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Drivers of plant invasions and their scale-dependency in grasslands☆

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ABSTRACT

Conservation and management policies for plant invasions often rely on coarse-scale data, while plant diversity effects on ecosystem functions and services are primarily driven by species interactions at small spatial scales. Yet, most evidence on invasion drivers at fine scales is limited to a single grain size, leaving uncertainty about their scale-dependency. Understanding such scale-dependency is essential for predicting and managing invasions effectively.

We sampled plant communities across grassland habitats in Ukraine to assess how native species richness, environmental factors, and anthropogenic disturbances influence community invasion level – the proportions of all alien species, and separately for invasive species (fast-spreading aliens at advanced stages of invasion), archaeophytes (introduced before 1500 CE) and neophytes (post-1500 CE aliens). By analysing these groups across six fine-grain areas (0.001–100 m^2), we tested for scale-dependent effects.

Native species richness was the strongest driver of invasions, showing negative effects that weakened with increasing scale. Alien species were dominated by archaeophytes and occurred most in dry grasslands, and least in fringe, alpine, and mesic types, driven by climatic and disturbance gradients. A range of abiotic and anthropogenic drivers, including precipitation, temperature, disturbance, land use and urbanization also influenced invasion levels, but their importance varied with scale. Notably, the scale-dependency of invasion drivers differed among archaeophytes, neophytes, and invasive species.

Our results highlight the importance of separating alien groups and considering multiple spatial grains to avoid overlooking key drivers of invasion. Focusing on scale- and group-specific factors can enhance the ecological relevance and efficiency of conservation and management strategies targeting plant invasions.

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1. Introduction

Understanding drivers of biological invasions has taken on new urgency given the unprecedented rates of biodiversity homogenization worldwide under an ever-growing human pressure (Richardson and Pyšek, 2008; Winter et al., 2009). Despite extensive research and various proposed hypotheses (Catford et al., 2009; Jeschke, 2014), the factors driving plant community invasions by non-native (hereafter alien) species remain controversial, largely due to inconsistencies in sampling grain sizes (Fridley et al., 2007; Hulme, 2008). The level of invasion, measured as the proportion of alien species in a community (Chytrý et al., 2008a; Richardson and Pyšek, 2008), is widely used to assess potential threats of aliens to ecosystems (Hulme, 2008), yet its interpretation may be scale-dependent if alien and native species richness within the same community respond differently to variations in sampling grain. Therefore, the assessment of invasion level and its perceived impact on ecosystem may be influenced by the scale of data collection (Hulme, 2008). While alien and native plants often differ in their distribution patterns across habitats (Chytrý et al., 2008b), whether their scale-dependency differs within the same community remains unclear. Some studies report strong scale-dependency in the proportion of alien plant species (Hulme, 2008), while others indicate scale-invariance (Stark et al., 2006).

High native species richness is expected to buffer communities against invasions by reducing resource availability to newly arriving species – an idea central to *diversity–invasibility hypothesis* (Elton, 1958). But the relationship between invasion levels and native species richness may also depend on the sampled spatial scale. The *invasion paradox* describes how this relationship often shifts from negative at plot scales (where species interactions dominate) to positive at broader scales (i.e., regional, continental, and global), where anthropogenic impact and abiotic filters outweigh the influence of competitive exclusion (Fridley et al., 2007). While experimental studies consistently report a negative relationship between native species richness and invasion success at fine scales (Hector et al., 2001), observational evidence remains inconsistent. Some studies even find positive relationships at 1-m^2 grains (Cleland et al., 2004; Keeley et al., 2003; Sax et al., 2002; Stohlgren et al., 2006). The scale at which the relationship shifts from positive to negative remains uncertain. Some studies report this shift even at very fine grains, such as 0.01 m^2 (Brown and Peet, 2003). Although fine plots ($<$100 m^2) are common sampling grain in invasion studies (Powell et al., 2011), scale-dependent patterns of native species-richness effects on invasion level remain debated due to sampling inconsistencies (Fridley et al., 2007; Smith and Côté, 2019). Moreover, the direction of this relationship may also vary across habitat type. For example, in forest fragments, native and alien species richness may be positively correlated, supporting a “rich-get-richer” pattern driven by shared environmental preferences (Trotta et al., 2023). Understanding how invasion success varies across spatial grains can enhance the efficiency of conservation and management efforts by enabling scale-appropriate monitoring and more accurate identification of areas with the greatest potential threat of invasions (Hulme, 2008).

The actual level of invasion (number or proportion of alien species) is a joint product of community invasibility (susceptibility to invasions), propagule pressure (the rate of influx of alien propagules into the target site), and the invasiveness of alien species (Chytrý et al., 2008a; Richardson et al., 2011; Richardson and Pyšek, 2008). Key factors influencing these processes, and thus determining community invasion levels, include resource availability (Davis et al., 2000), environmental heterogeneity (Davies et al., 2005; Melbourne et al., 2007), the harshness of environmental conditions (von Holle, 2013), and natural or anthropogenic disturbances (Clark and Johnston, 2011; Pinto and Ortega, 2016). These factors govern the interaction between native and alien species by either promoting competitive exclusion or facilitating species coexistence, depending on the spatial scale of observation (Cleland et al., 2004; Davies et al., 2007; Davis et al., 2000). The covariation of these environmental factors with sampled scale are suggested to drive their scale-dependent effects on invasions at large spatial scales (Clark and Johnston, 2011; Davies et al., 2005; Fridley et al., 2004; Kotowska et al., 2022; Melbourne et al., 2007). While the majority of studies compare the effects of invasion drivers across broader spatial extents, such as at plot vs regional vs landscape scale (Boscutti et al., 2022), how these drivers operate across fine spatial grains remains unclear. This knowledge gap is particularly relevant for grassland ecosystems, as at fine scales grasslands support the highest plant diversity (Petermann and Buzhdygan, 2021), and depend on this diversity for maintaining ecosystem functions and services (Buzhdygan et al., 2025b). Understanding how invasion drivers shape fine-scale patterns in grasslands is crucial for addressing the invasion paradox when native species richness may both resist and facilitate invasions depending on spatial scale (Smith and Côté, 2019), predicting invasion levels, and forecasting and mitigating changes in grassland species richness, ecosystem functions and services in the face of invasions (Essl et al., 2020).

In this study, we assess the scale-dependent effects of native diversity and environmental drivers (Table S1) on the invasion levels (proportion of alien species) of grassland plant communities sampled across all grassland habitat types in Ukraine at fine spatial grains spanning six orders of magnitude (0.001–100 m^2). We define *alien species* as those introduced outside of their native range and natural dispersal potential (Richardson et al., 2011). Within alien species we distinguish *invasive species* as those in the final stages of the introduction–naturalization–invasion continuum (Kalusová et al., 2024; Richardson et al., 2000). In our study, invasive species refer strictly to nonnative invaders, without addressing their perceived negative impacts on human society, since the rigorous assessment of these impacts has only recently been established on robust theoretical grounds (Blackburn et al., 2014). This contrasts with studies on native invaders (e.g., Axmanová et al., 2024). We distinguished invasive species from the total pool of alien species to better capture variation in impact on plant community, as invasive species produce reproductive offsprings, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over a large area (Pyšek et al., 2004). We further differentiate *neophytes* (recent aliens introduced after 1500 CE) from *archaeophyte* aliens (prehistoric to medieval invaders which arrived before 1500 CE). Archaeophytes are likely to be strongly dependent on climate and habitat type that meet their ecological requirements. In contrast, neophytes may not yet have reached their full distribution due to their shorter residence time in temperate Europe and are likely more influenced by recent propagule pressure from urban, industrial, and agricultural land use than by climate or habitat type (Chytrý et al., 2008a; Pyšek and Jarošík, 2005). Although invasive species and neophytes are often correlated, we treat them as distinct groups, as they do not fully overlap in our dataset (Fig. S3A-B). Archaeophytes dominated the pool of alien species in our data (Fig. S3C—D). Therefore, our expectation is that patterns and scale-dependencies might differ between all alien species (commonly used group in invasion ecology studies) and the subset of only invasive or only neophyte species due to differences in the potential of spread and residence time.

The study grasslands are located at the intersection of continental, steppe, and alpine biogeographical regions and are among Europe’s most biodiverse and ecologically significant habitats, including natural steppe and semi-natural mesic grasslands in the Carpathians. The study grasslands represent remnants of temperate grasslands increasingly threatened by human activity. Many of them are high nature value grasslands and some (e.g. in the Carpathians) are shaped by centuries of traditional low-intensity and low-input farming practices (Janišová et al., 2025). The invasion levels of these grasslands and their drivers are highly understudied in the scientific literature. Our study is the first to date examining the scale-dependent effects of environmental drivers and native species richness on the invasions of these grasslands. Specifically, we address the following questions:

(1) What is the relative importance of native species richness and of environmental factors on the invasion level of local plant communities across different grassland habitat types?
(2) Do the effects of these drivers on invasion level vary with the sampled grain size?
(3) Do these scale-dependent patterns differ between alien species groups: invasive alien species, archaeophytes and neophytes?

