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RESEARCH ARTICLE

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The Eurasian crane (*Grus grus*) as an ecosystem engineer in grasslands: Conservation values, ecosystem services, and disservices related to a large iconic bird species

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Abstract

Large bird species, such as cranes are involved in human-wildlife conflicts as they often forage in croplands. The Eurasian crane (*Grus grus*) is a large bird species, protected across Europe, which, thanks to conservation programmes and its ability to utilise croplands for foraging, shows a strongly increasing population trend. This exaggerates the existing conflicts between crop farmers and cranes and is spilling over to natural habitats, where foraging by large flocks can lead to land degradation. No studies have evaluated the effects of foraging cranes on grasslands, despite the fact that these habitats provide important feeding grounds for cranes across their whole range. To fill this knowledge gap, we evaluated the ecosystem engineering effect of foraging Eurasian cranes on the vegetation of dry grasslands in Hungary. We used indicators of vegetation naturalness, forage quality, and floral resource provision to evaluate the ecosystem state from multiple aspects. We sampled 100 quadrats in disturbed patches and 100 in undisturbed grasslands in two seasons and 2 years (800 observations). Cranes created distinct vegetation patches with different species composition from undisturbed areas. We identified important trade-offs between the positive and negative effects of the foraging activity of cranes on different structural and functional components of the ecosystems. The crane-disturbed early-successional patches increased plant diversity and floral resources but decreased the area of undisturbed grasslands. Although crane-disturbed patches could provide forage for livestock early in the season, the forage quality became poor later in the year. We highlight the importance of monitoring the landscape-level extent of the disturbed areas.

KEYWORDS

alkaline grassland, biopedturbation, forage quality, Gruidae, land degradation

1 | INTRODUCTION

Ecosystem engineer organisms create, alter, or maintain environmental conditions in a way that can considerably affect other organisms (Jones et al., 1994). The effect of engineer species varies across spatial scales (Coggan et al., 2018), from local microhabitat creation (e.g., several burrowing vertebrates create distinct microhabitat patches that provide shelter for other animals or establishment microsites for plants) to landscape-scale habitat alteration (e.g., beavers alter landscape-scape habitat structure and water flow that affect a wide range of species). Engineer animals mediate vegetation composition and dynamics through several mechanisms, including soil formation and affecting soil characteristics due to their metabolism (Clyde et al., 2021; Mallen-Cooper et al., 2019; Mosbech et al., 2018), forming establishment microsites through biopedturbation (Cavin & Butler, 2015; Davidson et al., 2012) or affecting seed dispersal and seedling establishment by scatter-hoarding (Godó et al., 2022; Pesendorfer et al., 2016).

Most studies on vertebrate engineers focus on mammals in general and rodents in particular (Mallen-Cooper et al., 2019). However, ecosystem engineering is also exemplified by charismatic birds, such as soil and sediment formation by seabirds or ducks on oceanic islands (Clyde et al., 2021; Mosbech et al., 2018), supporting forest recovery by scatter-hoarding corvids (Pesendorfer et al., 2016) or intentionally modifying fire regimes by raptors in Australia (Bonta et al., 2017). Ecosystem alteration by soil disturbance is rarely documented among birds and 96% of the studies on biopedturbation focus on mammals (Mallen-Cooper et al., 2019). Among birds, there are a few examples of burrow-nesting species, such as owls in deserts (Rengifo-Faiffer & Arana, 2019) or seabirds on oceanic islands (McKechnie, 2006) that are known to affect local habitat conditions by biopedturbation during the construction and use of burrow systems. The burrow systems of birds and mammals are usually permanent landscape features as they are inhabited by successive generations of animals (Whitford & Kay, 1999). These landscape features are often characterised by a unique vegetation. The structure and species composition of the vegetation developed on burrows are often distinct from the surrounding matrix, due to the continuous and concentrated trampling and nutrient input by the burrow dwellers (Valkó et al., 2021). Burrow networks can introduce a high level of environmental heterogeneity and biodiversity to the landscape (Cavin & Butler, 2015; Davidson et al., 2012; Valkó et al., 2021).

Ecosystem engineering during foraging might also be a relevant process in large-bodied birds inhabiting open landscapes, especially during migration when they forage in large flocks. Disturbed patches at foraging sites are probably less persistent as these areas are used only temporarily, but as large areas are affected worldwide this process might act as an important factor influencing habitat conditions in certain ecosystems. Despite the potential relevance of this process, we are not aware of any studies on the effect of foraging birds on the species composition, structure or environmental conditions of natural habitats.

Ecosystem engineer animals are often involved in human–wildlife conflicts and face negative public attitudes. Their effects are often disputed as from the agricultural viewpoint they are often considered as pests but from the conservation viewpoint they are important keystone species. For example, the burrowing activity of the plateau pika (*Ochotona curzoniae*) provides a critical ecosystem service by increasing the infiltration rate of water, hence reducing overland flow at the Quinghai-Tibetean Plateau (Wilson & Smith, 2015). Still, because the burrowing activity can decrease the quality of the pasture, rangeland managers considered pikas as pests and initiated mass poisoning campaigns that had serious negative impacts on regional-scale hydrological functioning. As shown by the above example, maintenance of the integrity of essential ecosystem functions requires the gathering of evidence and informing the decision makers about the full spectrum of impacts, ecosystem services and disservices provided by engineering species. This might contribute to avoiding the damage to these important species and many others that depend on them. This is especially important given the conservation importance and threatened status of many ecosystem engineer species (Davidson et al., 2012). Their global decline goes beyond the loss of certain species and involves several cascading effects on ecosystem structure and functionality.

