

Extreme droughts in oligotrophic mountain grasslands cause substantial species abundance changes and amplify community filtering

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Abstract

Questions: Mountain grasslands can be strongly affected by extreme droughts such as those related to climate change. What are the impacts of extreme droughts on community composition, diversity, Ellenberg indicator scores and species groups in oligotrophic montane *Nardus* grasslands, and what are the associated mechanisms of vegetation change?

Location: Rhön Mountains, Germany.

Methods: Over three consecutive years, we investigated the effects of yearly droughts (April–August) in an experimental setup with rainout shelters. Owing to the coincidence of ambient extreme dry conditions in those years and our artificial rainfall reduction, we evaluated the contribution to community change of ambient drought conditions and the treatments. We analysed changes in community composition by applying redundancy analysis to species differences in comparison with the pretreatment year, and used mixed-effects models to test for changes in community-weighted means of Ellenberg indicator scores, sociological and functional groups.

Results: We found significant changes in species abundance and community structures in response to drought. Evenness increased, but species richness remained rather stable over time. Ellenberg indicator scores for temperature and nitrogen increased, whereas the score for moisture decreased. Simultaneously, dominant species declined and subdominants increased. Changes occurred with a time lag and were driven largely by the high ambient drought level and less by the artificial treatments.

Conclusions: Our results show that drought-related changes in community composition in *Nardus* grasslands occur across community structures, characteristic species, and species groups. The post-drought recovery of the community is shaped by community filters, which in particular allow subdominants to take advantage of newly available niches in the matrix, even if they lack strong drought tolerance. Our findings indicate a certain resilience of the community to droughts related to climate change, which suggests that the observed changes should not lead to an accelerated short-term decline in these grasslands, but that this cannot be excluded in the long term.

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KEYWORDS

climate change, community diversity, *Nardus* grasslands, rainout shelter experiment, semi-natural mountain grasslands, species composition, vegetation change

1 | INTRODUCTION

Semi-natural grasslands are one of the most biodiverse ecosystems worldwide and provide multiple ecosystem services, particularly those related to fodder and livestock production and to cultural services (Bengtsson et al., 2019). However, these ecosystems are increasingly exposed to the impact of climate change, which is especially the case for mountain grasslands, because climatic conditions are important factors for their biodiversity and these are expected to change in the future (Bellard et al., 2012). However, many open questions remain about how the species composition of specific types of semi-natural grasslands responds to climate change impacts such as droughts (Gibson & Newman, 2019).

Seasonal droughts affect semi-natural grasslands differently. For example, spring and summer droughts have significant impacts on the diversity of grasslands, causing not only temporal, but also permanent changes in community composition and plant fitness (Gellesch et al., 2017; Ploughe et al., 2019). Studies in subalpine-mountain and in calcareous grasslands, however, have reported relatively high resilience in species and functional composition after short-term extreme droughts, but a marked decline in forage yields (Deléglise et al., 2015; Grime et al., 2008). Similarly, artificial drought in species-poor *Nardetalia* grasslands did not lead to considerable changes, either in dominant species or in above-ground biomass (Holub et al., 2013). Because of the given uncertainty and complexity of the impacts, the direction and net effects of droughts on vegetation in terms of community diversity, composition changes, and species functional composition of semi-natural mountain grasslands are currently poorly predictable (Fischer et al., 2020). This might particularly be the case in infertile grasslands that have been shown to be inherently slow to change (Pakeman, 2004).

Species-rich montane *Nardus* grasslands are typical semi-natural grasslands on oligotrophic, poorly buffered acidic soils in mountain areas (Peppler-Lisbach & Petersen, 2001). Despite their high conservation value and formerly wide distribution in Europe, different environmental drivers have led to a strong and widespread decline (Schwabe et al., 2019). For example, abandonment as well as later intensified land use led to a strong decline and degradation of remaining habitats, in which either nitrophilous plants or the dominance of *Nardus stricta* became problematic and reduced the habitat's biodiversity (Kurtogullari et al., 2020). On the other hand, eutrophication by nitrogen and reduced soil acidity led to significant changes in soil conditions and species composition (Peppler-Lisbach et al., 2020). Despite this well-developed knowledge about past and current vegetation changes in *Nardus* grasslands, we know little about the future impacts of droughts (Streitberger et al., 2016), which are not only projected by climate change scenarios for central Europe

(IPCC, 2014), but were also experienced recently in two consecutive drought years (2018 and 2019) (Hari et al., 2020).

Taking advantage of these extreme climate conditions in 2018/2019, we used an experimental setup installed in 2017 to investigate the effects of such drought conditions in spring and summer on montane *Nardus* grasslands. Originally, the experimental setup with rainout shelters aimed to investigate the effects of drought stress during the growing season, as projected by regional climate change scenarios (PIK/Potsdam Institute for Climate Impact Research, 2017). Ambient drought conditions in all years of the experiment, however, led to a natural water supply reduced to, or even beyond, that planned for the moderate drought treatment over the annual experimental term. Nonetheless, these circumstances gave us the opportunity to assess the common and partial effects of extreme droughts in combination with the designed further reduction in precipitation.

We expected: (a) changes in the structural parameters of the community (e.g., a decline in total cover and vegetation height); (b) shifts in plant-community composition towards more drought-tolerant and more thermophilous species (e.g., indicated by a decrease in Ellenberg indicator score for moisture and an increase in the indicator score for temperature, respectively) (Beierkuhnlein et al., 2014); and (c) a decline in *Nardus* grassland character species, especially those with a distinct montane distribution that have been shown to be sensitive to drought, like *Arnica montana* (Stanik et al., 2020), and that are expected to decline under climate change (Trivedi et al., 2008). Based on these expected changes, we would be able to evaluate whether the community shows signs of resilience to different drought levels.

