NKFIH KH 129483
(1st November, 2018 – 31th December, 2020)

FINAL REPORT

Grazing management effects and functional diversity in grasslands

1. Progress of research dissemination

In the proposal altogether 4 impacted publications were planned for the whole project period. In the project period 12 papers with an impact factor were published, in which the project support was stated (10 Q1 papers /incl. 5 D1 papers/, Cumulative IF: 38.117). With an international collaboration of the Global Arid Zone Project (GAZP) a paper was submitted to *Nature* (under external review stage), the PI is one of the 20 core authors. Two special issues in impacted journals were edited (*Flora*: Ecology and Evolution of Steppe Biodiversity, PI as lead guest editor with Barbara Neuffer, Karl-Georg Bernhardt and Karsten Wesche as co-editors, and *Journal of Vegetation Science*: Dispersal and Establishment, PI as lead guest editor with James M. Bullock, Borja Jiménez-Alfaro and Judit Sonkoly as co-editors). Most of the papers were published either in open access journals, open access by country agreement or provided in public repositories (REÁL or Library of the University of Debrecen).

We organised a workshop in the MTA DAB in Debrecen on 12th April 2019, entitled: "Növényi stratégiák és jellegek szerepe az ökológiai kutatásokban", where we discussed the current trends of trait-based ecology and proposed a unified database for plant traits for the Pannonian region (Pannonian Database of Plant Traits – PADAPT). The proposal was also listed in the funding. We organised three special sessions at the 62nd IAVS Symposium (14-19 July 2019, Bremen). The three special sessions were strongly linked to the topic of the present proposal. These were: "Plant reproduction and dispersal" (organised by Leonid Rasran, Péter Török & Judit Sonkoly), "Patterns, drivers, and conservation opportunities of grassland biodiversity" (organised by Didem Ambarli, Riccardo Guarrino, Alla Aleksanyan and Péter Török), and "Using plant traits for the recovery of ecosystem functions and services: Trait-based ecosystem engineering?" (Béla Tóthmérész and Péter Török). We participated at the 16th Eurasian Grassland Conference (29 May – 2 June 2020, Graz) and at the DarkDivNet2019 Workshop (20–23 November 2019, Tartu, Estonia). At the conferences we participated with nearly 20 oral or poster presentations. Unfortunately, most conference participation planned in the project was postponed or cancelled because of the COVID-19 pandemic.

2. Research results

Here we summarise the most important findings of the papers written during the project period and published with the support of the research grant.

2.1. Grazing effects of beef cattle are grassland type and intensity dependent

Overgrazing was identified as one of the key drivers of grassland biodiversity, but the functional analysis of increased grazing pressure on grassland vegetation is still lacking. We analysed vegetation patterns in dry alkali short-grass steppes, dry loess steppes, non-alkali wet grasslands and alkali wet grasslands along an intensity gradient of beef cattle grazing. We tried to answer how grazing intensity and grazed grassland type are interacting. We compared the studied grasslands by calculating community-weighted means for each single trait, and multi-trait functional richness, functional evenness, and divergence for four leaf traits. All species and functional diversity metrics were significantly affected by the grassland type, except leaf dry matter content. The effect of

interaction between grazing intensity and grassland type was also significant for functional richness, functional evenness, community-weighted means of leaf area, and for species richness and evenness. An upward trend of specific leaf area was detected in all grasslands with the highest scores for the overgrazed sites, but the change was also grassland type dependent. The detected trend suggests that with increased intensity the overall selectivity of grazing decreased. We found that evenness was affected but functional evenness was not affected by grazing intensity. Functional evenness scores were more related to the grassland type than to changes in grazing intensity, and displayed a high variability. We stressed that management strategies should be finetuned at the site level and beside intensity the subjected grassland type should be considered in designing a sustainable grazing management (Török et al. 2018a).

