Project type and number: **NKFI PD_18 128385**

Duration: **2018.09.01–2021.08.31.**

Project title: **Effects of disturbances on the productivity – species richness relationship**

Principal investigator: **Ónodi, Gábor**

Final report on the results of the research

The report follows the order of the hypotheses described in the detailed research plan and the workplan of the original proposal. For each of the three case studies, this final report covers both the results related to the original scientific questions and changes due to involving additional datasets. In summary, I have done all field works planned in the proposal. During the three years of this grant, we published twelve papers in peer-reviewed journals. I acknowledged the financial support provided by the National Research, Development and Innovation Fund (PD_18 128385) in two first-author papers and two second-author papers. Out of the eight papers not mentioning this grant, I have attached only one to this report that is strongly connected to the third dataset of this project and was published in PNAS in 2020. The publication phase has not been ended yet. Findings in Case study 1 allow us to frame more comprehensive ecological questions that extended the publication perspective in this part of the project. The publication process is delayed in Case study 2, because of adding more study years to the analysis, but the planned publications are fulfilled and completed by additional papers in Case study 3. Three additional manuscripts are in progress currently with the support of this NKFI grant. As many conferences in the research field were cancelled during the last one and a half years, my planned conference publications failed, except for two national conferences (MBT in November 2019 and MÖK in August 2021) and one international conference (Eurasian Dry Grassland Group Conference in May 2019).

1. Evaluation of productivity – species richness relationship in semiarid sand grasslands

(H1) The productivity – species richness relationship is hump-shaped in the studied semiarid ecosystem ranging from open to closed sand grasslands, while sampling year and productivity range affect the relationship.

1.1. Aims

We aimed at studying the productivity – species richness relationship at a wide range of productivity in natural sand grasslands using the extended dataset of an ongoing project started in 2017 (NKFI OTKA K 124671).

1.2. Activities

Besides fulfilling all planned field samplings in Ásotthalom and Orgovány sites as described in the Material and Methods section of the Detailed Research Plan, additional samplings were conducted in 2018 and in June 2019 in two additional study sites: in Deliblát (79 plots) and Kunadacs (82 plots) Sand Dune Areas. Productivity and species richness data from Ásotthalom and Orgovány sites were analyzed, but manuscript preparation was delayed because new findings changed publication goals as described in Results 1.3.A.

In addition, the dataset of an earlier regional-scale study has been involved in this research and the effects of different levels of human disturbance on plant diversity have been published in Flora in 2020.

1.3. Results

1.3.A

The most important statements of H1 has been tested and published in Case study 3 concerning the hump-shape of the productivity – species richness relationship in open sand grasslands. This paper also discusses the temporal and productivity range effects on the relationship (see 3.3.A). On the other hand, the analysis of the Ásotthalom-Orgovány dataset provided unique results due to the extension of the dataset into wetlands (meadows and reed stands). Our findings are in agreement with our first hypothesis (see the fitted line for the red plots in Figure 1), but they show multiple and overlapping humped-back relationships in adjacent sand (marked in red in Figure 1) and meadow habitats (marked in green in Figure 1) for both sites. The model applying common productivity - species richness relationship of Ásotthalom and Orgovány sites (black curve in Figure 1) does not explain a considerable part of the variation in richness, especially at the middle of the productivity range. By contrast, an alternative model applying unimodal curves fitted separately for sand and wetland plots of both sites better explain the relationship based on second-order bias-corrected Akaike's information criterion scores.

These findings may shed light on the problem of filled curves in the case of multi-site studies, and thus it may explain the processes suppressing species richness below the expected values based on the “common” model. These results suggest that low richness values at intermediate productivity levels indicate the boundary of two different vegetation complexes having distinct productivity – species richness relationships. Furthermore, we found that the shape of the relationship changes due to the transformation of the independent variable. These results are planned to be published in Methods in Ecology and Evolution (see *1.4.A*).