2 | METHODS

2.1 | Site description

The study site is located in the Rhön Mountains, a lower mountain range in central Germany. The experimental field is situated on a lateral plateau built on Tertiary basalt on the northeastern slope of the Wasserkuppe massif (50°30'25"N, 9°57'22"E; 813 m a.s.l.). The soil type at the site is a skeletal brown earth with 47.1% (SD 2.1) silt, 47.0% (SD 2.6) clay, and 5.9% (SD 1.1) sand. The mean topsoil pH (H₂O) value is 4.06 (SD 0.09) and was not significantly different among treatment plots (ANOVA: $F_{2,9} = 0.817$, $p = 0.472$). The study site and plot positions were selected to minimise environmental heterogeneity within and among plots and to be representative of the plant species community of the grassland location. The dominant plant communities are oligotrophic montane *Nardus* grasslands (*Nardetalia strictae*, *Violion caninae*) (Peppler-Lisbach & Petersen,

2001). A mean of 22 ± 2.9 plant species per plot was observed in this grassland at the beginning of the experiment. Most dominant species were narrow-leaved grasses, such as *Nardus stricta*, that comprised on average 65% of the cover in the pretreatment vegetation. Small-growing forbs, like *Potentilla erecta* and *Galium saxatile*, were also frequently present in the sward. This threatened habitat type is classified as a priority natural habitat (H6230*) by the EU Habitats Directive (Council Directive 92/43/EEC; European Council, 1992), thus conservation efforts by EU Member States aim to protect these grasslands in a favourable conservation state. Owing to the strict conservation requirements of the habitat at the study site, it was not possible for us to install measurement devices in or to make destructive sampling of the soil.

2.2 | Experimental design

In a fully randomised design with four replicates ($n = 12$), we simulated the effects of droughts on the grassland community between April and August over multiple years. The experimental site was set up in 2017, at which point we documented the pretreatment state of the vegetation. In that year, only the management of the grassland and not a reduction in precipitation was carried out. The intended drought simulation using rainout shelters was carried out in 2018, 2019, and 2020. For the rainout shelters, we followed construction guidelines from Yahdjian and Sala (2002) and recommendations of Vogel et al. (2013) and Kundel et al. (2018); the shelters have been shown to successfully reduce soil moisture (Carlyle et al., 2011). To minimise edge effects and lateral water input, the shelter ($3 \text{ m} \times 3 \text{ m}$) was constructed with a buffer zone of 50 cm on each side of the vegetation plot ($2 \text{ m} \times 2 \text{ m}$). Shelter roofs were made of 0.8-mm thick transparent trapezoid polycarbonate slats with 88% visible light transmission (Marlon CS Longlife; ThyssenKrupp Plastics). Greenhouse effects due to the rainout shelters were minimised by having an 80-cm space between the lower roof edge and the ground (Kreyling et al., 2017).

We installed drought treatments according to future monthly precipitation regimes for a period in spring and summer, as projected for the second half of the 21st century by the regionally specified RCP 4.5 climate change scenario for the Rhön Mountains (PIK/Potsdam Institute for Climate Impact Research, 2017). To define our drought treatments, we derived a moderate and a strong climate-change trajectory compared with the reference period (1961–1990). For the moderate (R30) and strong (R60) drought treatment, by arranging the roofing slats with wider and closer spacing, respectively, the rainout shelters reduced the ambient precipitation between 1 April and 30 August of each experimental year (2018–2020) by 30% and 60%, respectively. Following the projections, we did not reduce precipitation in the potential rainfall surplus period in autumn and winter, during which the climatic water balance is expected to be positive, and which would allow a phase of vegetative recovery. Thus, rainout shelters were removed by the end of August. The controls (KOD) remained unroofed and received ambient precipitation

amounts during that time. All plots were managed by once-a-year mowing on the date (15 July) used in traditional management of mountain grasslands in the study region. This regime had been applied to the whole grassland site as studied for at least 15 years before the current experiment.

2.3 | Environmental conditions

Climate parameters at the study site were recorded regularly. Temperature and humidity were logged hourly with EasyLog EL-USB-2 data loggers (Lasca Electronics Ltd, UK), which were shielded from sun exposure by thin white panels and were placed 40 cm above the ground in the experimental plots and, for the ambient climate of the study site, 2 m above the ground. To account for the combined effects of temperature and humidity (De Boeck et al., 2016), we used these measurements to calculate the vapour pressure deficit (VPD; Allen et al., 2018). Data on daily precipitation for the site were retrieved from the nearby weather station Wasserkuppe (1.4 km from the experimental site on the same massif) because no more closely situated measurement facilities were available (DWD Climate Data Center, 2020).

The experiment fell within a period of extreme climate conditions. Compared with the long-term climate of the study area, conditions during the experimental period were hotter and dryer, with 2018 being the most extreme year (Hari et al., 2020). Thus, the climate conditions of the experimental plots were decisively influenced by the ambient climate of each experiment year. Compared with precipitation during the annual experiment term (April to August) in the reference period (1961–1990), with a mean of 504.1 mm, and the pretreatment year 2017 with 580.1 mm, all experiment years had lower amounts of precipitation (2018: 285.9 mm; 2019: 366.0 mm; 2020: 378.9 mm) (Appendix S2.1). Thus, compared with the long-term mean for the reference period, the plots experienced a rainfall input reduced by –43%, –27%, and –24% in the experimental periods in 2018, 2019, and 2020, respectively. Moreover, drought notably coincided with high evapotranspiration. When compared with the reference period, temperature was significantly higher in the pretreatment year (2017) and all experimental years (2018–2020), but humidity was lower and VPD higher only in the experiment years (Appendix S2.2–S2.5).

Comparing the years 2018–2020 with the pretreatment year (2017), only 2018 showed differences in all climatic parameters (Appendix S2.6). Comparing treatments, there were no differences in temperature ($F_{2,50} = 0.127$, $p = 0.881$), humidity ($F_{2,50} = 0.776$, $p = 0.466$) or VPD ($F_{2,50} = 0.486$, $p = 0.618$) in the experimental years (2017–2020). To test the validity of the rainfall reduction induced by the rainout shelters and their additional drought effect under these naturally extreme climate conditions, differences in the soil-water content of the topsoil were measured after all other measurements had been carried out and after a 5-day rainfall period totalling 82.7 mm in August 2020. The reduction in precipitation due to the rainout shelters resulted in a significantly reduced

soil-water content in the strong drought treatment (R60), whereas the soil-water content in the moderate drought treatment (R30) was slightly, but not significantly, lower (Appendix S3). These climatic conditions, however, gave us the opportunity to evaluate the effects of the extreme ambient climate on *Nardus* grasslands compared with artificial drought as intended by the experimental design.