2. Materials and methods

2.1. Study area and sampling design

We sampled grasslands representing all major grassland habitats in Ukraine, based on the EUNIS habitat classification (Chytrý et al., 2020). Sampling took place between 2010 and 2022 and resulted in eleven datasets from different sampling campaigns (Table S2). The geographical extent of the data covered an area from 46.08° N to 51.87° N and 24.2° E to 37.76° E and within an elevational gradient 0–1805 m a.s.l. (Fig. 1A). For more details on the study area see Buzhdygan et al. (2025a).

We followed the standardized sampling protocol of nested plots, developed by the Eurasian Dry Grassland Group, EDGG (https://edgg.org; Dengler et al., 2016). In accordance with this methodology, our study plots were 100-m^2 squares, each comprised of two nested-plot series located in two opposite corners. Each of these nested-plot series included five square subplots differing by one order of magnitude: 10 m^2, 1 m^2, 0.1 m^2, 0.01 m^2, and 0.001 m^2 (Fig. 1A). Study plots were established within a single vegetation community for each grassland habitat type, classified according to the EUNIS system v.2018 (Table S2). We selected sites to represent the full diversity of EUNIS-classified grassland habitat types present in Ukraine (Schaminée et al., 2018; Kuzemko et al., 2022). In some cases, we used the EUNIS-ESy expert system (Chytrý et al., 2020) to assist in assigning sites to the appropriate EUNIS habitat types. Each studied site was classified at the third hierarchical level of the EUNIS system, which we then grouped into broader categories corresponding to the second hierarchical level of the EUNIS system (Table S2): dry (R1), mesic (R2), wet (R3), alpine (R4), fringe (R5), saline (R6), and habitat complex (X) *pody* – steppe depressions with diverse habitat types that vary across space and time, creating a dynamic mosaic of ecological conditions (Buzhdygan et al., 2025a; Shapoval and Kuzemko, 2021). The unequal number of plots across habitat groups reflects two main factors: (1) the higher diversity of subordinate EUNIS types within certain groups (e.g., 13 third-level types under dry grasslands, Table S2), and (2) the rarity of some habitat types in the study area (e.g., habitat complex *pody*). As a result, plot allocation was not uniform but rather aligned with the ecological representation and availability of each habitat type in the study area. We selected the locations of the 100-m^2 plots using random placement based on visual analysis of cartographic materials and satellite imagery publicly available through Google Maps. We prioritized areas with visually homogeneous grassland vegetation and avoided recently disturbed or highly heterogeneous patches. To ensure spatial independence, 100-m^2 plots were placed at least 500 m apart. The presence or absence of alien species was not considered during site selection to avoid bias in the sampling design, meaning that sites were selected randomly within each habitat type regardless of whether alien species were present.

Overall, we sampled 191 plots of 100 m^2 and 382 nested-plot series, resulting in a total of 2101 plots across all grain sizes. Of these, 22 plots contained no plant species and were excluded, thus only 2079 plots were considered for further analyses (Table S3). Our study focused on natural and semi-natural grasslands and deliberately excluded heavily anthropogenically modified sites. In each plot we recorded the presence of all vascular plant species using the shoot presence method, following the EDGG standardized sampling protocol (Dengler et al., 2016). In this method each plant individual is assigned to the whole area of the vertical projection of its aerial parts and thus can be counted in more than one nonoverlapping subplot (Dengler, 2008). In contrast to the rooted presence method, where species are recorded only in those plots in which they are rooted, the shoot presence method provides a more accurate representation of which species are interacting in the studied plot (Dengler et al., 2016). The shoot presence method is also better suited for analysing spatial scale-dependency across fine grain sizes than the rooted presence method (Dengler, 2008; Williamson, 2003).

2.2. Metrics of alien species

We used literature sources and open databases to extract information on the non-native status of the species and grouped them based on the time of introduction, geographical origin, and naturalization level (for detailed methodology and procedure, see Supplementary Methods). We first checked the non-native status of each species in our dataset according to the Ukrainian national data-sources (for details see Supplementary Data 1) and compiled a list of the alien species which were identified as *neophytes* (introduced after 1500 CE) and *archaeophytes* (introduced before 1500 CE) in at least one of the national data-sources. Further, we used the international databases available for the countries surrounding our research area to clarify the status of species with uncertain assignments, such as species with varying status according to different information sources or species with non-native status in a certain region of the country (Supplementary Data 1). We also classified alien species according to their invasive status, i.e. stage along the introduction–naturalization–invasion continuum based on Kalusová et al. (2024), as follows: (i) *casual* alien species that do not form self-sustaining populations in the invaded area; (ii) *naturalized* alien species that form self-replacing populations for several life cycles without or despite direct human intervention; (iii) *invasive* alien species that form self-replacing populations over many life cycles produce large reproductive offspring that often spread over long distances. Also, we identified the geographical origin for each non-native species. For detailed methods and data sources used to assemble the non-native status for each species and their time of introduction, geographical origin, and naturalization level see Supplementary Methods and Supplementary Data 1. We assessed the levels of invasion in each plant community at each spatial scale as the proportion of alien species relative to total species richness. Analyses were conducted for all alien species combined, and separately for archaeophytes, neophytes and invasive species. The occurrence and proportion of archaeophytes were strongly correlated with those of the total alien group (Fig. S3 C,D), indicating that archaeophytes made up the majority of alien species in our dataset.

2.3. Drivers and scale-dependency of alien species success

We considered a range of environmental variables as the potential drivers of plant invasions in the studied grasslands (Table S1). For each 100 m^2 plot, we extracted mean annual temperature and precipitation from the CHELSA climate database (Karger et al., 2017). These climate variables had strong negative correlation (Fig. S1). Therefore, we derived a single composite variable of climate gradient by applying principal component analysis (PCA) using the '*prcomp*' function in '*stats*' *R* (R Core Team, 2022). The first principal component explained 98 % of the variance and correlated positively with increasing precipitation and decreasing temperature, representing a gradient ranging from hot and dry to cold and wet climatic conditions (Fig. S1). Therefore, this first principal component was used as a single variable representing climate gradient of mean annual precipitation and temperate in our analysis (hereafter, climate gradient). This climate gradient can be viewed as the measure of site productivity and environmental stress, with the harsh environmental conditions on the low and high ends of the gradient (cold areas on the high end and hot areas with drought and associated lack of snow cover during winter on the low end) and the highest site