2.2 Static and dichotomic conservation paradigm is not sensitive enough for sustaining complex habitat gradients

Forest-steppes sustained by extensive free grazing or herded livestock grazing form the contact zone between closed-canopy temperate forests and treeless steppes and provide a textbook example of forest-grassland mosaics. Forests and grasslands have distinct environmental, structural and compositional characteristics, and the interactions of these characteristics result in the emergence of specific edge communities. We sampled the vegetation of relatively large forest patches, medium forest patches, small forest patches, north-facing edges, south-facing edges, and grassland vegetation. Our study question was whether these six habitat types can be grouped into two distinct habitat categories, which would support the above mentioned dichotomic description, or a different paradigm better fits this complex system. Our results indicate that the widely used dichotomic categorization of forest-steppe habitats into forest and grassland patches is too simplistic, potentially resulting in a considerable loss of information. The possible gradient-like arrangement of non-forest communities in the studied mosaic ecosystem calls for further studies to understand forest-steppe heterogeneity in the frame of the gradient-based paradigm of landscape structure. We suggest that forest-steppe vegetation better fits the gradient-based paradigm of landscape structure, which is able to reflect continuous variations. (Erdős et al. 2020).

2.3. Secondary grasslands can act as refuges for grassland and wetland plants

Vast landscapes with a historically high proportion of grasslands have largely been converted into arable lands, or into built-up areas or forest plantations. In such landscapes the role of secondary habitats like river embankments, which are one of the most extensive and widespread secondary habitats in former floodplains, became more and more important in sustaining landscape-scale biodiversity. In the research the diversity patterns of secondary dry and wet grasslands on river embankments were compared with those of semi-natural dry and wet grasslands. Species diversity, phylogenetic diversity and functional diversity were assessed. With the performed trait-based analyses we also tried to evaluate the ecosystem services provided by secondary grasslands on river embankments. Both dry and wet secondary grasslands of the embankments showed higher species diversity compared to their semi-natural counterparts. The cover of generalist species was high in the secondary grasslands, and secondary grasslands showed significantly lower phylogenetic diversity than the semi-natural grasslands. Functional diversity did not differ but higher community-weighted means of specific leaf area, plant height and flowering period were found related to important ecosystem services like biomass production and pollination in the secondary grasslands. We suggested that well-planned management actions and restoration activities could help further improve the ecological function and conservation value of secondary grasslands on river embankments, contributing to the maintenance of species diversity and sustaining the functionality of ecosystems in agricultural landscapes (Bátori et al. 2020).

2.4 Kurgans are biodiversity hotspots of grassland plants and arthropods outside nature reserves

Land use intensification (e.g., the replacement of low-intensity grazing by free grazers or livestock) over the past centuries has become one of the major threats to biodiversity at multiple scales. Many formerly extensive natural habitats have been transformed into agricultural fields or urban areas. In transformed landscapes, many populations of grassland specialist plant and animal species live outside the few protected areas and are often preserved on 'small natural features' such as road verges, field margins and rocky outcrops. In the steppe and forest steppe zones of Eurasia kurgans act as such refuges for grassland species. We found that kurgans could effectively support grassland biodiversity even outside the protected areas, since the species richness and abundance of the studied grassland specialist taxa were the same on kurgans outside and inside the protected areas. Given the considerable differences in the life strategies and dispersal ability of the studied taxa, this uniform pattern might be an outcome of different processes. We revealed that the presence of anthropogenic disturbances and encroachment of woody species are the most considerable threats to the long-term maintenance of biodiversity on kurgans located outside the protected areas. For their effective conservation a new approach is needed, which can cope with the small area and dispersed localities of the kurgans and can integrate them into the landscape-scale network of small natural features (e.g., river embankments or road verges). As the ecological importance of kurgans is disproportionate to their size, conservation actions focusing on their protection offers a greater rate of return of the efforts than what can be expected in case of larger continuous sites (Deák et al. 2020).

2.5 High resistance of grassland biodiversity mitigates the negative effects of native woody encroachment.

Woody encroachment often results in ecosystem degradation which is often associated with the decline of biodiversity. Woody encroachment is a worldwide phenomenon and occurs on many types of grasslands and open herb-dominated habitats. This process is often facilitated by altered frequency and intensity of management, e.g., management switch to intensive grazing or abandonment. With the analysis of grassland vegetation subjected to different levels of shrub encroachment we found that encroachment affected the total herb richness and the species richness of dry-grassland species. For most studied variables, lowest values were found for the highest woody encroachment groups. Grassland-age affected the species richness of the herb layer and that of dry-grassland species; lower values were detected in restored grasslands. In secondary, spontaneously recovered grasslands, species diversity and evenness were lower, while the cover of species with the highest abundance was higher than that in ancient grasslands. Species composition and richness displayed a relatively high resistance to moderate woody encroachment; the highest decrease in diversity was detected at a high level of woody encroachment. The research results suggested that moderately encroached loess grasslands can be easily restored by the suppression of woody species, as their species pool still contains many dry-grassland species targeted for restoration (Teleki et al. 2020).

