



Effects of mound building and caching by steppe mouse (*Mus spicilegus* Petényi) on the vegetation in agroecosystems

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ABSTRACT

Several rodent species are considered ecosystem engineers. They exert profound changes in agroecosystems by disturbing the soil during their activities. The steppe mouse (*Mus spicilegus*) inhabits various agroecosystems and constructs conspicuous mounds for overwintering using piled up plant material and soil. These mounds are widespread in many agroecosystems and may significantly affect the vegetation. In our study, we evaluated the effect of mound building activity of the steppe mouse on the vegetation of agroecosystems in Hungary. We sampled the cache content of 90 mounds in total located in old fields, alfalfa fields, and annual crop fields, and surveyed the aboveground vegetation of the mounds and their surrounding undisturbed matrix in 39 paired plots. Mice cached large amounts of seeds belonging mostly to weeds. In total we found 50,413 germinable seeds of 30 species in the cache content samples. However, the mound vegetation and the cache shared only a few species, suggesting that seeds cached by the mice do not contribute to the regenerating vegetation on the mounds. Soil disturbance by mice created distinct vegetation patches with species composition and structure different from the neighbouring undisturbed matrix. Early secondary successional vegetation patches on mounds introduced small-scale heterogeneity into the homogenous agricultural landscape, increased plant diversity and provided distinct flower resources for pollinators. The detected differences in the aboveground vegetation between the mound and the matrix in the studied habitats suggest that the steppe mouse acts as a facultative engineer species in agroecosystems.

1. Introduction

Animals play a crucial role in shaping open habitats through various means, one of which involves direct disturbance of soil (Root-Bernstein and Ebensperger, 2013). Several soil-disturbing animals are referred to as ecosystem engineers, as they exert profound changes in ecosystems by disturbing the soil during shelter creation or foraging (Mallen-Cooper et al., 2019; Neilly et al., 2022; Valkó et al., 2022a). For example, several rodent species excavate burrows and tunnel systems or build mounds by which they create disturbed surfaces (Mallen-Cooper et al., 2019). This activity involves moving, mixing, and loosening soil layers and facilitating the redistribution of nutrients. By these activities, rodents create

unique microhabitats with properties markedly different from the surrounding undisturbed areas (Platt et al., 2016). Soil relocation by ecosystem engineer mammals can also displace seeds within the soil seed bank (Tóth et al., 2022; Yusefi et al., 2023). On the open surface of the disturbed patch, displaced seeds may have a better chance of germination and establishment (Kiss et al., 2021; Godó et al., 2022). Gaps formed in this process may provide establishment sites for less competitive plant species, fostering greater diversity at the local and landscape levels, or can support unique plant groups important for conservation (James and Eldridge, 2007; Eldridge and Whitford, 2009; Godó et al., 2022; Valkó et al., 2022b). Through transforming vegetation, ecosystem engineer rodents provide ecosystem services and

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disservices (Godó et al., 2022), and can indirectly influence invertebrate species richness (such as pollinator communities) by altering vegetation composition and therefore resource availability (Yoshihara et al., 2010; Romero et al., 2015).

Studies on the ecosystem engineer rodents revealed that the nature and strength of the impact of disturbances are shaped by various factors, such as environmental conditions, community characteristics, and the availability of resources altered by the engineer (Wright et al., 2006; Romero et al., 2015). The impact of the same engineer rodent species can differ considerably in habitat types with different productivities, despite modifying the environment in the same way (Wright and Jones, 2006; Louw et al., 2019; Bongiovanni et al., 2024). Characteristics of the rodent species, such as body size, temporal persistence, and functional type (creating new habitat, modifying an existing habitat, or causing bioturbation) also have decisive role in influencing vegetation patterns (James and Eldridge, 2007; Romero et al., 2015). Some rodent species may also contribute to enhancing biodiversity through seed dispersal (Vander Wall, 1990; Godó et al., 2018; Valkó et al., 2022b; Godó et al., 2022). It is a characteristic of several rodent species to collect seeds or plant material into caches to survive harsh periods (Vander Wall, 1990; Godó et al., 2022). Other engineer rodent species may disperse seeds through endo- or epizoochory directly to the disturbed patch (Godó et al., 2022). These complex characteristics and activities of ecosystem engineer rodent species make it challenging to anticipate the changes that may occur in the habitat due to their presence (Louw et al., 2019).

To analyse the complex effects of caching rodents on agroecosystems, we selected the steppe mouse (*Mus spicilegus* Petényi, 1882) as a model species. The steppe mouse is a small outdoor mouse resembling to the sympatric house mouse (*Mus musculus* L.). It has a total length of 55–93 mm and a weight of 9–20 g, and typically has a lifespan of about 12–18 months (Aulagnier et al., 2009). The steppe mouse is a common rodent species with a special caching behaviour inhabiting grasslands and agroecosystems from eastern Austria to western Russia (Coroiu et al., 2016). It primarily feeds on various parts of plants, with a particular preference for weeds. Consequently, the presence and abundance of weeds play a crucial role in determining the distribution and population density of the steppe mouse, while the mouse also affects plant community dynamics by its feeding habits (Sokolov et al., 1998; Hölzl et al., 2009, 2011b; Szenczi et al., 2011). Local declines are observed in populations at the southern edge of the distribution range, while there is an expansion towards the northern, western, and eastern boundaries, probably due to the increasing mean temperature of the winter season (Beltcheva and Metcheva, 2018; Tytar et al., 2019). In autumn, a group of mice gather and build a mound above their burrow that provides protection against harsh environmental conditions and weather elements during the winter period. In spring, the mice mostly abandon this burrow, disperse, become more solitary, and establish territory, while focusing on foraging, and breeding (Poteaux et al., 2008; Szenczi et al., 2011). Typical densities of mounds are 1–20 mounds per hectare (Macholán and Vohralík, 1997). The mound consists of a thick layer of piled up inflorescences, fruits, and spikes (grain-bearing tip part of the stem) covered by shallow bare soil layer (Szenczi et al., 2011). Seeds of almost one hundred plant species have been reported in the mounds of steppe mouse throughout its distribution range (Sokolov et al., 1998). In general, mice do not feed on the cached plant material (Szenczi et al., 2011). This means that the collected seeds can stay intact and survive the winter after which some of them may be able to germinate from the mound. In addition, the bare soil surface of the mound may also be suitable for the establishment of seeds arriving from the environment.

The aim of our study was to evaluate the effect of the mound building activity of the steppe mouse on the aboveground vegetation in old fields and alfalfa fields, and to analyze the seed content of caches in mounds located in old fields, alfalfa fields and annual crop fields. We also aimed to evaluate the characteristics (i.e. traits) of the cached plant species and their potential role in the vegetation formed on the mounds. We asked

the following questions:

I) Mounds vs. matrix vegetation. How does habitat type (old field, alfalfa field) and position (mound or neighbouring matrix) affect the species composition, and vegetation characteristics in the aboveground vegetation?

II) Seed caches in different habitat types. What is the effect of habitat type (old field, alfalfa field, annual crop field) on the species composition, and characteristics of the cached seeds?

III) Mound vegetation and seed content of caches. Are the vegetation on the mounds and the seed content in caches similar in terms of plant traits and species composition?

Overall, we aimed to evaluate the effects of the mound building and seed caching activities of the steppe mouse on the species composition, structure, and functioning of the agroecosystems.