2.4 | Data collection and analysis

Vegetation and community structures were surveyed annually in mid-July by the same observer prior to management of the plots, using phytosociological relevés with a percentage scale (Dierschke, 1994). As community structures, we surveyed herb layer cover and height, moss cover and height, and litter cover. Following Facelli and Pickett (1991), we defined litter as undecomposed, dead plant material either standing and still attached and/or detached lying loose on the ground. The nomenclature follows the German taxonomic reference list (GermanSL, version 1.3; Jansen & Dengler, 2008). We assigned species to species groups according to two criteria (Appendix S1). First, we defined sociological groups based on their occurrence in certain syntaxa and, in the case of two groups, in combination with their nutrient demand:

1. Character species (*Nardetalia* specialists in open habitats according to Pepler-Lisbach & Petersen, 2001)
2. Low-productive grassland species (other species of anthropo-zoogenic heathlands/grasslands with an Ellenberg indicator score for nitrogen (N) of <4, according to Ellenberg et al., 2001),
3. Species of agricultural grasslands (species of anthropo-zoogenic heathlands/grasslands and with an Ellenberg indicator score for N of ≥ 4 , according to Pepler-Lisbach et al., 2020).

Second, we assigned species to basic functional groups: graminoids (all Cyperaceae, Juncaceae and Poaceae) and forbs. All other species were assigned as indifferent. For each relevé, we calculated community-weighted means (CWM) of Ellenberg indicator scores (Ellenberg et al., 2001) for temperature (T), moisture (F), and nitrogen (N), and the different sociological and functional groups by using the package *weimea* (version 0.1.18; Zelený, 2020). CWMs of these metrics proved to be informative not only for community properties, but also for ecosystem functioning (Garnier et al., 2004).

All statistical analyses were conducted in R (version 4.1.0; R Core Team, R Foundation for Statistical Computing, Vienna, AT). Data exploration was carried out following the protocol described in Zuur et al. (2010). To evaluate the effects of experimental treatment and year on changes in plant community composition (in terms of changes in the richness and relative abundance of species), we employed redundancy analyses (RDA) on species abundance changes per experimental year (2018–2020) compared with their pretreatment cover values in 2017 ($\Delta\sqrt{\text{cover}}$) of the vascular plant species

as response data). We used differences in species cover to account for repeated measurements and for the small-scale spatial species variability among the experimental units in our in situ replicated design (Kreyling et al., 2018). The significance of predictor variables and their interaction in the RDA was tested with Monte Carlo permutation tests (999 permutations), in which we considered plotID as strata to account for spatial autocorrelation. To complement RDA, we employed variance partitioning to quantify common and partial effects of treatment and year on changes in community composition. To compute the ordinations and their consecutive tests, we used the *vegan: Community ecology* package (version 2.5-6; Oksanen et al., 2019).

To analyse effects of treatment and year and their interaction on community structures (herb layer height: log-transformed to improve normality), community diversity (evenness and species richness; Pielou, 1966), Ellenberg indicator scores, and sociological and functional groups, we used the mixed-model approach (linear mixed-effects models for numeric data, and generalised linear mixed-effects models with Poisson error distribution for count data) and conducted consecutive ANOVA comparisons. All mixed models contained a corresponding response variable mentioned above as the dependent variable, treatment (three-level factor) and year (four-level factor) as independent variables and the plotID as random intercept to account for repeated measurements. Models were fitted with Restricted Maximum Likelihood using the package *lme4* (Bates et al., 2015).

3 | RESULTS

3.1 | Effects on plant community composition

Community composition changed markedly over the course of the experiment, as manifest in changes in cover rather than occurrence. We found a significant relationship between changes in community composition, compared with 2017, and treatment and year ($F = 9.676$, $p < 0.001$), which explained 55.53% of the total compositional variance. Year proved to be the most influential factor ($F = 15.243$, $p < 0.001$), before treatment ($F = 4.108$, $p < 0.001$), although their interaction was not significant. Variance partitioning quantified the partial effect of treatment and year as 0.064 and 0.433 (adjusted R^2), respectively. The R^2 value of the common effect was -0.03 . The results of the RDA are summarised by the ordination diagram in Figure 1. Axis 1 reflects mainly changes in community composition over the years (negative axis scores for 2018 and 2019, and positive scores for 2020). Axis 2 separates 2018 from 2019 plots and is additionally related to differences among treatments, with positive axis scores more associated with the control (KOD), and negative scores related to treatment R30. Unexpectedly, R60 plots showed an intermediate position. The relevés of 2018 had a positive association with temperature and VPD, and a negative association with humidity. Contrary to our

