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# Short-term seed banking enables adaptive, multi-year seeding strategies in grassland restoration

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ABSTRACT

*Ex situ* seed banks can play a critical role in supporting grassland restoration and mitigating the impacts of climate change by ensuring a continuous supply of native seeds. We investigated the effects of short-term seed storage (fresh, one-, two-, and three-year storage) and seeding year (2011–2014) on the restoration of open sand grassland using accessions from the Pannon Seed Bank in Hungary. Seeds of ten native species were sown in an abandoned sandy field, and vegetation was monitored for up to nine growing seasons. Clear directional development toward the reference grassland became evident from the fifth year onward. Target species reached up to 90% relative cover, primarily due to the sown species, while non-target natives and neophytes declined. Differences among storage treatments were only transient, e.g. higher species richness when using fresh seeds, and by the end of the monitoring period all seed storage durations converged toward the reference community. In contrast, seeding year had a lasting influence: plots sown in years with favorable precipitation (e.g., 2013) showed stronger establishment of target species, while less favorable years (e.g., drought in 2012) constrained recovery. These year-specific effects shaped both the long-term success of target species and invasion dynamics. Restoration outcomes were therefore more strongly influenced by seeding year than by storage duration, underscoring the need for adaptive restoration strategies tailored to year-specific conditions. We recommend multi-year, scheduled seeding as a buffer against adverse weather, supported by the short-term use of seed banks to ensure seed availability under variable climatic conditions.

## 1. Introduction

Global ecosystem restoration targets—such as those established by the Convention on Biological Diversity (2022) and by the pioneering European Regulation on Nature Restoration (European Commission, 2024) — require the large-scale introduction of native propagules, primarily seeds, into degraded areas (Berto and Brown, 2023; Leger et al., 2021; Merritt and Dixon, 2011). Prioritizing the

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restoration of grasslands and drylands offers a cost-effective strategy for global restoration efforts, thereby enabling broader implementation (Strassburg et al., 2020). Notably, biodiversity hot spots for vascular plants occupy more than three times larger area in open ecosystems compared to forests globally (Bond, 2021). These ecosystems hold significant conservation value, serving as vital habitats for numerous species, while also supporting livelihoods and cultural heritage—especially in temperate regions (Buisson et al., 2022). In addition, restoring grasslands on former arable lands can also enhance carbon sequestration, as grassland soils store approximately 50% more carbon than forest soils worldwide (Conant et al., 2017). Therefore, the restoration of native grasslands represents a key contribution to both global and EU targets, making improvement of the native seed supply—both in quantity and quality—an urgent priority (McCormick et al., 2021; Pedrini et al., 2020).

Currently, the native seed producer sector is struggling to meet the required standards for large-scale ecological restoration, so improvements in volume and quality must be considered (De Vitis et al., 2017; Goldsmith et al., 2022; Pedrini et al., 2020). One study found that only 32% of species essential for grassland restoration in Europe are commercially available in the native seed market (Ladouceur et al., 2018). This limitation presents a critical bottleneck, particularly for the restoration of species-rich grasslands (Berto and Brown, 2023). Spontaneous succession may serve as an alternative to active restoration when sufficient native propagules are present in the landscape or soil seed bank (Prach et al., 2019). However, dispersal limitation and habitat fragmentation frequently hinder natural recolonization. Additionally, the soil seed bank generally lacks sufficient perennial grassland species due to its long-term depletion as a result of cultivation, limiting its effectiveness for restoration (Török et al., 2020). While wild seed collection (Pedrini et al., 2020) and alternative seed sources (Kiehl et al., 2010) can supplement supply, seed production may be constrained by extreme climatic events in certain years, necessitating the use of *ex situ* seed banks as a bridging solution.

Seeds of wild species stored in *ex situ* seed banks hold great potential for ecological restoration (White et al., 2023). For instance, the Millennium Seed Bank conserves over 2.4 billion seeds representing nearly 40,000 taxa from around the globe (Royal Botanic Gardens, Kew, 2024) and has been actively used for biodiversity protection and habitat restoration in the UK (Chapman et al., 2019) and elsewhere (León-Lobos et al., 2012). Many national seed banks preserve local floras, and regional seed bank networks support the conservation of regional biodiversity (Eastwood and Müller, 2012; Kennedy, 2008; Sutherland, 2012). In addition to conserving wild species, these seed banks provide essential expertise in seed processing and seed ecology, and many contribute to reintroduction studies (White et al., 2023), but these reintroductions are generally considered risky and costly (Godefroid et al., 2011). However, most reintroduction efforts using stored seeds have focused on single, often protected species. In contrast, ecological restoration aims differ significantly, as the focus is not on individual at-risk species but rather on restoring entire communities composed of a diverse range of species, not all of which are of direct conservation concern. Currently, most seed banks lack the seed volumes required for large-scale restoration of multiple species in many countries. There are limited possibilities to produce seeds of native species in seed fields or to purchase native seeds on the seed market, suggesting that specialized restoration seed banks are needed (Merritt and Dixon, 2011).

Seed quality—particularly the proportion of pure, viable, and germinable seeds—is critical to increasing restoration success and seed use efficiency (Pedrini and Dixon, 2020; Shaw et al., 2020). While *ex situ* storage can extend seed longevity, eventual viability loss is inevitable (De Vitis et al., 2020). Despite the recognized potential of stored seeds in reintroduction (Bowles et al., 1993), empirical data on successful establishment from stored seeds remains scarce (White et al., 2023), and studies exploring the effect of storage duration on establishment success are even rarer (but see Kövendi-Jakó et al., 2021).

Global changes present additional challenges for seed-based restoration. The frequency and duration of droughts is expected to increase, which can severely hinder restoration efforts (Broadhurst et al., 2016). Early years after seeding are particularly critical (Vaughn and Young, 2010), as extreme drought during this period can jeopardize establishment. Thus, timing of seeding becomes increasingly crucial for seed germination, seedling establishment, and overall restoration success (Shaw et al., 2020). Another major threat to habitat restoration is biological invasion, which has prompted urgent calls for action from the scientific community (IPBES et al., 2023). Studies have shown that treating invasive alien plants is often insufficient, as seeds or rhizomes can persist and result in reinvasion of disturbed sites (Kollmann et al., 2011; Weber, 2011). Additionally, invasive species can leave ecological legacies that hinder native plant establishment and facilitate secondary invasion (Corbin and D'Antonio, 2012; Loydi et al., 2015). One effective restoration strategy is to timely reseed vacated sites with native species, thereby occupying ecological niches and increasing resistance to reinvasion (Bucharova and Krahulec, 2020; Halassy et al., 2023). However, it remains unclear whether native species seeded after storage can consistently maintain priority, and to what extent annual weather variation affects this outcome.