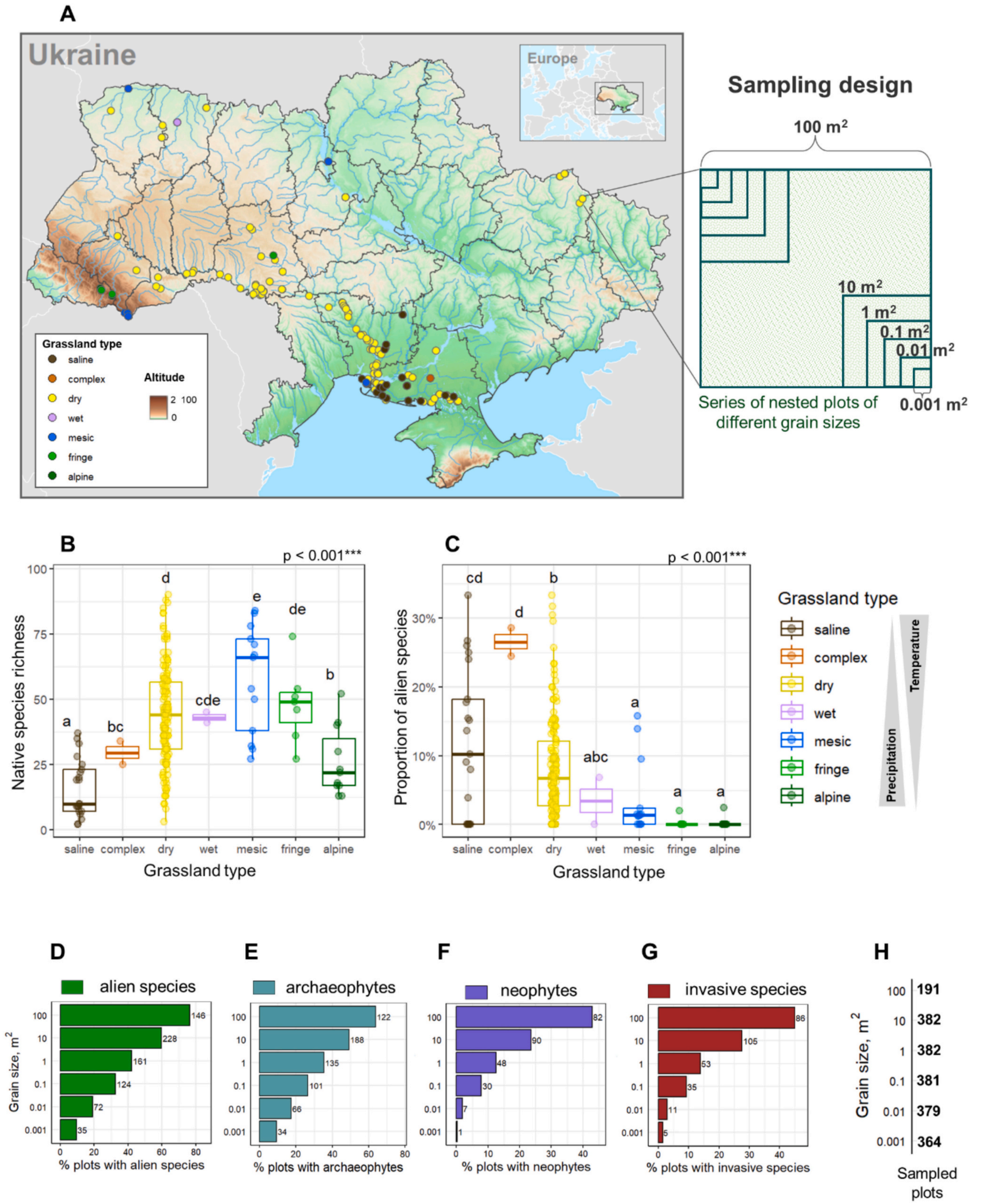

Fig. 1. (**A**) Map of the study area showing 191 vegetation monitoring plots and nested plot design. (**B**) Species richness of native species and (**C**) of proportions of alien species depending on the grassland habitat type, both sampled at the 100 m^2 plots. Habitat complex is the steppe depressions with combination of diverse habitat types that vary across space and time, creating a dynamic mosaic of ecological conditions. Letters on the boxplots show differences among the grassland types in the marginal means derived from the GLMs (Table S5). Proportions of plots (shown by bars) and number of plots (numbers near bars) containing all alien species (**D**), archaeophytes (**E**), neophytes (**F**) and invasive species (**G**) out of the total number of sampled plots (**H**), excluding those with no recorded species. See Table S3 for more details.

productivity in the middle of the gradient linked to warm and moderately wet conditions (Buzhdygan et al., 2025a). Climate gradient strongly positively correlated with altitude across our study area (Fig. S2). In each 10-m^2 sub-plot, we estimated cover of herbs, plant litter, stones and rocks, measured soil pH, and assessed microrelief (small-scale deviations from a smooth plane) and heat stress index (for details see Supplementary Methods). We considered herb-layer cover as a proxy for site productivity and plant litter cover – as a proxy for both productivity and disturbance, potentially influencing habitat invasibility (for details see Supplementary Methods). For the 100-m^2 plots, soil pH, microrelief, heat stress index, cover of plant litter, stones and rocks were calculated as the average of the values measured in the two 10-m^2 subplots located within each 100-m^2 plot. In each 100-m^2 plot we recorded grazing intensity, presence of mowing, and grassland abandonment. To quantify the influence of land use and urbanization in the surrounding landscape, we extracted the raster land cover data for cropland and urban built-up area from the Copernicus Global Land Cover Service (Buchhorn et al., 2020). We calculated the area of croplands and urban built-up land (i.e., surfaces covered by buildings and other man-made structures) within three buffer radii around each 100-m^2 plot: 250 m, 500 m, and 1000 m. For each plot we also extracted road density values using the spatial data from the OpenStreetMap (OpenStreetMap Contributors, 2025) and the '*raster*' (Hijmans et al., 2023) and '*sf*' (Pebesma, 2018; Pebesma and Bivand, 2023) packages in *R*. We estimated community-level disturbance severity and disturbance frequency proxies using species-level disturbance indicator values (Midolo et al., 2023). For more detailed methods on the sampling and measurements of the variables see Supplementary Methods.

We estimated the effects of the study drivers on the level of invasion at the local spatial scale, using 100-m^2 plots as a target plot size. We also tested if the proportions of all alien species, and particularly of invasive, archaeophyte and neophyte species depend on the richness of native species. Further, we tested the scale-dependency of the effects of each driver on the proportions of alien species for each study group by comparing their effects across all six grain sizes. At the smallest grains, invasive species were recorded in only 5 out of 364 plots (1.4 %) at the 0.001 m^2 scale and 11 out of 379 plots (3 %) at the 0.01 m^2 scale (Fig. 1E, Table S3), while neophytes occurred in just 1 and 7 plots (0.3 % and 1.8 %), respectively (Fig. 1F, Table S3). Due to these low occurrences, these two finest grain sizes were excluded from the further analysis of invasive and neophyte species, while all grain sizes were retained for the analysis of all alien species and of archaeophytes.

2.4. Data analysis

All data analyses were performed using *R* version 4.2.2 (R Core Team, 2022). To test the effects of environmental drivers and of native species richness on the proportions of all alien, invasive, archaeophyte and neophyte species we applied weighted generalized linear mixed effect models (GLMM) with binomial error distribution and logit link function, using plant total species richness per plot as model weights. We fitted GLMM models separately for each scale (grain size) using the '*lme4*' *R* package (Bates et al., 2015). For each response variable at each scale, we fitted three separate models (Table S6), each reflecting a distinct set of hypotheses, minimizing multicollinearity among predictors (Fig. S2) and to avoid model overfitting. Model 1 tested the effects of local environmental conditions (soil pH, heat index, microrelief), vegetation structure, management (grazing, mowing, abandonment), and land-use variables (cropland cover and urban built-up area in the surrounding landscape) at three buffer sizes (radius of 250 m, 500 m, and 1000 m). Each buffer size was tested in a separate model with all other predictors held constant (Models 1a–c, Table S6), to assess which spatial extent best captured the effect of surrounding land use on invasion level. This approach allowed us to evaluate the scale sensitivity of landscape drivers in a comparable framework, while avoiding high correlations among the buffer sizes ($r \geq 0.9$; Fig. S2). To avoid model overfitting and multicollinearity, Model 2 was limited to predictors related to road density, disturbance frequency, and disturbance severity (Table S6). We did not consider climate in this model, as in Model 1 climate had a strong signal and could override the effects of these disturbance-related variables in Model 2. Model 3 tested the effects of native species richness, with the climate gradient as a covariate in order to account for the climatic differences among the study sites (Table S6). Additionally, at 100-m^2 plots we tested if the proportions of alien species depend on the cover of native species in the plant community (Fig. S6) by fitting a binomial GLMM with native species cover as a predictor and with the climate gradient as a covariate.

Our data were collected through 11 distinct sampling campaigns (indicated by dataset ID, Table S2), which varied in sampling conditions, regions, observer identity and effort. To account for non-independence introduced by this variation, we modelled dataset ID as a random effect in all models. This approach captures both measured and unmeasured differences across campaigns, which cannot be fully accounted for by fixed covariates such as sampled year or region. Additionally, this strategy avoids overfitting and multicollinearity, which may arise when multiple correlated fixed effects are included. At finer spatial grains (0.001–10 m^2), data were nested with two 10-m^2 subplots per each 100-m^2 plot, containing several smaller grain sizes. To account for this hierarchical structure, we included a nested random effect of 100-m^2 plot ID within dataset ID in all models for these subplot scales (0.001–10 m^2). For models at the 100-m^2 grain size, we used dataset ID alone as a random effect. This structure accounts for within-plot dependencies and controls for autocorrelation due to shared environmental context and sampling history. Random effects are particularly important in this context because they avoid pseudo-replication by accounting for the non-independence of subplots within plots and within sampling campaigns.

We tested each model for model convergence, overdispersion and multicollinearity using the '*performance*' *R* package (Lüdecke et al., 2021). We found no multicollinearity (i.e., the variance inflation factor did not exceed 3). When we found overdispersion or underdispersion, we applied GLMM models with the quasibinomial family using the '*glmmPQL*' function from the '*MASS*' package (Venables and Ripley, 2002). We tested the spatial autocorrelation of the residuals for each model (for 100-m^2 plots) using Moran's I statistics. For this, for each GLMM model we extracted randomised residuals using '*simulateResiduals*' function of '*DHARMa*' package in R (Hartig, 2022). Then, on these residuals we performed Moran's I test using '*testSpatialAutocorrelation*' function of '*DHARMa*' package. The spatial matrix of weights for Moran's I test was calculated (using '*dist*' function in R) as the inverse distance matrix (Euclidean distances between pairs of plots) based on longitude and latitude of each study plot. The calculated Moran's I statistics revealed no significant autocorrelation of residuals for any of the models (i.e., as all $P > 0.05$, Table S6), indicating that spatial autocorrelation among study plots did not affect our results.