2. Material and methods

2.1. Study area

Our study area was located in the Great Hungarian Plain, East Hungary (47°31', 20°5'). The region is characterized by a continental climate with a mean annual precipitation of 550 mm and a mean annual temperature of 9.5°C with high interannual fluctuations (Fick and Hijmans, 2017). The area is a plain lowland landscape (elevation ranges between 88 and 102 m a.s.l.) and characterized by a mosaic of vast seminatural habitats such as alkaline and loess grasslands, wetlands, alkaline marshes, and agricultural lands (Deák et al., 2021).

In November 2020, we searched for newly built steppe mouse mounds. We selected six sites in each of the three habitat types where mounds are typical in the study region: old fields (secondary dry grasslands spontaneously developed from abandoned alfalfa fields), actively used alfalfa fields, and annual crop fields (Fig. 1). The old fields and alfalfa fields were managed by annual mowing. The annual crop fields were sown with corn or sunflower in 2020 and were harvested by the time of mound selection and sampling. At each site, we randomly selected five mounds. We assigned a unique ID to each mound and saved its GPS coordinates. We selected 30 mounds in each habitat type and surveyed a total of 90 mounds. The mean distances among mounds were 252.79 ± 247.54 , 155.60 ± 54.86 , 92.19 ± 69.42 m in old fields, alfalfa fields, and annual crop fields, respectively. The between site distances were $16,465.72 \pm 3647.80$, $15,530.10 \pm 2503.66$, $40,308.75 \pm 5427.55$ m in old fields, alfalfa fields and annual crop fields, respectively. For detailed data on the distance between mounds within sites and the distance between sites in a habitat type, please see Appendix Table 1.

2.2. Cache sample collection and the germination experiment

In November 2020, we collected interior samples from the caches (made of plant material) of each selected mound, using a soil auger (dimensions: length = 26 cm; diameter = 4 cm). The auger was placed on the top of the mound and was pushed down until it reached the original compact ground soil layer beneath the mound. We removed the sample from the auger in one piece. Then the upper and lower soil layers (with a thickness of 1.5–2 cm both) were removed. In order to sample a standard amount from each mound, we used the upper soil-free 20 cm of the samples for further analyses. The 20-cm samples were placed in paper bags and stored in a cold and dry place for four months to simulate winter conditions until the start of the germination experiment.

In March 2021 samples were concentrated by washing through sieves according to the method of Ter Heerd et al. (1996). Vegetative parts and fine soil materials were removed using a sieve with 3 mm mesh size followed by a fine sieve with a mesh width of 0.2 mm to reduce the sample volumes. The concentrated samples were spread in a thin layer (5 mm) in $60 \times 17.5 \times 14.5$ cm plant boxes filled with steam-sterilized potting soil (standard planting substrate containing turf,

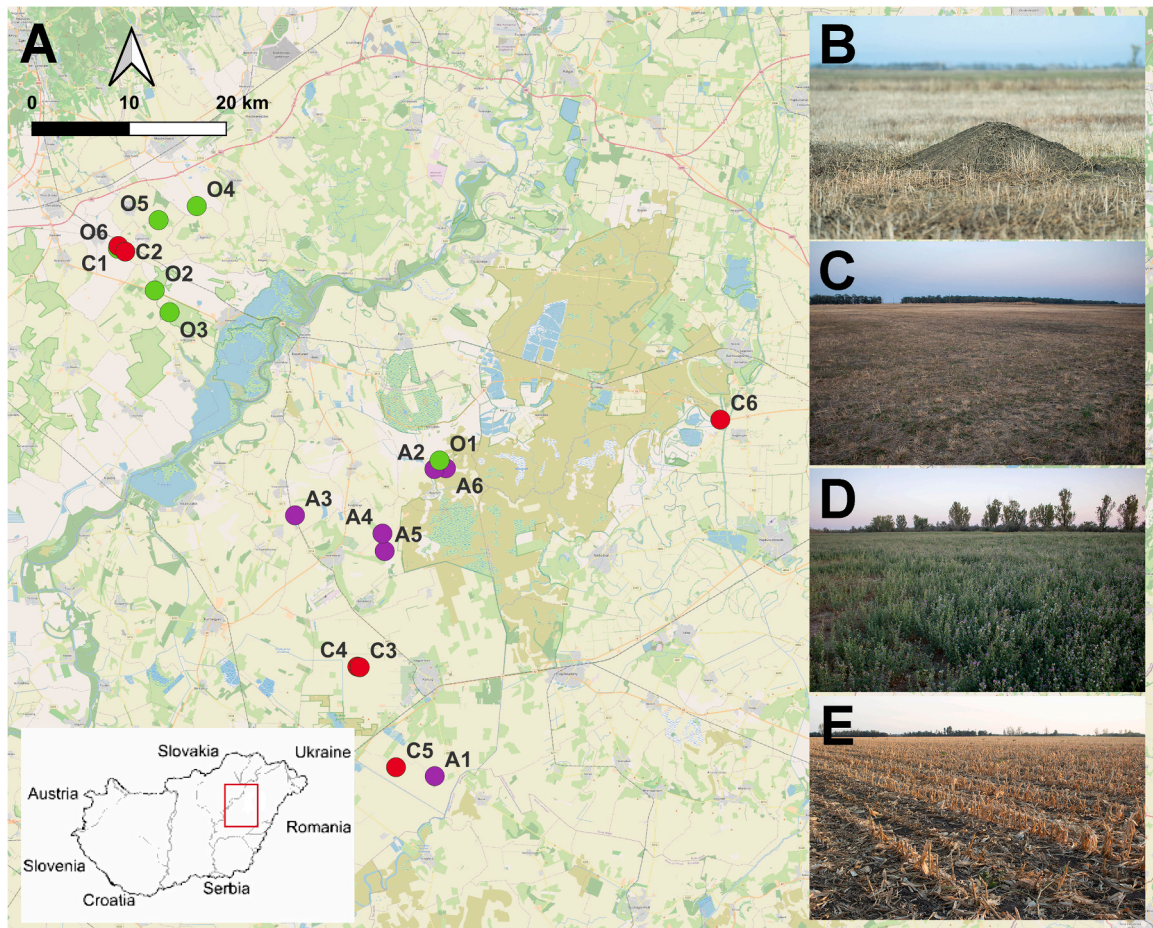


Fig. 1. Map of the sampling sites (A), and pictures about a typical mound of the steppe mouse (B), and the three studied habitat types (old field – C; alfalfa field – D; crop field – E). On the map, colours of the dots indicate the habitat type (green – old field; purple – alfalfa field; red – annual crop field). Photo credits: Sándor Borza.

humus, and manure). Nine control boxes were filled with the same steam-sterilized potting soil to filter out airborne contamination. The boxes were randomly placed in an unheated greenhouse in Nagyiván, Hungary, where germination was carried out from March 2021 to March 2022 under natural light conditions and regular watering. Seedlings were identified, and then removed. Any seedlings that could not be identified were transplanted into separate $8.5 \times 8.5 \times 8$ cm pots containing potting soil and grown until they could be identified. The nomenclature of the species followed Király (2009). To simulate natural summer conditions typical to the study area, and to enhance the germination of dormant seeds, we introduced a dry period of one month in August 2021, during which we did not water the boxes at all. Before this treatment all seedlings were removed from the boxes.