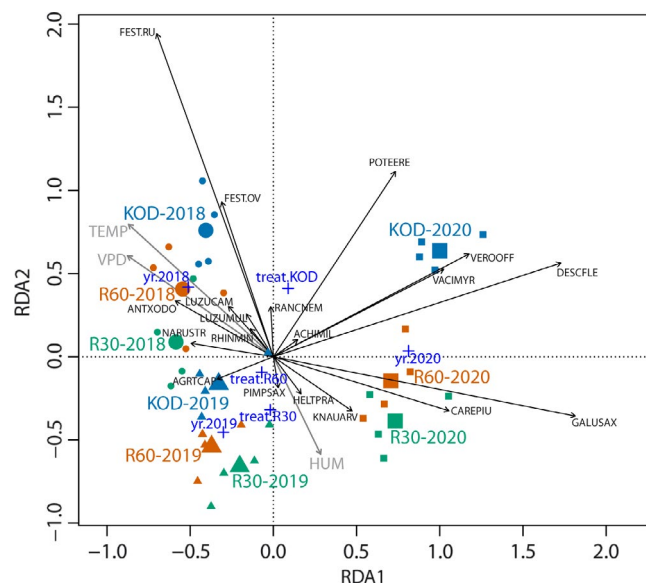


FIGURE 1 Ordination diagram of the redundancy analyses (RDA) for differences in species cover values compared with the pretreatment year (2017) as a function of year (yr.: 2018–2020) and drought treatment (treat.: KOD, control; R30, 30% reduction; R60, 60% reduction). Symbols: circles, 2018; triangles, 2019; squares, 2020. Large symbols indicate the centroid of each group. Inclusion criteria for species being displayed in the diagram (black arrows) were an explained variance >15% on axis 1 or 2. Species' codes: ACHIMIL, *Achillea millefolium*; AGRTCAP, *Agrostis capillaris*; ANT XODO, *Anthoxanthum odoratum*; CAREPIU, *Carex pilulifera*; DESCFLE, *Deschampsia flexuosa*; FEST.OV, *Festuca ovina* agg.; FEST.RU, *Festuca rubra* agg.; GALUSAX, *Galium saxatile*; HELTPRA, *Helictotrichon pratense*; KNAUARV, *Knautia arvensis*; LUZUCAM, *Luzula campestris*; LUZUMUL, *Luzula multiflora*; NARUSTR, *Nardus stricta*; PIMPSAX, *Pimpinella saxifraga*; POTEERE, *Potentilla erecta*; RANCNEM, *Ranunculus nemorosus*; RHINMIN, *Rhinanthus minor*; VACIMYR, *Vaccinium myrtillus*; VEROOFF, *Veronica officinalis*. HUM, annual experimental term mean humidity; TEMP, annual experimental term mean temperature; VPD: annual experimental term mean vapour pressure deficit

expectation, species that increased during strong drought years did not increase consistently with the concurrent experimentally intended drought treatments.

Changes in species cover were mostly associated with time, which corresponds to the identified role of year. Grasses, like *Festuca rubra* agg., *Festuca ovina* agg., *Anthoxanthum odoratum* and *Agrostis capillaris*, responded with a pronounced increase in cover in 2018, but declined markedly during the following two years. By contrast, the dominant graminoid *Nardus stricta* declined over the whole period. However, during 2018 and 2019 many species were stable in cover and first showed changes in 2020. For example, *Vaccinium myrtillus*, *Veronica officinalis*, and *Deschampsia flexuosa* increased in 2020, and this was more pronounced in the control plots, whereas *Knautia arvensis*, *Carex pilulifera*, and *Galium saxatile* increased predominantly under the drought treatments (R30, R60). Hence, changes in species cover were mostly nonlinear and became clear after two consecutive years of extreme drought.

3.2 | Effects on community diversity, community structures and Ellenberg indicator scores

We found a significant influence of year on evenness ($F_{3,27} = 43.78$, $p < 0.001$), which increased in 2018 ($\beta = 0.12$, $p < 0.001$), fell to the pretreatment level in 2019 and increased again in 2020 ($\beta = 0.13$, $p < 0.001$). The effect of treatment ($F_{2,9} = 5.684$, $p = 0.025$) on evenness was higher under the moderate drought treatment (R30) ($\beta = 0.06$, $p = 0.041$). The significant interaction between treatment and year ($F_{6,27} = 2.527$, $p = 0.045$) reflected the greater increase in evenness in the strong drought treatment (R60) towards 2020. No significant effect of treatment, year or their interaction was detected on species richness, although slightly increasing means suggested a positive trend (Appendix S4.1–S4.2). Most community structures of the grassland were influenced by both treatment and year (Figure 2; Appendix S4.3). The herb layer was influenced only by year ($F_{3,27} = 23.825$, $p < 0.001$), with significantly lower herb cover only in 2019 under all treatments. We could not detect any influence of treatment, or the interaction between treatment and year, on this parameter. We did find a significant influence of treatment ($F_{2,9} = 5.571$, $p = 0.026$) and the interaction between treatment and year ($F_{6,27} = 3.127$, $p = 0.019$) on herb layer height, which in 2019 already identifies the earlier decrease in herb height in both drought treatments, whereas the influence of year ($F_{3,27} = 150.365$, $p < 0.001$) first became significant in the control plots in 2020. Furthermore, moss layer cover was influenced by treatment ($F_{2,9} = 75.307$, $p < 0.001$), year ($F_{3,27} = 144.768$, $p < 0.001$) and the interaction between both factors ($F_{6,27} = 34.328$, $p < 0.001$). Under both drought treatments, moss cover declined earlier and markedly stronger than in the control and showed less recovery after 2018. A comparable pattern was observed for moss layer height, which was significantly influenced by treatment ($F_{2,9} = 26.123$, $p < 0.001$), year ($F_{3,27} = 22.686$, $p < 0.001$) and the interaction between treatment and year ($F_{6,27} = 4.827$, $p = 0.002$). For the litter layer cover, we detected a significant influence of year in all plots ($F_{3,27} = 221.896$, $p < 0.001$), mostly due to increasing values until 2019, and a subsequent moderate decline in 2020. Moreover, a significant influence of treatment ($F_{2,9} = 10.893$, $p = 0.004$), and an interaction between treatment and year ($F_{6,27} = 6.355$, $p < 0.001$), reflect higher litter accumulation in both drought treatments over the years compared with the control, especially in 2018. Hence, community structures responded immediately to factors that relate to ambient and artificial drought in the experiment.

