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RESEARCH ARTICLE

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Disturbance reshapes the productivity–diversity relationship

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Abstract

Question: We evaluated the effect of disturbance on the productivity–diversity relationship in a long-term monitoring study. We asked whether the same productivity–diversity relationship applies to 12 years of pre-fire (undisturbed) conditions and to eight years of post-fire succession studied in the same plots.

Location: Bugac, Kiskunság, Central Hungary.

Methods: We studied 20 permanent plots for 20 years in grassland patches of a forest–steppe vegetation complex, 12 years before (2000–2011), and eight years after (2012–2019) a severe wildfire. The cover values of each vascular plant species were visually estimated each year. We used total cover as a proxy for productivity and species richness as a measure of diversity. We assessed changes in the productivity–diversity relationship before and after the disturbance event. Temporal changes of the pre-fire and post-fire relationship were analysed separately by generalized estimation equations in the R environment.

Results: In the pre-fire period, we found a positive linear productivity–diversity relationship, and no time effect. However, in the post-fire period, we found a unimodal relationship, which changed gradually from year to year. The disturbance event moved the vegetation out of a stable state, increased the range of both productivity and diversity, and resulted in a decreasing linear component of the relationship after the fire. Our results provide a striking example of the influence of succession on the shape of the productivity–diversity relationship.

Conclusions: Disturbance may create considerable and long-lasting changes in the productivity–diversity relationship of formerly stable communities. The changing shape of the productivity–diversity relationship over time after disturbance suggests that the evaluation of broad-scale productivity–diversity relationships should control for disturbance history.

KEYWORDS

disturbance history, environmental stress, fire, humped-back model, post-fire succession, productivity–diversity relationship, semi-arid grassland, species richness, temporal pattern

1 | INTRODUCTION

The relationship between productivity and diversity is a focal issue in community ecology, and remains controversial despite a long history of study (Gillman & Wright, 2006), with competing theories and conflicting predictions (Grace et al., 2016). The humped-back model of Grime (1973, 1997) describes a unimodal productivity–diversity relationship. It suggests that plant species richness peaks at intermediate productivity because at low productivity, only a few species can tolerate the environmental stresses, while at high values only a few competitive species dominate. Since then, many studies have found hump-shaped productivity–diversity relationships, but meta-analyses have shown that there is no universal pattern, and non-significant or positive linear relationships are frequent (Waide et al., 1999; Mittelbach et al., 2001; Gillman & Wright, 2006). Since the 1990s, many authors have questioned the theory behind hump-shaped patterns because connections between biodiversity and productivity are complex (Gillman & Wright, 2006; Willig, 2011; Grace et al., 2016) and scale-dependent, both in space (Chase & Leibold, 2002) and time (Laughlin & Moore, 2009). The first global-scale studies also found conflicting results (Adler et al., 2011; Pierce, 2014; Fraser et al., 2015; Tredennick et al., 2016), and showed high spatial variability of the relationship. Recent papers highlight that more work is needed to determine the underlying causal mechanisms that drive productivity–diversity relationships (Grace et al., 2016; Duffy et al., 2017; Wang et al., 2019).

Most of the meta-analyses conducted on productivity–diversity relationships do not take into account key factors that may affect co-existence, such as disturbance history or successional state (Huston, 2014). These may contribute to highly divergent outcomes in the meta-analyses, as pointed out by Whittaker (2010). Disturbances such as drought or wildfire interact with environmental factors such as moisture, light, and nutrient availability in determining productivity–diversity relationship (Grace et al., 2007; Grace et al., 2016). Consequently, disturbances affect productivity and diversity in a complex way (Loreau et al., 2001). In particular, the effects of extreme events on diversity depend on ecosystem productivity (Huston, 2014), while their effects on productivity depend on diversity (Isbell et al., 2015; Kreyling et al., 2017). These complex connections may produce different productivity–diversity relationships at different levels of disturbance (Kondoh, 2001; Kadmon & Benjamini, 2006).

Guo (2003) studied changes in productivity–diversity relationship over time along successional gradients. While the study demonstrated that the relationship of a particular site can change over time, evidence of temporal changes after disturbance is still lacking. Temporal effects have only been included in a few studies in natural ecosystems so far (but see Cox et al., 2006; Laughlin & Moore, 2009; Li et al., 2017). These studies either lacked any disturbance effect (Cox et al., 2006; Laughlin & Moore, 2009) or did not consider annual changes following disturbance (Li et al., 2017). They showed time dependence of productivity–diversity relationships, and that disturbances influence both biomass and species richness (Grace et al., 2016; Collins et al., 2017; Sanaei et al., 2018). To our knowledge, no study to date has compared productivity–diversity relationships before and after a disturbance event.

