RESEARCH ARTICLE

Rapid functional but slow species diversity recovery of steppe vegetation on former arable fields in southern Ukraine

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Abstract

Questions: European steppes are among the most threatened ecosystems in the Palaearctic region, mainly because of conversion to arable land. Abandonment may allow for the passive recovery of steppes. We made use of an exceptional old-field succession chronosequence of nearly 100 years to answer the following questions: (a) Are the plant species composition, species richness and functional characteristics typical of virgin grass steppes able to self-restore during ca. 100 years after abandonment? (b) Do the rates of recovery of the above vegetation characteristics differ over the studied chronosequence? (c) Do topsoil carbon and nitrogen content change over the succession chronosequence, leading to concentrations similar to that of virgin steppes?

Location: Southern Ukraine.

Methods: We sampled vegetation and soil in a virgin grass steppe and in old fields abandoned for 6, 15, 31, 50 and ca. 97 years. We subjected the composition data to multivariate analysis. To test whether species richness, functional and soil characteristics of the old fields diverge from those of the virgin steppe, we used one-way analysis of variance with Tukey's honestly significant difference (HSD) statistic to create 90% confidence intervals.

Results: The vegetation composition of the three most recently abandoned old fields differed significantly from that of the virgin steppe. The species richness of vascular plants was lower in old fields than in the virgin steppe. The share of steppe habitat specialists was similar to the virgin steppe only in the field abandoned for ca. 97 years. Functional characteristics were significantly different from the virgin steppe only in the most recently abandoned old field. Contents of C_{org} and N_{tot} in fields abandoned for ≤50 years were lower compared with the virgin steppe.

Conclusions: The functional characteristics of steppe vegetation seem to recover much faster than its biodiversity. However, based on our results, 100 years can be enough time for the spontaneous re-establishment of typical steppe vegetation.

1 | INTRODUCTION

The conversion of natural ecosystems to arable land leads to habitat loss and strong biodiversity decline worldwide (Egli et al., 2018). In some regions of the world, the level of agricultural transformation of the landscape is extremely high. For example, in Eastern Europe, remnants of grasslands belonging to the Palaearctic steppe biome cover <10% of their original extent (Sunderland, 2004; Dengler et al., 2020). Despite this severe decline in several regions, Eurasian steppes are among the least protected biomes worldwide, and their unique biodiversity is highly threatened by still-increasing anthropogenic impact (Wesche et al., 2016; Török & Dengler, 2018).

Eurasian steppes host a high biodiversity of plants and animals well-adapted to continental climates characterized by low precipitation, periodic droughts, cold winters and strong winds (Wesche et al., 2016). Under such harsh conditions, grassland plant cover enhances ecosystem resilience and plays a crucial role in soil formation processes, protecting the soil against erosion and supporting water retention (Moon, 2013; Dudiak et al., 2020). Steppes also have a high potential for mitigating climate change through carbon sequestration (Rolinski et al., 2021). As revealed by experimental studies in other temperate grasslands, carbon sequestration can be regulated by plant species diversity and functional traits (Jones & Donnelly, 2004; Yang et al., 2019).

Destruction of a steppe by ploughing decimates local populations of native plants and leads to a decrease in the local diversity of both flora and fauna. Moreover, smaller, isolated remnant patches of such habitats cannot support populations of many steppe specialist species in the long term (Dembicz et al., 2021). The agricultural transformation of steppes also leads to significant changes in ecosystem functioning and to the decline of supportive and regulating ecosystem services due to altered soil structure and soil chemical properties, including a decrease in soil organic matter content (Cotton & Acosta-Martínez, 2018; Rolinski et al., 2021). Cessation or a substantial reduction of human impact may facilitate the renewal of natural ecosystem processes in the steppes and lead to the natural recovery of target plant communities, but only if the surrounding species pool is sufficiently large, sources of diaspores are constantly available, the risk of invasion by neophytes is low and habitat conditions allow for the establishment of target species (Tölgyesi et al., 2022). However, the development and maintenance of plant species diversity may be hindered by the absence of wild or domestic ungulates or the lack of natural wildfires in the highly fragmented steppes of Europe. Indeed, biomass removal through grazing and fires has been indicated as an important factor influencing plant community composition and structure in naturally recovering grasslands of the Eurasian steppe belt (Valkó et al., 2014; Brinkert et al., 2016).

The grass steppe zone of southern Ukraine is the westernmost part of the Palaearctic steppe biome that covers ca. 10.5 million km^2 in a belt stretching from Eastern Europe and Turkey to Manchuria (Wesche et al., 2016). Extensive areas of southern Ukraine that were previously covered by grasslands had been almost completely converted to arable land by the beginning of the 20th century (Lisetskii, 1992; Sunderland, 2004). The current landscape of the Ukrainian steppe zone is dominated by large, often irrigated, crop monocultures consisting mainly of wheat, sunflower, rape and corn. Steppe vegetation has been well preserved in only a few steppe reserves and other types of enclaves such as loess ravines and river escarpments, together covering ca. 1% of the territory of the country, compared with 40% in the 17th century (Burkovskyi et al., 2013; Moon, 2013).

In some regions of the Eurasian steppes, agricultural abandonment has become a unique opportunity for the recovery of steppe vegetation (Kämpf et al., 2016). Such abandonment was particularly pronounced in many post-Soviet countries after the transition from a state-command to a market-driven economy, resulting in tens of millions of hectares of abandoned agricultural land (Kraemer et al., 2015; Löw et al., 2015; Meyfroidt et al., 2016). The land reforms of the 1990s and the resulting changes in socio-economic conditions also led to widespread land abandonment (Hobbs & Cramer, 2007; Hartvigsen, 2014). As a consequence, many old fields underwent recovery towards steppe habitats, e.g. in Kazakhstan and Russia (Brinkert et al., 2016; Kämpf et al., 2016). By contrast, in other steppe regions such as southern Ukraine, management cessation was rarely observed, whereas the conversion of remnant grasslands to arable land still occurs (Korotchenko & Peregrym, 2012; Burkovskyi et al., 2013). In such circumstances, only planned land acquisition for nature conservation purposes may offer a real chance for grassland recovery and protection. However, it remains an open question whether spontaneous steppe recovery on the acquired fields will be successful. If this is the case, how quickly will the vegetation of these fields become floristically and functionally "indistinguishable" from the virgin steppe, and how quickly will the nutrient levels in old fields achieve characteristics close to the virgin steppe?