Ellenberg indicator scores for temperature, moisture, and nitrogen changed according to changes in plant community composition (Figure 3; Appendix S4.4). We detected a significant difference in Ellenberg T score among drought treatments ($F_{2,9} = 18.836$, $p < 0.001$), with higher scores in the moderate (R30) and strong (R60) drought treatments. Moreover, Ellenberg T score was influenced by year ($F_{3,27} = 111.724$, $p < 0.001$), with significantly increased scores in 2018 ($\beta = 0.09$, $p = 0.032$) and 2020 ($\beta = 0.28$, $p < 0.001$). A significant interaction between treatment and year ($F_{6,27} = 4.389$, $p = 0.003$) reflected the gradually increasing difference in Ellenberg

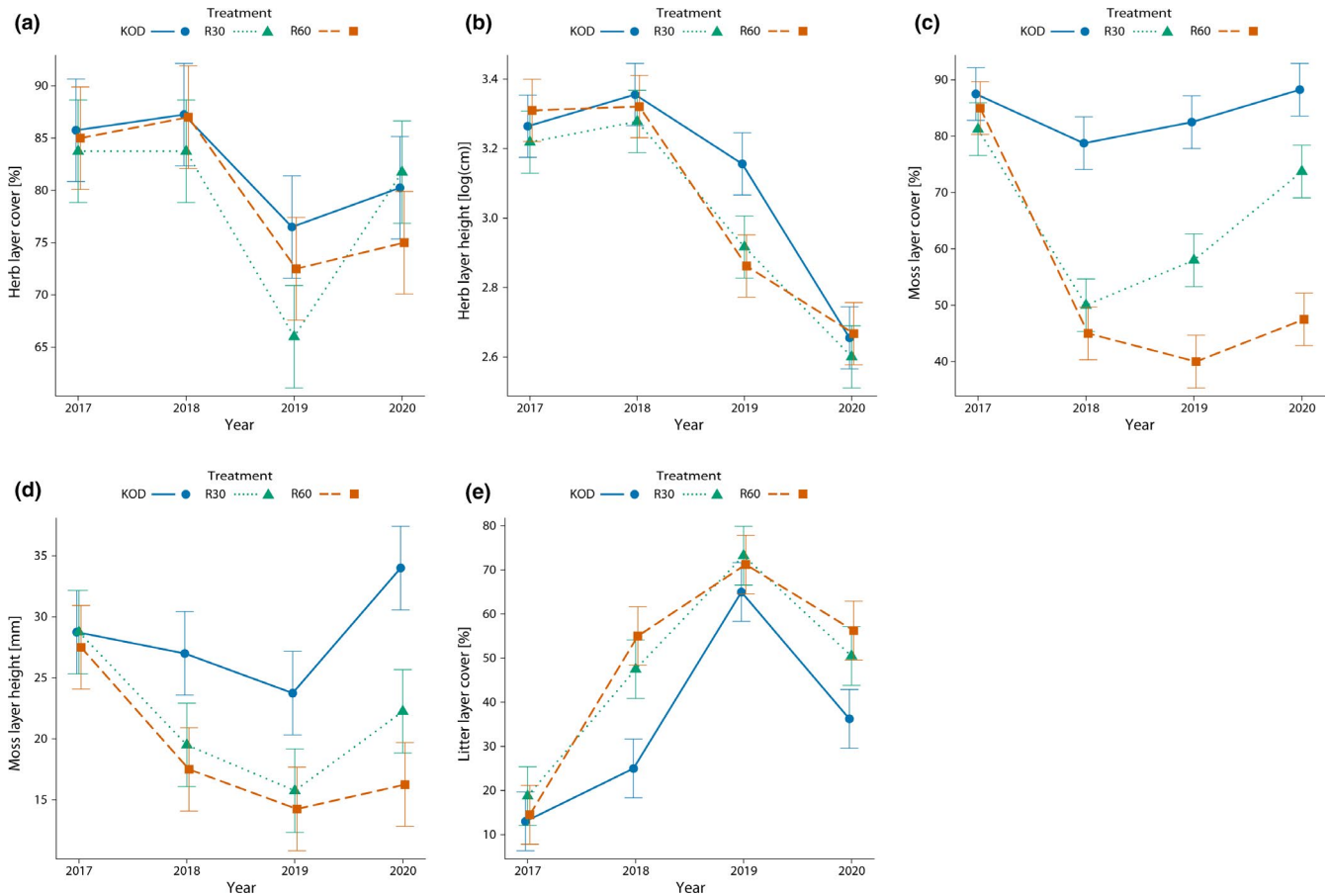


FIGURE 2 Changes in community structures in response to treatment and year (estimate and its standard error of the linear mixed effects model): (a) herb layer cover, (b) herb layer height, (c) moss layer cover, (d) moss layer height, and (e) litter layer cover

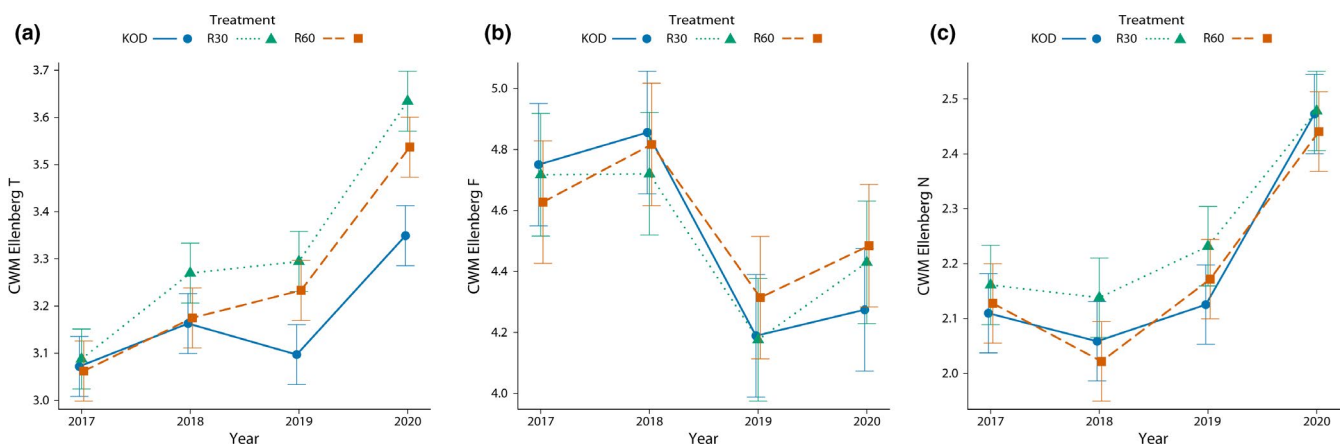


FIGURE 3 Changes in community-weighted means of (a) Ellenberg indicator scores for temperature (T), (b) moisture (F), and (c) nitrogen (N) in response to treatment and year (estimate and its standard error of the linear mixed effects model)