1.3.B

Our research focus moved to the application of single or multiple productivity – species richness relationships in different habitat complexes as described above. We intended to study this problem both in lowland and in mountain forest-steppe complexes in the Carpathian Basin. For this purpose, we studied diversity patterns using an earlier regional scale dataset containing also loess and dolomite complexes (besides lowland sand and marsh habitat complexes). As a first step, we published a paper in Flora in 2020 that studied disturbance effects on alpha, beta, and gamma diversity of six characteristic Pannonian habitat complexes

(see *1.4.B*). We found that the gamma diversity of the specialist species was higher in the natural sites of the loess and dolomite forest steppe and the freshwater marshland complexes compared to the moderately disturbed areas, while there were no significant diversity differences in the other complexes.

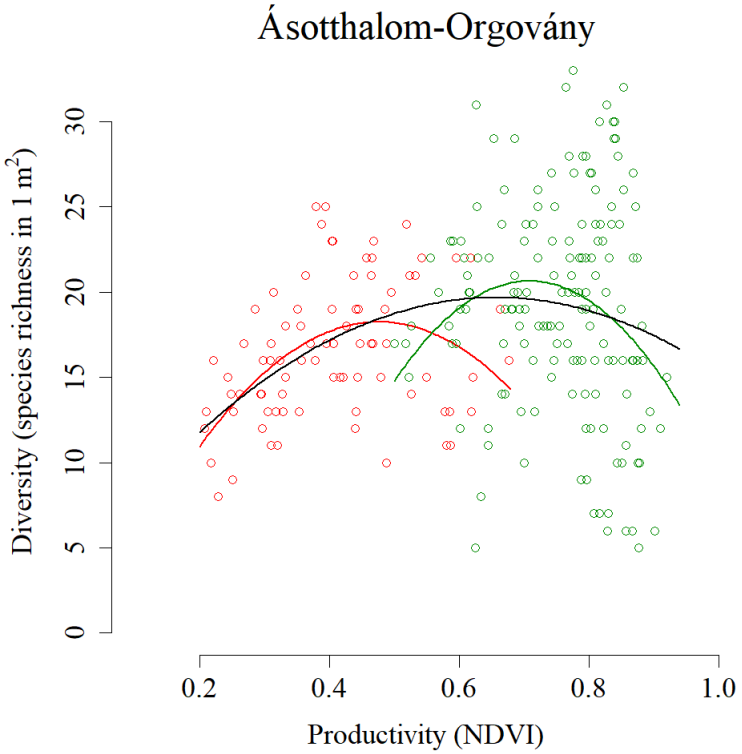

Figure 1 Productivity – species richness relationships in adjacent sand and wetland vegetation complexes in Ásotthalom and Orgovány sites. Sand plots are marked in red and wetland plots are marked in green for both sites. Significant ($p < 0.05$) unimodal relationships are marked in black, red, and green for all data plots, sand plots, and wetland plots, respectively.

1.4.A Planned publications

Ónodi, G., Kröel-Dulay, Gy., Kertész, M. and Botta-Dukát, Z. Planned title: The effects of the productivity range and the transformation of the productivity axis on the shape of the productivity – diversity relationship. Planned submission to Methods in Ecology and Evolution in November 2021.

1.4.B Publications

Kertész, M., Ónodi, G., Botta-Dukát, Z., Lhotsky, B., Barabás, S., Bölöni, J., Csecserits, A., Molnár, C., Nagy, J., Szitár, K., & Rédei, T. 2020. Different impacts of moderate human land use on the plant biodiversity of the characteristic Pannonian habitat complexes. Flora 267: 151591.

2. Studying the interactive effects of extreme drought and controlled precipitation gradient on the productivity – species richness relationship in open sand grasslands

(H2) Extreme drought and chronic precipitation change treatments have interactive effects on the productivity – species richness relationship, with extreme drought making the relationship steeper along the precipitation gradient.

2.1. Aims

To study the effects of disturbance and controlled precipitation gradient according to climate change scenarios using the dataset of an ongoing project started in 2013 (NKFI OTKA K 112576, K 129068).

2.2. Activities

The research on the aboveground biomass and species richness of vascular plants was carried out in the Fülöpháza site (ExDRain field experiment). We decided not to use species-level plant cover data for estimation of primary productivity but we used the experimentally modified precipitation values instead. Primary productivity depends on the amount of precipitation in the studied water-limited community, thus the observed variation in the primary production is a consequence of the experimental treatments. We are currently working on this manuscript, and it is planned to be published in 2022 in a Q1 journal. Additionally, I have contributed to other two papers during the period of the reported grant.