The post-agricultural recovery process for Eurasian steppe vegetation has attracted scientists since the end of the 19th century (Tanfiliev, 1898, see also Vedenkov, 1997 and Kazantseva et al., 2010). However, the existing literature on this topic is scattered (including many works published in Russian journals hardly accessible to international readers) and lacks a more comprehensive and long-term approach; the results are usually based on relatively short-time succession series and concentrated on delimitation of the main stages of steppe recovery (Shalyt, 1938). Also, modern long-term studies in Eurasian steppes are relatively rare, usually spanning only one or two decades (Török et al., 2011; Brinkert et al., 2016; Kämpf et al., 2016) and rarely exceed

40 years (Csecserits et al., 2007, 2011; Albert et al., 2014). One of the longest data time series conducted in the East European forest–steppe reaches ca. 100 years (Kazantseva et al., 2010). Recovery processes in the grass steppe in southern Ukraine attracted the interest of researchers in the first half of the 20th century (Shalyt, 1930, 1938; Tyulina, 1930), and such studies were continued later (Vedenkov, 1997). However, there is no agreement on the time needed for the full recovery of grass steppe vegetation. Studies carried out thus far mostly focused on the dominant functional groups of plants or the physiognomy of vegetation. A detailed analysis of the recovery trajectories of vegetation biodiversity, topsoil characteristics and functional composition in the Ukrainian grass steppe has not yet been performed.

To fill this knowledge gap, we undertook a study on grass steppe recovery on old fields comprising a period of almost 100 years. We performed the research in the largest European steppe protection site, the Askania-Nova Biosphere Reserve and its buffer zone, which are located in southern Ukraine. To achieve a sufficient temporal scope, rather than long-term research we applied an approach of substituting space for time, using old fields of different ages (Walker et al., 2010). The studied chronosequence offered an exceptional opportunity, because permanent abandonment is rarely observed in the studied region (usually, the land is ploughed again after several years). In this study, we wanted to assess the rate and overall effectiveness of passive recovery on old fields in the European grass steppe. To obtain a comprehensive picture of steppe recovery, we explored not only plant species diversity patterns and basic soil parameters, but also functional trait responses, which provide insights into the mechanisms shaping community assembly and triggering succession processes (Helm et al., 2018; Fantinato et al., 2019; Zhang et al., 2019; Krickl & Poschlod, 2023). We specifically asked the following questions:

1. Are plant species composition and species richness, as well as the ecological and functional characteristics of vegetation, fully restored after a recovery process lasting almost a century?
2. Are the rates of recovery of the above vegetation characteristics the same over the studied chronosequence?
3. Do topsoil carbon and nitrogen content change over the studied chronosequence, leading to concentrations similar to that of virgin steppes?

2 | METHODS

2.1 | Study area

We conducted field sampling in the Askania-Nova Biosphere Reserve and its buffer zone. The reserve is located in southern Ukraine, in the Kherson Region (Figure 1). The climate of the region is hot-summer fully humid warm temperate (Cfa) according to the Köppen–Geiger classification (Kottek et al., 2006), with an average annual precipitation of 398 mm and a mean annual temperature of 9.8°C. The coldest month (February) has a mean temperature of −1.8°C and the warmest month (July) has a mean of 23.0°C (weather station in Askania-Nova, period 1910–2010). In the Askania-Nova Biosphere Reserve, the
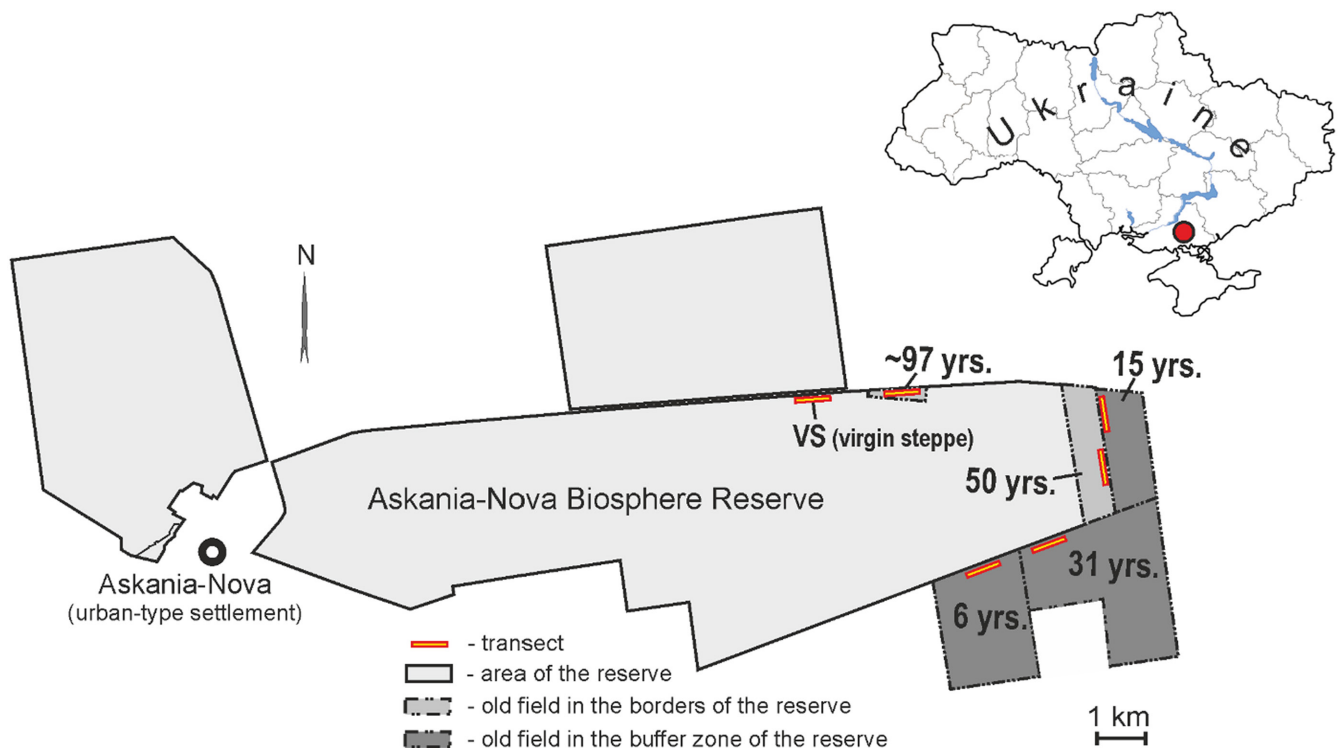

FIGURE 1 Locality of the studied reserve in Ukraine (red dot) and of the six studied transects within the borders of the reserve and in its buffer zone. The number of years indicates the time that had passed since management ceased.

steppe ecosystem has been preserved in its primary natural form over an area of 110 km[2] (Boiko, 1998), making it one of the largest patches of virgin steppe in Europe. The reserve includes the west Pontic grass steppe (Bohn et al., 2004), which is dominated by tussock-forming grasses (mostly from the genera *Stipa*, *Festuca* and *Koeleria*), although non-tussock-forming grasses, sedges and non-graminoid plants greatly contribute to the overall plant diversity. The reserve is located in a vast, flat loess plain with a maximum of 13.3 m elevation difference. The prevailing soil type of the reserve is dark-chestnut residual Solonetz with low humus content (Polupan et al., 2005), classified in the Soil Atlas of Europe (Jones et al., 2005) as Haplic Kastanozem.