Large bird species, such as the majority of the 15 crane species of the world are involved in human–wildlife conflicts as they often forage in croplands, even though they mainly feed on crop residue (Austin et al., 2018). König et al. (2021) investigated the ecosystem services and disservices of four iconic animal species, one of them being the Eurasian crane (*Grus grus*). They found that the negative effects associated with crane presence were the moderate decrease of yield on croplands and increased labour and prevention costs that act at short term and local scales, affecting mostly private farmers. In contrast, several positive effects were found which were associated with cranes, as these iconic birds can support tourism, quality of life, cultural identity; and these middle- and long-term positive effects go beyond the local scale. Since different stakeholders experience the negative and positive effects, the effective conservation of cranes should include the compensation of those stakeholders (i.e., farmers) who are affected by the negative effects. The growing populations of the world's two most abundant cranes—the sandhill (*Antigone canadensis*) and the Eurasian cranes—are associated with their ability to make use of the expansion of intensive agriculture by opportunistic foraging on croplands (Harris & Mirande, 2013; König et al., 2021). In the Eurasian crane, the positive population trend was also supported both by large-scale wetland conservation and restoration programmes and targeted management of safe roosting sites near large wetlands along the western flyway (Leito et al., 2015). By the designation of the Natura 2000 Special Areas of Conservation, the overall persecution pressure on cranes had considerably decreased. Milder winters further increase survival rates by shortening the migration routes (Nilsson et al., 2016). The growing abundance of these two crane species will probably further intensify the conflicts between cranes and farmers. There is a chance that these conflicts can spill over to natural habitats, where foraging by large flocks might lead to land degradation. The tendency to use technology that reduces crop residue might affect the habitat selection of cranes and might impose larger pressure on other habitat types including grasslands in the future (Nevard et al., 2018). In grasslands, farmer–wildlife conflicts and conflicts within the conservation sector can both occur if the intense disturbance by cranes decreases forage quality for livestock grazing or naturalness of the vegetation.

Crane species foraging in grasslands occur in many parts of the world (Austin et al., 2018); for instance, the sandhill crane in North-America, the Eurasian crane and the demoiselle crane (*Anthropoides*

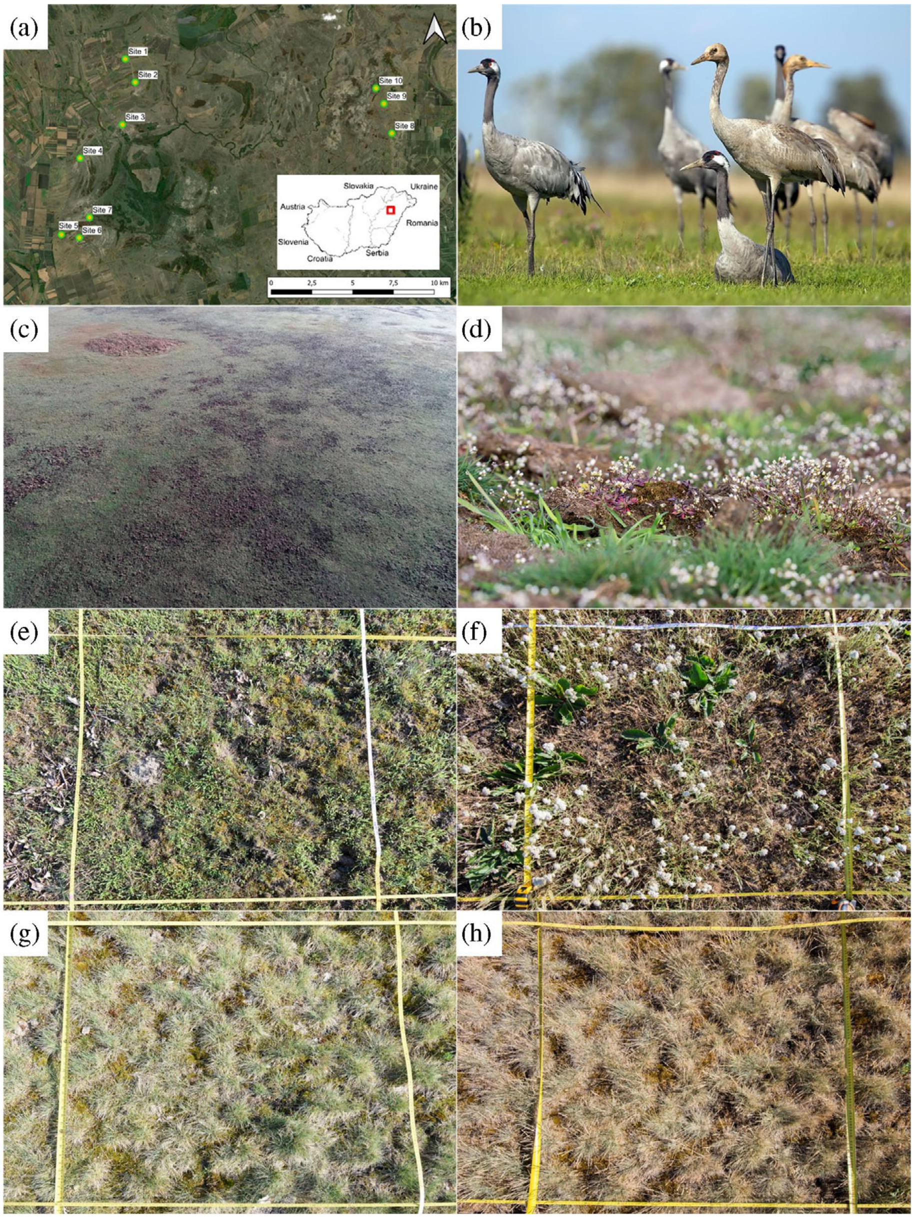

FIGURE 1 (a) Location of the study sites, (b) Eurasian cranes, (c) Grassland disturbed by cranes from the bird-eye's view, (d) Early successional vegetation with the dominance of *Erophila verna* on a disturbed patch; (e) Vegetation of a crane-disturbed quadrat in April 2021; (f) Vegetation of the same quadrat in June 2021; (g) Vegetation of an undisturbed grassland quadrat in April 2021; (h) Vegetation of the same quadrat in June 2021. Photos were taken by Attila Szilágyi (b), Sándor Borza (c) and Laura Godó (d–h). [Colour figure can be viewed at wileyonlinelibrary.com]