For each GLMM model and spatial scale we extracted the effect size (estimated slope) for each predictor. To plot these effects on a comparable scale across all predictors (Fig. 3) we standardized these obtained estimates using the '*coefs*' function from the '*piecewiseSEM*' package in R (Lefcheck, 2016). To test the scale-dependency of the effects of each study predictor (Fig. 4), we assessed the associations of the predictor slope estimates (obtained from the GLMMs) with the grain size of the study plot using the analysis of variance least-squares models ('*lm*' function in R). We tested both linear and quadratic relationships between driver slopes and plot size and used the likelihood-ratio test to select the most parsimonious models (Supplementary Data 3).

To test if the proportions of alien species and richness of native species differed among grassland habitat types (Fig. 1B-C, Table S5, Fig. S11), we fitted a binomial and a Poisson Generalized Lineal Models (GLM), respectively, and compared the differences in the model marginal means for each grassland type using the '*emmeans*' package in R (Lenth, 2023).

We analysed species composition of aliens using the nonmetric multidimensional scaling (NMDS) with the '*metaMDS*' function from the '*vegan*' package (Oksanen et al., 2018) applied to the occurrence matrices of alien species with species-specific cover in each 100-m^2 plot. To assess the alien composition based on their time of introduction, geographical origin and naturalization level, we quantified the community weighted mean (CWM) for each group, weighted by species cover. For this we used the '*functcomp*' function in the *FD* package (Laliberté et al., 2014). To test the effects of the environmental predictors on alien composition, we performed PERMANOVA tests on Bray-Curtis matrices with 1000 permutations using the '*adonis2*' function from the '*vegan*' package. The effects of the predictor variables were fitted post hoc to the NMDS ordination diagrams using the '*envfit*' function from '*vegan*' package.

3. Results

Out of the 1082 vascular plant species sampled across the study area, 87 species were aliens (8 %), of which 60 species were archaeophytes and 27 species were neophytes (Fig. S4). Among aliens, 14 species were classified as invasive (Fig. S4). Archaeophytes were the most frequently encountered across all spatial grains, followed by neophytes and invasive species (Fig. S4). Among archaeophytes, *Lamium amplexicaule*, *Veronica arvensis*, and *Bromus tectorum* were the most widespread species, each occurring in over 17 % of plots at the largest grain size (100 m^2). These species maintained relatively high frequencies even at smaller grains, with *Veronica arvensis* being the most frequent. Within neophytes, *Erigeron canadensis*, *Centaurea diffusa*, and *Erigeron annuus* showed the highest occurrences. For invasive species, *Bromus tectorum*, *Erigeron canadensis*, and *Centaurea diffusa* were the most common. At the 100 m^2 scale across all habitats, the proportion of alien species out of all species ranged from 0 % to 33 %, with a mean of 7.7 %. The same range (0–33 %) was observed for archaeophytes (mean = 6 %), neophytes (mean = 1.6 %) and invasive species (mean = 1.9 %) (Table S4). At smaller grain sizes (0.01–0.001 m^2) the proportion of archaeophytes reached up to 100 % in some plots, while neophytes reached up to 25 % and invasives up to 50 % of the total species composition. Archaeophytes showed significant variation among grassland types (Fig. S11C). Habitat complex *pody* and saline grasslands exhibited on average the highest proportions of archaeophytes, followed by dry grasslands (Fig. S11C). Mesic, wet, fringe, and alpine grasslands showed significantly lower proportions, with alpine and fringe types among the least invaded by archaeophytes (Fig. S11C, Fig. S5A). These patterns strongly match those in the overall proportion of all alien species (Fig. 1C), which is largely driven by archaeophytes, as they represent the majority of alien species in our dataset (Fig. S3C,D). Neophytes were most prevalent in dry grasslands, but we found no significant differences in neophyte proportions among the habitats (Fig. S11B). Wet and mesic grasslands also hosted neophytes to some extent, whereas fringe and alpine grasslands showed no neophyte presence (Fig. S5B). Proportions of invasive species also showed no significant differences among grassland types, with slightly higher value ranges in dry, mesic and saline grasslands (Fig. S11A).

Community composition of alien species and their groups based on introduction time, geographic origin, and invasion status in the study plant communities was correlated with climate gradient and community disturbance proxies (Tables S7-S8, Fig. S9-S10).

The proportions of alien species increased with sampled grain size (Fig. 2A,D,G,J) while their variability across samples decreased at larger grain sizes for all alien group and separately for archaeophytes and invasive species but increased for neophytes (Fig. S7). All groups showed strong negative relationships with native species richness (Fig. 2B,E,H,K), but weaker relationship with the cover of native species (Fig. S6). Moreover, the negative relationship between native species richness and the proportions of aliens strengthened as grain size decreased (Fig. 2C,F,I,L).

Among the environmental factors, the climate gradient (a PC ranging from hot and dry to wet and cold conditions) emerged as the strongest driver of alien species proportions, showing strong negative effects. However, these effects were weaker for neophytes compared with archaeophytes and invasives (Fig. 3, Fig. S8, Supplementary Data 2). Disturbance severity and frequency were important drivers for archaeophyte and invasive species, showing strong positive effects, but had little impact on neophytes (Fig. 3, Fig. S8). Soil pH negatively affected both invasive and neophyte species but had no significant impact on archaeophytes (Fig. 3). Microrelief had positive effects on the invasion level by archaeophytes and neophytes. Litter cover, herb-layer cover, grazing intensity and grassland abandonment positively influenced all alien group and archaeophytes, though these effects were not significant for invasive or neophyte species (Fig. 3). Invasion levels also tended to increase with higher cover of stones and gravel (Fig. 3), although these effects were not statistically significant. Croplands cover in the surrounding landscape was among the key drivers of neophyte proportions, showing positive effects, being the most influential at the 500 m buffer radius. In contrast, cropland cover had no significant effect on all alien, archaeophyte or invasive species. The proportion of both invasive and neophyte species increased with urban built-up area at all buffer scales, though the effects were not statistically significant for archaeophytes (Fig. 3). Similarly, road density had a significant positive effect on both invasive and neophyte species but not on overall alien group or archaeophytes (Fig. 3).

The effects of the climate gradient on the proportions of alien species did not vary with spatial grain (Fig. 4). In contrast, the effects of soil pH weakened with increasing grain size for archaeophytes, with marginally significant trends for invasive species and for all alien group (Fig. 4). The effects of gravel and stone cover showed strong scale-dependency. For all alien group and archaeophytes, this relationship was U-shaped, with strong positive effects at the finest grain (0.001 m^2), declining to neutral or slightly negative at 0.1–1 m^2, and increasing again at the largest grain size (100 m^2). In contrast, when invasives and neophytes were considered separately, the effect of gravel and stone cover weakened with increasing grain size, indicating a scale-dependent decline in their response (Fig. 4). The effects of litter cover on the proportions of alien species exhibited a slight U-shaped pattern across spatial scales, with strong positive effects at the finest grain (0.001 m^2), decline through intermediate grains (1–10 m^2), and a slight increase again at the largest grain size (100 m^2, Fig. 4A-B). This scale-dependency was not significant for neophyte and invasive species (Fig. 4C-D). Positive effects of grazing intensity on the percentage of invasive species increased with scale (Fig. 4D). For neophytes, grazing had negative effects at smaller spatial grains, but these effects weakened with increasing scale and became positive at the 100 m^2 (Fig. 4C). A negative scale-dependency was detected for the effect of road density on invasive species proportions (Fig. 4D). The effects of urban built-up area and disturbance severity decreased with grain size. For all aliens, the effect of cropland areas was negative across all grain sizes and buffer radii, with the strongest effects observed at intermediate grains (0.01–0.1 m^2), which weakened toward both finer and coarser grain sizes, also becoming marginally significant at the 500 m and 1000 m buffer radii (Fig. 4A). For neophyte and invasive species, the effect of cropland cover was positive and relatively constant along the scale gradient (Fig. 4C-D).

4. Discussion

We found that the level of invasions in grassland plant communities was associated with multiple drivers, including native species richness and abiotic variables describing climatic conditions, system disturbance, land use, urbanization, and local microrelief. However, the effects of these factors changed with the size of the sampled grain, suggesting that the drivers of invasions and their mechanisms are scale-dependent across fine spatial scales.