The main causes of land abandonment in the buffer zone of the reserve were economic and legal (e.g. farm bankruptcy, financial constraints concerning the availability of fuel or agricultural machinery, cessation of irrigation, lawsuits). During the long history of the reserve, its boundaries have changed several times. Some previous land acquisitions included formerly cultivated fields that ceased to be used as arable land. However, mowing continued sporadically on the acquired old fields as well as in the nature reserve (the hay is still used as winter fodder for animals kept in the zoological park belonging to the reserve). Also, fires accidentally caused by humans still occur in part of the reserve and its buffer zone; in the past 30 years, fire events have occurred every ca. 1.5 years in the strictly protected part of the reserve, affecting areas from a few to several thousand hectares. Both mowing and fires reduce litter accumulation in the large part of the reserve where, because of different constraints, herds of wild ungulates are not maintained.

2.2 | Field sampling

To study the chronosequence, we selected five arable fields abandoned in different years (6, 15, 31, 50 and ca. 97 years ago) and one reference site, a virgin steppe located in the never-ploughed part of the Askania-Nova Biosphere Reserve (Figure 1). The sizes of the studied old fields were 25.5, 186.2, 697.6, 228.1 and 360.1 ha, respectively. The close proximity of the old fields and the reference site (max. 5.5 km between sites) guaranteed a consistent landscape history and a set of environmental conditions that vary little over the studied area. Most of the studied old fields were adjacent to the virgin steppe; only one (abandoned for 15 years) was adjacent to another old field (abandoned for 50 years) and its distance to the virgin steppe was ca. 800 m (Figure 1). To be selected for inclusion in this study, ploughing must not have occurred after abandonment, but other uses (such as mowing) could have occurred sporadically. Because the virgin steppe area selected for our study had also been mown in the past, there was no apparent difference in management among the selected sites. Accordingly, we assume that the results of our study are not strongly biased by land-use factors, despite the fact that no replicates were made for old fields of a given age (because there were no other old fields in the research area).

We conducted field sampling from 20 to 26 May 2017. On each of the five old fields and in the virgin steppe we established a

transect ca. 600 m long (Figure 1). Transects were located parallel to the reserve border to minimize the effect of varying distances from potential diaspore sources on the studied vegetation recovery patterns. We collected vegetation data and soil samples from 12 square 10-m[2] plots regularly distributed along each transect. In every plot, we assessed the per cent cover of each vascular plant, bryophyte and lichen species. In addition, we took a mixed soil sample from the upper soil layer (depth 5–15 cm) consisting of subsamples collected at five evenly distributed points in the plot. The soil samples were first analysed to double-check the homogeneity of environmental conditions among the studied sites, and further to detect the trend informing how quickly the old fields achieve the topsoil organic carbon and total nitrogen contents close to the virgin steppe. Because of the flatness of the area, all of the 72 sampled plots were located at almost the same elevation (30–31 m a.s.l.), with a slope of 0°.

2.3 | Laboratory analysis of soil samples

After field sampling, soil samples were dried at room temperature (20 ± 2°C), and then stored in a refrigerator at −4°C. The pH was determined potentiometrically in a 1:2.5 (m/V) soil suspension in water and 1 mol/L KCl solution (according to the norm PN-ISO 10390: 1997). Electrical conductivity (EC) was measured in 1:5 water–soil suspension using a conductometer. The calcium carbonate content was measured using Scheibler's method (only for samples with pH in KCl ≥7; for the others, the carbonate content was assumed negligible). Total carbon content (C_{tot}) and total nitrogen content (N_{tot}) were determined in a Vario Macro Cube CN elemental analyser (Elementar Analysensysteme GmbH, Langenselbold, Germany) after dry combustion. Organic carbon content (C_{org}) was calculated as the difference between C_{tot} and carbonate content. The soil texture was analysed concerning the share of individual fractions of sand (diameter = 2.0–0.063 mm), silt (diameter = 0.063–0.002 mm) and clay (diameter < 0.002 mm) using a laser diffractometer, with textural classes defined according to World Reference Base for Soil Resources classification system (FAO, 2006).

2.4 | Data set preparation and analysis

Before the analyses, using expert assessment (Sudnik-Wójcikowska & Moysiyenko, 2006), we assigned all species of vascular plants to one of the following groups: steppe habitat specialists (non-synanthropic species occurring only in well-preserved steppe patches in southern Ukraine) or generalists (species occurring exclusively or at least occasionally in anthropogenically disturbed areas, i.e. native species of broader habitat spectra and non-native species). This classification, once elaborated for the west Pontic grass steppe zone in Ukraine (Sudnik-Wójcikowska & Moysiyenko, 2006), has been applied consistently in other studies conducted in that area (Dembicz et al., 2021). Moreover, to gain insight into vegetation resilience towards invasions during the steppe recovery process, we

assigned non-native species to two categories: archaeophytes (alien species that arrived in Ukraine before 1500) and neophytes (alien species that arrived in Ukraine after 1500).

We used the following functional traits obtained from the literature and our measurements supplemented with the TRY database (Kattge et al., 2020, A list of the individual data sources is found in Appendix S5): specific leaf area (SLA), vegetative height, seed mass, seed number per ramet (categorical variable; 1, 1–10 seeds; 2, 11–100; 3, 101–1,000; 4, >1,000), long-distance diaspore dispersal ability (further referred to as long-distance dispersal it is a binomial variable, with 1 indicating the ability of a species to disperse over long distances via zoochory or anemochory; based on the dispersal mode given in the TRY database or derived from the presence of structures on fruits indicating dispersal by wind or animals), Raunkiaer's life form, clonality (presence/absence of polycormones) and root depth (estimated in a three-step scale of shallow, medium or deep; Golubev, 1996). The latter is related to the adaptation to aridity, but can also be used as a rough proxy of carbon sequestration effectiveness (grassland plants with deep roots more effectively store carbon in the soil; Kell, 2011). Because of the high skewness of vegetative height and seed mass, we applied square root and $\log_{10}$ transformations, respectively. The species list and assignment of vascular plants to groups are given in Appendix S1. Raw data calculated or measured for each plot are available in Appendix S2.

We performed all the statistical analyses in R (R Core Team, 2017). Vegetation data from all plots were subjected to Detrended Correspondence Analysis (DCA) using the package *vegan* (Oksanen et al., 2017). To dampen the effects of dominant species in the DCA, we used square root transformed cover data. To compute indicator values for species and identify those typical for a given stage of steppe recovery, we used the "IndVal" function in the *labdsv* package (Roberts, 2019).