In Hungary, the post-socialist transition (1987–1999) led to widespread abandonment of agricultural lands, particularly in low-productivity areas (Mihók et al., 2017). While spontaneous succession can proceed relatively rapidly, invasive alien species have increasingly colonized these abandoned lands, necessitating active restoration (Csecserits et al., 2011). The Pannon Seed Bank (PSB) was established within the Pannon Seed Bank LIFE project (LIFE08 NAT/H/000288) to ensure the long-term storage of native plant seeds (Peti et al., 2015; Peti et al., 2017; Török et al., 2016). Building on a previous study in which we evaluated the reintroduction potential of PSB-stored species, as well as the effects of short-term seed storage (0–3 years) and year of seeding (across four consecutive years) at the early life stage (Kövendi-Jakó et al., 2021), we now investigate longer-term vegetation composition development. We used two species groups as indicators of restoration progress: target sand grassland species, and invasive neophyte species that threaten restoration success. Our research addressed the following questions: (1) Does seeding of sand grassland species stored in the PSB accelerate vegetation development toward the reference grassland? (2) How does short-term seed storage affect vegetation development over time? (3) How does the year of seeding affect vegetation development over time? We assessed the effects of storage time and year of seeding on (a) total plant cover and species richness, (b) the relative cover of target species (both seeded and spontaneously occurring), and (c) the relative cover of neophyte species (both annual and perennial).

## 2. Material and methods

### 2.1. Study area

A field experiment was established in 2011 on an abandoned cropfield located within the Kiskun Restoration Experiments at the Kiskun LTER Fülöpháza site (46°52'N, 19°23'E), Hungary (Fig. 1). The dominant soil types are calcareous sandy soils with humus content below 1%, developed on wind-blown inland sand dunes (Kovács-Láng et al., 2008). The climate is temperate continental with sub-Mediterranean characteristics. Based on meteorological records from 1936 to 2019, the mean annual temperature is 10.6 °C, and the mean annual precipitation is 534.2 mm (Orbán et al., 2023). Among the four consecutive seeding years (2011–2014), 2012 was marked by summer drought, whereas 2014 was a markedly wet year (Halassy et al., 2025; Orbán et al., 2023; Table S1).

The studied area is part of the forest-steppe biome, characterized by a mosaic of open oak forests, juniper-poplar groves, and dry sandy grasslands (Erdős et al., 2018). The driest grassland type, Festucetum vaginatae 'danubiale', is a semi-desert-like community rich in endemic species and dominated by the tussock grasses *Festuca vaginata* and *Stipa borysthenica*. This community typically occurs on the crests and southern slopes of nutrient-poor, coarse-textured calcareous sand dunes (Kovács-Láng et al., 2000). Extensive human activity—mainly agricultural and forestry interventions during the 19th and 20th centuries—has significantly fragmented and degraded the natural vegetation (Biró et al., 2013). According to the land-use assessment by Biró et al. (2013), the region is composed of agricultural land (57%), extensive semi-natural grasslands (19%), forests and plantations of non-native tree species (19%), and settlements (6%).

### 2.2. Seed collection and handling

Ten sandy grassland species were selected for the reintroduction experiment: *Centaurea arenaria* M. Bieb. ex Willd., *Dianthus serotinus* Waldst. et Kit., *Echinops ruthenicus* (Fisch.) M. Bieb., *Euphorbia seguieriana* Neck., *F. vaginata* Waldst. et Kit. ex Willd., *Gypsophila arenaria* Waldst. et Kit., *Koeleria glauca* (Spreng.) DC., *Onosma arenaria* Waldst. et Kit., *Scabiosa ochroleuca* L., and *Silene borysthenica* (Gruner) Walters (nomenclature follows Király, 2009). Species were selected based on the following criteria: inclusion of both grasses and forbs, representation of dominant and subordinate species typical of Pannonian sandy grasslands, classification as