Archaeophytes were the most frequently encountered across all

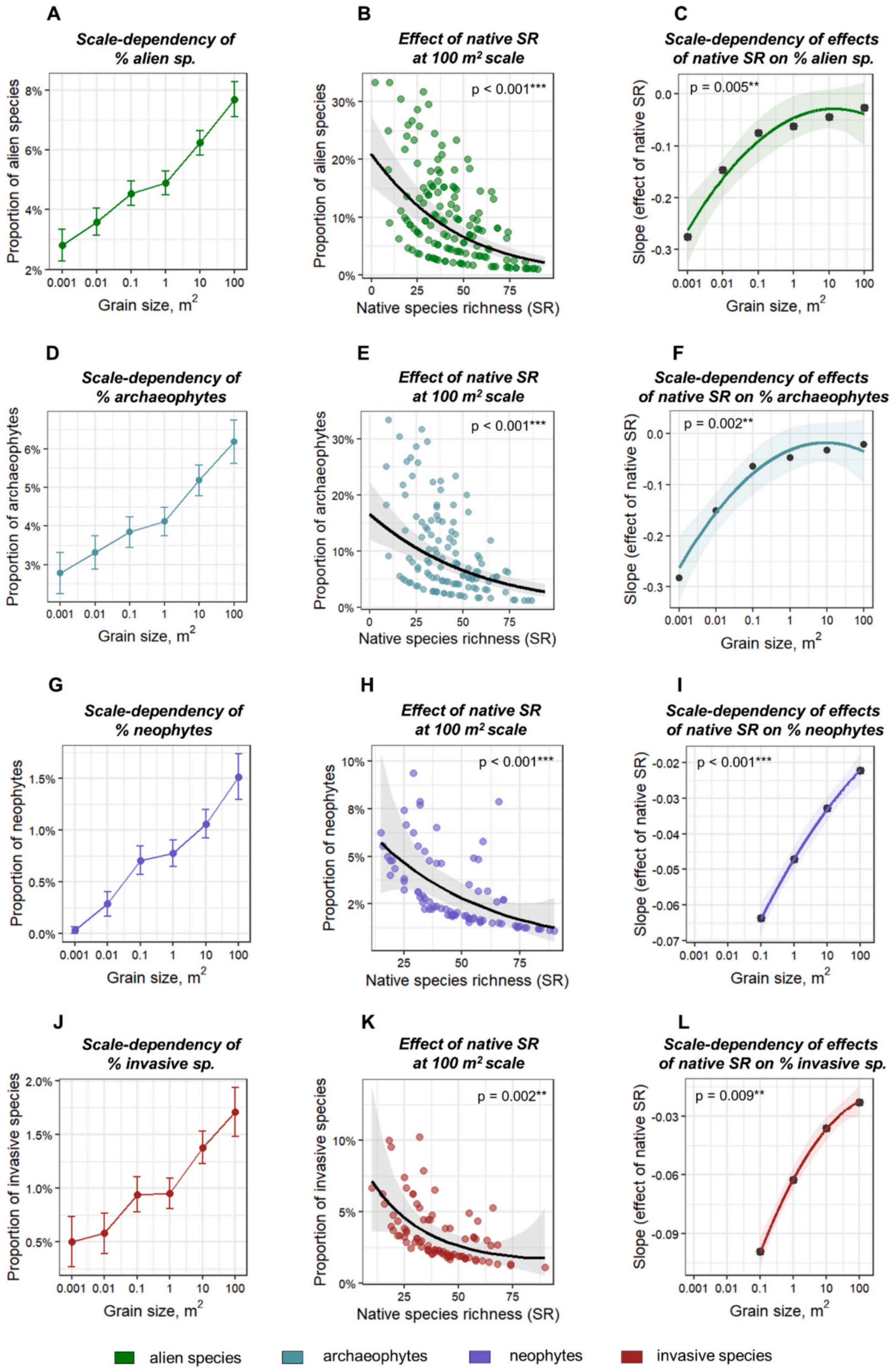

Fig. 2. Proportions of all alien species (**A**), archaeophytes (**D**), neophytes (**G**) and invasive species (**J**) across sampled grain sizes. Points show the mean value and error bars show the standard error (SE) of the mean. Relationships between native species richness and the proportions of alien species (**B**), archaeophytes (**E**), neophytes (**H**) and invasive species (**K**), sampled at the 100 m^2 plots. The lines represent predicted values from generalized linear mixed-effects models (GLMMs). Scale-dependency of the native richness effects on the proportions of alien (**C**), archaeophytes (**F**), neophytes (**I**) and invasive species (**L**), estimated as the slopes of native species richness effects (obtained from GLMMs at each grain size) regressed against grain size using least-squares linear models (Supplementary Data 3). Shaded areas around lines show 95 % confidence intervals. *P*-values shown above each panel indicate the significance of the tested relationships, based on a threshold of $\alpha = 0.05$.

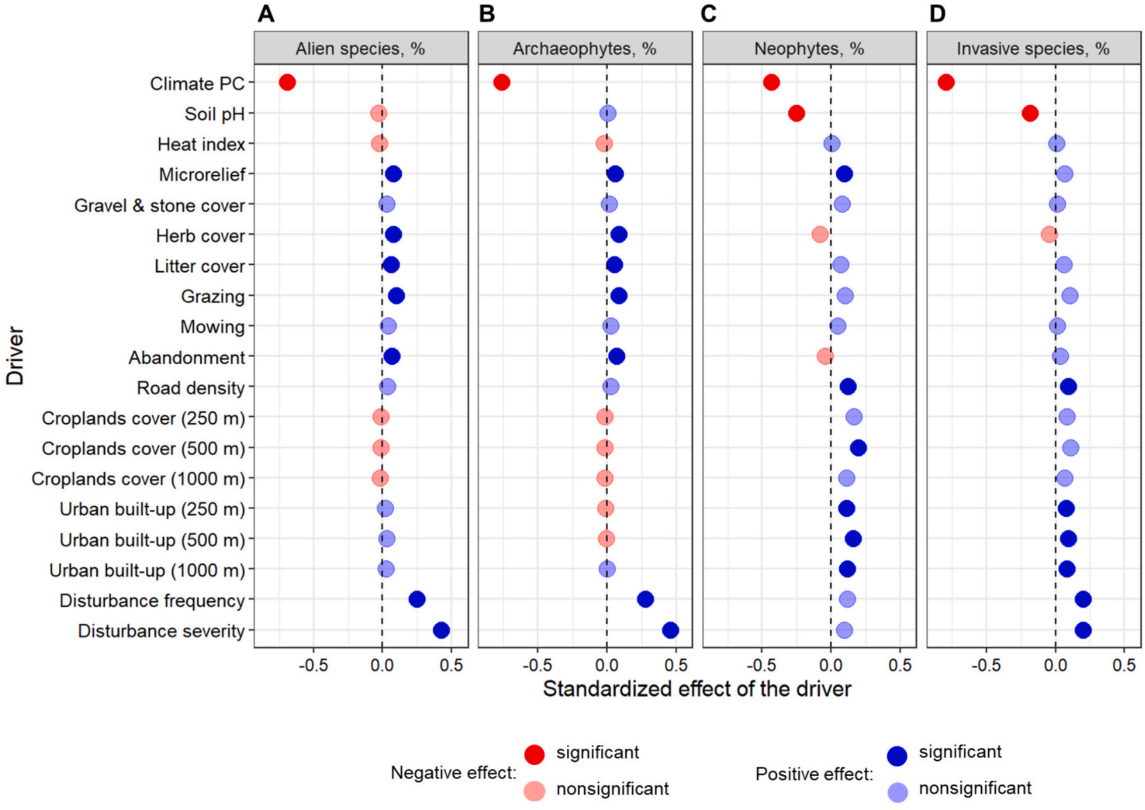

Fig. 3. The standardized effect sizes of environmental drivers on the proportion of all alien species (**A**), archaeophytes (**B**), neophytes (**C**) and invasive species (**D**) in plant communities sampled at the 100 m^2 plots. For the results for all spatial scales see Supplementary Data 2.

spatial grains and had some habitat specificity, particularly dominating in saline and dry grasslands and in habitat complex *pody* (Fig. S11). Neophytes had lower overall proportions and were relatively evenly spread across grassland types, with a slight tendency to be more common in dry and mesic grasslands. Fringe and alpine grasslands had low number of archaeophytes and no neophytes or invasive species. While all alien groups responded strongly to climate, there were some differences in their key environmental and anthropogenic drivers. Invasive species responded to urban area cover and road density, while neophytes were associated with road density, urban areas and cropland cover in the surrounding landscapes, reflecting their dependence on recent propagule pressure. In contrast, the broader group of all alien species, dominated by long-established archaeophytes, responded more strongly to overall disturbance severity and frequency, site productivity proxies and local management practices (grazing and grassland abandonment). These findings highlight that the drivers of plant invasion vary across alien species categories, likely due to differences in their residence time and spread potential.