Using the *FD* package in R (Laliberté et al., 2014), we calculated the share of habitat specialists, archaeophytes and neophytes in each plot, as well as the community-weighted means (CWMs) of metric (SLA, vegetative height and seed mass) and ordinal (seed number per ramet, depth of roots; treated as quasi-metric) functional traits. In the case of categorical (Raunkiaer's life forms) and binary (long-distance dispersal and clonal growth) traits, we used mean cover scores of the categories. By "share of species" we mean the percentage of the number of species representing a given group/trait in the total species pool of vascular plants in a plot. We applied that measure in assessing taxonomic composition and the share of steppe specialists and non-native plants in a community because this measure is independent of the total number of species and offers additional information on how strongly the given group contributes to overall richness (whether it is a small or large component at given stage of the succession). In the case of CWMs and the mean cover scores of functional traits, we used the "share in cover" calculated as a mean trait value of all species present in the community weighted by their relative abundances (covers in %) in a plot. We used "share in cover" here because it better reflects the functional strategies dominating in a community than non-weighted indices.

To test for differences in vegetation and soil parameters between reference plots in the virgin steppe and the plots located in old fields, we used one-way analysis of variance with Tukey's honestly significant difference (HSD) statistic to calculate confidence intervals (CIs) for the difference in true means (instead of using the *p*-value approach). We decided to use 90% CI for the mean effect size because it allows us to answer questions about a positive or negative influence of the studied factor with 95% confidence (focusing on one end of 90% CI). Thus, we only used the CIs to report and visualize the results of the tests. In the case of five functional traits (SLA, vegetative height, seed mass, seed number per ramet and long-distance dispersal) and soil data (C_{org}, N_{tot}, C/N ratio), we additionally applied the standardized effect size (SES; Sullivan & Feinn, 2012) allowing us to present the results for parameters having different units simultaneously. To calculate SES, we divided the results obtained from CIs by the standard deviation (*SD*) of that particular parameter found for plots located in the virgin steppe. We used 0.5 *SD* as a threshold to distinguish between "small" and "medium" effects, whereas differences exceeding 0.8 *SD* were interpreted as large effects (Cohen, 1992; Sullivan & Feinn, 2012).

3 | RESULTS

We did not detect statistically significant differences in the pH or EC of topsoil samples collected from the virgin steppe and the old fields. All soil samples were classified as silt loam. Because the content of texture classes differed only slightly between the studied sites and the sites lie close together and do not have a different topography, we could assume homogeneity of environmental conditions among the studied sites (for details on soil parameters see Appendices S2 and S4).

Within all of the plots, we found a total of 138 species of vascular plants, 30 species of bryophytes (Appendix S1) and 2 species of lichens (*Cladonia fimbriata* and *C. foliacea*). The sum of species found in all 12 plots in the virgin steppe was 116 (97 of which were vascular plants), whereas in old fields abandoned for 6, 15, 31, 50 and 97 years, the total numbers of species were 75 (62 of which were vascular plants), 68 (61), 76 (62), 96 (76) and 92 (80), respectively.

The vegetation composition of the most recently abandoned old field (6 years) was distinct from all other plots along the first DCA axis. Conversely, the vegetation of plots located in the two old fields abandoned 97 and 50 years ago constituted nearly one group together with reference plots in the virgin steppe (Figure 2; for the vegetation data, see Appendix S3). However, 20 species had a significant indicative value for the virgin steppe specifically, including *Tanacetum millefolium*, *Crepis ramosissima*, *Jurinea multiflora*, *Cruciata pedemontana* and *Iris pumila* (Table 1). The same number of indicator species was distinguished for the most recently abandoned old field, among them *Anisantha tectorum*, *Centaurea diffusa*, *Conyza canadensis*, *Lactuca serriola* and *Lamium amplexicaule* (Table 1). Fewer indicator species were significant in the case of other old fields, with only three being indicative for the stage 31 years after abandonment (Table 1).
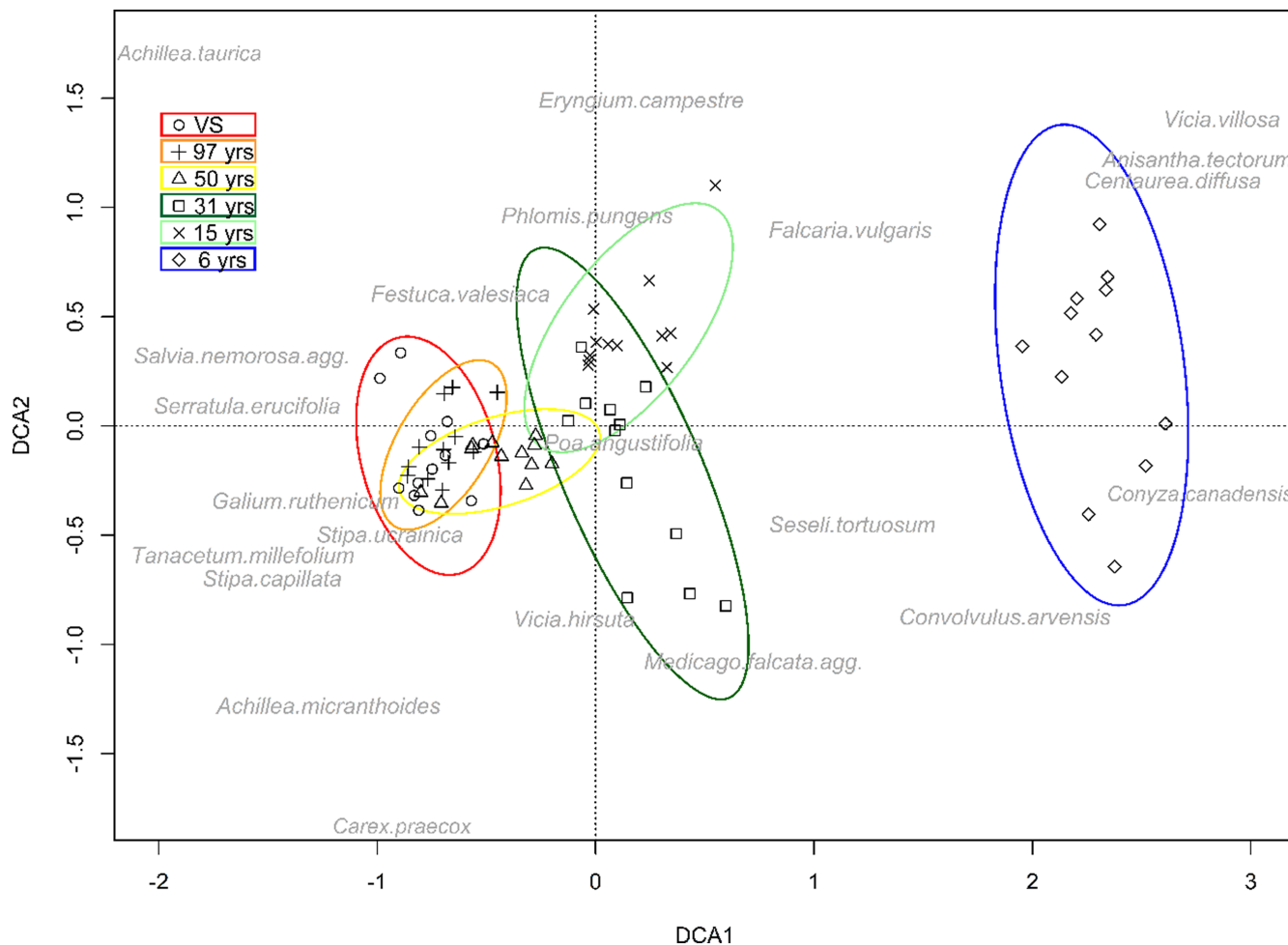
FIGURE 2 Detrended Correspondence Analysis of vegetation data. The obtained eigenvalues for the first two DCA axes were 0.5491 and 0.1526, respectively. Symbols indicate the age of the old field and reference plots in the virgin steppe (VS); ellipses indicate 95% confidence intervals. The 22 species with the highest cover are displayed.