virgo) in many parts of Eurasia, the black-necked crane (*Grus nigricollis*) in Tibet and the blue crane (*Anthropoides paradiseus*) in South Africa. Grazed grasslands provide suitable feeding grounds for cranes because livestock grazing recycles nutrients, keeps the landscape open, and supports large quantities of invertebrate food resources (Austin et al., 2018). Foraging crane flocks might have a considerable impact on grassland vegetation, although no studies have evaluated their effects in grasslands.

The aim of our study was to evaluate the effect of foraging Eurasian cranes on dry grassland vegetation. We used indicators of vegetation naturalness, forage quality for livestock grazing, and floral resource provision to evaluate the ecosystem state from multiple aspects. We specifically asked the following questions: (i) Do the species composition and structure of the vegetation in grasslands used as forage sites for cranes differ from undisturbed grasslands? (ii) Which plant functional groups are supported and suppressed by the foraging cranes? (iii) Does foraging by cranes affect forage quality and floral resources? The main objectives of this study were to evaluate the ecosystem engineering effect of foraging Eurasian cranes on the vegetation composition, plant diversity, naturalness, forage quality and flower resource provision of dry grasslands. Our study can contribute to the understanding of the ecosystem services and disservices provided by a large iconic bird species in grasslands. The results can be relevant not only for the Eurasian crane but also for the other crane species.

2 | MATERIALS AND METHODS

2.1 | Study system

The study sites are located in the Hortobágy National Park, East Hungary (Figure 1). Hortobágy is one of the largest continuous open landscapes in Europe where alkaline grasslands cover approximately 80,000 ha. The climate is temperate continental, with a mean annual temperature of 9.5°C and mean annual precipitation of 550 mm (Fick & Hijmans, 2017). The soil reference group of the study area is classified as Vertic Solonetz, characterised by high salt content (IUSS Working Group, 2015). Hortobágy is a lowland plain area, the elevation ranges between 87 and 110 m above sea level. The landscape is characterised by a high diversity of dry grassland, wet meadow and marsh habitats as well as a small amount of croplands. Alkaline grasslands, meadows and marshes are included in the Annex I of the Habitats Directive (92/43/EEC) as ‘Pannonic salt steppes and salt marshes (1530)’, a priority habitat type of the European Union. The most widespread dry grassland type is *Achilleo setaceae–Festucetum pseudovinae*, which are short, dry grasslands that occur on moderately alkaline soil and are managed by extensive grazing. The dominant grass species covering 50–80% of the vegetation is *Festuca pseudovina*, characteristic forb species include *Achillea collina*, *A. setacea*, *Plantago lanceolata*, *Podospermum canum* and *Trifolium* spp. (Deák et al., 2014).

The Eurasian crane is a large-bodied bird species with a Palaearctic distribution. Its global population is currently strongly increasing and estimated as approximately 500,000 individuals (Wetlands International, 2015). It is a protected species in Hungary and across the European Union, being a bird of community interest and listed in the Annex I of the Birds Directive (2009/147/EC). Hortobágy is the largest stopover area on the Baltic-Hungarian Flyway, connecting the eastern part of Scandinavia, western Russia, the Baltic states and Tunisia, crossing Poland, Hungary and the Balkan Peninsula. During autumn migration, the highest crane numbers can be observed between mid-September and late November in Hungary. Since 2000, the total number of cranes found simultaneously roosting at the Hortobágy National Park has exceeded 150,000 individuals several times and averaged over 130,000 birds (database of the Hortobágy National Park Directorate). The peak number of cranes recorded at the Hortobágy National Park were 158,740 in the autumn 2019 and 95,400 in 2020 (www.hnp.hu).

While staying in the Hortobágy, the cranes spend most part of daytime foraging in croplands, especially in maize stubbles, whereas they occasionally also utilise grasslands as feeding habitats (Végvári, 2002). They spend the nights on fishponds where they are more protected from predators. In grasslands, cranes display a special feeding habit that is called as ‘crane-ploughing’. This means that the birds search for invertebrates in the grasslands (Anteau et al., 2011) and during this activity they remove the vegetation and heavily disturb the soil surface (usually the upper 1–2 cm) using their bills. The disturbed soil surface resembles a ploughed area (Figure 1). The area of the disturbed patches typically ranges between 10 and 100 m^2, but occasionally, larger ploughed areas also occur.

2.2 | Study sites and sampling

We designated 10 study sites in October 2019 when disturbed patches created by the foraging cranes are the most apparent on the sites. We used the following criteria for site selection: (1) the sites were situated at least 1 km from each other, (2) the sites were characterised by dry alkaline grassland vegetation (*Achilleo setaceae–Festucetum pseudovinae*); (3) all the sites were managed by extensive grazing, (4) within each site vegetation patches disturbed by cranes as well as undisturbed areas occurred within a distance of 0.5 km in alkaline dry grasslands and (5) the disturbed and undisturbed areas were at least 50 m^2 large.