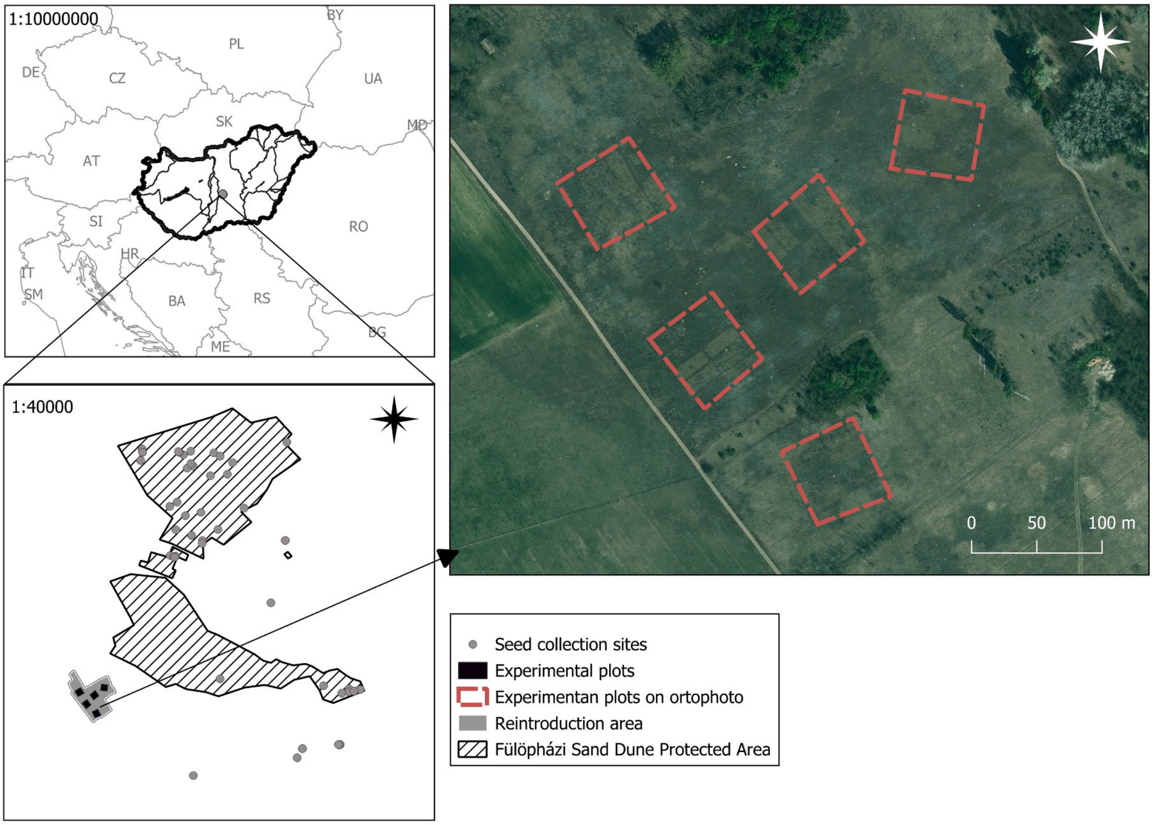


**Fig. 1.** Location of the Pannon Seed Bank experiment in the Fülöpháza Sand Dune Protected Area, Hungary, Europe. The site is located within the Kiskunság National Park. Projected coordinate system: EOV–1972. Maps were created in QGIS using orthophotos provided by the Lechner Knowledge Center, Budapest (2019).

orthodox species (i.e. seeds can be dried and stored at 0 °C without loss of viability), and the feasibility of collecting sufficient quantities. Both protected and specialist sandy grassland species were included. Table S2 provides a summary of the life form, average germination capacity, seeding density, protection status and species characteristics of each study species.

Seeds were collected in 2011, 2012, and 2013, following the Seed Collection Guide (Peti et al., 2015; Zsigmond, 2011) developed for Hungary and based on the ENSCONET collection manual (ENSCONET, 2009). Due to extreme drought conditions in 2012, seeds of native species could only be collected in small quantities, and *G. arenaria* produced no seeds that year.

Collected seeds were transported to the PSB in Tápiószele, where they were cleaned and prepared for storage following standard protocols (ENSCONET, 2009; Rao et al., 2006). Seeds were dried in a drying chamber at 16 ± 1 °C to a 15–20% relative humidity and subsequently stored at 0–4 °C. Germination tests were performed on all collected seed lots after collection, further information on the procedures can be found in Kövendi-Jakó et al. (2021).

### 2.3. Experimental design

We selected an 11-hectare abandoned field for the experiment. The site, which is state-owned and part of the Kiskunság National Park, had previously been used for crop production and was abandoned for 10–15 years prior to establishment of the experiment.

The experimental layout consisted of five blocks, each measuring 60 × 65 m (Fig. 1), with ten treatment parcels per block (11 × 28 m). Treatments were randomly assigned to parcels. Nine seeding types were applied, resulting from combinations of seed collection year (2011, 2012, 2013), seed storage duration (0, 1, 2, or 3 years), and seeding year (2011–2014). The tenth parcel in each block served as unseeded control. In addition, a reference area with open sand grassland vegetation was selected outside the old field in 2015 (Table 1).

As a pre-treatment, the invasive common milkweed (*Asclepias syriaca*) was spot-sprayed with an 8% Medallon solution in July 2011. Each parcel, including the control, was mown, and the hay removed just prior to seeding. Seedbeds were prepared by strip-plowing ten rows (1 m apart, 25 m long, 10–15 cm deep) with a rototiller (except in control parcels). Seeds as a mixture were sown manually into the plowed strips. The seeds were covered with 1–2 cm of soil in late September each year to avoid loss by wind and seed predation. Seeding density varied by species but remained constant over the years (Table S2). Due to a severe drought in 2012, seed production was low. As a result, only a single 25 m row and five rows in a 5 × 5 m plot were seeded in each parcel with seeds collected in that year, although seedbed preparation remained the same.

### 2.4. Data recording

Vegetation data were collected once in September before each seeding, and then twice a year (in late May and in early September) from 2012 to 2017, and again in 2020 (Table S3). In each parcel (except for those seeded in 2012, which had only one plot), we surveyed three 5 × 5 m plots to estimate the percent cover of each vascular plant species. For each plot, we calculated: species richness (i.e., number of species), total vegetation cover (sum of species cover values, which may exceed 100%), relative cover of target species (seeded and spontaneous), and relative cover of neophyte (invasive) species (annual and perennial). Data from the two sampling dates within each year were merged using the maximum cover value for each species. Target species were defined as characteristic species of sand grasslands in the Kiskunság region according to Csecserits et al. (2011). A total of 30 species were considered target species — 10 seeded and 20 spontaneously colonizing species. Invasive species were classified according to the list of invasive alien species in Hungary (Balogh et al., 2004), considering only neophytes (species introduced to Europe after 1492). Of the ten neophyte species recorded, six were annuals and four were perennials, including woody species. A complete species list with their classification is provided in Table S4.

**Table 1**
Summary of treatment types and monitoring schedule. Nine seeding types resulted from combinations of seed collection year (2011, 2012, 2013), seed storage duration in 0, 1, 2, 3 years (T0, T1, T2, or T3), and seeding year (2011–2014). The design also included a control (within experimental blocks) and a reference area (outside the experimental blocks). Number of 0–9 indicates the years in which vegetation surveys were conducted.

| Collection year | Storage duration (years) | Year of seeding | Survey years | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2020 |
| 2011 | T0 | 2011 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 9 |
| | T1 | 2012 | | 0 | 1 | 2 | 3 | 4 | 5 | 8 |
| | T2 | 2013 | | | 0 | 1 | 2 | 3 | 4 | 7 |
| | T3 | 2014 | | | | 0 | 1 | 2 | 3 | 6 |
| 2012 | T0 | 2012 | | 0 | 1 | 2 | 3 | 4 | 5 | 8 |
| | T1 | 2013 | | | 0 | 1 | 2 | 3 | 4 | 7 |
| | T2 | 2014 | | | | 0 | 1 | 2 | 3 | 6 |
| 2013 | T0 | 2013 | | | 0 | 1 | 2 | 3 | 4 | 7 |
| | T1 | 2014 | | | | 0 | 1 | 2 | 3 | 6 |
| Unseeded control | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 9 |
| Reference area | | | | | | | 1 | 2 | 3 | 4 |

### 2.5. Statistical analysis

We applied Principal Response Curves (PRC; Van den Brink and Braak, 1999) to assess vegetation development over time in relation to seed storage and seeding year, analyzed separately. Data processing was conducted with the "*vegan*" package (Oksanen et al., 2025). The untreated control served as the zero-line, and the reference grassland was considered benchmark. Restoration treatments were grouped according to seed storage and seeding year. The time factor encompassed monitoring years from 2011 to 2020. Species cover data were used as response variables without standardization or data transformation. The significance of the first PRC axis was tested using randomization tests with the reduced model and 999 permutations. We selected the first axis of PRC (PRC1) for display, including all species exceeding the 80% percentile of the cumulative cover across all plots and monitoring years within each site. Details on species contributions are provided in Table S5.