2.6. Secondary succession revisited: Trait neutrality and filtering effects drive assemble of species in sand grasslands

There are several contrasting views of species assembly and the course of succession in grasslands. One approach is the neutral theory, which suggests that succession is governed by stochastic process during species dispersal and arrival and fluctuations in established populations drive the temporal change in vegetation. In contrast, the filtering theory suggests that community assembly is strongly determined by functional trait filtering governed by more or less definite interaction of abiotic and biotic filtering processes selecting species from the available local species pool. We used a permanent plot setup and trait-based analyses of a successional dataset from acidic sand

grasslands. We expected high fluctuations in the trait values in the first years; and later a temporally divergent change in trait patterns of sites with different vertical position. We also assumed that there are different temporal patterns in the functional diversity of regenerative and vegetative traits. We confirmed that trait neutrality and filtering effects are jointly responsible for vegetation changes during the initial stages of secondary grassland succession. First, species establishment is influenced by local abiotic conditions and it is a highly stochastic process that is reflected by the high fluctuations in trait values. Later, with increasing rate of clonality, the community became more stable and the species assembly became governed by abiotic and biotic filtering. High fluctuations in some trait values, however suggest that the effect of stochastic processes was especially important also in later stages in vegetation development (Török et al. 2018b).

2.7. The trait spectrum of reproductive traits regenerates faster than that of vegetative ones during succession

Grassland recovery by spontaneous succession represents a cost-effective and the most natural solution for grassland restoration, and it can effectively substitute technical reclamation methods in slightly fragmented landscapes, when propagule sources are nearby. Since reproductive and vegetative processes operate on different scales and at different stages of plant community assembly, we investigated whether their recovery times were different during spontaneous succession. While there are many studies addressing the compositional changes during succession, little is known about the spontaneous recovery of grassland functionality and recovery of fundamental ecological processes and structures that assure the provision of ecosystem services. We compared the spectra of reproductive and vegetative traits between old-fields of different age and pristine grasslands used as reference. We assessed which of the two sets of plant traits in old-field spontaneous succession first showed a spectrum comparable to that of pristine grasslands. We found that during spontaneous succession the composition of reproductive traits in recovered grasslands became similar to that of pristine grasslands earlier than the composition of growth forms. Our approach also highlighted that vegetative traits are informative on the successful restoration at different timescales. As the reproductive trait spectrum recovers more quickly than the vegetative trait spectrum, vegetative traits might be more effective in the assessment of restoration success than the reproductive ones (Fantinato et al. 2019).

2.8 Establishment gaps act as artificial biodiversity hotspots for target species establishment in grasslands

Soil seed banks can be a source of species which contribute to the spontaneous recovery of grasslands, but its restoration potential can be limited because there are lot of grassland species that have no persistent seed banks. Thus, to overcome dispersal limitation, transferring seeds of target species into restoration sites is essential for a successful recovery process. We tested the effectiveness of creating establishment gaps of various size and we sowed seeds of target grassland species, monitored their establishment success and analysed the dynamics of their spread to the surrounding species-poor grasslands. We found that the creation of $4m^2$-sized establishment gaps together with the sowing of high-diversity seed mixtures containing both short-lived and perennial species is an effective method for increasing species richness in species-poor grasslands. Gaps sown with high-diversity seed mixtures were highly resistant to unfavourable climatic conditions and increasing grass abundance in dry years did not hamper the recovery of target grassland species in the short run, but provided an effective weed suppression (Kiss et al. 2020).

2.9 Leaf trait measurements for the analyses of grazing effects and establishing a database

The Pannonian ecoregion harbours a large number of endemic species due to its geographical location, and for the majority of steppe species, which have large continental distribution ranges, the Pannonian ecoregion harbours the most western occurrences. This means that most of these species are missing or underrepresented in large world databases like for example the TRY database. By collecting and measuring the leaves of a high number of plant species in the Pannonian ecoregion we provided original leaf trait data for 4,041 samples belonging to 491 species (27 woody, 464 herbaceous) vascular plant species from the Pannonian ecoregion. We stress that our data have the potential to fill a knowledge gap setting back trait-based studies, and we hope that further data will be published in the near future, representing rare species from other geographical regions. Having a more complete coverage of species in trait databases can help us better understand not only the role rare species play in ecosystem functioning, but also more general questions in functional ecology (E-Vojtkó et al. 2020).