2.3. Vegetation survey

In May 2021, we conducted a vegetation survey on the mounds that were subject to cache sampling. During the vegetation survey we considered each mound as an individual sampling unit. This approach allowed us to encompass the potential variety within the vegetation of the entire surface of each mound. We designated the control plots in the neighbouring vegetation in a place that was not affected by the activity of the mice. We surveyed the vegetation in a patch with exactly the same shape and area as the paired mound. To achieve this, we aligned a measuring tape along the edge of the mound, which we then used to designate a control plot of identical size. The distance between the mound and control vegetation was one meter. We recorded the total percentage of vegetation cover as well as the occurrence and percentage

cover of each vascular plant species. Additionally, we documented the base and the top surface radius and height of each mound (treating its shape as a truncated cone) to be able to calculate the volume. The average base radius of mounds was 61.19 cm (SD = 7.79) in old fields and 53.68 cm (SD = 8.84) in alfalfa fields. The average top radius of mounds was 24.20 cm (SD = 9.39) in old fields and 19.37 cm (SD = 4.49) in alfalfa fields. The average height of mounds was 13.95 cm (SD = 8.93) in old fields and 18.85 cm (SD = 5.95) in alfalfa fields. The average volume of mounds was 109.56 dm^3 (SD = 49.65) in old fields and 94.11 dm^3 (SD = 43.51) in alfalfa fields.

We could not survey the vegetation on mounds located in annual crop fields, as they were all destroyed due to agricultural works. In two old fields and two alfalfa fields, all the mounds were destroyed, either due to agricultural works or by animals, presumably by red foxes or badgers. One mound in one of the old field sites was also destroyed by animals. Therefore, we could sample the vegetation of 19 mounds and 19 undisturbed plots in old fields and 20 mounds and 20 undisturbed plots in alfalfa fields, in total 39 paired mound-matrix plots.

2.4. Data processing

2.4.1. Vegetation data

To express the number and abundance of species typical of natural habitats in the cache and in the aboveground vegetation, we applied naturalness scores. For this, we calculated the community weighted means of the social behaviour type (SBT) scores of all plant species in a sample. SBT scores ranges from -3 (AC – adventive competitors) to $+10$ (Su – unique specialist species) (Borhidi, 1995). These categories

represent a gradient from species typical of degraded habitats to those typical of natural habitats. Seed mass (expressed by thousand seed-weight) scores were derived from Török et al., (2013). We calculated seed shape index as described by Bekker et al., (1998) by using seed length, width, and thickness data that were collected for each species from Schermann (1967). Seed shape was quantified as the variance in three dimensions (length, width, and thickness), with standardization applied to all three values. This involved normalizing the values so that the length was set as 1 (by dividing all three values by the length). Consequently, the seed shape index became independent of the seed size. A seed with a more rounded shape exhibited an index value closer to 0, whereas an elongated seed resulted in an index value closer to 1. We obtained Ellenberg ecological indicator values of the species for temperature (TB), water (WB) and nutrients (NB) adapted to the Hungarian conditions (Borhidi, 1995). Species were assigned to two groups based on their lifespan: short-lived (annual and biennial) and perennial species.

Based on Chytrý et al., (2021) we assigned the pollination type(s) to each species and assigned species to two groups: i) insect-pollinated, i.e., species that obligatorily or facultatively rely on insect pollination (referred thereafter as 'insect-pollinated species'), and ii) not insect-pollinated, i.e., species that are completely independent from insect pollination, e.g., wind-pollinated or autonomous species. To each insect-pollinated species we assigned the colour of the flower based on Király (2009) according to which seven colour categories were established: white, yellow, red, pink, purple, blue, and green. For each plot, we calculated the total cover of insect-pollinated species belonging to each colour. Based on the percentage cover, we also calculated the Shannon and Simpson diversities of the flower colours of the insect-pollinated species in each plot. The full list of the recorded species, their functional characteristics, and their assignment to groups are provided in Appendix Table 2.

We calculated community-weighted scores of all traits and functional groups both for the aboveground vegetation relevés and cache samples. We calculated the Jaccard similarity of the species composition of the seed content of caches and the aboveground vegetation of the mounds.

2.4.2. Statistical analyses

To assess the species composition of the aboveground vegetation and the cache samples in the mounds, we used separate principal coordinates analyses (PCoA). For the calculations we used the percentage cover of the species in aboveground vegetation data, and abundance of germinated species in cache samples. For aboveground vegetation we calculated the models both on the habitat and site levels. For the multivariate analyses we used the CANOCO 5.0 program (ter Braak and Šmilauer, 2012).

For exploring the effects of habitat type (old field, alfalfa field, and annual crop field) and position (mound and neighbouring matrix) on aboveground vegetation and seed cache characteristics, we used generalised linear mixed models (GLMMs).

In the first set of models, we tested the effect of habitat type (old field and alfalfa field) and position (mound and neighbouring matrix) on the total species richness, total vegetation cover, number and cover of short-lived and perennial species, cover weighted NB, TB and WB scores, naturalness scores, Shannon and Simpson diversity of flower colours in aboveground vegetation samples.

In the second set of models, we studied the effect of habitat type (old field, alfalfa field, and annual crop field) on the total seedling and species number, seedling number of short-lived and perennial species, seed mass, seed shape index, weighted naturalness score, and weighted TB, WB and NB scores of the cached seed samples.

In the third set of models, we compared the cached seed samples and the aboveground vegetation on the mounds in terms of proportion of short-lived and perennial species, seed mass, seed shape index, and naturalness score, and Jaccard similarity index in the different habitats

(old field and alfalfa field).

In all GLMM models we used sites nested in habitat types as a random factor. In the case of the species richness scores, we used Poisson distribution with a log link, while in the case of all other dependent variables we used Gaussian distribution with a log link. Post hoc pair-wise comparisons were calculated using the Fisher's Least Significant Difference (LSD) method. For the calculations of GLMMs we used the SPSS v. 22 program (IBM Corp. Released, 2013).

3. Results

3.1. Aboveground vegetation

We recorded a total of 130 vascular plant species, from which 109 species occurred in old fields, and 98 in alfalfa fields.

The vegetation composition of the two habitats (old fields and alfalfa fields) was well separated based on the multivariate analyses. At the habitat level the mounds and the matrix differed regarding their species composition, and at the site level the differences were even more emphasised. Characteristic species on the mounds in old fields included short-lived forbs such as *Chenopodium album*, *Lamium amplexicaule*, and *Stellaria media*, while the matrix was characterised by perennial graminoids such as *Carex melanostachya*, *Festuca pratensis*, and *Poa angustifolia*. The mounds in alfalfa fields were characterised by short-lived (*L. amplexicaule*, *Veronica hederifolia*) and perennial forbs (*Cirsium arvense*), while short-lived forbs (*Capsella bursa-pastoris*, *Matricaria chamomilla*) and the perennial alfalfa (*Medicago sativa*), were abundant in the matrix (Fig. 2).

Total number of species and the number of short-lived species were similar on the mounds and in the neighbouring matrix (Fig. 3, Appendix Table 3). The number of perennial species was lower on the mounds than in the matrix in old fields. Total percentage vegetation cover and percentage cover of perennial species were lower on mounds compared to the matrix. The percentage cover of short-lived species was higher on the mounds than in the matrix in the case of old fields. Compared to the matrix, mounds were characterised by species with higher demand for nutrients. In old fields, mounds were characterised by lower naturalness scores and species with a higher temperature demand compared to the matrix. In alfalfa fields, mounds were characterised by species with lower demand for water than in the matrix.