2.3. Results

2.3.A Our results indicate a strong disturbance effect on the productivity – species richness relationship (Fig. 2). In the pre-treatment year (2013) we had only one productivity group for the 48 sampling plots, and productivity measurements showed a very narrow productivity range for the sampling plots. In the second year (2014), extreme drought treatment was conducted, thus we have two groups for productivity, while within-group (extreme or control) productivity values were identical. In 2015, recurring precipitation treatments were started. Extended precipitation gradient initiated trend-like changes in the shape of the productivity – species richness relationships both in extreme and control plots. Depending on the presence of the previous extreme event, the relationship developed to positive or negative linear. A significant positive linear relationship is characteristic for extreme plots since 2016, while in the lack of the disturbance negative linear relationship is significant since 2017 ($p < 0.05$). These results are remarkable because the effects of a single disturbance turned the slope of the relationship from negative to positive and this effect is persistent three to six years after the disturbance. This phenomenon may be linked with extreme event effects on the perennial grass matrix (especially *Festuca vaginata*) that collapsed after the extreme drought.

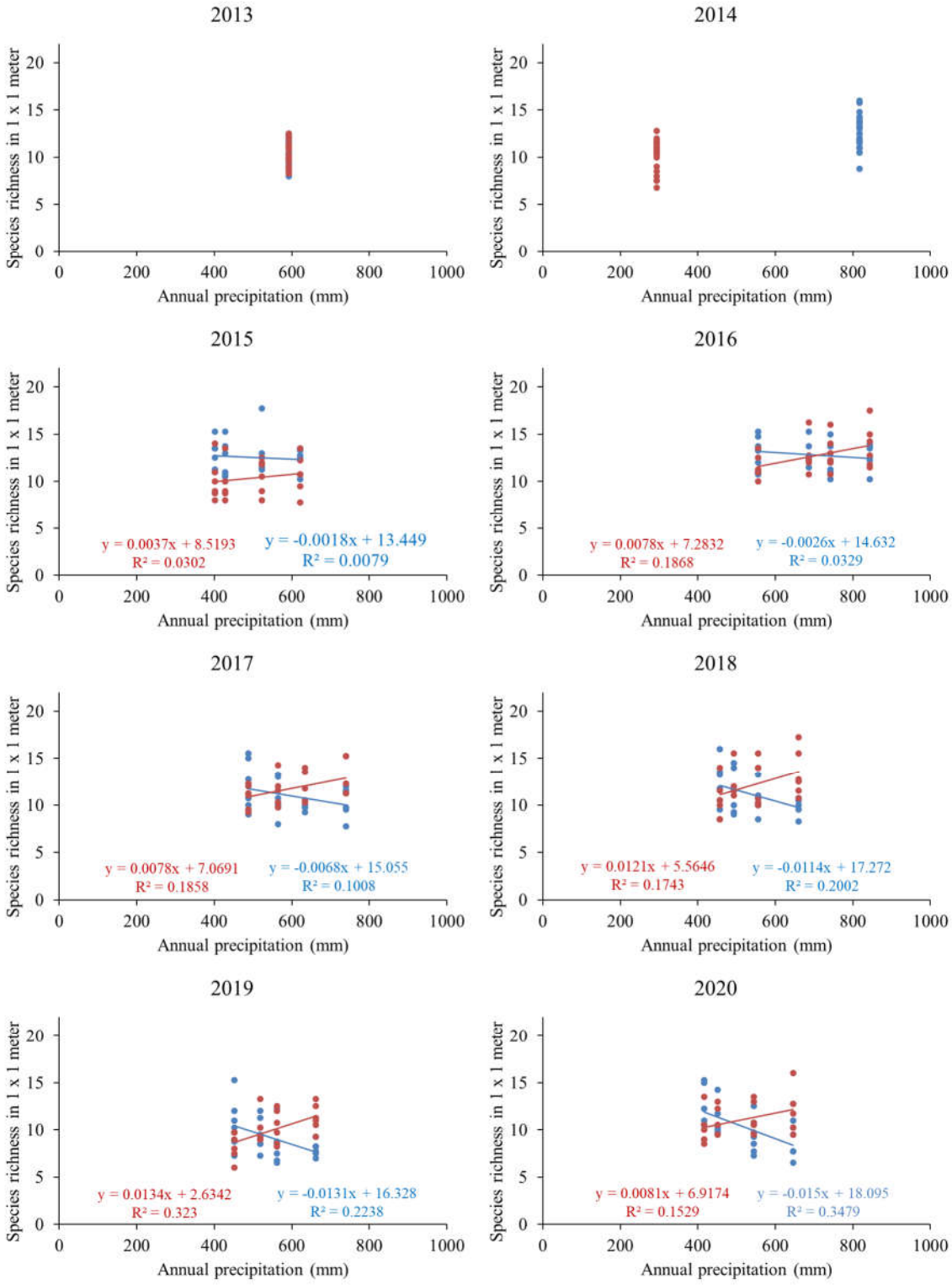

Figure 2 Temporal changes in the productivity – species richness relationships along a controlled productivity gradient due to the application of one-year extreme drought treatment in 2014. Productivity is expressed as the sum of yearly precipitation. Plots and fitted linear relationships are marked in red and blue for extreme treatment and control, respectively.

These findings may provide new insights into the expected climate change effects on productivity and plant species diversity, highlighting the role of competition and propagule limitation in grassland communities. Our results support the hypothesis (H2), because extreme drought made the relationship steeper.,However, increasing versus decreasing slopes of the relationship present more contrasting results than was expected. Nevertheless, publication of these results is planned for 2022, because we decided to present the persistence of the extreme effect via including samplings taken in 2020 and 2021 into the analyses.

