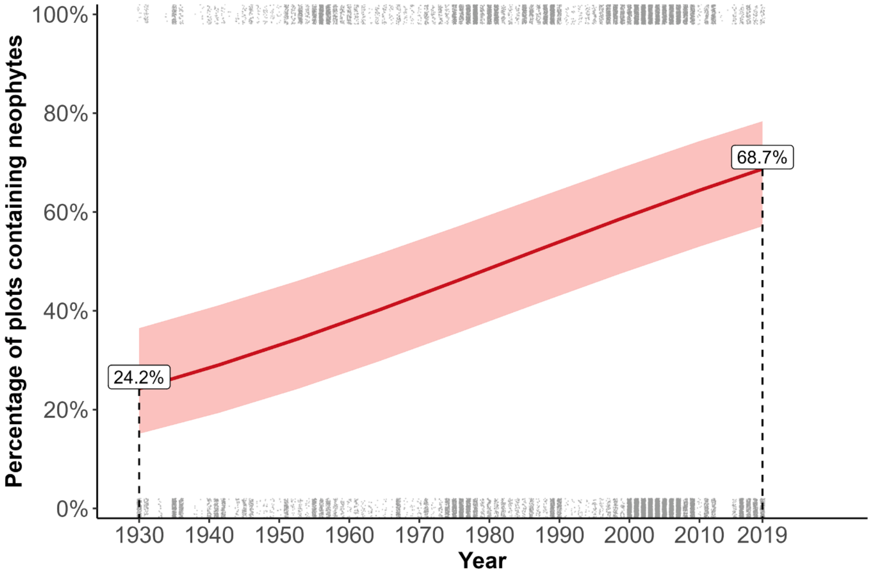

Fig. A.1. Partial regression plot for the percentage of plots containing neophytes (red line) over time using the reduced dataset containing only plots with area information (60 % of the whole data set). The shading shows the 95 % confidence interval. The dots above and below the regression line show the invasion status of a plot (bottom: uninvaded, top: invaded) over time. The model parameters are described in Table A.1. Random effects for the month when the vegetation plot was surveyed, study (indicated by bibliographic reference), and crop type are incorporated for all models