The mounds were characterised by a higher proportion of pink-coloured insect-pollinated species compared to the matrix. Compared to the matrix, on mounds some flower colours (such as red or green) were present with greater proportion. In old fields there was no difference in the Shannon diversity of flower colours of insect-pollinated species between the mounds and the matrix, and in two sites, mounds were characterised by higher total percentage cover of insect-pollinated species, while in the other two sites we experienced lower total percentage cover of insect-pollinated species compared to the matrix. In alfalfa fields, mounds were characterised by higher Shannon diversity of flower colours of insect-pollinated species and higher proportion of blue-coloured flowers compared to the neighbouring matrix, but lower total percentage cover of insect-pollinated species. Simpson diversity of flower colours of insect-pollinated species did not show any significant pattern (Fig. 3, Fig. 4).

3.2. Seed content of caches

We recorded a total of 50,413 seedlings belonging to 30 vascular plant taxa germinating from the cache samples, of which 29 could be identified at the species level (Appendix Table 4). The three most abundant species were *Chenopodium album* (17,886 seedlings), *Amaranthus retroflexus* (16,616 seedlings), and *Setaria viridis* (10,725 seedlings), which together made up 89.71 % of all seedlings germinated from the samples. A total of 17,519 seedlings of 20 species germinated from samples collected from old fields, 18,323 seedlings of 12 species from

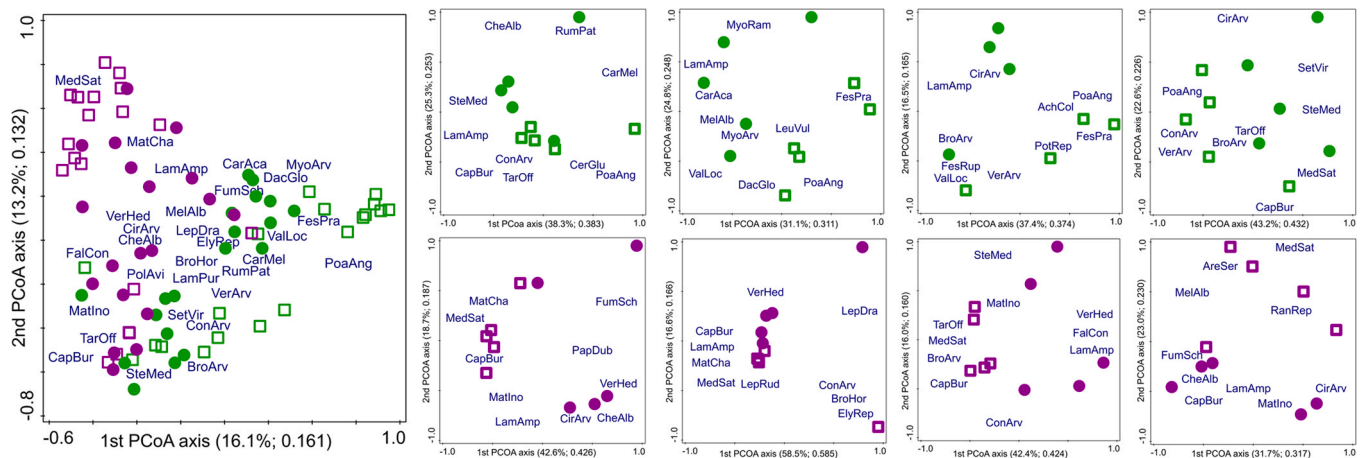


Fig. 2. Ordination diagrams from the principal coordinates analysis (PCoA), displaying the species compositions of the aboveground vegetation in the studied habitat types (green – old field; purple – alfalfa field; filled circle – mound; empty square – matrix). The large panel shows the species composition at the habitat level, whilst small panels show the species composition at the site level (one point represents one plot). We plotted the fifteen-fifteen most frequent species (at the level of the habitat type) on the large panel, and the ten most frequent species (at the site level) on the small panels. Species names are abbreviated using the first three letters of the genus and the first three letters of the species names (AchColl – *Achillea collina*; AreSer – *Arenaria serpyllifolia*; BroArv – *Bromus arvensis*; BroHord – *Bromus hordeaceus*; CapBur – *Capsella bursa-pastoris*; CarAca – *Carduus acanthoides*; CarMel – *Carex melanostachya*; CheAlb – *Chenopodium album*; CerGlu – *Cerastium glutinosum*; CirArv – *Cirsium arvense*; ConArv – *Convolvulus arvensis*; DacGlo – *Dactylis glomerata*; ElyRep – *Elymus repens*; FalCon – *Fallopia convolvulus*; FesPra – *Festuca pratensis*; FesRup – *Festuca rupicola*; FumSch – *Fumaria schleicheri*; MatCha – *Matricaria chamomilla*; MatIno – *Matricaria inodora*; MedSat – *Medicago sativa*; MelAlb – *Melandrium album*; MyoArv – *Myosotis arvensis*; MyoRam – *Myosotis ramosissima*; LamAmp – *Lamium amplexicaule*; LamPur – *Lamium purpureum*; LepDra – *Lepidium draba*; LepRud – *Lepidium ruderale*; LeuVul – *Leucanthemum vulgare*; PapDub – *Papaver dubium*; PoaAng – *Poa angustifolia*; PolAvi – *Polygonum aviculare*; PotRep – *Potentilla reptans*; RanRep – *Ranunculus repens*; RumPat – *Rumex patientia*; SetVir – *Setaria viridis*; SteAnn – *Stenactis annua*; SteMed – *Stellaria media*; TarOff – *Taraxacum officinale*; ValLoc – *Valerianella locusta*; VerArv – *Veronica arvensis*; VerHed – *Veronica hederifolia*). Percentage of variance explained by the first and second axes, and eigenvalues are indicated in brackets in their label.

alfalfa fields and 14,571 seedlings of 15 species from annual crop fields. From one sample from an alfalfa field and one from an annual crop field no seedlings emerged. We found a minimum of one and a maximum of seven germinated species per sample.

Species composition of the cache samples of old fields, alfalfa fields, and annual crop fields were not separated in the PCoA ordination (Fig. 5). In total, 16.9 % of the cache samples (15 samples out of 90) contained seeds of only one species, namely *Amaranthus retroflexus*, *Chenopodium album*, *Echinochloa crus-galli* or *Setaria viridis*. Seed content of mounds was characterized by two or three dominant species in old fields, one to three dominant species in alfalfa fields and one to four dominant species in annual crop fields (Appendix Table 5).

Total species and seedling number, seedling number of short-lived and perennial species, seed mass, seed shape index, and weighted TB, WB and NB scores of the cache samples were similar in old fields, alfalfa fields, and annual crop fields. The naturalness score of the cache samples were significantly higher in old fields compared to alfalfa fields and annual crop fields (Appendix Table 6).