The objective of this study was to evaluate the effect of a disturbance event on the stability of the productivity–diversity relationship. Monitoring vegetation dynamics before (Ónodi et al., 2014; Kertész et al., 2017) and after a severe wildfire in a long-term project in Bugac, Central Hungary, allowed us to detect changes in both productivity and diversity over time. We asked whether the same productivity–diversity relationship applies to 12 years of undisturbed conditions and eight years of post-fire succession observed in the same plots. The unburnt areas in the studied landscape were previously found to have a more stable species composition than the burnt areas (Kertész et al., 2017). Therefore, we hypothesized that the productivity–diversity relationship does not change over time before the disturbance, but changes after the event.

2 | METHODS

2.1 | Study site

The study site belongs to the KISKUN Long-term Ecological Research platform (KISKUN LTER, https://deims.org/124f227a-787d-4378-bc29-aa94f29e1732). It is located in the Bugac Nature Reserve of the Kiskunság National Park, central Hungary. The region has a continental climate with sub-Mediterranean influence (Zólyomi et al., 1997). Annual mean precipitation is 592 mm, and mean monthly temperatures range from −0.2°C in January to 22.1°C in July (KISKUN LTER Fülöpháza Meteorological Station, 2001–2019). The soil is calcaric arenosol with low humus content (FAO-ISRIC-ISSS, 1998), sustaining an edaphic variant of the zonal forest–steppe, the sand forest–steppe (Kovács-Láng et al., 2000; Fekete et al., 2002). The studied habitat is a fine-scale mosaic consisting of patches of open perennial sand grassland and woodlands. The grassland patches are dominated by perennial grasses (*Festuca vaginata*, *Stipa borysthenica*, and *Calamagrostis epigeios*) or by annuals (*Bromus tectorum*, *Bromus squarrosus*, and *Secale sylvestre*). The woodlands mostly consist of juniper (*Juniperus communis*) and white poplar (*Populus alba*). The grassland harbours several rare and endemic species (Molnár et al., 2012), and thus has high nature conservation value.

The sand forest–steppe is sensitive to climate change and extreme weather events (Kovács-Láng et al., 2000; Kovács-Láng et al., 2005), and has a long history of climate change impact research (Kovács-Láng et al., 2000; Ónodi et al., 2014; Kröel-Dulay et al., 2015). While the historical fire regime is unknown and the majority of the recent wildfires were human-induced (Cseresnyés & Tamás, 2014), extreme events such as drought and wildfires are predicted to become more frequent in the future in Hungary (Bartholy et al., 2009). Apparently meeting the latter prediction, the Bugac Nature Reserve was burnt in April 2012 in a severe wildfire (Szatmári et al., 2016). More details of the Bugac site can be found in the article that describes vegetation dynamics before the 2012 wildfire (Ónodi et al., 2014). The annual precipitation, which strongly affects productivity, did not show any temporal trend during the study period (Appendix S1).

2.2 | Field sampling

This study is part of an ongoing monitoring survey established in the forest–steppe vegetation of Bugac site in 1997 (Ónodi et al., 2014). Here we have used data collected since 2000, with the presence of the same personnel (GÓ and MK) guaranteeing consistency of sampling. We investigated the pre-fire (2000–2011) and post-fire (2012–2019) changes of the productivity–diversity relationship at the study site.

The samples were taken from 20 grassland patches (referred to as plots hereinafter) of the open juniper–poplar forest–steppe in two adjacent one-hectare blocks (46°38.91′ N, 19°36.43′ E; 46°38.88′ N, 19°36.21′ E) of 10–10 plots. Each plot consisted of five 1 m × 1 m subplots arranged in the five-point pattern on dice. Some of the plots contained woody species, i.e. white poplar suckers and parts of juniper shrubs growing around the plots.

Plots were sampled for canopy cover of vascular plant species twice a year, in late May or early June, and then in late September or early October, covering seasonal variation in composition, so that we collected a complete list of species each year. Species richness was considered as a measure of diversity in this study.