Total species richness, species richness of vascular plants and the number of steppe habitat specialists per plot were significantly lower in all old fields compared with the virgin steppe (Figure 3a; Table 2). However, in the case of the two old fields abandoned 97 and 50 years ago, the difference from the virgin steppe was smaller than in the more recently abandoned old fields (where there were on average ca. 17–21 species of vascular plants fewer than in the plots in the virgin steppe) (Figure 3a; Table 2). We did not find any significant difference in the species richness of cryptogams between the studied old fields and the virgin steppe (Figure 3a). The share of steppe habitat specialists was significantly lower in all old fields compared with the reference plots, with the exception of the oldest, where we did not find such a difference (Figure 3b). The share of non-native plants was highest in the most recently abandoned old field, with the share of archaeophytes and neophytes on average ca. 23% and 8% higher than in the virgin steppe, respectively (Figure 3b).

Only the most recently abandoned old field had a significantly higher cover of annual plants (on average nearly 70% more) and a lower cover of hemicryptophytes (on average 65% less) than the reference plots (Figure 4). The share of geophytes in cover remained similar in all old fields, and there was no significant difference from the virgin steppe (Figure 4). Chamaephytes were absent in plots located in three old fields: 6, 15 and 31 years old (Figure 4). They occurred in the other old fields, but their cover share was still lower than in the virgin steppe (where it reached ca. 5%) (Appendix S2).

In the old field abandoned for 6 years, plants with shallow root systems had a higher share in total vegetation cover, whereas plants with deep root systems had a lower share than in the reference virgin steppe (Figure 5). Vegetation of this old field also had a significantly lower share of plants with clonal growth (Figure 5), but taller vegetation and higher SLA, seed number, seed mass and long-distance dispersal than the virgin steppe (Figure 5; see also Appendix S2). In most of the other old fields, there were no or much smaller differences from the virgin steppe (Figure 5).

We found significantly lower contents of C_{org} and N_{tot} in the upper soil layers from almost all old fields compared with soils from the virgin steppe; only in the oldest one did we not find such a difference (Figure 6). In general, the younger the old field, the larger the difference in C_{org}, N_{tot} and the C/N ratio in the upper soil layer compared with the virgin steppe (Figure 6).

TABLE 1 Species of vascular plants with the highest indicator values (IndVal) for virgin steppe and old fields of a given age.

	IndVal	*p*-value		IndVal	*p*-value
Virgin steppe			Old field 50 years (continued)		
Tanacetum millefolium	0.788	0.001	Sisymbrium polymorphum	0.435	0.001
Crepis ramosissima	0.551	0.001	Stipa ucrainica	0.395	0.001
Jurinea multiflora	0.499	0.001	Arabidopsis thaliana	0.375	0.006
Cruciata pedemontana	0.486	0.001	Poa angustifolia	0.340	0.009
Iris pumila	0.448	0.001	Old field 31 years		
Achillea micranthoides	0.444	0.001	Bromopsis inermis	0.785	0.001
Linum austriacum	0.388	0.001	Potentilla semilaciniosa	0.435	0.011
Carduus uncinatus	0.360	0.004	Seseli tortuosum	0.325	0.019
Galatella villosa	0.333	0.005	Old field 15 years		
Inula oculus-christi	0.333	0.003	Eryngium campestre	0.657	0.001
Phlomis scythica	0.333	0.003	Goniolimon tataricum	0.386	0.003
Ranunculus scythicus	0.333	0.004	Buglossoides arvensis	0.347	0.003
Valerianella sp.	0.333	0.003	Medicago minima	0.302	0.047
Elisanthe viscosa	0.302	0.007	Leymus ramosus	0.249	0.026
Koeleria cristata	0.279	0.024	Filago arvensis	0.214	0.025
Herniaria besseri	0.263	0.021	Old field 6 years		
Dianthus lanceolatus	0.250	0.023	Anisantha tectorum	0.999	0.001
Phlomis hybrida	0.250	0.020	Centaurea diffusa	0.953	0.001
Bellevalia sarmatica	0.247	0.029	Conyza canadensis	0.916	0.001
Pastinaca clausii	0.220	0.037	Lactuca serriola	0.903	0.001
Old field 97 years			Lamium amplexicaule	0.898	0.001
Galium ruthenicum	0.809	0.001	Capsella bursa-pastoris	0.831	0.001
Salvia nemorosa agg.	0.585	0.001	Vicia villosa	0.806	0.001
Serratula erucifolia	0.562	0.001	Salvia aethiopis	0.793	0.001
Poa bulbosa	0.460	0.005	Viola kitaibeliana	0.685	0.001
Artemisia austriaca	0.439	0.001	Tripleurospermum inodorum	0.658	0.001
Vicia lathyroides	0.400	0.004	Pterotheca sancta	0.577	0.001
Stipa capillata	0.400	0.002	Chenopodium album	0.500	0.001
Veronica verna	0.371	0.005	Convolvulus arvensis	0.496	0.002
Limonium sareptanum	0.359	0.009	Chondrilla juncea	0.423	0.003
Euphorbia leptocaule	0.324	0.023	Cerastium pumilum agg.	0.413	0.006
Scorzonera mollis	0.315	0.001	Elytrigia repens	0.410	0.002
Valerianella carinata	0.244	0.043	Anthemis ruthenica	0.359	0.009
Old field 50 years			Linaria biebersteinii	0.336	0.024
Euphorbia seguieriana	0.770	0.001	Bromus squarrosus	0.333	0.004
Potentilla argentea agg.	0.435	0.002	Galium spurium	0.274	0.022

Note: The indicators were calculated based on vegetation data from 10-m^2 plots in the studied old fields ($n=12$ on each old field) and virgin steppe ($n=12$) in Askania-Nova Biosphere Reserve and its buffer zone. For a full list of species and nomenclature references see Appendix S1.