T score between the control and both drought treatments in 2019 and 2020. Ellenberg F score was influenced only by year ($F_{3,27} = 25.5$, $p < 0.001$), and not by treatment or their interaction, with F scores being smaller in 2019 ($\beta = -0.56$, $p < 0.001$) and 2020 ($\beta = -0.48$, $p < 0.001$). Similarly, the Ellenberg N score was influenced by year

($F_{3,27} = 110.355$, $p < 0.001$) but not by treatment. There was also no different development under the drought treatments over time. Ellenberg N score showed a marked increase in the final experiment year 2020 ($\beta = 0.36$, $p < 0.001$). Hence, the factor year, with its linked ambient dry conditions, proved to be the most influential

factor on Ellenberg indicator scores. Moreover, Ellenberg T and N scores, in particular, indicated an increasing trend over the years.

3.3 | Effects on sociological and functional groups

Sociological groups showed nonlinear responses to treatment and year (Figure 4; Appendix S4.5). Character species changed according to year ($F_{3,27} = 26.280$, $p < 0.001$), with a short-term decrease in 2018 ($\beta = -0.122$, $p = 0.008$) and a subsequent increase in 2019 ($\beta = 0.112$, $p = 0.015$) that remained almost stable at the same level in 2020 ($\beta = 0.087$, $p = 0.052$). We found neither an effect of treatment nor a significant interaction between treatment and year on character species. For low-productive species, we found a significant difference among drought treatments ($F_{2,9} = 4.791$, $p = 0.038$), with a higher proportion in the moderate (R30) drought treatment ($\beta = 0.041$, $p = 0.04$), and an effect of year ($F_{3,27} = 22.387$, $p < 0.001$). The proportion of low-productive species was higher in 2018 ($\beta = 0.076$, $p < 0.001$) and in 2020 ($\beta = 0.071$, $p < 0.001$). No interaction between drought treatment and year was detected. Agricultural grassland species were influenced by year ($F_{3,27} = 16.679$, $p < 0.001$), responding with an increase in 2018 ($\beta = 0.046$, $p = 0.002$) and subsequent reduction to the pretreatment level of 2017. Furthermore, we found no effect of drought treatment or the interaction between drought treatment and year.

Functional groups responded in different directions over the years (Figure 5; Appendix S4.6). The proportion of forbs showed a significant response to year ($F_{3,27} = 82.838$, $p < 0.001$), with the CWM of forbs being significantly higher, especially in 2020 ($\beta = 0.15$, $p < 0.001$). There was an effect of treatment ($F_{2,9} = 10.075$, $p = 0.005$), showing that the plots under the moderate drought treatment (R30) had a slightly higher proportion of forbs. No interaction between treatment and year was detected, which reflects a similar change in forbs for all treatments during the experiment. By contrast, the CWM of graminoids was influenced by treatment ($F_{2,9} = 4.639$, $p = 0.041$) and year ($F_{3,27} = 47.201$, $p < 0.001$). The proportion of

grasses decreased in all treatments, moderately in 2019 ($\beta = -0.048$, $p = 0.043$) and strongly in 2020 ($\beta = -0.124$, $p < 0.001$). A significant interaction between treatment and year ($F_{6,27} = 4.924$, $p = 0.002$) reflected different developments among treatments over time: graminoids in both drought treatments declined after a short-term increase in 2018, but to a lesser degree than in the control.

4 | DISCUSSION

Our study of the effects of ambient and experimental drought in oligotrophic mountain *Nardus* grasslands showed that the species community responded to the multi-annual drought regime with significant changes in species cover and community characteristics during the observation period. Measured temperature, humidity, and VPD underpin the severity of these droughts, of which 2018 proved to be most extreme year, with significantly reduced precipitation and increased temperature during the growing season. Hence, changes in community composition were most strongly related to the effect of year, reflecting the driving influence of these unintentional natural drought extremes during the experiment. Nonetheless, we were able to detect significant effects of the artificial drought treatments on community composition, structure, and Ellenberg indicator scores. These effects were, however, considerably weaker than the effect of year, were partly opposite and were not always as we initially expected.

Regarding community composition, we expected that drought treatments would amplify the effects of ambient drought conditions over the years (or vice versa). However, the RDA results revealed no common effects of treatment and year on community composition, hence species responded differently and in an unrelated way to ambient drought compared with the artificial drought caused by the rainout shelters. Variance partitioning showed a small negative adjusted R^2 value for the common effect, which can also be interpreted as zero (Legendre, 2008). Moreover, compared with the control, changes were less pronounced in the strong drought treatment

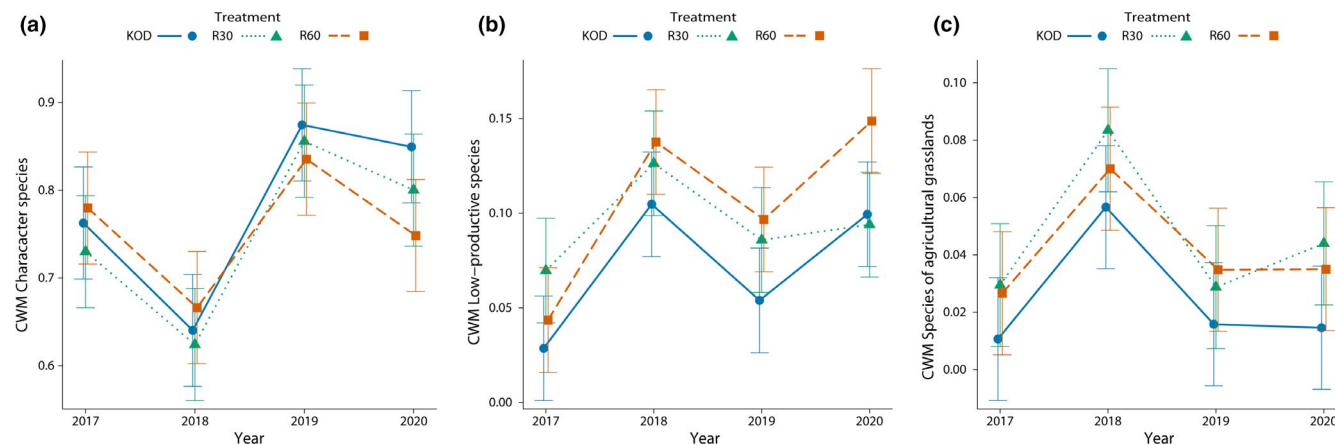


FIGURE 4 Changes in community-weighted means of sociological groups in response to treatment and year (estimate and its standard error of the linear mixed effects model): (a) character species, (b) low-productive species, and (c) species of agricultural grasslands