2.3.B

During the three years of the project, we published a paper in Oecologia that presents the experimental design and extreme drought effects on the perennial grass matrix and the abundance of an invasive annual weed.

An additional manuscript was submitted in September to Global Change Biology studying changes in decomposition due to the altered precipitation regime. All of these papers acknowledge the financial support provided by the National Research, Development and Innovation Fund (PD_18 128385).

2.4.A Planned publications

I plan to submit the results of the second case study (described in *2.3.A*) to Journal of Vegetation Science in 2022.

Seres, A., Kröel-Dulay, Gy., Szakálas, J., Nagy, P.I., Boros, G., Ónodi, G., Szitár, K., Mojzes, A.: Effects of drought on litter decomposition: the importance of altered species dominance, biomass allocation, and rooting depth in a temperate grassland. Submitted to Global Change Biology in September 2021.

2.4.B Publications

Mojzes, A., Ónodi, G., Lhotsky, B., Kalapos, T., & Kröel-Dulay, G. 2020. Experimental drought indirectly enhances the individual performance and the abundance of an invasive annual weed. Oecologia 193: 571–581.

3. Changes of productivity – species richness relationship along the post-fire succession

The productivity – species richness relationship changes as a function of time since fire along post-fire succession in open sand grasslands, while unburnt (control or pre-fire) stands change only slightly.

3.1. Aims

Evaluation of temporal changes in P-SR relationship along post-fire succession in a long-term study using the dataset of a long-term monitoring study on post-fire succession in Bugac.

3.2. Activities

We carried out all field samplings and data analyses planned for this case study in the workplan. Results were published in the Journal of Vegetation Science in 2021.

We also published a paper in Applied Vegetation Science in 2021 describing temporal changes in species richness at the Kéleshalom site between 2008 and 2018. This study has many similarities to Case studies 2 and 3, and we plan to analyze the productivity – species richness relationship using this database, therefore this paper strongly connects to the present grant.

We contributed to an international teamwork by providing our long-term dataset overlapping the dataset used in Case study 3. Results were published in PNAS in 2020.