To evaluate the effects of seed storage duration, seeding year, and time since seeding on vegetation development after seeding (control and reference data excluded), we used generalized linear mixed models fitted with the glmmTMB package (Brooks et al., 2017). In the first set of models, we tested the effect of seed storage length (fixed factor, four levels: fresh (T0), one (T1), two (T2) or three (T3) years of storage) and time since seeding (continuous) as interacting factors. In the second set of models, we tested the effect of seeding year (fixed factor, four levels: 2011–2014) and time since seeding (continuous) as interacting factors. In both sets, plot

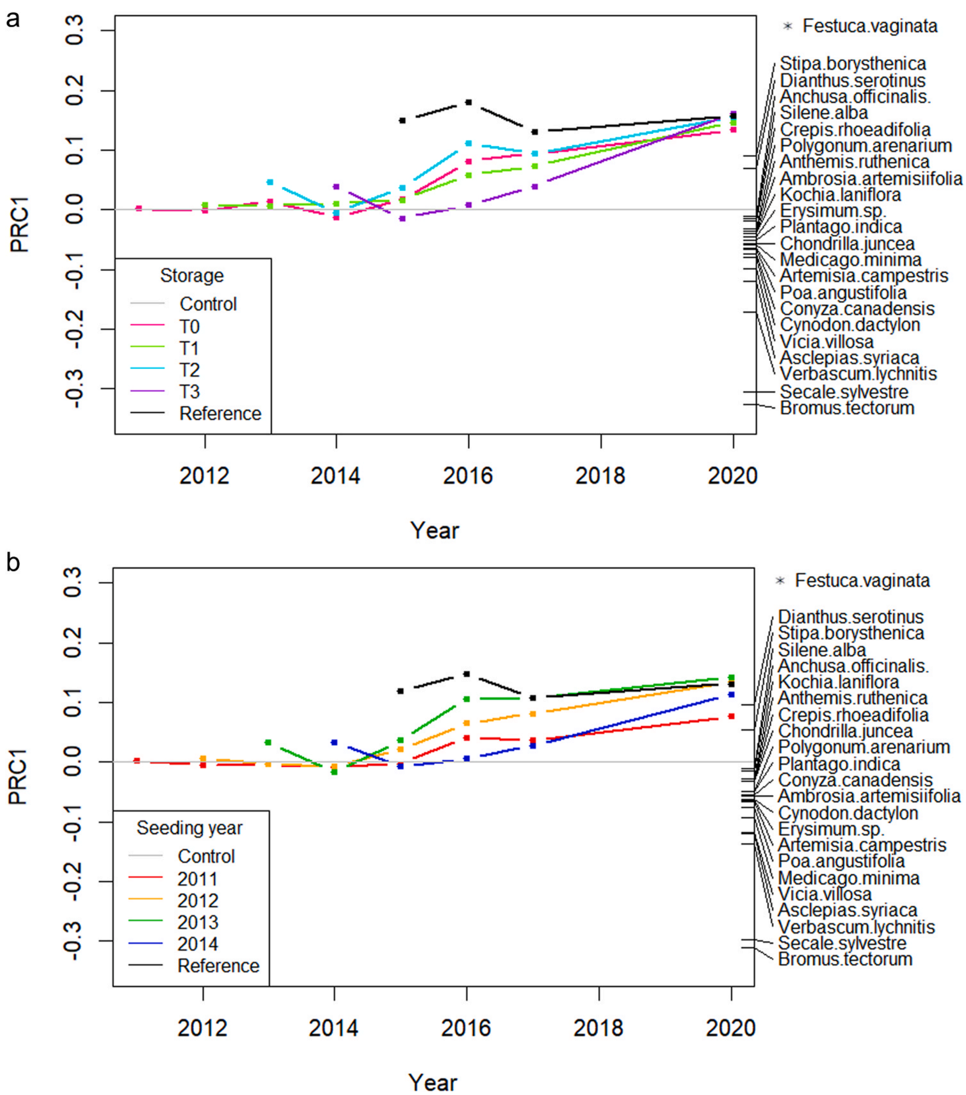


**Fig. 2.** Principal response curves (PRC) show the effect of seed storage (A) and sowing years (B) (2011–2014) on vegetation development over time at all sites. The zero line represents the control, while the other lines show the effect of restoration treatments (seed storage or sowing year) and reference grassland over time (2011–2020). The Y-axis of the treatment scores (PRC1) has been truncated to make the treatment trends more visible. The second axis shows the species weights. Note that *F. vaginata* had very high weights (33.495 and 33.932, respectively), so it was removed during truncation. See Supplementary Table 5 for species weights. Abbreviations: T0–T3 – seeds stored in the *ex situ* seed bank for 0, 1, 2, or 3 years.

nested within block and treatment was included as a random intercept. We separately analysed the following response variables: total cover, species richness, relative cover of all, seeded and spontaneous target species, as well as all neophytes, and annual and perennial neophyte species. We did not analyze the number of target and neophyte species separately due to insufficient data. For species richness, we used a negative binomial distribution; for cover data, a beta distribution was applied. Total cover values were rescaled by normalization (using the min-max scaling method) to fall within a specific range [0.001, 0.999] due to the beta distribution. The DHARMa package (Hartig, 2022) was used to assess model assumptions and fit. Relative cover of seeded target species was log-transformed to meet assumptions of normality and homoscedasticity. All statistical analyses were conducted in R version 4.4.0 (R Core Team, 2024).