2.10 Dispersal and species establishment in vegetation dynamics and resilience

Understanding the balance of processes that regulate plant community dynamics at local and landscape scales is among the greatest challenges of current vegetation ecological research. One of the most crucial topics in it is the clarification of the role that dispersal and establishment play in the resilience of communities subjected to natural and anthropogenic disturbances. In our paper we reviewed the current status and trends in the research of dispersal and establishment in plant communities with a clear focus and links to vegetation science. We concluded that propagule dispersal and plant establishment play a decisive role in the resilience of plant communities. Dispersal and establishment should not be considered as a random or stochastic process; disturbance dynamics emphasize the influence of multiple environmental factors on the regeneration process, but we are a long way from understanding the links between disturbance related drivers of plant regeneration. The most important aspects and processes of disturbance and regeneration dynamics are summarised in Figure 1. Future research should be directed to understanding the relationships between disturbance and the availability of regeneration niches in space and time. Despite the regeneration niche being a long-standing concept in vegetation ecology, its role in vegetation dynamics is considered much less than the traits and environmental tolerances of adult plants. We emphasised that there is a need to understand how species traits for dispersal, propagule banks and establishment are linked, and processes of dispersal and establishment should be included in the classic filter concept for species assembly. To understand spatial and temporal vegetation dynamics, the importance of seed traits, not only adult plant traits, should be considered (Török et al. 2020a).

2.11 Eurasian steppes in transition

Steppes are among the largest continuous terrestrial natural habitats of the world; steppe grasslands and forest steppes are stretching from Central and Eastern Europe to Northern China across the whole temperate zone of Eurasia. Because steppes are often characterised by fertile soils, they are subjected to large-scale degradation and area loss by intensive crop production, or other forms of overuse. We concluded in our paper that steppes are among the most threatened and least protected habitats globally, and therefore, the conservation and restoration of steppe biodiversity, especially in agriculture-dominated landscapes, are key priorities for research and practice. Effective biodiversity conservation and restoration depend strongly on the knowledge of ecological properties and processes that are responsible for the sustainment of crucial ecological functions and services in pristine steppes. We stressed that most recent and novel research in steppe

biodiversity and ecology highlighted the enormous levels of biodiversity at multiple scales shaped by a complex interaction of a long-term evolutionary history, macroclimate and local factors including disturbances such as overgrazing. Fine-tuned management, for example in a form of low-intensity and extensive grazing is urgently needed for maintaining steppe resistance and resilience to climate change extremities (Török et al. 2020b).