3.3. Comparison of aboveground vegetation on mounds and seed content of cache samples in old fields and alfalfa fields

The proportion of short-lived species was significantly higher and the proportion of perennial species was significantly lower for the cached seeds compared to the aboveground vegetation on the mounds in both habitat types. Compared to the aboveground vegetation, naturalness, seed mass, and seed shape scores were significantly lower in the cache samples. Number of seedlings was similar between old fields and alfalfa fields (Fig. 6; Appendix Table 7). Jaccard index for the cached seeds and the aboveground vegetation of mounds ranged from 0.04 to 0.43 in old fields and from 0.05 to 0.27 in alfalfa fields, and habitat type had no effect on the degree of similarity (Appendix Table 7). Out of the eleven most abundant species (present with at least 20 seedlings) germinated from the cache samples, three species were not found in the aboveground vegetation, and six species were found only in the aboveground

vegetation of the mounds but not in the matrix (Appendix Table 8).

4. Discussion

We found that the mound-building activity of the steppe mouse affected the aboveground vegetation both in old fields and alfalfa fields, and the mounds were characterized by distinct species composition compared to the surrounding matrix. Mounds were also characterised by different vegetation structure compared to the matrix, which was expressed by a lower total vegetation cover and cover of perennials, and a higher cover of nutrient-demanding species. Thus, the steppe mouse created early secondary successional patches in the landscape. The percentage cover, and the ratio and occurrence of flower colours of insect-pollinated species was different on mounds compared to the matrix, creating a distinct feeding patch for pollinators. Although the aboveground vegetation of the mounds situated in old fields and alfalfa fields differed, the species composition of the cache samples was similar in the habitat types. We found that the species composition of the vegetation and the corresponding cache samples of the mounds were different both in old fields and alfalfa fields, so, the species cached by the mice might not be the ones growing on the mound.

4.1. Aboveground vegetation on the mounds and in the matrix

The mounds and the matrix showed slightly different species composition on the habitat level, while at the site level we found marked differences both in old fields and alfalfa fields. This indicates that steppe mice have a considerable effect on species composition of the vegetation, but the impact can only be assessed at the local scale.

The total species number and also the number of short-lived species were similar on the mounds and in the surrounding matrix both in old fields and alfalfa fields. The finding that soil disturbance by rodents did not change species numbers corroborates with other studies conducted in natural habitats such as dry grasslands (Mallen-Cooper et al., 2019; Valkó et al., 2022b). In general, the increase in species richness on

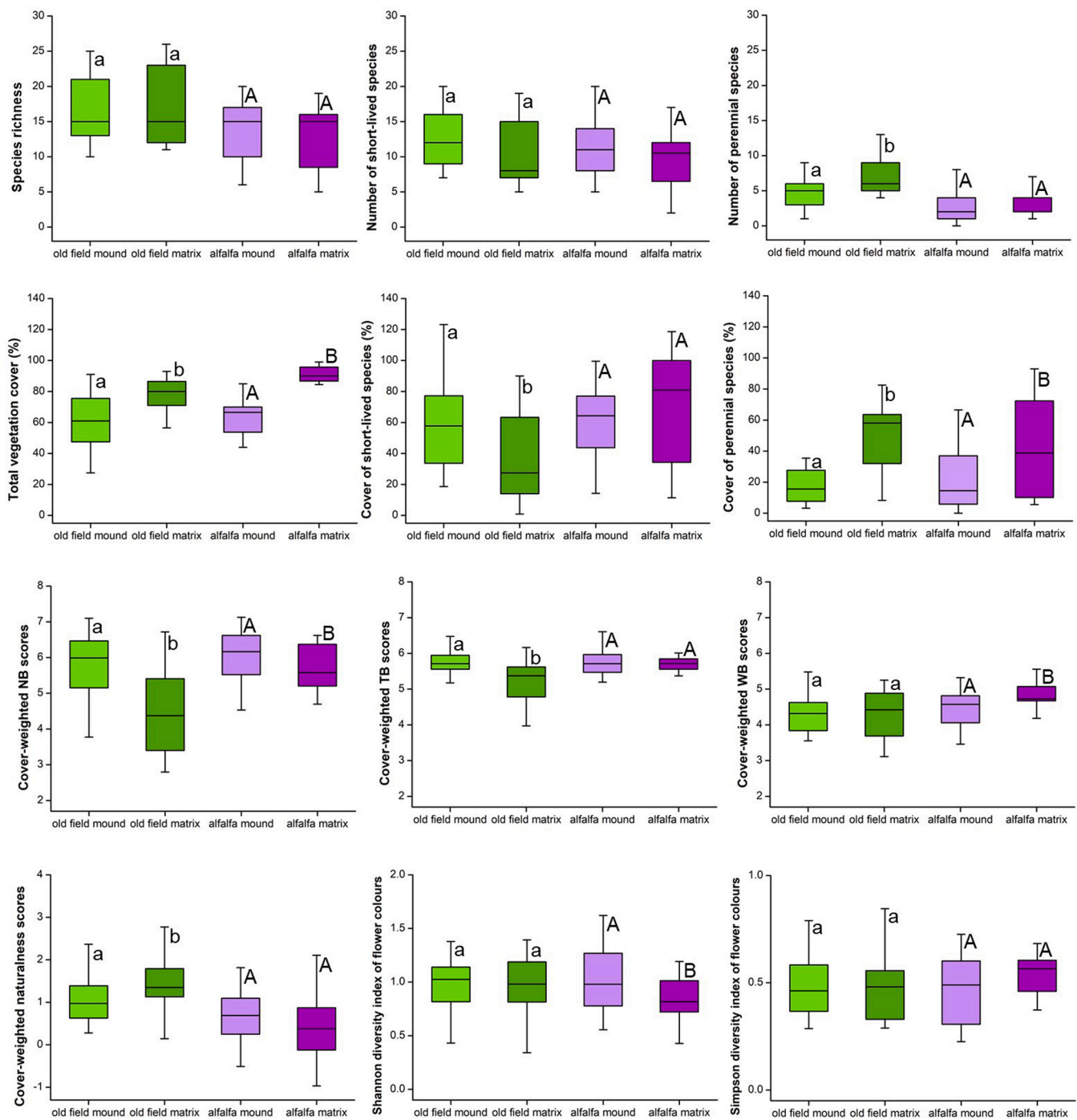


Fig. 3. Aboveground vegetation characteristics of the mounds and the matrix in old fields and alfalfa fields (Generalised Linear Mixed Models with LSD posthoc tests). Green boxes – old field; purple boxes – alfalfa field; light boxes – mound; dark boxes – matrix. Lowercase letters denote significant differences between the mounds and the matrix in old fields, and uppercase letters code the differences between the mounds and the matrix in alfalfa fields.

rodent mounds is caused by the appearance of short-lived species that find more suitable establishment conditions on mounds than in the closed vegetation of the matrix (Eldridge and Simpson, 2002; Müller et al., 2014). Since the studied systems were disturbed per se, where establishment gaps were not limiting, the number of short-lived species did not change with disturbance, we did not observe a marked increase in the total species number either. Although there was no significant difference in the total species richness between the mound and matrix habitats, we found that 21 species (16 % of the total species pool), were present exclusively on the mounds. This implies that mounds can provide establishment opportunities for certain species which are not able

to become established in the matrix. The appearance of these species on the mounds did not necessarily cause an increase in the total species number, but represented an exchange in species composition. The lower number of perennial grassland species on the mounds in old fields can be attributed to the disturbance caused by the mouse. On the disturbed mound surface, the perennial grassland species present in the surrounding matrix were unable to establish themselves in the subsequent vegetation period. Alfalfa fields are more disturbed habitats than old fields due to occasional ploughing, re-sowing and the mowing of alfalfa. Because of this, the number of perennial species was very low both in the matrix and on the mounds. It would be interesting to follow the