3.3. Results

3.3.A

Concerning the JVS paper, our results are in line with our original hypothesis (H3). We found a stable productivity–diversity relationship before the wildfire (Fig. 3), while the relationship changed gradually from year to year after the fire (Fig. 4). Furthermore, before the fire, the relationship was positive linear, while a significant quadratic component made it unimodal after the fire. The disturbance moved the vegetation out of a stable state, by initiating a post-disturbance succession. We assume that the stress caused by frequent moisture and nutrient shortage of the coarse sand soil, combined with the competition for moisture with the shallow-rooting juniper bushes and with the cryptogam layer, kept the overall productivity constrained before the wildfire. The humped-back shape of the productivity–diversity relationship developed gradually after the fire, and it has been formed by the eight post-fire unimodal curves of subsequent years, together.

We conclude that disturbance can be an important factor inducing considerable and long-lasting changes in the productivity–diversity relationship in formerly quasi-stable habitats. Disturbance may alter the range of productivity and diversity as well, leading to trend-like changes in the relationship. Our study proposes that the results of global scale studies may depend on controlling for disturbance.

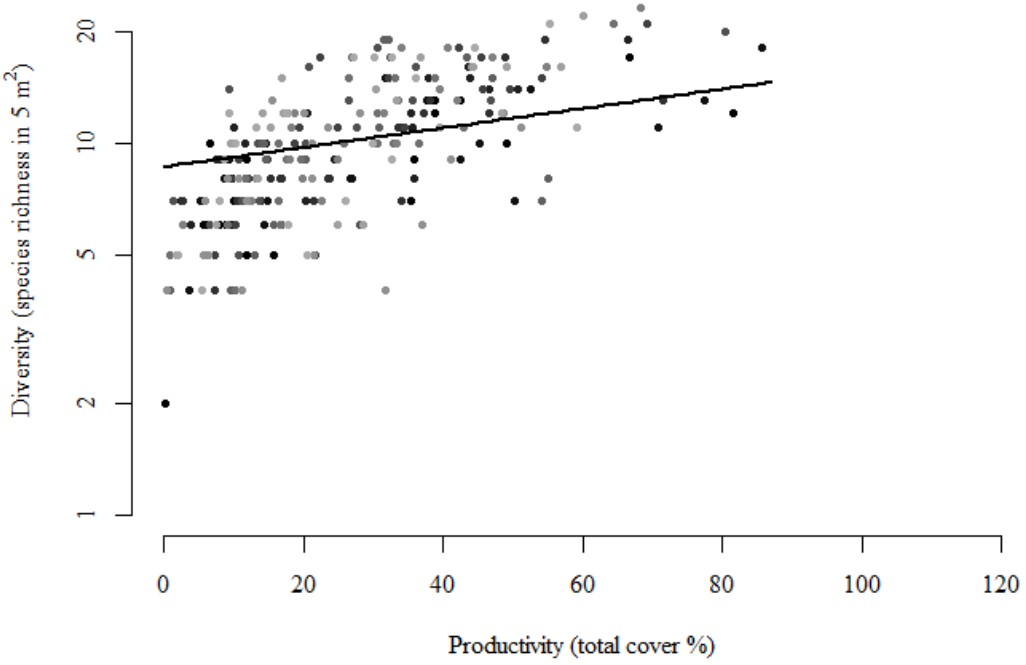

Figure 3 Relationship between productivity and diversity of vascular plant species before the wildfire (2000–2011). Cover value of 100% corresponds to 208 g/m2 live aboveground biomass. Note that diversity is shown on logarithmic scale, thus low diversity values seem to be more distant from the fitted line. Fitted line depicts the regression function for the whole data set. Shading marks time, with the darkest marking representing 2000 and the lightest marking 2011.