4.1. Diversity–invasions relationships and their scale-dependency

The proportions of alien species across studied grasslands increased with grain size (Fig. 2A,D,G,J), supporting the idea that the mechanisms underlying plant invasions depend on the sampled scale (Fridley et al., 2007; Powell et al., 2013). This scale-dependency arises because alien species are generally more locally rare than native species, resulting in higher spatial turnover and a faster accumulation of alien species with increasing grain size (Hulme, 2008; Powell et al., 2013). This is primarily due to the relatively smaller species pool of alien than native species, which underlies their rarity and turnover at fine spatial grains. Important to note, this pattern is not unique to invasions but is an inherent property of biodiversity processes involving locally rare species, e.g. endemism patterns (Daru et al., 2020). We found negative effects of native species richness on invasion levels (Fig. 2B,E,H,K), aligning with the *diversity–invasibility hypothesis* (Elton, 1958), which suggests that species-poor communities are more susceptible to invasions. While broad-scale studies often report a positive correlation between native species richness and invasions (Gaertner et al., 2009; Knight and Reich, 2005; Powell et al., 2013, 2011; Stohlgren et al., 1999), fine-scale studies, like ours, tend to observe negative diversity-invasibility relationships (Hector et al., 2001). At fine grains the individual plants and their immediate neighbours interact more directly, creating stronger competition (both intra- and interspecific) for limited space and resources (Davies et al., 2007). High native plant richness at these fine scales leads to more complete resource utilization and niche occupation (Buzhdygan et al., 2020), leaving fewer open niches for invader colonization (Levine, 2000; Shea and Chesson, 2002; Smith and Côté, 2019). However, even within fine-grain observations, evidence for the strength of the diversity–invasion relationship remains inconsistent (Fridley et al., 2007), and the area thresholds at which direct species competition is overridden by the environment-driven coexistence mechanisms are not defined. Positive diversity-invasion relationships have even been reported at fine grains, such as 100 m^2 (Brown and Peet, 2003; Stohlgren et al., 2006), 10 m^2 (Gilbert and Lechowicz, 2005; Smith and Knapp, 1999; Stohlgren et al., 2006) and as small as 1 m^2 (Cleland et al., 2004; Keeley et al., 2003; Sax et al., 2002; Stohlgren et al., 2006). In our study, decreased grain size led to a stronger negative effect of native richness on invasion levels (Fig. 2C,F,I,L; Fig. S8). The effects on the proportion of alien species, particularly archaeophytes, were steep up to 0.1 m^2 and then saturated at 1 m^2 (Fig. 2C-F). The variance explained by native richness was 8–43 % higher for archaeophytes, 14–30 % higher for invasive species and 10 % higher for neophytes at grain sizes up to 1 m^2 compared to larger grain size (10–100 m^2; Fig. S8). This aligns with previous findings that herbaceous communities exhibit direct plant-plant interactions predominantly at grain sizes up to 1 m^2, while larger grains are less influenced by local inter-

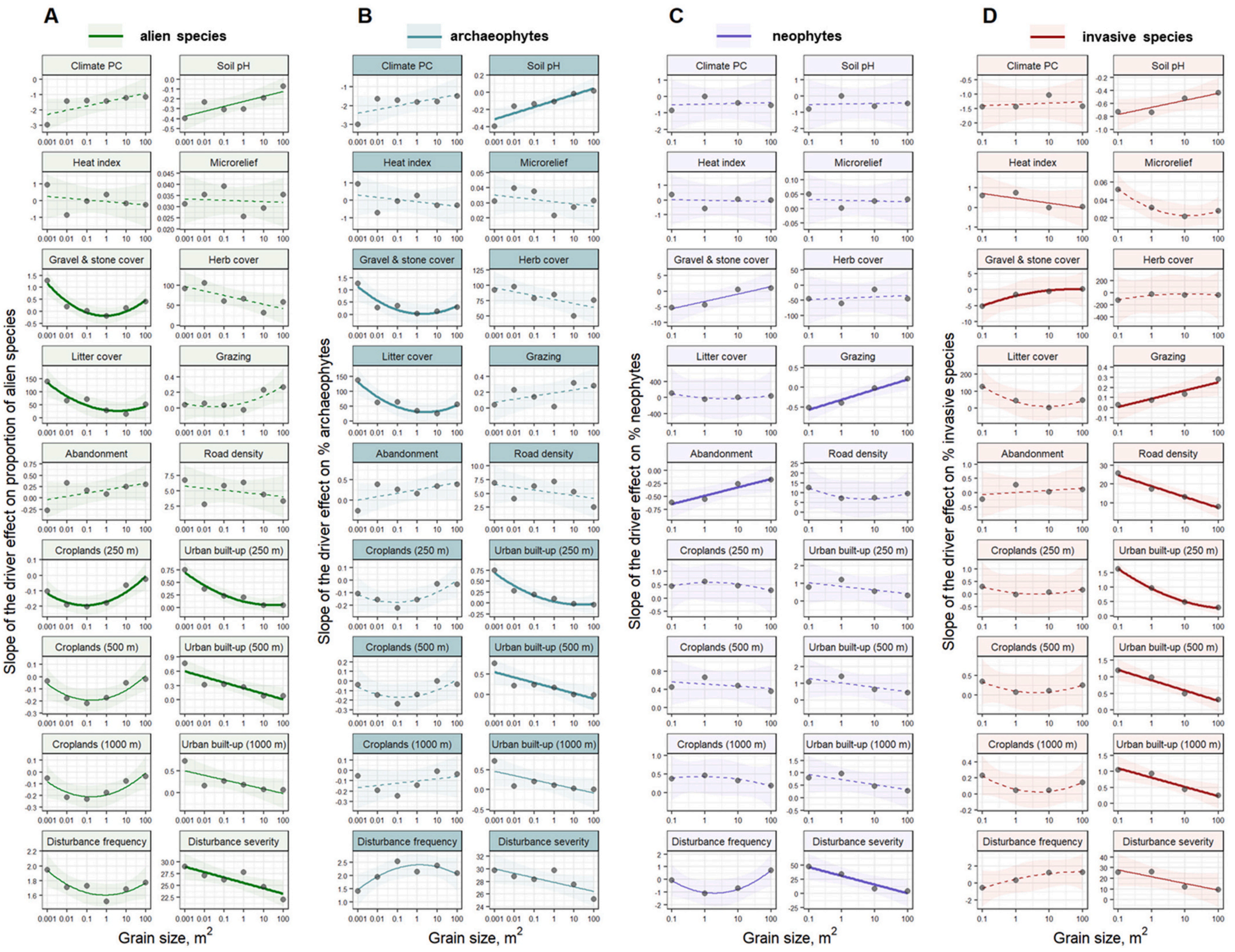

Fig. 4. Scale-dependency of the driver effects on the proportion of all alien species (**A**), archaeophytes (**B**), neophytes (**C**) and invasive species (**D**). Regression lines show association of the predictor slope (obtained from the GLMMs) with the grain size of the study plot using the analysis of variance least-squares models (Supplementary Data 3). Shaded areas around lines show 95 % confidence intervals. Solid thick lines show significant effects ($P < 0.05$), solid thin lines show marginally significant effects ($0.05 \leq P \leq 0.09$), and dashed lines show non-significant effects ($P > 0.09$).

and intraspecific competition and more by environmental drivers (Davies et al., 2007).

4.2. Environmental drivers of invasion level

The ability of alien plant species to invade a region depends not only on native plant diversity, but also on habitat characteristics (Chytrý et al., 2008a, 2008b). Although alien species occurred in all habitat types, their proportions were highest in drier and wormer ecosystems, especially in complex, saline and dry grasslands, and lowest in fringe and alpine grasslands (Fig. 1C, Fig. S5, Fig. S11, Table S4). Previous studies in Europe suggest that prehistoric and recent invaders occupy different habitats (Pyšek et al., 2005), with archaeophytes more often associated with low rainfall and well drained soils (Chytrý et al., 2008a) and occurring most commonly in dry to mesic open habitats, while neophytes tend to show stronger affinity for wet habitats and disturbed vegetation (Chytrý et al., 2008b). In our study, archaeophytes were the most common alien group across all spatial scales (Table S4), with high proportions particularly in saline, complex, and dry grasslands (Fig. S11). Many archaeophytes were found in at least two grassland types (Fig. S5A), including habitats with very different environmental conditions and disturbance regimes (whether anthropogenic or natural). This is likely due to their long reside in Ukraine, which has allowed them to adapt to a wide range of local conditions, including extremes such as periodic drought or high soil salinity. Neophytes were generally less frequent and abundant than archaeophytes (Table S3), but more evenly distributed across grassland types, with a slight preference for dry and mesic grasslands (Fig. S11). Some neophyte species showed distinct habitat preferences (Fig. S5B), for example, *Dianthus barbatus* and *Oenothera biennis* were confined only to mesic grasslands, while *Elaeagnus angustifolia* occurred mainly in saline areas, likely due to its salinity tolerance. Some neophytes in dry grasslands were woody or shrubby species that could spread rapidly if not managed, leading to grassland overgrowth. Invasive species, regardless of whether they are archaeophytes or neophytes, showed low habitat specificity (Fig. S11, Fig. S5C). Their high spread potential and broad ecological tolerance allows them to establish across multiple grassland types, even those with very different environmental conditions, as seen for *Erigeron annuus*, which was recorded in both dry and moist grasslands (Fig. S5C).