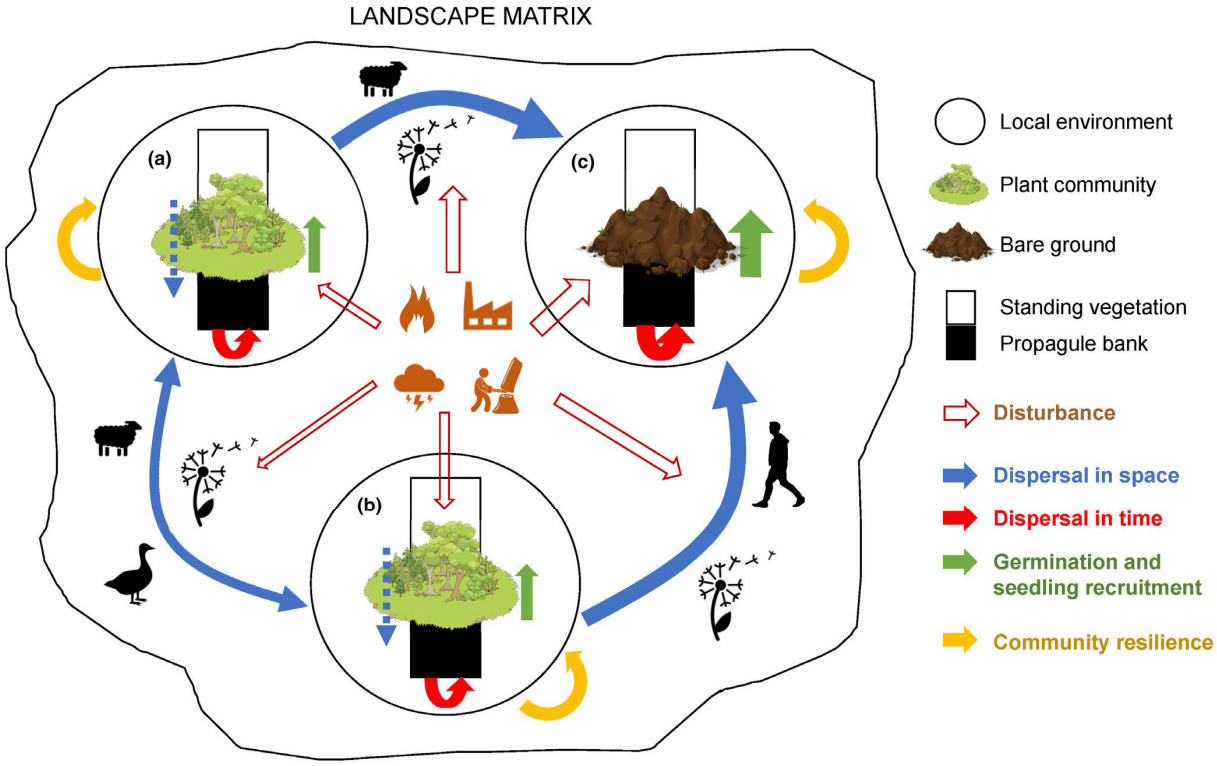

Fig. 1. Disturbance and regeneration processes in relation to community resilience. Disturbance is a crucial driver of community composition. While low intensity and/or frequency disturbance facilitates species coexistence by creating suitable microsites for germination and establishment, high intensity and/or frequency mostly anthropogenic disturbances may completely destroy vegetation (subfigure c). In such cases, vegetation recovery by germination and seedling recruitment relies exclusively on dispersal in space and/or on local propagule banks. Humans may also disrupt or supplement dispersal in space, for example, between community "b" and "c", where a wild vector is lost, but humans themselves disperse propagules. These are all key processes determining community resilience and vegetation dynamics at local and landscape scales (Figure from the open access paper of Török et al. 2020a).

3. International collaboration in the reporting period

An important goal of the project was to develop international collaborations, increasing the embeddedness of the research in the international mainstream research and establishing links to the scientific community. The PI joined several international projects including the dark diversity research consortium (DarkDivNet és Soil DarkDivNet, Macroecological Research Group, University of Tartu, Estonia), and another dealing with the restoration of arid land (Global Arid Zone Project, Colorado University at Boulder, USA). The PI was a member of a consortium project proposal for EU H2020-LC-CLA-2018-2019-2020 (Building a low-carbon, climate resilient future: climate action in support of the Paris Agreement) (866568 - N-SCRiBE), but the project was not

supported by the research grant agency. The PI also applied with „PRO-GRASS: New foundations for grassland restoration: Cross-disciplinary research on species filtering and assembly" to the ERC 2019 Consolidator Grant. The proposal was ranked to the 85-91% category with the scoring B and was not selected for the second round of the evaluation. With the participation of the PI an international LIFE Project (Sustainable Viticulture for Climate Change Adaptation - LIFE19 CCA/DE/001224) received support with a total budget of 2.8 million Euros.

The PI was invited to join to the editorial board of several highly respected journals including *Land Degradation and Development* (D1, 2018- Associate Editor), *Frontiers in Plant Science* (D1, 2018- Review Editor), *Applied Vegetation Science* (Q1, 2018-2020 Editorial board member; 2020- Associate Editor), *Tuexenia* (Q2, 2017- Associate Editor-), *Flora* (Q2, 2018- Editorial Board member), *Diversity* (Q3, 2018- Editorial Board member) and *Restoration Ecology* (Q1, 2018- Associate editor). In the reporting period the PI edited more than 40 manuscripts for these journals and reviewed further 60 manuscripts mostly for Q1/D1 journals.