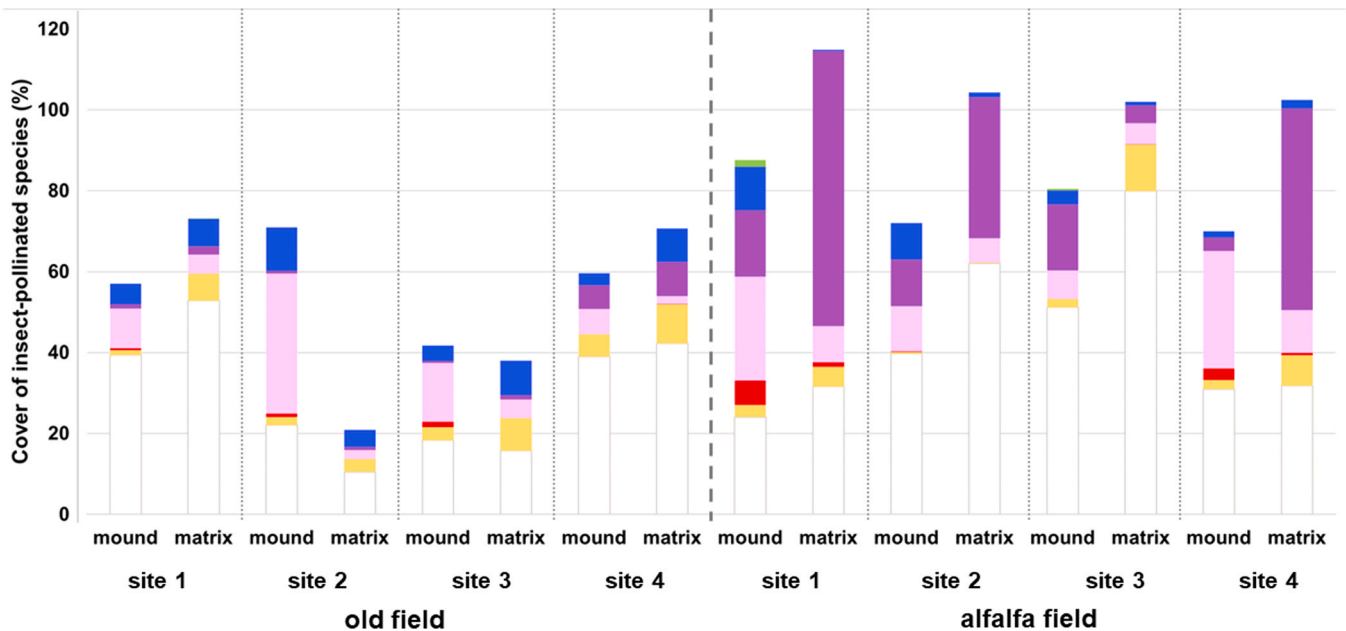


Fig. 4. Mean percentage cover of insect-pollinated species in the aboveground vegetation on the mound and in the matrix in each site, grouped by colour of the flower (white, yellow, red, pink, purple, blue, and green).

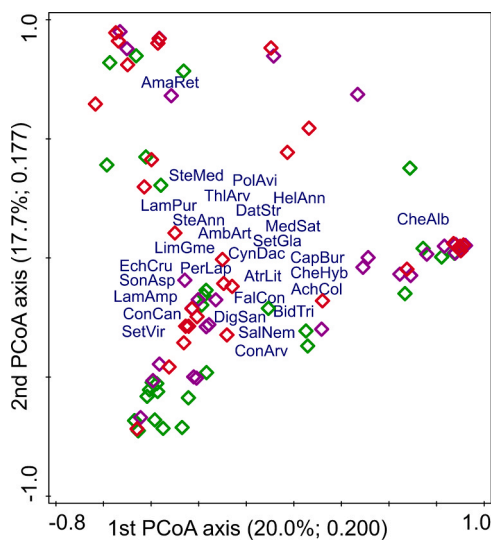


Fig. 5. Ordination diagrams from the principal coordinates analysis (PCoA), displaying the species compositions of the cache samples in the habitat types studied (green – old field; purple – alfalfa field; red – annual crop field). We plotted all of the germinated species identified to the species level (N = 29) on the figure. Species names are abbreviated using the first three letters of the genus and the first three letters of the species names (AchColl – *Achillea collina*; AmaRet – *Amaranthus retroflexus*; AmbArt – *Ambrosia artemisiifolia*; AtrLit – *Atriplex littoralis*; BidTri – *Bidens tripartita*; CapBur – *Capsella bursa-pastoris*; CheAlb – *Chenopodium album*; CheHyb – *Chenopodium hybridum*; ConArv – *Convolvulus arvensis*; ConCan – *Conyza canadensis*; CynDac – *Cynodon dactylon*; DatStr – *Datura stramonium*; DigSan – *Digitaria sanguinalis*; EchCru – *Echinochloa crus-galli*; FalCon – *Fallopia convolvulus*; HelAnn – *Helianthus annuus*; LamAmp – *Lamium amplexicaule*; LamPur – *Lamium purpureum*; LimGme – *Limonium gmelinii* spp. pannonicum; MedSat – *Medicago sativa*; PerLap – *Persicaria lapathifolia*; PolAvi – *Polygonum aviculare*; SalNem – *Salvia nemorosa*; SetGla – *Setaria glauca*; SetVir – *Setaria viridis*; SonAsp – *Sonchus asper*; SteAnn – *Stenactis annua*; SteMed – *Stellaria media*; ThlArv – *Thlaspi arvense*; see also Appendix Table 4). Percentage of variance explained by the first and second axes, and eigenvalues are indicated in brackets in their label.

development of the vegetation on mounds in subsequent years, as the effects of ecosystem engineer species may appear and intensify on longer temporal scales (Mallen-Cooper et al., 2019). Nevertheless, due to the characteristic of our study system, long-term monitoring of the mounds is challenging, because they are usually destroyed within a short period due to mowing or ploughing (Sokolov et al., 1998).

Both in old fields and alfalfa fields, the newly created microhabitats were characterized by lower total vegetation cover and lower cover of perennial species, which is a general characteristic of disturbed surfaces (Valkó et al., 2022a, b). The higher cover of short-lived species in mounds located in old fields suggests that mice had stronger effect on the vegetation in this habitat type by opening the dense vegetation structure of the matrix. Accordingly, the mounds provide better establishment opportunities for subordinate species of the old field matrix owing to reduced competition from perennial plants and increased nutrient availability (Clark et al., 2007).