## 3. Results

### 3.1. Vegetation development based on trajectory analysis

The first Principal Response Curve (PRC1) accounted for 54.3% of the treatment-related variance in vegetation composition for seed storage ($F = 67.86$, $p = 0.001$) and 50.5% for seeding year ($F = 109.32$, $p = 0.001$) (Fig. 2). Both PRCs showed broadly similar trajectories. Reference plots consistently diverged from the control throughout the study, with no sign of convergence. Reference grasslands were dominated by perennial grasses, primarily *F. vaginata* and to a lesser extent *S borysthenica* and the perennial forb *D. serotinus*, both associated with positive species weights, indicating their higher abundance in plots that deviated positively from the control line. In contrast, control plots remained dominated by annual grasses (*Bromus tectorum* and *Secale sylvestre*), which had negative species weights and tracked communities remaining close to the control line (Table S5). Neophyte species, besides *A. syriaca, Ambrosia artemisiifolia* and *Conyza canadensis,* also made substantial contributions and were negatively associated with PRC1. Restored plots initially clustered with the control community but progressively shifted away from it and toward the reference vegetation.

For seed storage treatments, trajectories across storage durations were highly similar, with slight differences observed throughout the monitoring period (Fig. 2A). All storage treatments gradually diverged from the control and converged with the reference grassland over time. By 2020, vegetation composition across all storage durations resembled the reference plots, with T0 showing the lowest similarity and T3 the highest.

A comparable pattern was found across seeding years, although with more pronounced differences among treatments (Fig. 2B). Plots seeded in 2011 tracked closely with the control until 2015, after which they began to diverge positively, yet remained distinct from the reference even by 2020. Plots seeded in 2012 also resembled the control until 2015 but subsequently surpassed the 2011 cohort and became more similar to the reference by 2020. The 2014 cohort overlapped with the control during the first two years after seeding, then showed a modest positive divergence and eventually exceeded the 2011 cohort by 2020. In contrast, plots seeded in 2013 diverged more strongly and consistently from the control, approaching the composition of the reference grassland by the end of the monitoring period. Notably, the 2013 cohort showed the steepest and most sustained shift toward reference conditions, surpassing the other seeding years and even slightly exceeding the reference by 2020.

Based on the relative cover data, both control and seeded plots were dominated by non-target native species (~72%) at the start of the study, with similar proportions of spontaneously occurring target species and neophytes. In control plots, spontaneous target species *Poa angustifolia*, and non-target *Cynodon dactylon*, *Kochia laniflora* and *S. sylvestre* were most abundant, whereas seeded plots were dominated by non-target *Artemisia campestris*, *Anchusa officinalis, B. tectorum, Erysimum sp., K. laniflora*, *Plantago indica* and *S. sylvestre*. In the seeded plots spontaneous target species such as *Stipa borysthenica* and *Verbascum lychnitis* were present, alongside neophytes including *A. artemisiifolia*, *A. syriaca*, and *C. canadensis*. We also recorded occasional occurrences of seeded species prior to sowing of the respective parcels (Tables S6 and S7); however, their relative cover was consistently very low (below 1%).

From the second year onward, seeded target species expanded substantially, reaching a peak relative cover of ~82% by year seven. This shift was mainly driven by seeded *F. vaginata* (up to 69%) and *D. serotinus* (up to 13%), which, together with spontaneously establishing *S. borysthenica*, strongly contributed to the community's convergence toward reference grasslands. Although most seeded target species persisted throughout the study, their cover declined by year nine. Three species— *E. ruthenicus*, *G. arenaria*, and *O. arenaria*—were no longer recorded in the monitoring plots, though still present in the treated parcels. In contrast, native non-target

**Table 2**
Results of generalized linear mixed models (glmmTMB) testing the effects of seed storage duration and elapsed time after seeding on vegetation development. Results are considered significant when $p < 0.05$. Note: The number of target and neophyte species was not analyzed due to insufficient data.

| Indicator | Seed storage | | | Elapsed time after seeding | | | Interaction | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi2$ | df | p | $\chi2$ | df | p | $\chi2$ | df | p |
| Total cover | 0.919 | 3 | 0.821 | 0.495 | 1 | 0.482 | 1.529 | 3 | 0.676 |
| Species richness | 15.601 | 3 | 0.001 | 129.42 | 1 | < 0.001 | 11.021 | 3 | 0.012 |
| All target species (relative cover) | 2.94 | 3 | 0.401 | 1022.52 | 1 | < 0.001 | 8.44 | 3 | 0.038 |
| Seeded target species (relative cover) | 1.271 | 3 | 0.736 | 1374.124 | 1 | < 0.001 | 45.923 | 3 | < 0.001 |
| Spontaneous target species (relative cover) | 3.503 | 3 | 0.32 | 3.714 | 1 | 0.054 | 13.729 | 3 | 0.003 |
| All neophyte species (relative cover) | 5.489 | 3 | 0.139 | 12.041 | 1 | < 0.001 | 28.974 | 3 | < 0.001 |
| Annual neophyte species (relative cover) | 14.942 | 3 | 0.002 | 50.460 | 1 | < 0.001 | 25.902 | 3 | < 0.001 |
| Perennial neophyte species (relative cover) | 4.351 | 3 | 0.226 | 8.636 | 1 | 0.003 | 15.576 | 3 | 0.001 |

species and neophytes declined, with *A. artemisiifolia* disappearing entirely and *A. syriaca* persisting at lower cover.

### 3.2. The effect of seed storage and elapsed time on vegetation development

Seed storage duration significantly affected species richness and the relative cover of target and neophyte species in interaction with the time elapsed since seeding but did not influence total cover (Table 2).

Total cover started at 60–70%—based on a single late-summer sampling rather than the annual maximum derived from two seasonal samplings as for the rest of the years—and showed a temporary increase in the first three years before stabilizing around 100% (Fig. 3A).

Species richness increased over time in all treatments, starting from 12-15 species and reaching a peak of 29–31 species mid-study, then stabilizing at around 25 species by the end (Fig. 3B). In the year of seeding, treatments using freshly collected seeds had higher species richness than those with stored seeds. By the ninth year, performance among seed storage durations converged.