Linked to the proposal we organised three special issues in the international journals *Journal of Vegetation Science*, *Flora* and *Restoration Ecology* – two were published in the reporting period (See Török et al. 2020a and 2020b), and the one in *Restoration Ecology* will be completed in the first half of 2021. The PI participated at a kick-off meeting in Germany and contributed to an international LIFE Proposal (Germany, France, Austria and Hungary), which was submitted in early September. The PI also started a collaboration with the recently started LIFE-IP Grassland-HU project, which falls strongly in the subject of the present proposal.

The PI became a founding member of Hungarian Young Academy and was elected as the first Co-chair of the young academy (2019 May onwards). The PI was invited to be a member of the Hungarian Accreditation Committee (MAB), expert committee for Natural Sciences (2019-2026), and the Co-chair for the Multidisciplinary expert committee (2020-). The PI was elected to the council of the International Association for Vegetation Science (2019-2024).

References

Bátori Z., Kiss P.J., Tölgyesi C., Deák B., Valkó O., Török P., Erdős L., Tóthmérész B., Kelemen A. (2020): River embankments mitigate the loss of grassland biodiversity in agricultural landscapes. *River Research and Applications*, DOI: 10.1002/rra.3643

Deák B., Valkó O., Nagy D. D., Török P., Torma A., Lőrinczi G., Kelemen A., Nagy A., Bede Á., Mizser S., Csathó A.I., Tóthmérész B. (2020): Habitat islands outside nature reserves – threatened biodiversity hotspots of grassland specialist plant and arthropod species. *Biological Conservation*, DOI: 10.1016/j.biocon.2019.108254

Erdős L.*, Török P.*, Szitár K., Bátori Z., Tölgyesi C., Kiss P.J., Bede-Fazekas Á., Kröel-Dulay G. (2020): Beyond the forest-grassland dichotomy: the gradient-like organization of habitats in forest-steppes. *Frontiers in Plant Science* **11**: 236. *társ-elsőszerzőség

E-Vojtkó, A., Balogh, N., Deák, B., Kelemen, A., Kis, S., Kiss, R., Lovas-Kiss, Á., Löki, V., Lukács, K., Molnár V, A., Nagy, T., Sonkoly, J., Süveges, K., Takács, A., Tóth, E., Tóth, K., Tóthmérész, B., Török, P., Valkó, O., Vojtkó, A., Lukács, B.A. (2020): Leaf trait records of vascular plant species in the Pannonian flora with special focus on endemics and rarities. *Folia Geobotanica* **55**: 73–79.

Fantinato E., Sonkoly J., Silan G., Valkó O., Tóthmérész B., Deák B., Kelemen A., Miglécz T., Del Vecchio S., Bettiol F., Buffa G., Török P. (2019): Pollination and dispersal trait spectra recover faster than the growth form spectrum during spontaneous succession in sandy old-fields. *Applied Vegetation Science* **22**: 435–443.

Kiss R., Deák B., Tóthmérész B., Miglécz T., Tóth K., Török P., Lukács K., Godó L., Körmöczi Zs., Radócz Sz., Kelemen A., Sonkoly J., Kirmer A., Tischew S., Švamberková,E., Valkó O. (2020): Establishment gaps in species-poor grasslands: artificial biodiversity hotspots to support the colonization of target species. *Restoration Ecology*, DOI: 10.1111/rec.13135

Teleki B., Sonkoly J., Erdős L., Tóthmérész B., Prommer M., Török P. (2020): High resistance of plant biodiversity to moderate native woody encroachment in loess steppe grassland fragments. *Applied Vegetation Science*, DOI: 10.1111/avsc.12474

Török P., Penksza K., Tóth E., Kelemen A., Sonkoly J., Tóthmérész B. (2018a): Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. *Ecology and Evolution*, **8**: 10326–10335.

Török P., Matus G., Tóth E., Papp M., Kelemen A., Sonkoly J., Tóthmérész B. (2018b): Both trait-neutrality and filtering effects are validated by the vegetation patterns detected in the functional recovery of sand grasslands. *Scientific Reports* **8**: 13703.

Török, P., Bullock, J.M., Jiménez-Alfaro, B., Sonkoly, J. (2020a): The importance of dispersal and species establishment in vegetation dynamics and resilience. *Journal of Vegetation Science* **31**: 935–942.

Török P., Neuffer B., Heilmeier H., Bernhardt K.-G-, Wesche K. (2020b): Climate, landscape history and management drive Eurasian steppe biodiversity. *Flora* **271**: 151685.