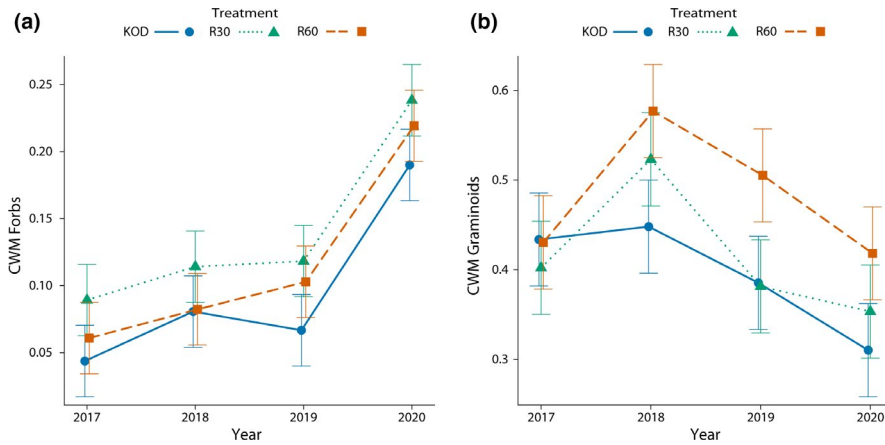


FIGURE 5 Changes in community-weighted means of functional groups in response to year and treatment (estimate and its standard error of the in response to treatment and year (estimate and its standard error of the linear mixed effects model): (a) forbs and (b) graminoids

(R60) than in the moderate treatment (R30). The identified changes in community composition over the years were mostly undirected and largely driven by annual changes in climate conditions. Similarly to the study of Holub et al. (2013), which considered montane species-poor *Nardetalia* grasslands in the Czech Republic, total species richness remained rather constant under drought. However, we detected significant community changes, which were not observed in the species-poor community by Holub et al. (2013). Our results showed a significant increase in evenness, which can be associated with increases in subdominant species (e.g., *Vaccinium myrtillus*, *Veronica officinalis*) and decreases in dominant species (e.g., *Nardus stricta*, *Deschampsia flexuosa*). In our study, the observed species changes were likely induced by the more severe drought conditions (especially in 2018), which triggered the potentially critical response threshold of many species that was not reached in the other study (Hillebrand et al., 2020; Ratajczak & Ladwig, 2019).

Compared with effects on community composition, the effects of drought on community structure were more consistent. For example, the decrease in the herb layer height was strongly related to year, indicating a gradual decrease, but this decrease was seen earlier under the drought treatments (2019) than in the control (2020). The strongest decreases in moss cover and height were observed in the drought treatments, whereas both parameters decreased less in the control. Hence, this treatment-specific trajectory suggests that structural characteristics of the moss layer are particularly sensitive to drought. Litter cover increased under the drought treatments and after the most severe drought conditions in 2018, when plant mortality and senescence were increased and decomposition hampered (Oddi et al., 2019; Sanaullah et al., 2012).

Results from CWMs of Ellenberg indicator scores and species groups demonstrated the specific response pattern of *Nardus* grasslands. Ellenberg indicator scores increased for temperature (T) and decreased for moisture (F), as expected. The strong increase in the T indicator score in the drought treatments during the years suggests that the increase of thermophilous species in the *Nardus* grassland community was more pronounced and accelerated at higher drought levels (Ploughe et al., 2019). Moreover, the Ellenberg indicator score for nitrogen (N) increased consistently across treatments in the last

year of the experiment due to the decline in dominant species with low N indicator scores (e.g., *Nardus stricta*), but not by increases of nutrient-demanding species. The response of sociological and functional groups showed an antagonistic pattern (i.e. character species vs low-productive species and species of agricultural grassland as well as forbs vs graminoids). By accessing deeper water resources in the soil, many perennial forbs with conservative growing strategies can persist better than grasses under dry conditions (Nippert & Knapp, 2007).

In sociological groups, character species decreased in 2018, when subdominant species (i.e. low-productive species) and species from agricultural grasslands increased, which changed to an increase in character species later in the experiment. This subsequent increase also included species with a clear montane distribution, like *Arnica montana*, for which negative functional trait responses to climate stress have been identified (Stanik et al., 2020). However, these low competitive species might have benefited from more suitable community structures, owing to the less dense and lower herb and moss layer in the years after the most severe drought in 2018 (Hollmann et al., 2020). This positive community-based feedback may have overridden direct negative drought effects on these species.

Our observations demonstrate that many changes in the vegetation community were rather time-lagged in the next or even two years after the extreme drought. For example, significant shifts in Ellenberg indicator scores or functional groups first became evident in 2019. Furthermore, because of the high number of slow-growing species in *Nardus* grasslands, many changes in species first became significant in 2020, whereas the year 2019 was not associated with any specific species change compared with the pretreatment state of 2017. These findings are similar to results from earlier studies that describe the year-to-year dynamics of species in response to weather patterns in perennial-dominated dry grasslands (Fischer et al., 2020) and annual-dominated grasslands (Dudney et al., 2017). Those studies identified weather fluctuations within and across years as one factor creating time lags in species' responses in oligotrophic grasslands (Herben et al., 1995). In these cases, the previous years' climate led to cascading changes in the community structure, to senescence in dominant species, and a delayed recovery in

perennials, which favoured dynamic species. The latter species benefited from the decline in less drought-tolerant species and buffered drought impacts on the community level (Zhang et al., 2020).