Plant invasions across different grassland habitat types in our study were driven by multiple factors, highlighting that invasive success cannot be attributed to a single predictor (Chytrý et al., 2008a). The climate gradient was among the key environmental drivers (Fig. 3, Fig. S8), with the proportions of overall alien species, as well as separately archaeophytes, neophytes and invasive species significantly decreasing under wetter and colder conditions. These results challenge the conventional perception that macroclimatic factors predominantly govern plant invasions at broader scales (continental, regional, and landscape), while having limited effects at fine spatial grains (Czarniecka-Wiera et al., 2020; Milbau et al., 2009). The climate gradient in our study was strongly correlated with elevation ($r = 0.97$; Fig. S2), suggesting that higher invasion levels along the elevation gradient are primarily driven by climatic constraints, as supported by previous studies (Table S1). The decrease in the proportion of alien species at the benefit of native species with increasing altitude is a common pattern reported in Central Europe (Chytrý et al., 2008a, 2005).

Local land-management practices, such as grazing intensity and grassland abandonment, increased alien species proportions, though the effect was not significant for invasives or neophytes. Cropland cover in the surrounding landscape showed positive tendency for the proportion of invasive species and this effect was more pronounced for the neophytes (particularly at buffer radius of 500 m). Previous research shows that abandoned croplands are sensitive to the immigration of many invasive species, such as *Ambrosia artemisiifolia*, *Asclepias syriaca*, and *Solidago* spp. and act as hotspots for their further spread in the landscape (Chytrý et al., 2008a).

In line with the previous evidence (Table S1), we found a positive relationship between the proportion of alien species and site productivity proxies (i.e., herb-layer cover and litter cover, Fig. 3A-B). However, Davies et al. (2007) suggest that community invasions are determined by the availability of unused resources rather than by site productivity itself. These resources become accessible when competition with resident species is reduced due to natural or anthropogenic disturbances creating gaps in the vegetation. For example, patches of bare ground caused by grazing (through trampling or digging) or patches of plant litter from the abandonment of grassland management can create localized unexploited resources where alien species can establish. In our study, we found evidence supporting this pattern, as invasion levels increased with litter cover and grazing intensity (particularly for invasive species) (Fig. 3). In addition to creating local patchy microsites for invasion, grazing animals may import non-native plant propagules into native vegetation or directly modify resident vegetation in such a way that invading species can establish (Hobbs and Huenneke, 1992). In line with these disturbance-driven dynamics of resource availability, plant invasions are also predicted to increase in environments experiencing pulses of resource supply, such as nutrient releases from flooding or fluctuating water supplies in dry regions (Davis et al., 2000). Previous research across different biogeographical regions of Europe show that many aliens appear in frequently disturbed habitats with fluctuating nutrient availability (Chytrý et al., 2008b).This aligns with our findings, as the highest proportion of alien species, particularly archaeophytes, occurred in habitat complex (Fig. 1C, Fig. S11C) – the unique steppe depressions characterized by highly heterogeneous mosaics of grassland habitats, which are subject to pronounced temporal and spatial fluctuations in resource supply from periodic enrichments and frequent disturbances (Shapoval and Kuzemko, 2021).

The effects of litter and grazing patches on plant invasions can also be understood through the lens of spatial heterogeneity. Small-scale disturbances, such as these vegetation patches or gaps, create spatial heterogeneity across multiple scales (Turner, 2010), which can significantly influence invasion dynamics. Indeed, previous studies suggest that environmental heterogeneity plays a key role in determining whether a community can resist new invasions and the speed at which an invasion progresses (Melbourne et al., 2007). We also found a positive effect of microrelief on the proportion of both archaeophytes and neophytes. Invasion levels also showed a tendency for these proportions to increase with the cover of gravel and stones (Fig. 3). Both microrelief and cover of gravel and stones serve as proxies for small-scale environmental heterogeneity, causing localized differences in vegetation cover, soil moisture, soil depth, microclimate and erosion (Dembicz et al., 2021). Interestingly, invasion theory shows that while environmental heterogeneity increases community invasions (Davies et al., 2005), it simultaneously reduces the impact of invasive species on native species by promoting coexistence mechanisms that are not possible in homogeneous environments, known as the *environmental heterogeneity hypothesis* of invasions (Melbourne et al., 2007).

Urbanization is another recognized driver of biological invasions (Table S1). In our study, the levels of invasion increased with the urban built-up area and road density, though the effects were significant only for invasive and neophyte species, not for archaeophytes (Fig. 3). Studies at broader regional and landscape scales showed that urbanization pressure was a major driver of spread for both neophytes and archaeophytes, but these effects were strongly scale-dependent and influenced by the configuration and complexity of landscape (Boscutti et al., 2022). Roads, in particular, are widely recognized as key facilitators of invasion, acting as dispersal pathways, significantly contributing to propagule pressure from road margins (Tikka et al., 2001). Roads can also facilitate alien spread indirectly through the local modification of the neighboring environment by road infrastructure (Gelbard and Belnap, 2003).

Our results demonstrated that communities experiencing higher overall disturbance severity and disturbance frequency supported significantly higher proportions of alien species, particularly archaeophytes and invasive species (Fig. 3A-B,D), reinforcing the widely recognized ability of alien species to dominate disturbed and degraded ecosystems (Chytrý et al., 2008b; Clark and Johnston, 2011; Hobbs and Huenneke, 1992; Pinto and Ortega, 2016). As disturbances become more frequent and severe due to climate change and increasing human pressures (Turner, 2010), alien species are likely to thrive in these altered environments, posing an increasing threat to native biodiversity.

Our results support the conceptual distinction between archaeophyte, neophytes and invasive species by revealing differences in the relative importance of environmental and anthropogenic drivers for each group (Fig. 3). Invasive species, defined as those actively spreading in the final stage of the introduction–naturalization–invasion continuum, responded significantly to urban built-up areas and road density. Neophytes, which have a shorter residence time in temperate Europe than archaeophytes, also showed strong associations with human activities, including road density, urban built-up areas, and cropland cover in the surrounding landscape. These patterns suggest that the spread of neophytes is facilitated by propagule availability and transient establishment opportunities provided by urban, industrial, and agricultural land-use areas. As expected, climatic effects were less pronounced for neophytes compared to the broader group of all aliens and particularly of archaeophytes, likely because many neophytes have not yet reached their full distribution and remain more influenced by recent anthropogenic pressures than by long-term climatic or habitat constraints (Chytrý et al., 2008a). In contrast, the broader group of all alien species showed weaker responses to urbanization and cropland cover but stronger associations with local system productivity and disturbance (herb-layer and litter cover), as well as with the local management practices such as grassland abandonment and grazing. This pattern reflects the strong prevalence within the broader alien group of naturalized archaeophytes. These species may have already saturated their suitable range and thus respond more strongly to local habitat properties and to climatic conditions and related environmental disturbance regimes than to contemporary propagule pressure (from roads and the surrounding urban and agricultural areas). These results reinforce our decision to consider invasive species, neophytes, and archaeophytes as separate groups, and demonstrate that environmental and anthropogenic filters vary in importance across these categories, likely due to differences in their spread potential and residence time.

4.3. Scale-dependency of abiotic and anthropogenic drivers of invasion level

Interaction of environmental drivers with the sampled scale has been shown to change the patterns of fine-grain plant diversity in grasslands (Dembicz et al., 2021), including evidence from our study sites (Buzhdygan et al., 2025a). However, the extent to which the invasion drivers differ in their effects along the fine-grain size gradient in grasslands and the scales at which they are most relevant remains largely unclear. In our study, the importance of the invasion drivers varied as a function of grain size (Fig. 4, Fig. S8). The positive effects of urban built-up area, road density and disturbance severity on invasion levels were most pronounced at the finest grain sizes (up to 0.1–1 m^2, depending on the driver), where competition among species is most intense due to the space limitation (Davies et al., 2005). These effects weakened at larger spatial grains (10–100 m^2), likely because direct competition among individual plants diminishes at these scales, while factors such as environmental heterogeneity and broader community-level interactions become more influential (Davies et al., 2005; see sections 4.1–4.2). Previous research has emphasized the role of spatial scale in shaping the effects of urbanization and disturbance at regional and landscape levels (Boscutti et al., 2022). Our findings complement this by demonstrating that scale-dependency also occurs at local scales across fine-grain sizes. This scale dependency highlights the risk of overlooking important invasion drivers when focusing on a single spatial grain, as evidenced by the diminished effects of urban built-up area or disturbance severity at our 100-m^2 plots (Fig. 4). However, the strong negative effect of native richness on invasion level at the finest grains (0.001–0.01 m^2, Fig. 2C,F, I,L) and the high variance explained (Fig. S8) suggest that high native species richness remains a critical barrier to invasions at the finest scales, even under disturbance. Notably, the negative effect of grassland abandonment on neophyte proportions was strongest at the smallest scale and progressively weakened with increasing grain size, likely reflecting reduced species competition at broader spatial grains.