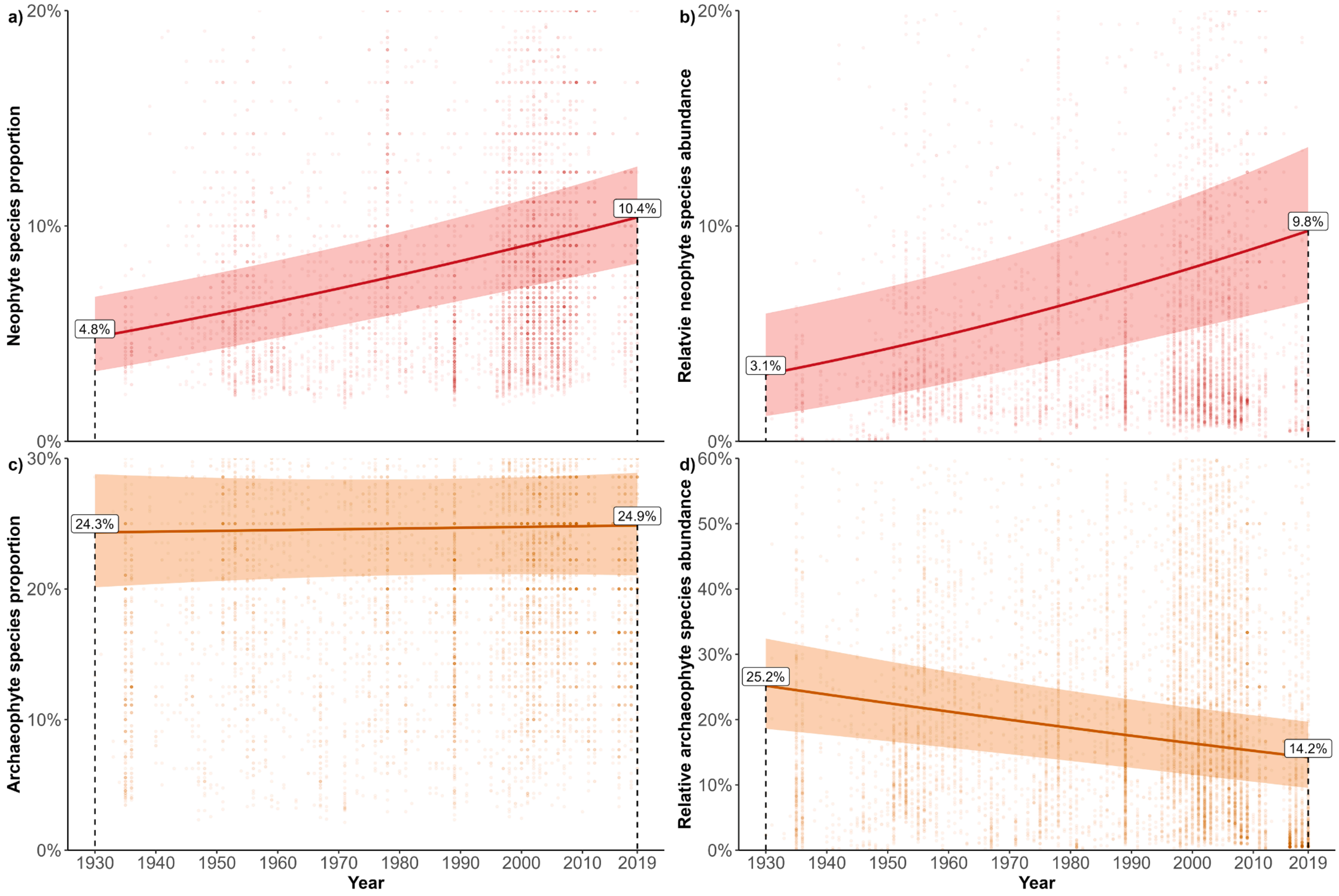

Fig. A.2. Partial regression plots using the reduced dataset containing only plots with area information (60 % of the whole data set) showing (a) neophyte species proportion, (b) relative neophyte species abudance, (c) archaeophyte species proportion, and (d) relative archaeophyte species abundance, each plotted against time. The shaded areas show the 95 % confidence interval. The response variable is depicted as small dots, outliers were omitted from the plot. The model parameters are depicted in Tables A.2 and A.3. Random effects for the month when the vegetation plot was surveyed, study (indicated by bibliographic reference), and crop type are incorporated for all models

Table A.1
Results of the model for the percentage of plots containing neophyte plant species, including log area (available for 60 % of plots). Note that all predictors were scaled for analysis. Significance codes: $p <$ -1e-4 = '****', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'

Parameter	Estimate	Std. Error	Z-value	P-value	Significance
(Intercept)	0.155	0.225	0.690	0.490	ns
Year (scaled)	0.495	0.0851	5.821	5.83e−09	****
Number of species (scaled)	0.930	0.0419	22.202	< 1e−12	****
Latitude (scaled)	−0.294	0.071	−4.144	3.42e−05	****
Longitude (scaled)	0.347	0.0762	4.550	5.36e−06	****
Temperature (scaled)	−4.44e−03	0.0268	−0.166	0.868	ns
Log area (scaled)	0.226	0.0945	2.394	0.0167	*
Random effect	**Variance**	**Std. Dev.**	**Groups**		
Study	1.866	1.366	265$^{\#}$		
Crop type	5.61e−02	0.237	6		
Month	0.218	0.467	12		