To estimate productivity, we chose non-destructive biomass estimation, which is widely applied in ecosystem research (Guo, 2003; Virtanen et al., 2013; Li et al., 2017; Brun et al., 2019). The cover estimate provides an accurate proxy for annual above-ground live biomass production in our habitat (Ónodi et al., 2017). According to the corresponding data set of a nearby site, the relationship between estimated cover and biomass is linear and 100% cover value corresponds to 208 g/m^2 live above-ground biomass. In our study, we consider the summation of peak covers of plant species as an estimate for primary productivity (Sala & Austin, 2000; Huenneke et al., 2001) using canopy cover values in the following way: the within-year maximum cover of each species was summed up in each subplot and then averaged for the plot (hereinafter, called total cover) to achieve a proxy of productivity in each sampling year. The cover of each vascular plant was assessed in the sampling plots, by visually estimating percentage cover between 0 and 100, while decimal fractions were used below 2% (Hahn & Scheuring, 2003). Total cover values may exceed 100% due to overlapping canopies at a certain sampling period, and also because of the summation of yearly maximum covers of each species, which were sometimes reached at different sampling periods (Ónodi et al., 2017).

TABLE 1 Generalized linear models of relationship between productivity and diversity of vascular plants

Explanatory variables	Estimate	Std. error	Wald test	*p*
2000–2011				
Intercept	2.3155	0.0700	1,094.3	<0.001
Total cover	0.1213	0.0337	12.90	<0.001
2012–2019				
Intercept	2.5039	0.0536	2,180.55	<0.001
Total cover	0.1376	0.0298	21.28	<0.001
Year	0.1829	0.0259	49.68	<0.001
Squared total cover	−0.0649	0.0229	8.06	0.005
Total cover * Year	−0.0762	0.0259	8.66	0.003

Note: In the case of years 2000–2011, model selection excluded the following variables: year and its interactions and squared total cover; while for the years 2012–2019 only the interaction squared total cover ∗ year was excluded.

2.3 | Statistical analyses

We analysed productivity–diversity relationship following traditional settings; thus diversity (in our case species richness) was the dependent variable, while productivity (in our case total cover) was the independent variable, including its quadratic term to allow the humped-back shape of the curve. Since we tested possible temporal changes of curves, sampling year and its interaction with linear and quadratic terms of total cover were also included in the full model. To avoid collinearity between linear and quadratic terms and improve interpretability of parameters, cover and year were centred and standardized to unit standard deviation (Schielzeth, 2010). Since species richness values are discrete, we assumed that they follow a Poisson distribution and applied a log link function. Productivity values may be temporally auto-correlated; therefore, models were fitted by generalized estimation equations (Liang & Zeger, 1986) using first-order autoregressive [AR(1)] correlation structure. The geeglm function does not set the scale parameter to 1 in the case of a Poisson distribution but estimates it from the data (as with the quasi-Poisson distribution in GLM), allowing overdispersion. To improve parameter estimates, the full model was sequentially simplified, by removing at each step the term with the highest *p*-value in a Wald test comparing the full and restricted models, until all non-significant terms were removed. The potential spatial auto-correlation was graphically checked by plotting residuals against blocks, and there was no significant block effect. Data from before and after fire periods were analysed separately. Analyses were done in the R environment using the *geepack* package (Halekoh et al., 2006).

3 | RESULTS

In the pre-fire period (2000–2011), only the linear effect (see Table 1: total cover) was significant on species richness, while the year, the quadratic effect (squared total cover), and interactions between the variables were not. Thus, there is one general (i.e. time-independent) linear productivity–diversity relationship, based on the model applied (Figure 1).

In the post-fire period (2012–2019), the linear effect (total cover), the year, the quadratic effect (squared total cover), and the interaction between the year and the linear effect were found to significantly affect species richness (Table 1). Therefore, we represented the productivity–diversity relationship with a series of yearly quadratic (unimodal) functions (Figure 2). The linear component of the function decreases from the first year: in the first year after the fire, the relationship seems almost linear, becoming less steep and more unimodal later.

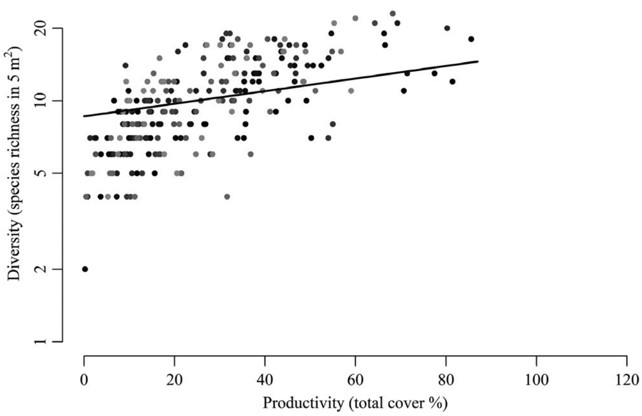

FIGURE 1 Relationship between productivity and diversity of vascular plant species before the wildfire (2000–2011). The cover value of 100% corresponds to 208 g/m^2 live above-ground biomass. Note that diversity is shown on a logarithmic scale, thus low diversity values seem to be more distant from the fitted line. The fitted line depicts the regression function for the whole data set. Colouring marks time, with the darkest marking representing 2000 and lightest marking 2011. Data points are plotted using a non-transformed *y*-axis in Appendix S4