4 | DISCUSSION

4.1 | Restoration of vegetation characteristics during steppe recovery

The vegetation composition of the studied old fields showed a successional trajectory with increasing similarity to the reference steppe community over time. The overall species composition was successfully restored ca. 50 years after abandonment. In some studies on Hungarian steppes (Csecserits et al., 2007, 2011; Török et al., 2009; Albert et al., 2014) and Ukrainian steppes (Vedenkov, 1997), even a decadal timescale was reported to be sufficient to achieve a state close to a reference steppe. Tyulina (1930), one of the first investigators of Askanian grassland recovery, reported that it takes ca.
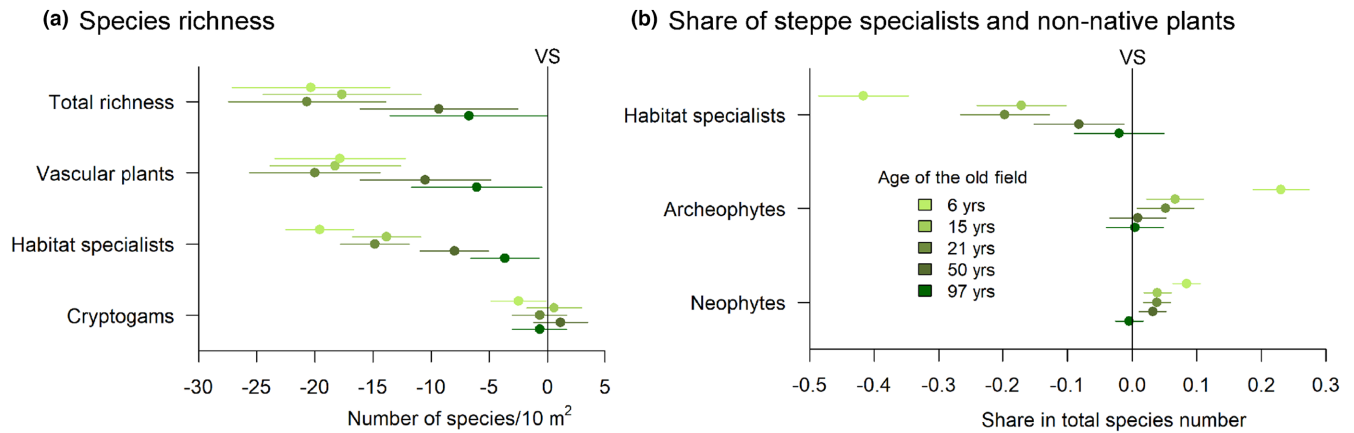
(a) Species richness

(b) Share of steppe specialists and non-native plants

FIGURE 3   Mean differences with 90% confidence intervals of species richness of three taxonomic groups and steppe habitat specialists (a) and share of habitat specialists and non-native vascular plants in total species number (b) between virgin steppe (VS) in Askania-Nova Biosphere Reserve (mean from $n = 12$ plots represented as a vertical line at $x = 0$) and studied old fields ($n = 12$ per each old field).

TABLE 2   Species richness of all species, vascular plants, steppe habitat specialists and cryptograms in 10-m^2 plots in the studied old fields ($n = 12$ on each old field) and virgin steppe ($n = 12$) in Askania-Nova Biosphere Reserve and its buffer zone

		Virgin steppe				Old field 97 years				Old field 50 years			
	n	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Total richness	12	46.42	8.86	31	62	39.67	6.89	29	53	37.08	3.18	32	42
Richness of vascular plants	12	43.17	7.21	31	53	37.08	6.07	26	48	32.67	2.39	29	38
Number of habitat specialists	12	22.00	4.18	14	28	18.33	3.73	12	25	14.00	2.70	10	17
Richness of cryptograms	12	3.25	3.22	0	9	2.58	2.15	0	7	4.42	2.11	0	8

		Old field 31 years				Old field 15 years				Old field 6 years			
	n	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Total richness	12	25.75	6.23	19	38	28.75	6.72	17	40	26.08	3.87	20	33
Richness of vascular plants	12	23.17	4.82	18	33	24.92	5.81	16	35	25.33	3.20	20	31
Number of habitat specialists	12	7.17	1.53	5	10	8.17	1.47	6	11	2.42	1.17	1	4
Richness of cryptograms	12	2.58	2.19	0	6	3.83	1.90	1	7	0.75	1.14	0	3

Note: The years indicate how many years had passed since the field was abandoned.
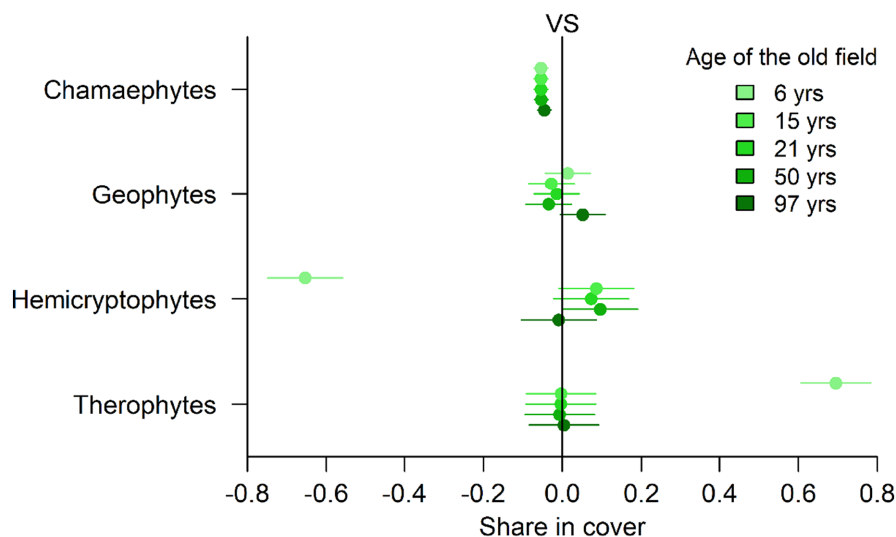