In addition to habitat filters, which select species at higher levels to constitute the habitat itself, community filters for niche differentiation are important for within-habitat species composition (Maire et al., 2012). Increasing drought due to climate change will act as a habitat filter and presumably lead to a long-term shift in species pools due to changed species' beta niches, i.e. the range of physical environmental conditions under which species fitness is maintained (Peppler-Lisbach & Schröder, 2004). Conversely, community filters are more likely to control short-term effects on community composition and to affect species' alpha niches, i.e. the niche differentiation that arises when plant species use resources differently and thus co-exist and persist within a community (Wilson et al., 2019).

In *Nardus* grasslands, a regular reciprocal replacement of dominant species has been identified, even under normal environmental conditions (Herben et al., 1997). Our results indicate that the drought-related decline in the dominant graminoid, *Nardus stricta*, was at least partly compensated for by increases in other matrix graminoid species such as *Deschampsia flexuosa* and *Festuca ovina* agg., which share a similar (alpha) niche space. This suggests that under drought conditions, mechanisms underlying the internal structuring of dominant species in this habitat were largely maintained, even if total herb layer cover decreased. When disturbances and environmental severity increase, the number of available niches for plants to coexist also increases (Harpole & Tilman, 2007). In the grassland system we studied, species that benefited from this newly available alpha niche space were predominantly small-growing forbs with stolons (*Veronica officinalis* and *Galium saxatile*) or graminoids with rather high vegetative persistence (*Carex pilulifera* and *Helictotrichon pratense*) that are characteristic of this type of grassland. Other species from more productive grasslands were not able to develop dominance after their short-term increase in the following years. The competitive ability and regeneration of these species proved to be strongly constrained by consecutive droughts in oligotrophic systems (van Daele et al., 2017). Therefore, the observed changes in abundance of low-productive and character species, together with the relative stability of species richness, indicate that community filters, which generate an altered set of alpha niches, may play an increased role in recovery of the community after droughts. Interestingly, even species with less suitable beta niche requirements, for example species with relatively high Ellenberg F scores, could benefit from extreme drought in the short term, if they show suitable adaptations to altered alpha niche situations (e.g., *Galium saxatile* with its fast vegetative spread by stolons).

Limitations in our experiment arise from strong year effects (Werner et al., 2020). Under the exceptionally dry ambient conditions during most of the annual experimental period in 2018 and 2019, the additional rainfall exclusion did not develop its full treatment effect (Aguirre et al., 2021). However, by considering year effects together with the treatment effects in our analyses, we were able to separate the relative importance of these natural

and artificial factors for the observed community changes. Owing to the decreasing predictability and projected higher frequency of extreme climate events, results from in situ rainout shelter experiments become increasingly difficult to interpret. Thus, to better separate year and treatment effects, and better control for unintended soil-water differences resulting from natural droughts, future experiments should include not only drought, but also wetting treatments, and collect observations over multiple years (Werner et al., 2020). Further limits to linking the community changes to our monitored climate variables may arise from drought periods prolonged into autumn and early winter, and thus beyond the considered growing season, which was particularly the case in 2018 (Appendix S2.1). Contrary to the underlying climate-change models for our experiment, precipitation amounts in autumn 2018 were below the long-term mean, which could have hampered or delayed recovery and partial regrowth of the vegetation (Deléglise et al., 2015; Herben et al., 1995). In the case of repeatedly prolonged drought seasons, hampered species' recoveries could promote species turnover in the long term, particularly by affecting slow-growing or short-lived species (Fischer et al., 2020), which we may not have observed within our limited experimental period. Furthermore, limitations arise from the small number of replicates per treatment, even if experiments to study climate change effects on grasslands have likewise been conducted with a small number of replicates (Bruehlheide, 2003). With a small number of replicates, variation in the data analysed increases, which may lead to over-/underestimated model results. However, most results of the assessed indicators for community change were statistically significant and therefore a robust basis for result interpretation.

In conclusion, despite the significant abundance-related community changes in response to multiple droughts, our findings indicate a short-term resilience of species-rich *Nardus* grasslands to drought in spring and summer (April to August). We could neither detect a significant shift of the community state nor a decline in species richness or erosion of sociological and functional groups. Changes were largely buffered by species already present in the community that utilised newly available alpha niches. Therefore, our findings support modelled projections, as well as an expert-based habitat conservation assessment that assumed a moderate sensitivity of *Nardus* grasslands to climate change in Europe (Beierkuhnlein et al., 2014; Petermann et al., 2007). However, possible long-term effects of climate change need to be considered, such as fitness decline, shifts in species pools and, finally, the exclusion of drought-intolerant montane species (Jung et al., 2020; Silvertown & Charlesworth, 2001). Implications for the future conservation of this threatened grassland type that arise in this context are: more frequent and more intense droughts may induce long-term effects and push the community beyond critical resilience thresholds. Increased efforts are thus required to reduce the pressure of other environmental change drivers and to improve the current quality of these grasslands. In parallel, long-term monitoring at the community and species levels is necessary to identify which plant traits mediate the coexistence of competing plants in oligotrophic grasslands under altered climatic conditions (Tredennick et al., 2017).

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AUTHOR CONTRIBUTIONS

NS and GR designed the experiment. NS collected the data and analysed it together with CPL. All authors contributed to the interpretation of the results. NS led the writing of the manuscript, on which CPL and GR gave critical comments and suggested revisions.

DATA AVAILABILITY STATEMENT

The data about the vegetation (vegetation relevés) and the environmental conditions of the experiment plots that support the findings of the study are available at Zenodo.org under <https://doi.org/10.5281/zenodo.5553177>

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Assignment of species to species groups

Appendix S2. Climate parameters among years and treatments

Appendix S3. Differences of soil water content among treatments

Appendix S4. Detailed results for changes in significant community structures, diversity indices, Ellenberg indicator scores, and for changes in sociological and functional groups

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