The relative cover of target species increased substantially, reaching 80–90% by year seven, then declined in the final year (Fig. 3C). Initially, overseeding with fresh seeds resulted in lower cover of target species but surpassed the performance of stored seeds by year seven. Early target cover was primarily due to spontaneous species, but over time, seeded species became dominant (Fig. S1).

The highest initial relative cover of neophyte species was 37%, but by the seventh year it had decreased to below 6% across all treatments (Fig. 3D). Initially, the highest neophyte cover occurred in plots seeded with three-year stored seeds, but treatment differences diminished over time. In contrast, neophyte cover increased temporarily for fresh and one-year stored seeds in the medium term. Annual neophytes were reduced to below 1% (Fig. S2A), while perennial neophytes increased early on but declined later and persisted at low levels (Fig. S2B).

### 3.3. The effect of seeding year and elapsed time on vegetation development

Seeding year and elapsed time significantly affected total cover, species richness, and the relative cover of both target and neophyte species in interaction (Table 3).

Total cover was initially highest in plots seeded in 2013 and 2014 but was the highest mid-term in plots seeded in 2011 and 2012. Eventually, cover stabilized at approximately 100% across all seeding years (Fig. 4A). The highest initial species richness was recorded

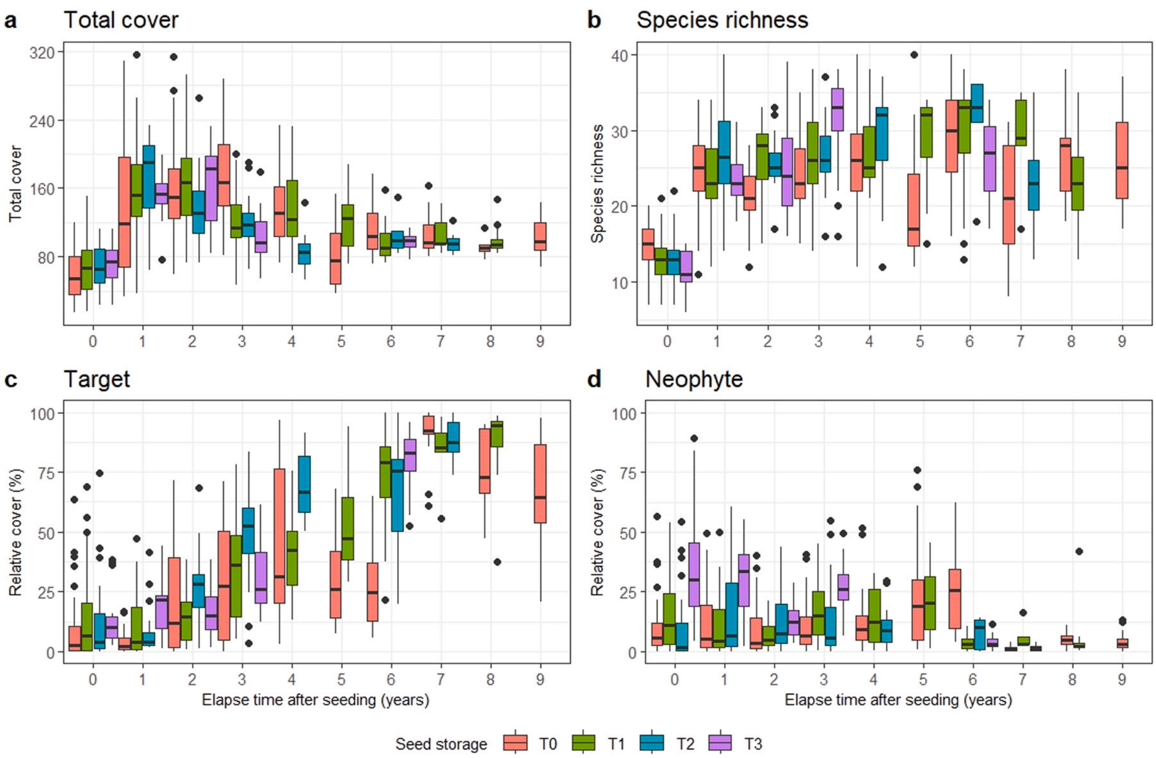


**Fig. 3.** Effect of seed storage duration and elapsed time after seeding on vegetation characteristics from 2011 to 2020. (a) Total cover (sum of the maximum cover values of individual species); (b) species richness (number of species per plot); (c) relative cover of target species (seeded and spontaneous combined); and (d) relative cover of neophyte species (annual and perennial combined). Boxplots show minimum, first quartile, median, third quartile, and maximum values. Abbreviations: T0–T3 – seeds stored for 0, 1, 2, or 3 years in the *ex situ* seed bank. Note: the maximum elapsed time of nine years applies only to seeds not stored (T0).

**Table 3**
Results of generalized linear mixed models (glmmTMB) testing the effects of seeding year and elapsed time after seeding on vegetation development. Results are considered significant when $p < 0.05$. Note: The number of target and neophyte species was not analyzed due to insufficient data.

| Indicator | Year of seeding | | | Elapsed time after seeding | | | Interaction | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi 2$ | df | p | $\chi 2$ | df | p | $\chi 2$ | df | p |
| Total cover | 8.974 | 3 | 0.03 | 0.721 | 1 | 0.396 | 12.701 | 3 | 0.005 |
| Species richness | 14.088 | 3 | 0.003 | 140.754 | 1 | < 0.001 | 29.843 | 3 | < 0.001 |
| All target species (relative cover) | 104.318 | 3 | < 0.001 | 987.697 | 1 | < 0.001 | 51.091 | 3 | < 0.001 |
| Seeded target species (relative cover) | 101.045 | 3 | < 0.001 | 1426.881 | 1 | < 0.001 | 65.594 | 3 | < 0.001 |
| Spontaneous target species (relative cover) | 99.499 | 3 | < 0.001 | 5.013 | 1 | 0.025 | 37.616 | 3 | < 0.001 |
| All neophyte species (relative cover) | 10.663 | 3 | 0.014 | 11.787 | 1 | < 0.001 | 39.346 | 3 | < 0.001 |
| Annual neophyte species (relative cover) | 23.647 | 3 | < 0.001 | 48.898 | 1 | < 0.001 | 31.615 | 3 | < 0.001 |
| Perennial neophyte species (relative cover) | 6.217 | 3 | 0.102 | 8.454 | 1 | 0.004 | 15.217 | 3 | 0.002 |