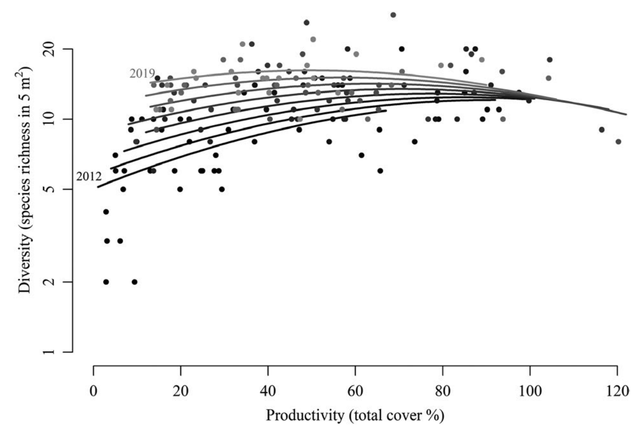

FIGURE 2 Relationship between productivity and diversity of vascular plant species in years after the wildfire (2012–2019). The cover value of 100% corresponds to 208 g/m^2 live above-ground biomass. Note that diversity is shown on a logarithmic scale on the *y*-axis, thus low diversity values seem to be more distant from the fitted line. The lines depict the regression functions separately for each year. Colouring 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. Data points are plotted using a non-transformed *y*-axis in Appendix S5

4 | DISCUSSION

We found a stable productivity–diversity relationship before the wildfire, while the relationship changed gradually from year to year after the fire, in line with our research hypotheses. Furthermore, before the fire, the relationship was positive linear, while a significant quadratic component made it unimodal after the fire. Consequently, our results show a strong disturbance effect on the productivity–diversity relationship. This suggests that the disturbance moved the vegetation out of a stable state, by initiating a post-disturbance succession. The productivity–diversity relationship showed directional change over time after the fire, similar to the temporal changes described by Guo (2003). Furthermore, the pattern of changes with decreasing disturbance effect (i.e. increasing time elapsed since the disturbance) matches the productivity–disturbance–diversity model of Kondoh (2001). Our study offers a unique opportunity to assess changes in the productivity–diversity relationship in a vegetation complex both before and after a strong disturbance event. It fulfils all the three criteria of Gou (2003): (a) both diversity (i.e. species richness) and productivity (i.e. total cover) were monitored; (b) the study covered a long successional sequence; and (c) all vascular plant species were recorded.

Humped-back productivity–diversity relationships are more often detected at a regional scale than locally (Rajaniemi, 2003). Thus, the extension of local studies to a regional scale, i.e. across community boundaries, may lead to the appearance of the quadratic effect (Mittelbach et al., 2001; Brun et al., 2019). On the contrary, we conducted a local-scale monitoring study (fine grain, cf. Whittaker, 2010; Virtanen et al., 2013), which was started in an open sand grassland community containing few white poplar and common juniper shrubs. Until the wildfire, we detected a positive linear relationship without a significant quadratic component. Although according to Gou (2003) this relationship is typical of vegetation of an early successional stage, we found it to be stable through time. This stable relationship is probably the consequence of the limited changes in local species composition in the studied grassland patches (Ónodi et al., 2014) during a slow patch dynamics of unburnt stands (Kertész et al., 2017). The maximum species richness occurred at a moderate cover level without decreasing diversity at the high-productivity end, similar to findings of other vegetation studies in semi-arid habitats (Zhou et al., 2006; Ashouri et al., 2016; Fattahi et al., 2017). 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.

A local-scale investigation may provide a unimodal productivity–diversity relationship in case of extension in time, pooling more stages of the successional sequence (Guo, 2003). The few published case studies on temporal changes in this relationship do not explicitly deal with the effect of disturbance. However, they all show a decreasing diversity at the high-productivity end of the relationship when later successional stages are involved. In line with our results, each of these studies reported a considerable change in the productivity range. Guo (2003) detected it at the end of a four-year study of post-fire succession in semi-arid shrublands, Li et al. (2017) found it during the later stages of old-field succession, and Laughlin and Moore (2009) noticed that it appeared as the effect of wet years in a semi-arid habitat. In our case, the humped-back shape of the productivity–diversity relationship developed gradually after the fire, and it has been formed by summation of the eight post-fire unimodal curves of subsequent years.