Within each site we designated two 30 m^2-sized permanent plots; one in disturbed area and one in undisturbed grassland. In October 2020 we re-visited all the sites to record whether the areas disturbed in 2019 were disturbed again in 2020 and whether the areas undisturbed in 2019 remained undisturbed also in 2020. In each plot, we designated ten 1 m × 1 m sized quadrats, which were precisely marked with metal sticks placed underground so we could precisely re-visit the quadrats with the help of a metal detector. In total there were 100 disturbed and 100 undisturbed quadrats. We have chosen the mentioned plot and quadrat sizes because (i) we aimed to choose a size that fits to the average size of the ploughed areas, and (ii) we aimed to study fine-scale vegetation composition. Thus, we optimised our sampling strategy toward large number of small quadrats, rather than sampling more plots with fewer quadrats.

We recorded the species list and percentage cover of vascular plant species in each quadrat at four sampling dates: early April 2020, mid-June 2020, early April 2021 and mid-June 2021. This resulted in 800 observations in total. Nomenclature of vascular plants followed the work of Király (2009). We also recorded the total cover of vascular plants and that of cryptogams (i.e., the summed cover of mosses, lichens and *Nostoc* cyanobacteria).

2.3 | Data analysis

We assigned the recorded vascular plant species to four morphological groups: short-lived forbs, short-lived graminoids, perennial forbs and perennial graminoids. The full list of the recorded species and their assignment to morphological groups are provided in Appendix S1.

We used two proxies for conservation values: Shannon diversity and naturalness score. We calculated the Shannon diversity of the vascular plant species in each plot. For expressing the naturalness of the vegetation, we classified the recorded plant species into Social Behaviour Types (SBT) according to the classification system of Borhidi (1995). The classification system assigns a naturalness value to each SBT category, ranging from −3 (AC—adventive competitors) to +10 (Su—unique specialist species). We calculated cover-weighted naturalness scores for all plots.

We used two proxies of forage quality for livestock grazing: forage quality index based on a Hungarian classification system (Balázs, 1949) that takes multiple palatability criteria into account and specific leaf area (SLA), which is a proxy for hydrated and more attractive leaves. We classified the species according to their forage quality based on the classification system of Balázs (1949). Forage quality scores range from −3 (toxic plants) to +8 (highly valuable forage plants). The average of the reported SLA values was derived from a regional database (Vojtkó et al., 2020) and for the species not represented in the regional database, the LEDA database (Kleyer et al., 2008) was used. We calculated cover-weighted forage quality and SLA scores for all plots.

We characterised the availability of floral resources with two proxies: flowering period and the cover of insect-pollinated species. Flowering period was calculated as the number of months when a species is flowering using the work of Király (2009). We calculated the community-weighted means (CWM) of flowering period for all plots.

We used generalised linear mixed models (GLMMs) for testing the effect of disturbance (two levels: disturbed patches, undisturbed grasslands; fixed predictor), and season (two levels: spring, summer; fixed predictor) of the R statistical programming environment (R Core Team, 2021), using the R-packages 'lme4' and 'lmerTest' (Bates et al., 2015; Kuznetsova et al., 2017). Dependent variables were: total vegetation cover, cryptogam cover, perennial forb cover, perennial graminoid cover, short-lived forb cover, short-lived graminoid cover, Shannon diversity, naturalness score, forage quality score, CWM of specific leaf area, CWM of flowering period and the cover of insect-pollinated plants. Site ID and sampling year were included as random factor. As in linear mixed models the appropriate denominator degree is ambiguous (Burnham & Anderson, 2002), the 'lme4' package designed to fit linear mixed models intentionally omits *p*-values from model summaries and provide *t*-values instead. Accordingly, absolute values of the *t*-statistics larger than 2.0 indicate 'significant' relationships, which are analogous to $p < 0.05$ for balanced data (Bates et al., 2015).

To assess the species composition of the vegetation in the disturbed patches and undisturbed grasslands across the two study years and two seasons, non-metric multidimensional scaling (NMDS) based on percentage cover of the species was calculated using CANOCO 5.0 program (ter Braak & Šmilauer, 2012). For the multivariate analysis, quadrats from the same plot, season and year were averaged.

To investigate if plant abundances differed among (i) disturbance types (disturbed patches vs. undisturbed grasslands), (ii) years (2020 vs. 2021) and (iii) seasons (spring vs. summer), we applied permutational analysis of variance (PERMANOVA). To do so, first we calculated a continuous distance matrix using the raw abundance records of each of the 68 plant species, considering Bray–Curtis distance coefficients. In the following step, we fitted six PERMANOVA tests treating types, years and seasons as well as their interactions as grouping factors in comparison with abundance distances, employing the PERMANOVA function available in the 'PERMANOVA' package (Vicente-Gonzalez & Vicente-Villardon, 2021) in R.

We carried out an indicator species analysis to identify species characteristic of the crane-disturbed patches and the undisturbed grasslands (Dufrêne & Legendre, 1997). For the analyses, we used the 'IABabdsv' package in R.