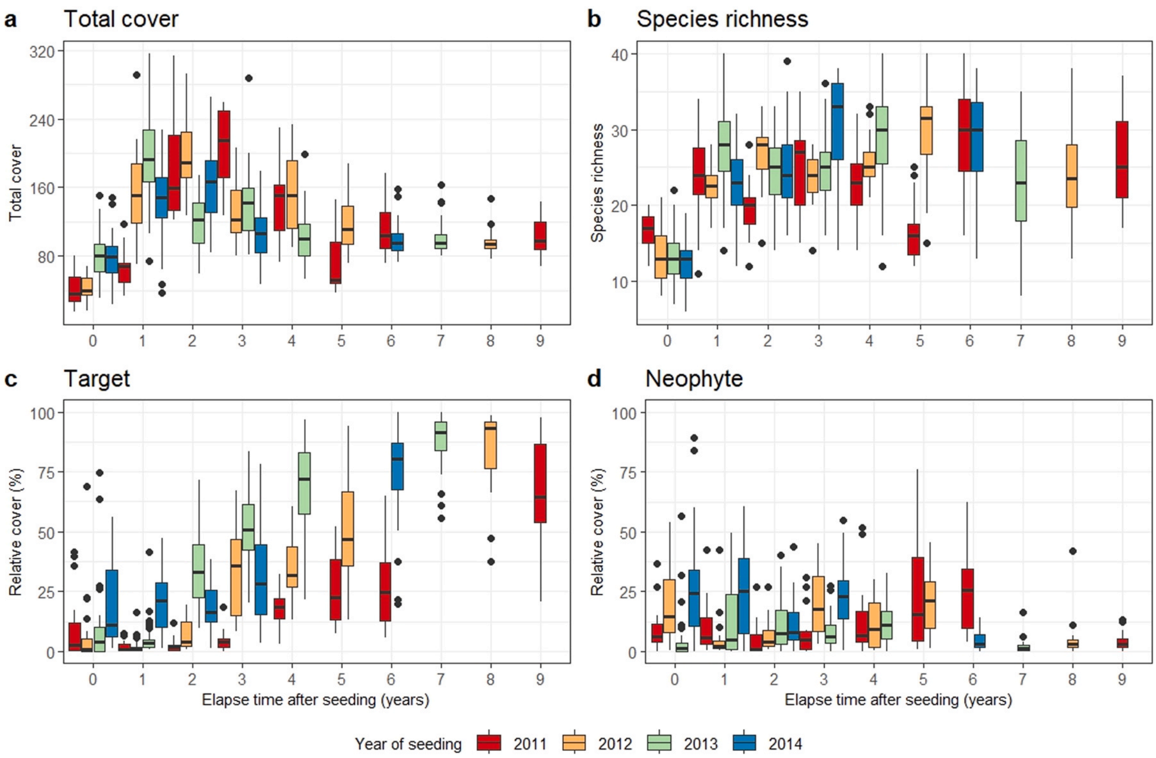


**Fig. 4.** Effect of seeding year and elapsed time after seeding on vegetation characteristics from 2011 to 2020. (a) total cover (sum of the maximum cover values of individual species); (b) species richness (number of species per plot); (c) relative cover of target species (seeded and spontaneous combined); and (d) relative cover of neophyte species (annual and perennial combined). Boxplots show minimum, first quartile, median, third quartile, and maximum values. Note: the maximum elapsed time of nine years applies only to seeds sown in 2011.

in plots seeded in 2011. However, species richness in other seeding years soon caught up and surpassed 2011, with all treatments stabilizing around 25 species by the end of the study (Fig. 4B).

Target relative cover was initially below 10% across all seeding years, with 2014 showing the highest initial value (Fig. 4C). Relative cover increased more rapidly in the 2012 and 2013 seedings and ultimately reached higher levels than in the 2011 and 2014 seedings. Spontaneous target species initially accounted for most of the target cover but seeded species became dominant over time (Fig. S3).

Initial neophyte relative cover varied greatly across seeding years, with 2014 having the highest values, followed by 2012 (Fig. 4D). Neophyte relative cover also increased temporarily in plots seeded in 2011 and 2013 but declined strongly in all treatments over time. Annual and perennial neophyte species followed similar temporal trends, with the relative cover of annuals declining to below 1%, and that of perennials decreasing after the mid-study period and remaining at low levels thereafter (Fig. S4).

## 4. Discussion

### 4.1. The effectiveness of seeding in accelerating grassland recovery

Our study shows that using both fresh and short-term (1–3 years) stored seeds can speed up the restoration of sandy grassland on abandoned arable field compared to spontaneous processes. This impact was apparent only from the fifth year, before that the species composition of treatment plots was very similar to control plots and later on became more similar to the reference grassland. Numerous factors influence the trajectory of plant community assembly in old fields, including the type of former agricultural use and associated disturbances, soil characteristics, landscape fragmentation, seed dispersal mechanisms and colonization potential, as well as the presence of invasive species (Cramer et al., 2008). Among these, increased nitrogen availability is a key driver affecting both the rate and direction of plant and soil community reassembly in old fields (Paschke et al., 2000). Habitat fragmentation and the high abundance of invasive species in the surrounding landscape can further constrain the regeneration of sandy grasslands (Reis et al., 2022). Despite the proximity of semi-natural grasslands, regenerating abandoned fields in the region exhibit substantial weed and invasive species infestations (Csecserits et al., 2011). This pattern is also evident in the old field under investigation, which initially displayed a high relative cover of weedy and neophyte species, such as the annual *A. artemisiifolia* and *C. canadensis*, and the perennial *A. syriaca*. Despite that *A. syriaca* was spot-sprayed with Medallon solution as a pre-treatment, this treatment proved to be insufficient alone for controlling milkweed. Eradicating invasive species poses a significant challenge and is unlikely to be achieved through a single treatment, as many species are capable of re-establishing from rhizomes or seeds, particularly following soil disturbance (Kollmann et al., 2011; Weber, 2011). Successful management requires an integrated approach involving repeated chemical and/or mechanical treatments and additional measures (Bakacsy and Bagi, 2020; Berki et al., 2023). In our study, although seeding native species was insufficient to reduce the cover of *A. syriaca*, it effectively decreased the abundance of annual neophytes after 7–9 years (see also Sáradi et al., 2025).