The higher cover of nutrient-demanding species on the mounds suggests an increase in the nutrient availability compared to the matrix; however, we did not measure this feature directly. This phenomenon was also described by other studies. Compared to the surrounding undisturbed area, mounds built by various animal taxa – such as ant species (*Formica* spp.; Jurgensen et al., 2008), the bird malleefowl (*Leipoa ocellata*; Neilly et al., 2022), and the pocket gopher (*Thomomys talpoides*; Yurkewycz et al., 2014) were reported to have higher soil nutrient content compared to the surrounding matrix. Also, it was shown that mounds of malleefowl can affect soil functions by altering bacterial community composition leading to enhanced enzyme activity and unique soil chemistry (Decker et al., 2023). The reason for increased nutrient availability on the mounds can be caused by that, when building the mounds, mice mostly collect the topsoil from the neighbouring areas (approximately from a 45–140 m²-sized area), which is characterised by a higher level of nutrient content (Jobbágy and Jackson, 2001; Szenczi et al., 2011). As mice do not feed on cached plant material (Szenczi et al., 2011, 2012), by spring it starts to decompose which can further increase nutrient content on mounds. This is somewhat similar to the effect of surface caches of plant material created by pikas (*Ochotona* spp.), with the difference that pikas do not cover the cache with soil. As the unused plant material decomposes over time, it creates nutrient-rich soil in a certain patch that can enhance the growth

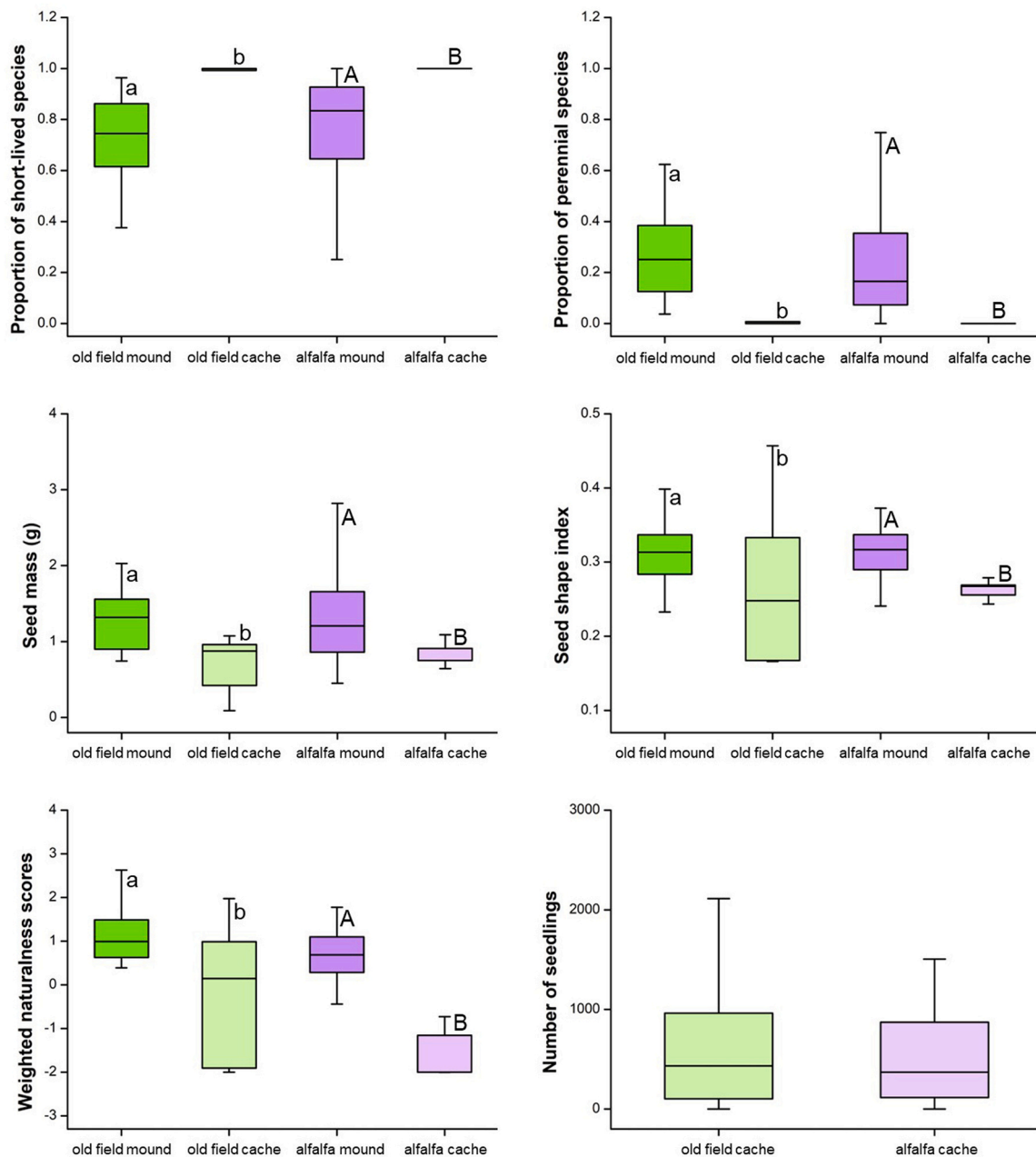


Fig. 6. Characteristics of the aboveground vegetation of the mounds and the cached seed content of the mounds in old fields and alfalfa fields (Generalised Linear Mixed Models with LSD posthoc tests). Green boxes – old field; purple boxes – alfalfa field; pale boxes – cache samples; light boxes – mounds' aboveground vegetation. Lowercase letters denote significant differences between the mounds and the matrix in old fields, and uppercase letters code the differences between the mounds and the matrix in alfalfa fields.

of nutrient-demanding species (Aho et al., 1998; Popov et al., 2023). Moreover, in the Ellenberg system, high NB scores are assigned to disturbance-tolerant species, so the high NB scores does not reflect only high nutrient content of the soil, but also indicates the presence of the disturbance-tolerant species (Borhidi et al., 1995).

In old fields, the disturbance by steppe mouse probably created a new microclimatic niche, because the cover of heat-demanding species was higher on mounds. Reduction of plant cover by disturbance is an important factor that increases soil temperature (Song et al., 2013). The probable reason why the cover of heat-demanding species in alfalfa fields did not differ between the mound and the matrix could be that in this habitat mowing and occasional ploughing result in a high proportion of bare soil surface also in the matrix.

The only characteristic that was different between the mounds and

the matrix in alfalfa fields but not in old fields, was the cover-weighted WB scores. The smaller cover of water-demanding species on mounds situated in alfalfa fields could be caused by the lower alfalfa cover on the mounds. Alfalfa, as a cultivated species, has relatively higher water demand than species which occurred on the mounds in alfalfa fields (Borhidi, 1995, Appendix Table 2, 5).

Our results showed that the cover of insect-pollinated species was generally lower on mounds, and mounds differed considerably in the ratio and occurrence of flower colours of insect-pollinated species from the matrix. The higher Shannon diversity of flower colours of insect-pollinated species on mounds situated in alfalfa fields suggest that mounds may offer a wider variety of flower resources for pollinators than the neighbouring matrix. Different flower colour spectrum and the elevated structure of the mounds provide a visual contrast between the

mound and the matrix, which can support pollinators to detect pollen and nectar resources (Trunschke et al., 2021; Yoshihara et al., 2010). So far, relatively few studies investigated disturbance-induced changes related to flowers and pollinators (but see Labadessa and Ancillotto, 2023; Yoshihara et al., 2010; Valkó et al., 2021, 2022a). In the same landscape, Valkó et al. (2022a) studied the effect of crane ploughing, and found that in a closed perennial grass matrix, there are more insect-pollinated species in the disturbed patches. In the current study, the investigated habitats originally harboured many insect-pollinated species, still the effect of the steppe mouse may be important by diversifying the flower resources for pollinators.