FIGURE 4   Mean differences with 90% confidence intervals of mean cover scores of Raunkiaer's life forms in the total vegetation cover between virgin steppe (VS) in Askania-Nova Biosphere Reserve (mean from $n = 12$ plots represented as a vertical line at $x = 0$) and old fields ($n = 12$ per each old field).
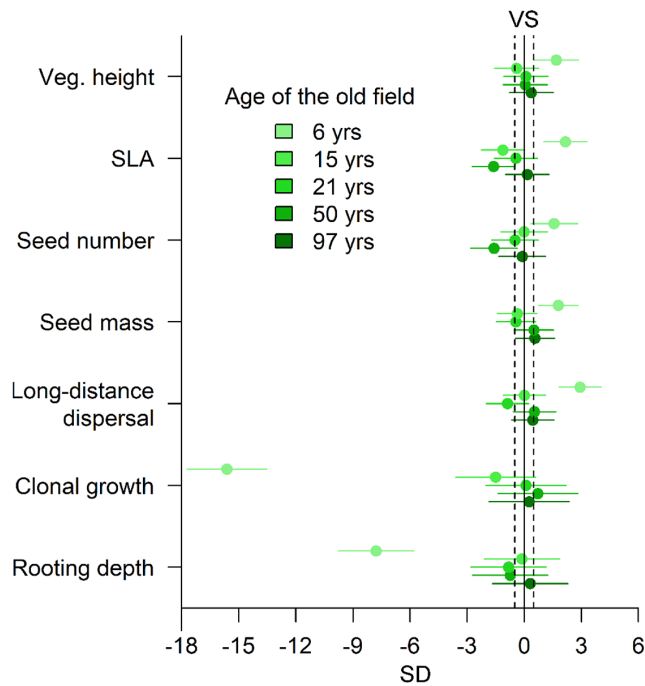
FIGURE 5 Mean differences with 90% confidence intervals (90% CI) of standardized differences in community-weighted mean (or mean cover score for non-metric data) of functional traits between virgin steppe (VS) in Askania-Nova Biosphere Reserve (mean from $n=12$ plots represented as a vertical line at $x=0$; CIs as dashed lines) and old fields ($n=12$ per each old field). Veg. height: vegetative height; SLA: specific leaf area; long-distance dispersal: the ability of diaspores to disperse over long distances

FIGURE 6 Means and 90% confidence intervals (90% CI) of standardized difference in chemical properties of soil between virgin steppe (VS) in Askania-Nova Biosphere Reserve (mean from $n=12$ plots represented as a solid line at $x=0$; CIs as dashed lines) and old fields ($n=12$ per each old field).

30–40 years to develop steppe vegetation with a dominance of *Stipa* spp. However, this result did not indicate overall species composition recovery. Shalyt (1930) observed that the process of recovery of steppe vegetation on old fields takes ca. 60–70 years. He proposed to divide the process into four phases: (a) weeds typical of arable fields (first year after abandonment); (b) spreading grasses (mostly *Leymus ramosus*, 2–3 years after abandonment); (c) encroachment of clumping grasses (*Festuca* ssp., *Stipa* ssp.) ca. 22–24 years after abandonment; and (d) fully recovered steppe ("secondary virgin steppe") after 60–70 years.

Our results show that the major change in vegetation composition occurred during the first decade, after which succession slowed (as indicated on the DCA plot). This may be explained by the stabilization of dominance between species groups (Myster & Pickett, 1994; Foster & Tilman, 2000), increasing resistance of communities to colonization because of more complete resource utilization (Sperry et al., 2019) or decreasing availability of microsites to establish (Harper, 1977), as well as certain interspecific (e.g. allelopathic) interactions (Foster & Tilman, 2000).

As expected, the vast majority of species indicative of the virgin steppe were steppe habitat specialists, whereas generalist species (including some archaeophytes and neophytes) were strong indicators for the most recently abandoned old fields. The lower number of indicator species for the int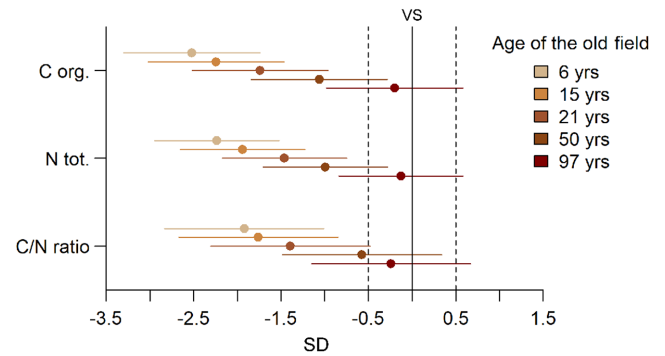ermediate stages of succession can be explained by the overlap of species from early and late succession stages. Interestingly, some target steppe species of tumbleweed strategy appeared to be good indicator species for the "intermediate" stages, namely *Goniolimon tataricum*, *Eryngium campestre* (both 15 years after abandonment) and *Seseli tortuosum* (31 years after abandonment). This indicates the high colonizing potential of tumbleweeds in the studied landscape, but not on recently abandoned old fields.

Species richness increased throughout the studied chronosequence and reached a level very close to the virgin steppe after almost 100 years. Remarkably, the species richness of the studied old-field succession did not follow the classic hump-backed model with maximum diversity at intermediate stages (Grime, 1973), although several studies on grassland recovery have confirmed such a pattern, e.g. Sun et al. (2017) and Chen et al. (2014) on the Loess Plateau in China. This unimodal relationship of species richness over time assumes low species diversity during the early stages of succession, when only pioneer plants colonize the area after disturbance; increasing species diversity in intermediate stages when mid-successional species arrive; and a decrease of species diversity in late stages due to competitive exclusion (Sun et al., 2017) or changing environmental conditions (Pickett, 1982). In our study, high species richness in late successional stages can be supported by occasional disturbances, i.e. mowing and fires that occurred in all of our transects. Mowing with hay removal together with fires counteracted litter accumulation and hindered the exclusion of less-competitive species (Kelemen et al., 2013), particularly in the absence of large steppe ungulates (Cingolani et al., 2014).

The share of habitat specialist species in the oldest abandoned field was very close to the target community, which indicates a highly satisfactory recovery effect after nearly a century. Seeds of dry grassland specialists usually persist in the seed bank only for a short time (Bekker, 1998). Thus, the more probable source of target species in studied transects are propagules immigrating there from other steppe patches. According to Cousins and Lindborg (2008), grassland specialists disperse more slowly and in a stepwise manner

compared with generalist species. However, diaspores of grassland plants are known to attach to mowing machinery (Auffret & Cousins, 2013), which could enhance their spread from the virgin steppe to the old fields that have been incorporated into nature reserve borders and are thus managed by the same authorities.

Non-native species were particularly abundant in the most recently abandoned old fields, with their share of total richness declining gradually in the studied chronosequence. Because most of the archaeophytes and neophytes in the studied area are annual or biennial plants, their presence is strongly related to both the former management of arable fields and disturbance. Therophytes prevailed in cover in the early phase of succession, being gradually replaced by perennial herbs and grasses. Annual species easily colonized fields soon after abandonment, because they were present in the vegetation of former and adjacent arable fields, as well as in the seed bank (Bekker et al., 1998). These species are usually characterized by high seed production and fast growth (Coomes & Grubb, 2003). Nevertheless, their share decreased quickly during the course of succession, mainly because of the sensitivity of annual species to competition from perennial plants (Fenner, 1978). Still, early dominant annual species were not completely excluded, and some alien weeds remaining after cultivation or penetrating from neighbouring agrocoenoses were still present even in the oldest abandoned fields. This sequence is consistent with other observations from Eurasian steppes (Drohobych & Vedenkov, 1993; Vedenkov, 1997; Feng et al., 2007) and forest steppes (Csecserits et al., 2007; Török et al., 2009; Albert et al., 2014), as well as North American prairies (Bomberger et al., 1983; Samuel & Hart, 1994; Sinclair & Weiss, 2010). Interestingly, the share of chamaephytes did not fully recover in any of the old fields. Chamaephytes usually have relatively small cover in the grass steppe of southern Ukraine, but many of them are rare and endangered species, e.g. *Astragalus corniculatus* and *Jurinea multiflora*, both of which occurred in our plots. Such results can indicate potential problems with their propagule dispersal or seedling establishment in formerly ploughed land. Additional studies on this issue are needed to develop proper restoration methods for steppe species belonging to this group.