Table A.2
Model results for the proportion of alien plant species, a) neophytes and b) results for the archaeophytes, including log area as a predictor (available for 60 % of plots). Significance codes: $p <$ -1e-4 = '****', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'

a) Neophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	−0.973	0.362	962	−2.687	7.33e−03	**
Year	1.2e−03	1.77e−04	1089	6.756	2.31e−11	****
Latitude	−0.0204	1.73e−03	577	−11.794	< 1e−12	****
Longitude	−6.74e−03	9.44e−04	1917	−7.138	1.34e−12	****
Temperature	1.42e−04	4.1e−05	4394	3.465	5.36e−04	***
Log area	−7.96e−03	2.38e−03	2853	−3.351	8.16e−04	***
Random effect	**Variance**	**Std. Dev.**	**Groups**			
Study	4.65e−03	0.0682	202$^{\#}$			
Crop type	3.39e−04	0.0184	6			
Month	2.15e−03	0.0463	10			
Residual	5.72e−03	0.0756				

b) Archaeophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	0.832	0.519	1323	1.602	0.109	ns
Year	6.98e−05	2.49e−04	1629	0.280	0.779	ns
Latitude	−7.84e−03	2.59e−03	752	−3.033	2.5e−03	**
Longitude	−6.86e−03	1.39e−03	2426	−4.936	8.53e−07	****
Temperature	1.56e−04	5.91e−05	6315	2.638	8.37e−03	**
Log area	7.37e−03	3.27e−03	4223	2.255	0.0242	*
Random effect	**Variance**	**Std. Dev.**	**Groups**			
Study	1.2e−02	0.110	229$^{\#}$			
Crop type	7.76e−04	2.79e−02	6			
Month	2.4e−03	4.9e−02	11			
Residual	1.67e−02	0.129				

Table A.3
Model results for the relative abundance of alien plant species, a) neophytes and b) results for the arachaeophytes, including log area as a predictor (available for 60 % of plots). Significance codes: $p <$ -1e-4 = '*** *', $p < 0.001$ = '*** ', $p < 0.01$ = '**', $p < 0.05$ = '* ', ns = not significant. $^{\#}$We excluded entries with NA values, using the default *na.omit* function in 'lme4'

a) Neophytes

Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	−1.969	0.709	501	−2.779	5.66e−03	**
Year	1.58e−03	3.49e−04	536	4.527	7.38e−06	****
Latitude	−0.0161	3.31e−03	384	−4.855	1.75e−06	****
Longitude	−4.36e−03	1.91e−03	1011	−2.285	0.0225	*

(*continued on next page*)

Table A.3 (*continued*)

Log area	−0.0143	4.89e−03	1718	−2.913	3.63e−03	**
Temperature	1.38e−05	8.83e−05	4425	0.156	0.876	ns
Random effect	Variance	Std. Dev.	Groups			
Study	0.0116	0.108	202$^{\#}$			
Crop type	2.05e−03	0.0453	6			
Month	3.36e−03	0.0579	10			
Residual	0.0267	0.163				
b) Archaeophytes						
Parameter	Estimate	Std. Error	df	t value	Pr(>|t|)	Significance
(Intercept)	4.364	0.769	1060	5.676	1.77e−08	****
Year	−1.56e−03	3.7e−04	1261	−4.217	2.66e−05	****
Latitude	−0.0114	3.79e−03	643	−3.005	2.76e−03	**
Longitude	−0.0115	2.07e−03	1876	−5.541	3.43e−08	****
Temperature	−1.11e−05	9.04e−05	6330	−0.123	0.902	ns
Log area	−0.0244	4.94e−03	3613	−4.936	8.35e−07	****
Random effect	Variance	Std. Dev.	Groups			
Study	0.0225	0.150	229$^{\#}$			
Crop type	5.85e−03	0.0765	6			
Month	7.72e−04	0.0278	11			
Residual	0.0391	0.198				

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109483.

Data availability

The data/code has been shared at the Attach File step.
Alien Plant Species Accumulation 2024_v1 (GitHub)

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