In contrast to former studies, we showed that the shape of the relationship changed as a function of time since the disturbance. After the wildfire, both productivity and diversity increased in the study plots; however, different plant functional groups contributed to different degrees to these changes. The short-lived group (annuals and biennials) increased both in species richness (pre-fire vs. post-fire means were 2.9 vs. 4.9) and in cover (1.1% vs. 3.2%), while the long-lived group (herbaceous and woody perennials) did not have an increased richness compared to pre-fire level (7.6 vs. 7.4), but yielded the bulk of the cover increase (25.4% vs. 42.1%, see also Appendices S2, S3). According to former investigations conducted in this habitat, the flora does not change after fire, but some large and deep-rooting long-lived species (*Populus alba*, *Stipa borysthenica*, and *Calamagrostis epigeios*) may become temporarily dominant (Ónodi et al., 2014; Kertész et al., 2017). We suggest that the expansion of the productivity range towards higher values after wildfire was driven mainly by persistent long-lived species, while the species richness of short-lived plants increased without a considerable further increase in productivity. In combination, these changes are responsible for the increase in diversity of the low-productivity plots, and thus for the temporal decrease of the positive linear component of the productivity–diversity relationship. In line with our results, Zhou et al. (2006) found significantly altered productivity–diversity relationships at different intensities of disturbance in a semi-arid steppe ecosystem. As the effect of disturbance caused by fire diminished with time, the slope of the linear component of the productivity–diversity relationship changed from increasing to decreasing, in consonance with the findings of Kondoh (2001) and Kadmon and Benjamini (2006).

Disturbance effects on the shape of the relationship may have important implications for broad-scale studies, which are based on snapshots of multiple sites and are rarely checked for disturbance (Huston, 2014). In a recent worldwide study (Fraser et al., 2015), a hump-shaped relationship was found to be generally valid in grasslands. While this study reported various disturbance histories such as fire and grazing in the different sites, it was not stratified according to disturbance. Furthermore, as a selection criterion, they applied a three-month-long regeneration time after the last disturbance, which is much shorter than the duration of the disturbance effect on the productivity–diversity relationship in our study. Pierce (2014) also found a hump-shaped relationship after the reanalysis of a former global-scale study (Adler et al., 2011). However, the productivity–diversity relationship has been considered sensitive to site selection in these studies (Pierce, 2014; Tredennick et al., 2016). Pierce (2014) questioned the exclusion of some habitats considered outliers in the original analysis of Adler et al. (2011). They applied upper boundary regression (i.e. curve-fitting only the top 20 points in each 100 g/m^2 productivity interval) for the whole data set without considering anthropogenic disturbance history, which resulted in a unimodal relationship (Pierce, 2014). However, even the upper limit of species richness may increase at high and decrease at low productivity due to disturbance (Kondoh, 2001; Rajaniemi, 2003), causing steeper and more linear productivity–diversity relationships in more disturbed habitats (Kondoh, 2001; Kadmon & Benjamini, 2006), similar to the relationship we found in the year of the fire. Although the productivity range of our study plots is at the lower level of the mentioned global studies (below 300 g/m^2, see also Fraser et al., 2015), and similar studies in productive grasslands are still wanting, our results call for multivariate approaches in order to reveal linkage between productivity and diversity (Grace et al., 2016; Wang et al., 2019). Otherwise, including sites in broad-scale bivariate analyses focusing only on the effects of productivity on biodiversity requires consistent control for disturbance history (Zhou et al., 2006; Grace et al., 2007; Graham & Duda, 2011; Virtanen et al., 2013). This is particularly true at the extremities of the productivity range because these points may strongly influence the regression parameters due to their high leverage (Zuur et al., 2007).

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. While broad-scale studies may help to explain global patterns and global-change effects on both biodiversity loss and productivity changes, their results may depend on controlling for environmental covariates (Duffy et al., 2017) and site selection (Pierce, 2014; Tredennick et al., 2016). We have presented striking changes in the productivity–diversity relationship after disturbance. This suggests that controlling for disturbance is desirable in multi-site studies.

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AUTHOR CONTRIBUTIONS

GÓ conceived the study. MK and GÓ contributed to data collection. ZB-D and GÓ performed statistical analyses. GÓ led the writing of the manuscript with major input from GK-D and MK. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article (Appendix S3).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Diagram of annual precipitation at the study site during the study period.

Appendix S2. Diagrams of changes in total cover and species richness in different species groups.

Appendix S3. Original data tables.

Appendix S4. Diagram of data points in Figure 1 using non-transformed *y*-axis.

Appendix S5. Diagram of data points in Figure 2 using non-transformed *y*-axis.

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