TABLE 1 Results of indicator species analyses for the species of the crane-disturbed patches and undisturbed grasslands

	Indicator value	*p* value
Species characteristic of crane-disturbed patches		
Achillea setacea	0.312	0.001
Bromus hordeaceus	0.813	0.001
Cerastium brachypetalum	0.946	0.001
Erophila verna	0.709	0.001
Hordeum hystrix	0.308	0.001
Koeleria cristata	0.265	0.001
Matricaria chamomilla	0.428	0.004
Myosotis stricta	0.377	0.001
Ornithogalum kochii	0.328	0.001
Polygonum aviculare	0.827	0.001
Potentilla argentea	0.250	0.002
Scleranthus annuus	0.543	0.001
Spergularia rubra	0.234	0.021
Stellaria graminea	0.334	0.001
Ventenata dubia	0.505	0.001
Veronica verna	0.436	0.001
Species characteristic of undisturbed grassland		
Cardaria draba	0.223	0.003
Carex praecox	0.300	0.001
Carex stenophylla	0.648	0.001
Elymus repens	0.681	0.001
Inula britannica	0.497	0.001
Lotus corniculatus	0.535	0.001
Poa angustifolia	0.203	0.034

3 | RESULTS

3.1 | Species composition

In total we recorded 68 vascular plant species, out of which 62 species occurred in the disturbed patches and 57 in the undisturbed grasslands. We found in total 16 characteristic species in the crane-disturbed patches and 7 in the undisturbed grassland (Table 1). Characteristic species of the disturbed patches included early-successional short-lived forb (*Erophila verna*, *Myosotis stricta* and *Polygonum aviculare*) and graminoid (*Bromus hordeaceus* and *Hordeum hystrix*) species, and a few disturbance-tolerant perennial forbs, such as *Achillea setacea* and *Ornithogalum kochii*. Undisturbed grasslands were characterised by perennial graminoids (*Carex stenophylla*, *Elymus repens* and *Poa angustifolia*) and forbs (*Inula britannica*, *Lotus corniculatus*, Table 1). Species composition of the disturbed patches and undisturbed grasslands were separated along the horizontal axis of the NMDS ordination (Figure 2). We observed a separation between spring and summer vegetation in the crane-disturbed plots, while the species composition of undisturbed grasslands was similar

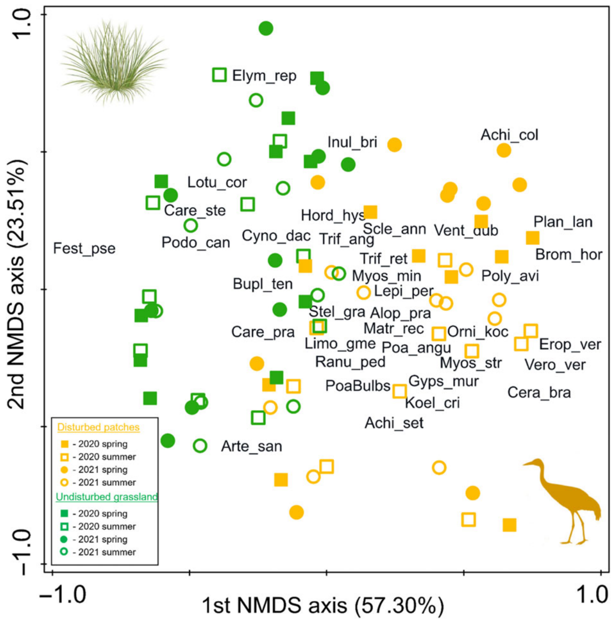

FIGURE 2 Non-metric multidimensional scaling (NMDS) of disturbed patches and undisturbed grasslands in the two study years and two seasons. Notations: Yellow symbols—Disturbed patches; green symbols—Undisturbed grassland; squares—Year 2020, circles—Year 2021; empty symbols—Spring; full symbols—Summer. Species names are abbreviated by using the first four letters of the genus and first three letters of the species names (for the full list, please see Appendix S1). Eigenvalues for the first and second axis were 0.573 and 0.235. Percentage of variance explained by the first and second axis were 57.30% and 23.51%, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

across seasons. There was no clear separation in the vegetation between the 2 years.

The PERMANOVA analysis confirmed the patterns of the ordination. The species composition of the disturbed patches and the undisturbed grasslands was significantly different ($F = 40.11$, $p = 0.048$). The vegetation was different between the two seasons ($F = 2.62$, $p = 0.001$) but there was no separation among years ($F = 1.69$, $p = 0.131$). The interaction of disturbance × year ($F = 14.52$, $p = 0.001$) and disturbance × season ($F = 15.52$, $p = 0.001$) resulted in significantly different species compositions, while year × season interaction ($F = 1.61$, $p = 0.101$) had no effect on vegetation composition.

3.2 | Plant functional groups, conservation values and ecosystem services

All the plots disturbed in 2019 were disturbed again in 2020, while all plots undisturbed in 2019 remained undisturbed also in 2020. The effect of disturbance was significant on all the studied parameters (Table 2). Total vegetation cover, cryptogam cover and the cover of perennial graminoids were smaller in the disturbed plots than in the undisturbed grasslands, while perennial forbs, short-lived forbs and short-lived graminoids were more abundant in the disturbed patches (Figure 3a–f). The disturbed patches were characterised by larger Shannon diversity (Figure 4a) and smaller naturalness score (Figure 4b) than the undisturbed grasslands. Forage quality (Figure 4c) decreased and specific leaf area (Figure 4d) increased as a result of the disturbance. Plant species tended to have longer flowering period in the disturbed patches (Figure 4e). The cover of insect-pollinated plants was larger in the disturbed patches compared with the undisturbed grasslands (Figure 4f). Total vegetation cover as well as the cover of perennial forbs, perennial graminoids and short-lived forbs increased from spring to summer, while the cover of cryptogams decreased. Shannon diversity increased but naturalness score declined with the progression of the vegetation period. From spring to summer, CWMs of specific leaf area decreased, while flowering period became longer and the cover of insect-pollinated plants increased (Table 2).