Our study confirmed previous results that seeding of native species is of paramount importance for accelerating recovery of grasslands on degraded land (Berto and Brown, 2023; Reis et al., 2022; Török et al., 2020). Sowing low-diversity seed mixtures, typically composed of generalist species, has proven effective for the rapid establishment of dense vegetation cover (Török et al., 2011) and for enhancing resistance to invasion by occupying available niche space (Bucharova and Krahulec, 2020; Halassy et al., 2023). Our results suggest that seeding a few native species, including competitive native species (e.g., *F. vaginata*) after initial invasion control measures can be an effective restoration strategy. However, the continued presence of some perennial neophyte species and mid-term increases of annual neophyte species highlight the need for ongoing surveillance and adaptive management (Shaw et al., 2020).

### 4.2. Restoration potential of short-term stored seeds

Our results suggest that seeding fresh seeds is more efficient in enhancing species richness in the short term, but in the longer term, both fresh and stored seeds are equally effective in increasing both species richness and the cover of target species, accelerating the regeneration of sand grasslands compared to spontaneous processes. Due to the ecological stability of ancient grasslands, species adapted to these habitats have evolved traits that enhance seedling establishment and competitive ability, rather than long-term seed persistence (Kiss et al., 2016). Consequently, typical grassland species, including those of sandy grasslands, often produce transient or short-lived seeds (Halassy, 2001; Kiss et al., 2016). In addition to *ex situ* seed banks with the goal of long-term preservation of seeds of conservation importance (Godefroid et al., 2011), our results highlight that restoration seed banks (Merritt and Dixon, 2011) could be supplemented with a short-term storage function. This would effectively address the needs of species with short-lived seeds, such as many typical grassland species. Consequently, this approach would allow for more flexible and responsive use in restoration projects. In such cases, the seed pool requires regular replenishment to maintain viability and ensure the continued availability of target species.

### 4.3. Climatic variability and the timing of seeding

The year of seeding significantly influenced early vegetation dynamics across all studied aspects of our experiment that had lasting effects throughout the study period. As seeding occurred at the end of September, the weather of the following spring (February–April) was most critical for seedling establishment. For example, seeding in 2013 was followed by 2014, a year with exceptionally high precipitation (817 mm; Table S1), which promoted strong establishment and cover of target species. In contrast, seeding in 2011 was followed by the drought year 2012 (439 mm precipitation, SPEI index: –1.34), resulting in weak seedling establishment and low cover of seeded species. The frequency and duration of dry periods, along with shifts in precipitation patterns due to climate change, can pose significant challenges to seed-based restoration (Broadhurst et al., 2016). Compared to yearly averages, temperature and water availability during the emergence period are especially crucial in determining seedling establishment and the number of seedlings that survive by the end of the first growing season (Denton et al., 2024). Adverse conditions during seedling establishment, such as summer droughts, can lead to juvenile mortality and ultimately hinder recruitment in arid systems (James et al., 2011).

The year of seeding also influenced the presence and cover of neophyte species, largely through the interplay of vegetation development and climatic conditions. Higher proportions of neophytes were associated with plots seeded in 2012 and 2014, representing two climatic extremes: a drought year and a wet year. In drought years, dominance shifts were mainly driven by annual neophytes, whereas under wet conditions both annual and perennial neophytes were promoted. Our findings suggest that year-specific climatic conditions play a key role in shaping invasion dynamics. Although drought can have direct negative effects on invasive species, their rapid resource utilization, particularly in the case of annual invaders, often enables them to recover quickly after drought events and gain a long-term competitive advantage over native perennial species (Diez et al., 2012; Halassy et al., 2025). As sand grasslands are generally water-limited, the vegetation cover is low with spaces suitable for establishment once water limitation is overcome due to excess precipitation (Burke et al., 1998). Therefore, the increasing frequency of extreme weather events (both drought and excessive precipitation) under climate change presents a dual challenge for ecological restoration. These events not only directly influence the success of seed-based restoration efforts but also alter invasion dynamics, potentially facilitating the establishment and spread of invasive species in response to shifting environmental conditions.

## 5. Conclusions

We present the first multi-year, field-based evidence that short-term stored seeds can perform as effectively as fresh seeds in community-level restoration, addressing a key limitation caused by seed supply shortages. By incorporating temporal replication across four consecutive years, we also demonstrate that inter-annual climatic variability strongly influences both the establishment of target species and invasion dynamics. These findings highlight the importance of combining short-term seed storage with adaptive, climate-aware restoration planning. Our results further indicate that gradual, multi-year seeding, for instance by phased application across multiple years or sections, is a viable strategy for mitigating seed losses during drought, reducing the abundance of annual neophyte species, and enhancing overall restoration success, thereby reinforcing earlier conclusions (Kövendi-Jakó et al., 2021). Based on our results, *ex situ* restoration seed banks, if supplemented with a short-term storage function, could serve as strategic reservoirs to buffer the impacts of extreme climatic events. By storing seeds collected in favorable years, such seed banks ensure seed availability during periods when collection is unfeasible or when drought renders direct seeding ineffective. Together, these insights emphasize that integrating short-term seed storage with multi-year, climate-informed seeding strategies can substantially increase the reliability and resilience of seed-based restoration under future climate change.

## Ethics Statement

Not applicable: This manuscript does not include human or animal research.

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## Author contributions

KS, AM and KT conceived the experimental design of the study; KT principal investigator; KS, AM, KH, AKJ, MH, BPR, NS, and KT performed experiment and data collection; AKJ, BPR, NS performed the statistical analyses; KS statistical consultant; AKJ primary author; KT, MH, BPR, NS wrote parts of the manuscript; MH and KS provided revisions to scientific content of manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## CRediT authorship contribution statement

**Anna Kövendi-Jakó:** Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation. **Krisztián Halász:** Writing – review & editing, Investigation. **Melinda Halassy:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition, Formal analysis, Data curation. **Andrea Mojzes:** Writing – review & editing, Methodology, Investigation. **Katalin Szitár:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Bruna Paolinelli Reis:** Writing – review & editing, Visualization, Software, Investigation, Formal analysis, Data curation. **Nóra Sáradi:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Katalin Török:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

## 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.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04156.

## Data availability

Data are available from ZENODO: https://doi.org/10.5281/zenodo.17396129 (Kövendi-Jakó, 2025).

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