Regarding other functional characteristics, only a decade was needed to develop high shares of clonal species and plants with deep root systems (because of the high abundance of species like *Leymus ramosus*, *Goniolimon tataricum* and *Falcaria vulgaris* in the 15 years old field), which are typical for a virgin steppe. At the same time, environmental filtering also had a negative impact on both the vegetative height and SLA of recovering vegetation. This may imply that only a decade after abandonment, the community becomes more resistant to drought. Traits related to diaspore dispersal also showed strong filtering at early stages of succession; only the vegetation of the most recently abandoned old field was characterized by a higher share of plants with large seed number, higher seed mass and long-distance dispersal abilities compared with the vegetation of a reference steppe. Large seed number and diaspore adaptations to long-distance dispersal are typical traits of pioneer species, so we expected that such species would prevail in the community in the first years after abandonment. However, most of the pioneer species are dispersed by wind and have low seed mass. Thus, the higher share of plants with high seed mass can be better explained by other groups typical of recently abandoned old fields: arable weeds and ruderal plants that often produce relatively large seeds exhibiting high longevity in a soil seed bank (Fried et al., 2021), e.g. *Vicia villosa*, *Convolvulus arvensis*, *Centaurea diffusa* and *Anisantha tectorum*.

To summarize, we found that basic functional characteristics of the Pontic steppe in Askania-Nova regenerated in a decadal timescale, thus much faster than composition and diversity indices. Similar findings were reported by Tölgyesi et al. (2019) on 20-year-old restored grasslands in a forest–steppe in Hungary. Observations of relatively fast "superficial recovery" of temperate grasslands have also been reported from the North American prairies, which are analogues of the Eurasian steppes. Weaver and Flory (1934) stated that "the area may appear like prairie" after a decade, but the re-establishment of former interrelations between vegetation and soil tends to require much longer. Forty years have been reported as necessary for recovery from abandoned cropland to prairie in Oklahoma and Kansas (Sinclair & Weiss, 2010) but even after 40 years of succession in the tallgrass prairie of Nebraska (Bomberger et al., 1983) or mixed-grass prairie in Wyoming (Samuel & Hart, 1994), the plant community composition of old fields was still significantly different from that of the adjacent undisturbed vegetation.

4.2 | Soil carbon and nitrogen content in the old-field chronosequence

We noticed increasing soil organic carbon content over time in the topsoil of the old fields. Post-agricultural steppe soils have the potential for carbon sequestration, whereas persisting cultivation causes significant soil organic carbon losses (Guo & Gifford, 2002; Wang et al., 2009). The Haplic Kastanozems with a high clay fraction (up to 20%) and slightly acidic to neutral pH (6.1–7.3; Appendix S4) create favourable conditions for the microbial decomposition of organic residues and accumulation of organic substances, probably through the creation of stable organo-mineral complexes (Pozniak, 2019). Cessation of ploughing and the disappearance of related excessive soil aeration limit the mineralization processes of organic matter and contribute to organic carbon sequestration (Pozniak, 2019).

We detected signs of soil recovery reflected in nitrogen levels in the upper soil layer of the oldest abandoned fields very close to the reference state. Increased soil nitrogen content was also found by Feng et al. (2007) in an old-field succession chronosequence of regenerated grasslands on the Loess Plateau in China, and by Kalinina et al. (2011) in grasslands of the forest–steppe region in Russia. Kalinina et al. (2011) found a constant C to N ratio along the studied chronosequence. In our study, we detected a trend of increasing C to N ratio in topsoil samples. Such a trend is rather typical during succession and can be explained by faster accumulation of carbon than nitrogen due to changes in microbial processes, as shown in the meta-analysis by Zhou et al. (2017). Moreover, the revegetation of former agricultural soils and the appearance of steppe grasses with a long vascular root system (also confirmed in our study) causes an

increase in plant residues, resulting in higher organic carbon content in the soil (Kell, 2011; Karelin et al., 2015). Thus, one may assume that the old fields dominated by typical steppe plants can be regarded as reaching carbon sequestration potential comparable with a virgin steppe (see also Karelin et al., 2015), which can be further enhanced in later successional stages by increasing the species richness of grassland plants (Yang et al., 2019). However, our correlative results on vegetation recovery in old fields and their topsoil organic carbon and nitrogen content should be treated with caution because of a lack of information about the physical and chemical characteristics of these soils from the time of their agricultural use (as such data are not available for the studied sites), and limited knowledge on the long-term alterations to ecological and geochemical soil processes in the area. Thus, our interpretation of the results is based on a trend analysis of parameters in the upper soil layer, and we could not clearly indicate how the intensity and duration of agricultural use before abandonment influenced the studied soil parameters.

5 | CONCLUSIONS

Our results demonstrated that it is possible to achieve some functional characteristics close to a zonal grass steppe within a decadal timescale. Yet, more time is needed to achieve the species composition, species richness and shares of ecological groups of the target steppe community. It seems that a century-scale is needed to develop vegetation close to that of the Pontic grass steppe.

Spontaneous succession on former arable fields can lead to restoration of the original steppe ecosystem, but probably only if there is preserved habitat in the surroundings (as a source of diaspores; Albert et al., 2014; see also Molnar & Botta-Dukat, 1998), low risk of invasion by ecosystem engineering neophytes (Wilson, 1989) and if some sporadic disturbances (like fires and mowing in this study) reduce the accumulation of above-ground biomass and litter, and can facilitate the establishment of specialist target species (see also Tölgyesi et al., 2022). Thus, we conclude that passive recovery is a promising choice in areas with high availability of target species propagules when no rapid results are expected.

AUTHOR CONTRIBUTIONS

ID and MZ conceived the research concept with the support of IM and VS; ID, IM, VS, MZ and BS-W collected data in the field; BS performed laboratory analyses of the soil samples; NZ determined cryptogams; ID performed statistical analyses; VS and ID prepared the map; DV and AD collected the data on the functional characteristics of plants; HS thoroughly revised the text linguistically; ID led manuscript preparation with contributions from all authors.

DATA AVAILABILITY STATEMENT

All data subject to analyses in the study are available in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of all vascular plant and bryophyte species found within 10-m^2 plots, and the assignment to groups analysed in the study.

Appendix S2. Analysed plot characteristics data.

Appendix S3. Analysed vegetation composition data.

Appendix S4. Summary statistics of soil data.

Appendix S5. References of the individual sources of trait data.