4 | DISCUSSION

4.1 | Vegetation composition of crane-disturbed versus undisturbed patches

We found that foraging cranes created vegetation patches with different vegetation structure and species composition compared with undisturbed stands of dry alkaline grasslands (Figure 2). The disturbed patches were characterised by sparse vegetation with small cover of vascular plants and cryptogams. The cover of perennial graminoids decreased, while that of perennial forbs and short-lived graminoids and forbs increased as a result of crane disturbance (Table 2, Figure 3). The availability of open microsites and the low cover of competitor perennial graminoid species probably supported the germination of several plant species which resulted in larger plant diversity in disturbed areas compared with undisturbed grassland (Deák et al., 2011). Similar patterns were found in Peruvian deserts where avian biopedturbations by burrow-nesting birds created more favourable areas for seedling establishment compared with undisturbed patches (Rengifo-Faiffer & Arana, 2019).

In their meta-analysis Romero et al. (2015) showed that the overall effect of ecosystem engineers on diversity is positive and corresponds to a 25% increase in species richness, indicating that ecosystem engineering is a facilitative process globally. We detected a significant, approximately two-fold increase in plant diversity in the crane-disturbed plots compared with undisturbed grasslands (Table 2, Figure 3). This is particularly interesting, as such strong effect of engineer species has not been found for foraging bird species before and engineer effect was reported to be weaker at latitudes higher than 23° (Romero et al., 2015).

The species composition of disturbed and undisturbed areas was clearly separated as shown by the multivariate analysis (Figure 2) which implies that cranes create distinct vegetation patches within the grasslands. Disturbed patches were characterised by early successional short-lived graminoids and forbs that are natural elements of the open, trampled and grazed patches of alkaline grasslands (Deák

TABLE 2 The results of the generalised linear mixed models testing the effect of type (disturbed patches vs. undisturbed grasslands; fixed factor), and season (spring vs. summer; fixed factor) on the dependent variables related to vegetation structure, plant functional groups and ecosystem state

	Type (disturbed/undisturbed)			Season (spring/summer)		
	Estimate	SE	*t* value	Estimate	SE	*t* value
Total vegetation cover	18.700	2.039	**9.169**	6.965	2.039	**3.415**
Cryptogam cover	9.960	0.879	**11.330**	−4.931	0.879	**−5.609**
Perennial forb cover	−10.084	0.751	**−13.422**	5.448	0.751	**7.252**
Perennial graminoid cover	45.334	1.120	**40.462**	2.963	1.120	**2.645**
Short-lived forb cover	−12.070	0.569	**−21.210**	−0.164	0.569	−0.288
Short-lived graminoid cover	−8.858	0.602	**−14.716**	5.111	0.602	**8.491**
Shannon diversity	−0.706	0.023	**−30.109**	0.141	0.023	**6.019**
Naturalness score	0.944	0.039	**23.912**	−0.080	0.039	**−2.017**
Forage quality score	0.790	0.028	**28.432**	0.026	0.028	0.936
Specific leaf area	−5.369	0.202	**−26.540**	−1.458	0.202	**−7.207**
Flowering period	−0.215	0.039	**−5.497**	0.114	0.039	**2.916**
Insect pollination	−21.251	0.962	**−22.088**	3.336	0.962	**3.468**

Note: Significant effects (t ≤ 2) are denoted by boldface.

et al., 2015). Invasive or strong competitor weed species were absent on the disturbed plots, which might be due to the high salt content of the soil (see also Tóth et al., 2022; Valkó et al., 2017). The disturbed plots were characterised by high inter-annual vegetation fluctuation, while this seasonality was less apparent in the undisturbed grasslands.

4.2 | Conservation values, ecosystem services and disservices

We observed increased diversity but decreased naturalness score in the crane-disturbed patches. This was due to the high cover of early-successional natural pioneer and disturbance-tolerant species and lower cover of generalists and competitors, especially *Festuca pseudovina*, the dominant grass species of alkaline grasslands. Patches of early-successional vegetation formed by grazing animals are integral parts of the studied ecosystem, so in the current extent, these early-successional patches do not pose a considerable conservation problem (Deák et al., 2015; Valkó et al., 2017).

We evaluated the effects of cranes on the forage quality for livestock grazing using two proxies. Forage quality expressed by the Balázs-score was lower in the disturbed patches compared with undisturbed grasslands (Table 2, Figure 4), as disturbed patches were characterised by pioneer species that sprout and dry out early in the season, so they did not provide suitable forage in the summer and autumn (Balázs, 1949). This implies that in large extent, the foraging activity of cranes can be problematic for grazing management. However, the negative consequences of decreased overall forage quality in the disturbed patches can be counterbalanced by the increased availability of forage plants in early spring. Specific leaf area is another proxy of forage quality, as livestock tends to select species with fresh, hydrated leaves characterised by large SLA (Balogh et al., 2021). We found that the disturbed patches were characterised by plants with larger SLA (Table 2, Figure 4). This can be important for grazing management especially in the springtime, where the early-sprouting pioneer vegetation formed on the disturbed patches can provide important complementary forage for the livestock compared with the undisturbed grasslands. The fresh sprouts of short-lived graminoids (such as *Bromus hordeaceus*, *Hordeum hystrix* and *Poa bulbosa*) growing on crane-disturbed areas can provide good forage for livestock in early spring (Molnár, 2017).

We found that crane-disturbed areas provided floral resources for a longer time and in larger quantity than undisturbed grassland (Table 2, Figure 4). This can support the maintenance of insect diversity, especially pollinator assemblages and palynivores (Bátori et al., 2020). This service has an especially high conservation importance in grass-dominated habitats such as the studied ecosystem with relatively few nectar-producing plants. Similar phenomenon was reported on the burrows of Siberian marmots (*Marmota sibirica*), where the larger number of flowers and their higher visibility attracted more pollinators compared with undisturbed grasslands (Yoshihara et al., 2010).