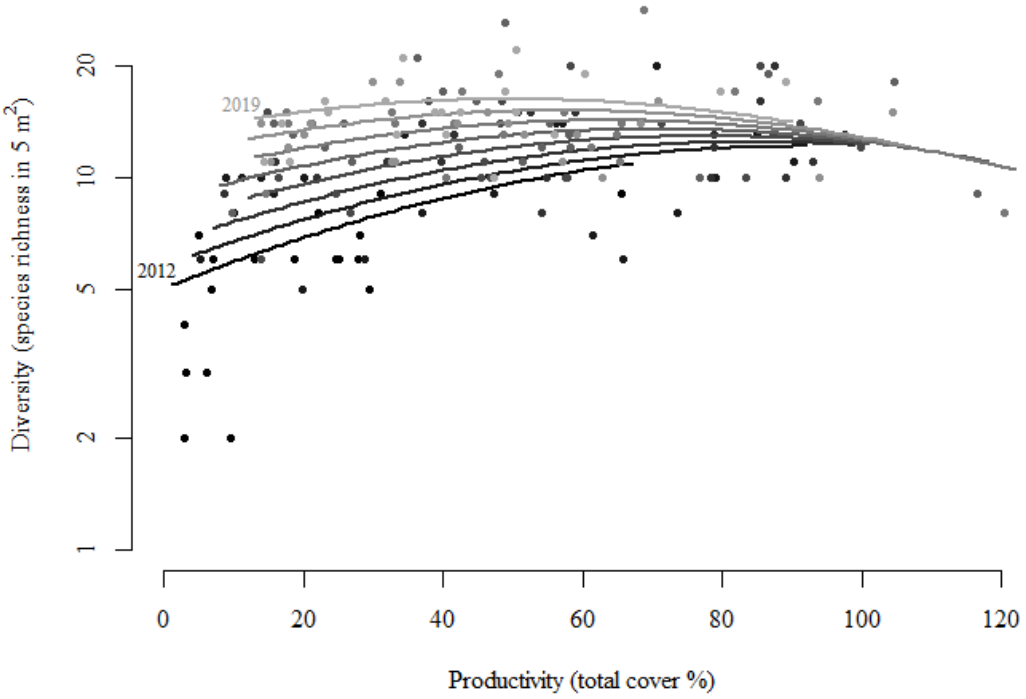

Figure 4 Relationship between productivity and diversity of vascular plant species in years after the wildfire (2012–2019). Cover value of 100% corresponds to 208 g/m2 live

aboveground biomass. Note that diversity is shown on logarithmic scale on the y-axis, thus low diversity values seem to be more distant from the fitted line. The lines depict the regression functions separately for each year. Shading marks time, with the darkest marking representing 2012 and lightest marking 2019, for both points and lines. The domains of the separate functions show the ranges of the cover values in the given years.

3.3.B

The AVS paper presents the effects of wildfire and juniper shrub encroachment on species richness and composition of open sand grasslands in Kéleshalom. *Juniperus communis* acts as a strong competitor in the studied grasslands by increasing productivity (Fig. 5) and decreasing the diversity of the colonized plots (Fig. 6c), while wildfire results in open surfaces in the studied grasslands (Fig. 6d). Similar to Case study 2, we found that increasing productivity and the lack of disturbance together lead to decreasing the diversity of the colonized plots.

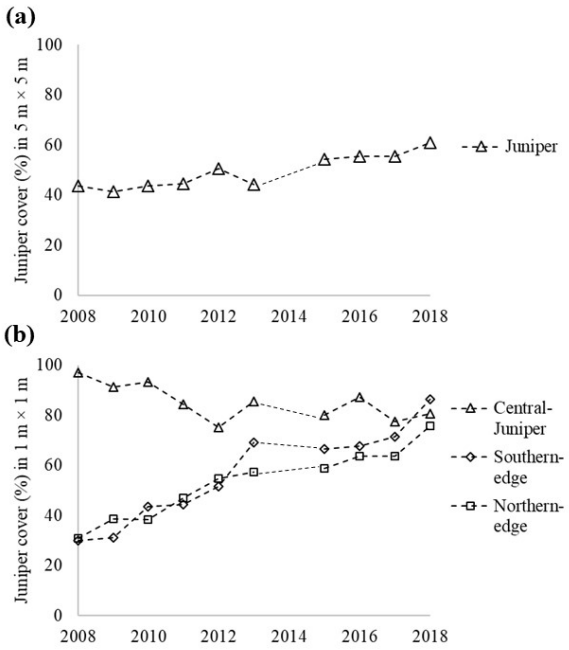

Figure 5 Increasing canopy cover of *Juniperus communis* (a) in the unburnt Juniper plots of 5 by 5 meters, and (b) in the unburnt Central-Juniper, Southern- and Northern-edge microplots of 1 by 1 meter