The scale-dependent effects of both disturbance and site productivity on community invasion levels are linked to the effects of environmental heterogeneity, as more disturbed sites, as well as more harsh environments (and therefore less productive sites) tend to exhibit greater heterogeneity at fine scales compared to more productive or more undisturbed sites (Davies et al., 2007). While the scale-dependent effects of landscape heterogeneity on plant invasions have been observed across gradients of relatively large area sizes (e.g., Kotowska et al., 2022), the scale-dependency of fine-grain heterogeneity (i.e., within-plot heterogeneity) remains largely understudied (Davies et al., 2007). In our study, the positive effects of litter cover, as proxies for productivity (at high litter amounts) and disturbance (at both low and high litter levels), as well as the cover of gravel and stones (as a proxy for small-scale environmental heterogeneity) on the proportions of alien species, particularly archaeophytes, were strongest at the finest scale (0.001 m^2) and decreased with grain size, reaching their lowest effect at intermediate scales (1–10 m^2). This pattern contrasts with the expectation that the effects of heterogeneity on invasions should steadily increase with spatial scale (Davies et al., 2007; Fridley et al., 2007; Melbourne et al., 2007). This may be because at the finest scales (0.001–1 m^2) the entire plot can be dominated by the direct physical influence of individual litter patch or single microrelief objects, such as a single stone, molehill, or erosion patch. These physical barriers dominating the space at very fine scales could have detrimental effects on native vegetation, thereby altering local competition dynamics in favour of invaders. In some cases, however, such objects can also limit the establishment of aliens, as shown in our study by negative effects of gravel and stone cover on the proportions of invasive species and neophytes, which weakened with increasing grain size (Fig. 4C-D). Our results indicate that land management and conservation strategies should account for fine-scale variability in within-plot heterogeneity, as litter amount and microrelief features in grasslands can significantly influence competitive dynamics between native and invasive species.

The positive effect of grazing on the proportion of invasive species increased with grain size (Fig. 4D) and showed an increasing trend for archaeophytes (Fig. 4B), likely due to the reduced effects of competition with native species richness with increasing scale (Fig. 3F, Fig. S8). For neophytes, grazing effects followed a different pattern: shifting from strong negative effects at small scales to positive effects at 100-m^2 grain (Fig. 4C). Overall, this scale-dependent pattern may reflect the role of grazing animals as dispersal vectors (Janišová et al., 2025), that can facilitate the spread of alien species across larger areas. Cropland area in the surrounding landscapes showed contrasting patterns for neophyte species compared to archaeophytes. For neophytes, the effect of cropland cover was consistently positive across all grains, suggesting that croplands may facilitate neophyte establishment. When considering all alien species, and separately archaeophytes, the effect of cropland area was consistently negative, with the strongest effects at intermediate grains. These contrasting responses likely reflect differences in ecological strategies and introduction histories: neophytes are more recent introductions and are often associated with ongoing anthropogenic disturbances, such as those in agricultural landscapes, whereas archaeophytes are long-established and more integrated into semi-natural habitats, making them at fine scales less tolerant of, or even disfavoured by the impacts of intensive cropland use. This contrasts with findings from previous studies conducted at broader spatial extents, which reported that archaeophytes were positively associated with agricultural land use at regional and landscape scales (Boscutti et al., 2022).

4.4. Conservation and management implications and future directions

Conservation and management policies often focus on large-scale areas, such as national parks or even entire grassland habitats, thus underestimating the relevance of fine-scale processes (Vellend, 2017). However, coarse-scale data may overestimate the role of macroscale relative to other local invasion drivers (Hulme, 2003). The effects of plant diversity on ecosystem functioning are derived from the inherently small-scale nature of plant species interactions (Buzhdygan et al., 2025b). Consequently, if ecosystems experience biodiversity losses at local scales, their functioning may decline, even if regional plant diversity shows an overall increase (Vellend, 2017). Therefore, without an appropriate understanding of the invasibility drivers at the fine scale, large-scale conservation studies may misinterpret the relative risks posed by invasions on biodiversity and ecosystem functions and services (Hulme, 2003; Vellend, 2017).

Our findings indicate that the level of invasion of grassland plant communities is influenced by native species richness at the local scale, with higher fine-grain diversity predicting lower invasion levels. This suggests that native biodiversity at the local scale may buffer against the severity of non-native invasions in grasslands, consistent with findings across different ecosystem types (Cheng et al., 2024; Levine, 2000). However, we conclude this with caution, as recent advancements in neutral theory suggest that negative diversity–invasions relationships at fine spatial scales may be a result of neutral processes due to constraints of the limited space available to accommodate high numbers of both native and alien species within the small number of individuals (Stark et al., 2006). Further fine-scale studies should benefit from incorporating neutral null-modelling approaches (assuming no species interactions, e.g., Fridley et al., 2004; Stark et al., 2006) to better understand variability in invasion patterns. Nevertheless, our study highlights that perceptions of invasion success and its relationship to native plant species richness are heavily influenced by the spatial grain of observations. Consequently, these spatial artifacts can impede the accurate identification of areas where conservation and management efforts should be prioritized to mitigate the most significant invasion threats. For example, maps highlighting invasion hotspots (areas with particularly high proportions of alien flora) should be interpreted with caution, as these patterns are influenced by the grain size used for species monitoring (Hulme, 2003). Furthermore, given the widespread use of the proportion of alien species as an indicator of biodiversity homogenization, our findings on its scale-dependency emphasize the need for considerable caution when synthesizing data collected at inconsistent grain sizes.

Our data also revealed a scale-dependency in the effects of environmental and anthropogenic drivers on the invasion levels of grassland plant communities, highlighting that the identification of factors controlling invasions cannot be readily decoupled from the science of spatial scale. Furthermore, the scale-dependency of these drivers often differed depending on whether we considered all alien species (dominated by archaeophytes) or focused separately on invasive species and neophytes. This reinforces our decision to analyse all these groups separately and demonstrates that scale-dependency and environmental filtering operate differently across alien species categories due to differences in their spread potential and residence time. Focusing on neophytes is particularly important because, unlike archaeophytes, they are still expanding their ranges and are more responsive to propagule pressure from urbanization and agricultural landscapes. Understanding the drivers and scale-specific responses of neophytes can help anticipate future invasion risks and guide early intervention strategies before these species become widespread. Similarly, by focusing on the scale-specific drivers of invasive species, management strategies can more effectively target those at advanced stages of invasion, ensuring that conservation efforts are both ecologically informed and resource-efficient.

The comparison between alien species richness and cover revealed that the proportion of cover contributed by alien species was generally lower across most habitat types than their proportion based on species richness (Fig. 1C, Fig. S11, Fig. S12). This suggests that alien species were often present but not dominant in community biomass or cover. Although accounting for cover instead of richness did not substantially change the overall patterns of alien species distribution across habitat types in our study area (Fig. 1C, Fig. S11, Fig. S12), cover of alien species provides important complementary information to their species richness. Because species cover was only estimated within the 10-m^2 and 100-m^2 plots, our analyses of the scale-dependency of invasion levels and their drivers did not incorporate species abundance or cover. Future studies would benefit from including abundance or cover data for both native and alien species across multiple spatial scales and grassland types. This is particularly important, as even a single invasive species can become highly dominant in the landscape (Martin and Wilsey, 2015) and significantly alter ecosystem functions (Buzhdygan et al., 2016). Moreover, the scale-dependency of alien–native relationships may operate through shifts in species abundances, not just presence–absence patterns (Powell et al., 2013; Valone and Weyers, 2019).

Our findings provide a framework for actionable conservation planning. By identifying which drivers operate most strongly at specific spatial grains, practitioners can match the scale of intervention to the ecological processes at play. For example, fine-scale actions, such as reducing litter accumulation may be effective in reducing establishment opportunities for invaders, while broader-scale measures like regulating grazing pressure or managing surrounding land use (e.g., cropland expansion and urban increase) are relevant for controlling invasive species spread across the landscape. Tailoring management strategies to both the stage of invasion and the relevant spatial scale can improve the efficiency and effectiveness of monitoring, prevention, and restoration efforts in grassland ecosystems.

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CRediT authorship contribution statement

Oksana Buzhdygan: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Selina Baldauf:** Writing – review & editing, Visualization, Software, Formal analysis, Data curation, Conceptualization. **Britta Tietjen:** Writing – review & editing, Methodology, Conceptualization. **Svitlana Iemelianova:** Writing – review & editing, Data curation, Conceptualization. **Dariia Borovyk:** Writing – review & editing, Data curation, Conceptualization. **Denys Vynokurov:** Writing – review & editing, Data curation. **Olha Chusova:** Writing – review & editing, Data curation. **Vasyl Budzhak:** Writing – review & editing, Data curation. **Joana Bergmann:** Writing – review & editing. **Jürgen Dengler:** Writing – review & editing, Data curation. **Iwona Dembicz:** Writing – review & editing, Data curation. **Monika Janišová:** Writing – review & editing, Data curation. **Iuliia Vasheniak:** Writing – review & editing, Data curation. **Jonathan Chase:** Writing – review & editing, Conceptualization. **Anna Kuzemko:** Writing – review & editing, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Data availabilityAll data and code to reproduce the analyses of this study are available at https://doi.org/10.5281/zenodo.17491739. Also, data are available as Supplementary Data 1, Supplementary Data 2 and Supplementary Data 3.

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