5 | CONCLUSIONS

Our results suggest that the effects of foraging cranes from the conservation and rangeland management viewpoint are complex. We identified important trade-offs between the positive and negative effects of the foraging activity of cranes on different structural and functional components of the studied grassland ecosystems. Cranes create early-successional open vegetation patches that increase the landscape-scale biodiversity and floral resources but decrease the area of undisturbed alkaline grasslands. Crane-disturbed patches can provide forage for livestock early in the season, but later on the forage quality of the vegetation becomes poor. Disturbed patches similar to those created by foraging cranes have been an important component of many open landscapes. Indeed, creating such focal soil

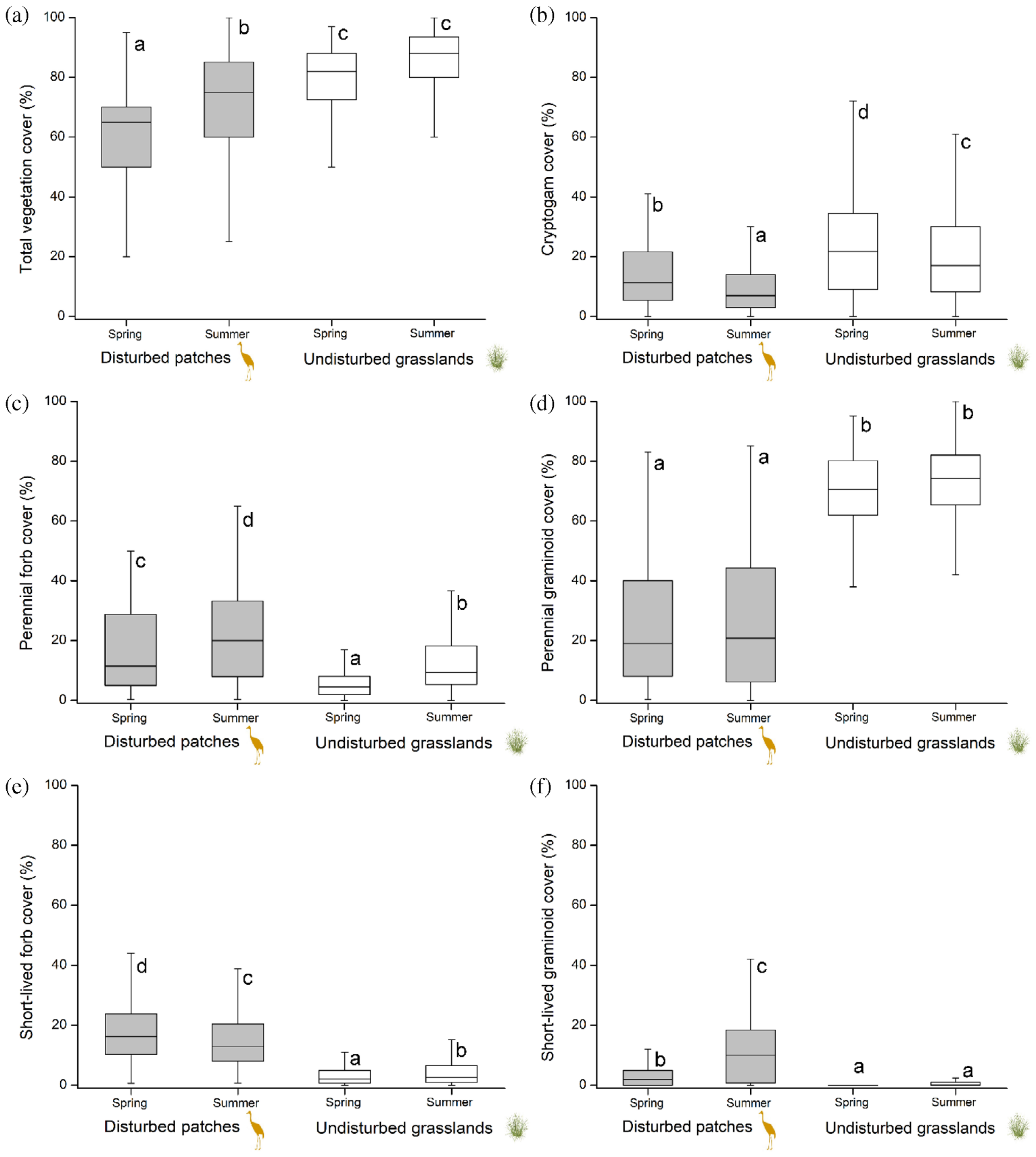

FIGURE 3 Vegetation characteristics related to vegetation structure and plant functional groups in the disturbed patches (grey boxes) and undisturbed grasslands (white boxes) in the two seasons (spring, summer). Data from the 2 years were pooled. Different superscript letters indicate significant differences between the groups [Colour figure can be viewed at wileyonlinelibrary.com]

perturbations artificially was found to be effective for increasing environmental heterogeneity and provide establishment microsites for subordinate plant species (Limb et al., 2010).

Due to the site fidelity of cranes, the disturbed patches seem to be permanent landscape elements, that are maintained in an early successional stage across years. It is an interesting question for future studies why do cranes prefer their already used foraging sites. It is likely that it is easier to forage in the already disturbed patches, but it is still to be studied whether the foraging activity of cranes and the associated disturbance increase the abundance of some of their preferred food items, such as certain soil-dwelling arthropods.

Given the increasing global population of Eurasian cranes (Wetlands International, 2015) and the mild winters as a consequence of climate change, it is expected that cranes will be more abundant and stay for longer in stopover areas, and the number of overwintering birds is also expected to increase (Harris & Mirande, 2013).