When comparing the steppe mouse with larger burrow-dwelling species found in our study area, such as the European rabbit (*Oryctolagus cuniculus* L.), the scale and ecological impact of soil disturbance may differ considerably. Due to the small size and the special behaviour of the steppe mouse, they affect only small patches of vegetation. Soil disturbance caused by the mice is primarily represented by the mounds that are used only during a single winter. Once abandoned, these mounds provide an opportunity for vegetation to regenerate quickly on a small, well-defined disturbed area. In contrast, rabbits create large burrow systems used year-round by multiple generations. As central-place foragers, rabbits exert a gradient of influence on the surrounding plant communities. Their digging, combined with constant grazing and trampling, permanently eliminates vegetation near burrow entrances, while the intensity of their impact diminishes with distance from the burrow entrance (Gálvez-Bravo et al., 2011). The larger size of rabbits and their more intensive activity leads to greater and long-lasting ecosystem changes, concentrated in fewer locations. The eroded bare areas created by rabbits often experience weed encroachment (Mutze et al., 2016). In contrast, the impact of the steppe mouse is more sporadic, creating small gaps for plant establishment that are scattered over the area and do not promote weed encroachment. Thus, these small disturbed patches do not have the same ecological function as rabbit warrens.

4.2. Seed content of caches

We found that the species composition of seeds in the cache material was very similar regardless of the habitat type. Many of our samples (81.1 %) were characterized by a few dominant species along with sine incidental subordinate species. The highest densities were typical in both monocots and dicots, such as *Amaranthus retroflexus*, *Chenopodium* spp., *Echinochloa crus-galli*, and *Setaria* spp. Previous studies also found these species in caches of steppe mouse mounds. However, according to those studies, the studied caches generally contain the parts of only one plant species (Hözl et al., 2009, 2011b; Szenczi et al., 2011), while we discovered that the caches contained 1–4 dominant species.

We found that the naturalness score of old field cache samples was higher than in the other two habitats (alfalfa fields and annual crop fields) suggesting that the proportions of species collected by the mouse may be somewhat influenced by the species pool in a given habitat (Hözl et al., 2009; Szenczi et al., 2011, 2012; Csanády et al., 2019). Nevertheless, the high abundance and frequency of certain species in the samples regardless of the habitat type (Appendix Table 8) suggest a strong preference of the mice for a few species that they collect.

The specific preference for certain species can be explained by the fact that steppe mice build their mound not for storing food, as believed earlier, but rather for thermoregulatory and water-insulation purposes (Sokolov et al., 1998; Hözl et al., 2011a; Szenczi et al., 2011, 2012). The collected plant parts of preferred species share the same characteristics, e.g., they are fluffy, able to retain heat, hold air, or absorb a lot of water. Hözl et al. (2011a) showed that there is a significant difference between different plant materials in their ability to take up heat, with *Setaria* spp. being the most effective compared to *Amaranthus* spp. and *Chenopodium* spp. Surprisingly, in our samples, *Setaria* spp. was only the third most abundant species collected by mice. This could also be

explained by the fact that the preferences regarding the collected plant material could also be shaped by the previous experiences and habits of the individuals (Patris et al., 2002; Csanády et al., 2019).

4.3. Comparison of aboveground vegetation and cache samples in old fields and alfalfa fields

When comparing the characteristics of the species in the caches and the aboveground vegetation on the mound, we found that caches contained more short-lived species with lighter and rounder seeds. These are the characteristics of several weed species typical of the region. This is consistent with previous findings suggesting that the steppe mouse prefers weeds (Hözl et al., 2011b; Szenczi et al., 2011; Csanády et al., 2019). These findings were also supported by the observation that naturalness scores were lower for the species germinated from the cached material than for the aboveground vegetation of the mounds. Despite all these, the similar patterns of seed characteristics of the species germinated from the cache material (i.e., weeds with light and round seeds) may only be a coincidence, because mice do not specifically collect the seeds; rather they carry larger parts of the plants.

Some species that germinated in large numbers from the cache samples occurred only on the mounds but were absent in the matrix, while others did not occur either on the mounds nor in the neighbouring matrix plots. One possible reason for this pattern is that a certain proportion of the aboveground vegetation germinated on the mound likely originated from the seed bank of the top soil layer of the neighbouring areas that the mouse hoarded on top of the collected plant material (Yusefi et al., 2023). Another reason could be that during mound building, seeds of some species might be dispersed by the mice from a more distant location in the matrix by synzoochory or by endo- or epizoochory (Godó et al., 2022), as some of these species are present in the diet of the mouse, or having appendices which support epizoochory (Schermann, 1967; Szenczi et al., 2011; Appendix Table 8). The absence of species in the matrix that were present on mounds highlights that mice mostly collect the plant material from areas farther from the mound, and are willing to go a longer distance to collect the most preferred species. In doing so, they do not reduce the vegetation cover next to the mound, which provides greater protection from predators.

5. Conclusions and outlook

Our results imply that small-scale disturbances, such as the mound-building activity of the steppe mouse, play an important role in maintaining small scale heterogeneity of the vegetation in otherwise homogenous agroecosystems. Mounds provide sites with reduced competition and altered resource availability, which can lead to the formation of small vegetation patches with a species composition that differs from the neighbouring matrix. We suggest that the steppe mouse might be a facultative engineer species as its effects on the vegetation were influenced by the habitat type. However, the changes might not persist for a long period as mounds often become destroyed by agricultural activities. Therefore, the steppe mouse populations form and maintain a fluctuating system through their mounds, where presence of mounds is constant at a certain area, but exhibit a dynamically changing spatio-temporal pattern. As the spatial location of mounds changes annually, it creates each individual mound as a suitable site for plant establishment for a short time window.

The seed content analysis of the cache material provided evidence that mice have a strong preference for a few weed species regardless of the habitat type. Interestingly, only a few of the cached weed species only a few appeared in the aboveground vegetation that formed on the mound, although many other early secondary successional species appeared. Thus, we can assume that despite the mounds provide suitable conditions for the establishment of the cached weed species, they do not appear abundantly in the aboveground vegetation of the mound. This result may help in shaping the attitudes of farmers towards steppe mice.

The steppe mouse and other rodents are often considered pests in agricultural areas; however, we found no evidence of weed encroachment on the mounds of the steppe mouse from the cached plant material. There is a need for further studies on ecosystem services and disservices provided by the steppe mouse, including their effects on soil nutrients, soil microbiome, and crop pollination, which can affect agricultural production and potentially shape the public perception of these rodents.

Given that the steppe mouse is a common species, with a wide distribution range, and is adapted to living in secondary and disturbed habitats, it can be present in various agroecosystems. Since the distribution range of the steppe mouse appears to be expanding northward, westward and eastward, probably owing to the milder winters, it has the potential to play an increasingly important role in shaping the structure and functioning of various agroecosystems in Europe.

CRediT authorship contribution statement

Laura Godó: Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Orsolya Valkó:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Sándor Borza:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Attila Ferenc:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Réka Kiss:** Writing – review & editing, Investigation. **Katalin Lukács:** Writing – review & editing, Investigation, Data curation. **Balázs Deák:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, 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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.109359](https://doi.org/10.1016/j.agee.2024.109359).

Data availability

Data will be made available on request.

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