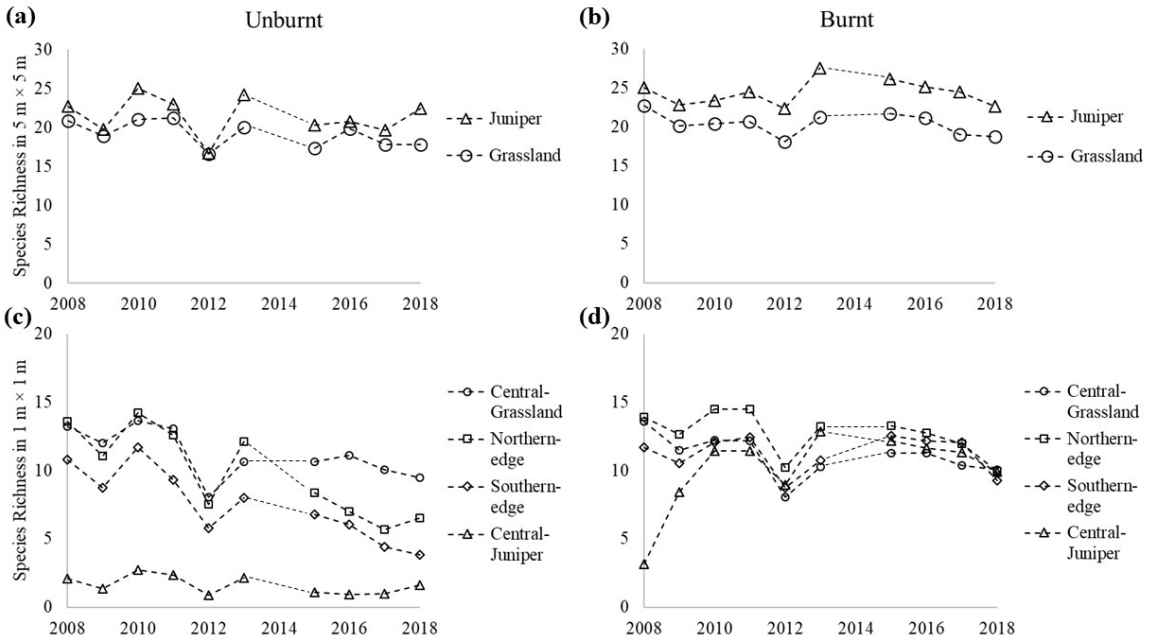

Figure 6 Changes in species richness in burnt and unburnt plots during the study period (2008-2018). Subplots (a) and (b) show results for 5 m × 5 m plots, while (c) and (d) are for 1 m × 1 m microplots

3.3.C

The PNAS paper presents the effects of species richness and synchrony on the stability of different plant communities on a global scale.

3.4. Publications

Ónodi, G., Kröel-Dulay, G., Botta-Dukát, Z., & Kertész, M. 2021. Disturbance reshapes the productivity–diversity relationship. Journal of Vegetation Science 32: e13030.

Ónodi, G., Kertész, M., Lengyel, A., Pándi, I., Somay, L., Szitár, K., & Kröel-Dulay, G. 2021. The effects of woody plant encroachment and wildfire on plant species richness and composition: Temporal changes in a forest-steppe mosaic. Applied Vegetation Science 24: e12546.

Valencia, E., Bello, F. de, Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A., Klink, R. van, Carmona, C.P., Danihelka, J., Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E., Gómez-García, D., Harrison, S.P., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N., Kertész, M., Klumpp, K., Louault, F., Marrs, R.H., Ogaya, R., Ónodi, G., Pakeman, R.J., Pardo, I., Pärtel, M., Peco, B., Peñuelas, J., Pywell, R.F., Rueda, M., Schmidt, W., Schmiedel, U., Schuetz, M., Skálová, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, M., Stock, M., Val, J., Vandvik, V., Ward, D., Wesche, K., Wiser, S.K., Woodcock, B.A., Young, T.P., Yu, F.-H., Zobel, M., & Götzenberger, L. 2020. Synchrony matters more than species richness in plant community stability at a global scale. Proceedings of the National Academy of Sciences 117: 24345–24351.