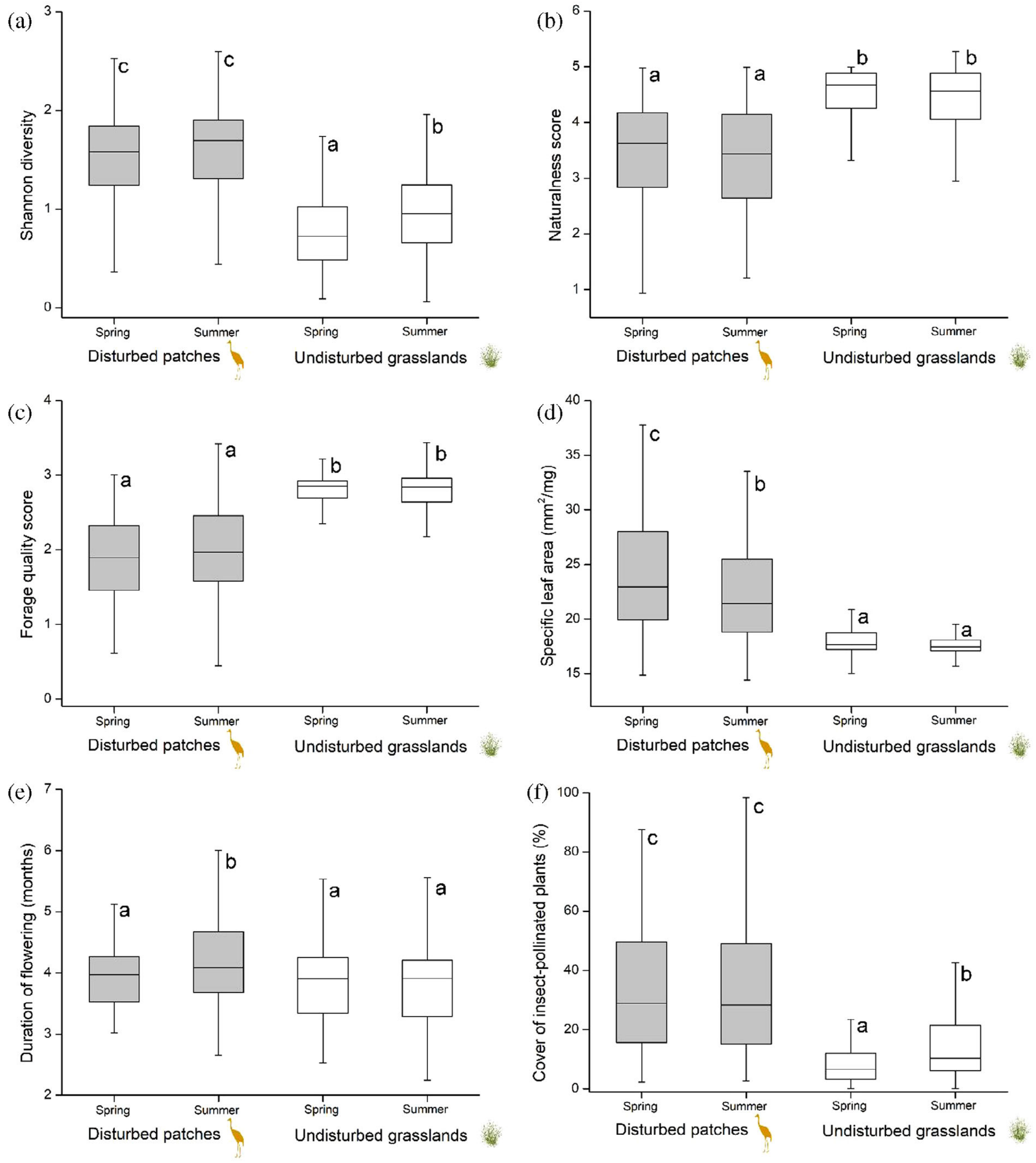

FIGURE 4 Vegetation characteristics related to ecosystem state in the disturbed patches (grey boxes) and undisturbed grasslands (white boxes) in the two seasons (spring, summer). Data from the 2 years were pooled. Different superscript letters indicate significant differences between the groups [Colour figure can be viewed at wileyonlinelibrary.com]

This predicted increase in crane pressure will probably affect not only the grassland patches currently used for foraging but also currently undisturbed grasslands as well. Additionally, the current warming trends of the winters across Europe have already resulted in the northward shift of the wintering ranges of the Eurasian Crane. For example, significant part of the Northwest-European breeding population of the study species has shifted its wintering grounds by over 1000 km within 15 years (Prange, 1999). As observational evidence is mounting that the same behavioural change is happening in the Baltic-Hungarian Flyway, the effects of the foraging of cranes are expected to be stronger in winter than in the autumn months, owing to the increasingly wet soil conditions. This might amplify the transformation of local habitats. Therefore, a surveillance system monitoring the landscape-level extent of the disturbed areas, for example, by satellite imagery would be important to keep track on the vegetation changes. Our results support previous findings that it would be important to maintain the currently used croplands in the stopover areas to provide primary feeding grounds for cranes and to avoid a considerably larger crane pressure on grasslands (Végvári, 2002). In these areas, cultivation of corn would be the best option, as its crop residue is a preferred food item of cranes.

It is important to note that in less harsh environments, intense foraging activity and the resulting disturbed patches created by cranes might be of greater concern due to the possible encroachment of weed and invasive plant species that were limited by the harsh environmental conditions in our studied system. We can also expect that in lower latitudes the engineering effect of cranes can be even higher (Romero et al., 2015). These call for future studies in other ecoregions and habitat types.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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