

# The effect of winter and summer warming on productivity, biodiversity and aboveground competition in grassland communities

climate warming, plant communities, competition, productivity

## Abstract

The effects of temperature warming and an increase in extreme events will have on grassland communities will be a very pertinent question to answer in the coming decades, as we struggle to grow enough food to feed world populations even now. We examined the effects of winter and summer warming on biodiversity, productivity and aboveground competition in experimental plots on semi-natural grasslands located at the University of Bayreuth. In terms of biodiversity, our results suggest a significant difference in biodiversity between the control and summer warming treatments which may be due to a difference in species composition. For productivity, we found a significant difference between the control and winter warming treatments. This could be due to an extended growing period from the heat lamp. Finally, for above ground competition, we found no significant difference between all treatment plots which may be due to an increase in below-ground competition.

## Introduction

Climatic change has the potential to affect many types of flora and fauna. Phenomena such as flooding, coastal inundation, extreme rainfall, and extreme drought, that were once observed to be relatively rare incidents, are due to become frequent occurrences. IPCC reports suggest future climates with an increased mean temperature may lead to warmer winters and hotter, drier summers (Roberts 2015). Jentsch et al. 2011, found extreme drought to reduce activity in below ground microbial communities, and reduce leaf gas exchange, leaf protein content, and leaf water potential. An increase in mean temperature means warmer summers and winters. We intend to investigate how grassland communities will react on these changes. Shedding light on vegetation reactions and adaptations on manipulated seasonal temperature may help to better understand the plants' needs, and to develop target-oriented measures to adapt to futures climate conditions and to ensure the provision of our basic needs such as food production.

Reaction to extreme events can be variable depending on vegetation type and the type of stressor (Jentsch and Beierkuhnlein 2008). Sometimes this results in higher or lower productivity, and, in the case of drought events which decrease invasion, but also decreases post-drought reproductive success. Often compounding this are slow adaptation rates (reacting to potentially quick onset extreme events) by plants with long life cycles. Blüthgen et al. 2016 found long term stability to be driven by species' population health and communities contributing a full range of ecosystem functioning. They found arthropods to show a 2x fold and birds a 3.7x fold higher fluctuation in grasslands than in forests, arguing that forest conversion shows a negative impact. This suggests that the health of these ecosystems can be intertwined, making data on how they may adapt or be impacted all the more crucial.

It is predicted future climate will feature more extreme precipitation events and severe events in European altitudes. However, we expect higher productivity with winter warming (less stressors, more time to grow, more microbial activity, and potentially more access to water (melted snow/ice) with

warming). Isbell et al.'s 2015 results, gathered through examining grassland plant communities, point to biodiversity stabilizing ecosystem productivity by increasing resistance and resilience to climatic events. Their findings also suggest that biodiversity rich communities are able to more quickly recover after drought events (portfolio effect). They found, across all studies and extreme events, low diversity communities of 1-2 species changed by around 50%. High diversity communities, with 16-32 species, were more resistant, changing only around 25%. However, a year after each climate event, both low and high diversity communities recovered and, in some cases, overshot normal levels of productivity. This puts forward evidence that ecosystem resilience is not necessarily dependent on biodiversity, and that biodiversity mainly stabilizes productivity after an event, by increasing resilience. Another example is in Jentsch and Beierkuhnlein 2010, who found that while biomass did not react so strongly to extreme events, single species performance was specific. The study found drought, heavy rain, and increased freeze thaw cycles to affect processes in nutrient cycling, gas exchange, and reproductive fitness. Biodiversity both buffered extremes and in other cases, accelerated stress.

Further, we expect productivity and above ground light competition during summer warming to be more linked with precipitation rates, and, therefore, highly variable. This is based on the assumption that droughts represent additional stressors to the communities, whereas warm and moist conditions can be highly beneficial. Finally, we expect an increase in above ground competition in winter, as for some plots, there are more beneficial environmental conditions leading to increased growth rates, and therefore higher competition. We expect to see an increase in above ground competition because of increased leaf area, allowing for more light competition. This follows the novel approach developed by DeMalach et al. in 2017, investigating the 'light asymmetry hypothesis'. In the paper, they found that an increase in light asymmetry is a main driver of the negative effect of nutrient enrichment on species richness, giving a possible explanation into species loss observed in terrestrial plants (DeMalach et al. 2017, Hautier et al. 2009). However, Craven et al. in 2016, has argued against this, finding that plant diversity effects were robust to changes from drought and by nutrient enrichment. We investigated the effects of winter and summer warming on semi natural grassland communities. We hypothesize biodiversity will remain unchanged in both scenarios - summer- and winter warming. Further, we expect that productivity as well as above ground competition will increase, where winter warming was simulated. In case of the summer warming scenario, we expect the productivity and above ground competition to be linked with precipitation rates and highly variable, as droughts represent additional stressors, whereas warm and moist conditions can be highly beneficial. The goal of these studies is to provide data for the development of policy and adaptation strategies to these extreme weather events, in a way that monitoring would inevitably take too long to gather. This is critical, as extreme events pose a greater threat to ecosystem services and functioning than global shifts in average climate conditions (Jentsch and Beierkuhnlein 2008).

## Research Hypothesis

*"We hypothesize that biodiversity will remain unchanged in both scenarios- Summer- and Winter warming. Further we expect the productivity as well as the above ground competition to increase, where winter warming was simulated. In case of the Summer warming scenario, we expect the productivity*

*and above ground competition to be linked with precipitation rates and highly variable, as droughts represent additional stressors, whereas warm and moist conditions can be highly beneficial."*

## Methods



Figure 1: Location of the Experiment

source: © OpenTopoMap (CC-BY-SA)

### Site characteristics

The Event 2 Experiment is located in the ecological botanical garden of the University of Bayreuth, Germany (49°55'18.7"N 11°35'01.3"E) on a semi-natural grassland (Fig. 1). The soil is characterised as Gleysol, whereby the Ap horizon has a depth of 0.3m. Below lays a clayey Bg horizon. The mean pH of the topsoil is 4.1 (1 M KCL) (Grant et al. 2017).

The yearly temperature mean lies by 10,25°C for the last 5 years. However the last two years with 10,36°C in 2018 and 10,73°C in 2019 were lying slightly over the average. The comparison of the average air temperature of the different month indicate especially warmer month in spring (Wetterstation Bayreuth)(Fig.2). The precipitation average for Bayreuth lies by 756mm per year. However in 2018 and 2019 the precipitation was decreased to 523mm in the year 2018 and 486mm in the year of 2019 (Fig.3).

### Experimental manipulations

Our Experiments are part of the EVENT experiments that tries to assess impacts of future climate conditions by creating certain extreme conditions and analysing their effect on the plant communities (Jentsch and Beierkuhnlein 2010). We intend to study the effect of rising temperatures in summer and winter on plant communities, their productivity and aboveground competition. For each treatment, winter warming, summer warming and no treatment (control), five plots were created and arranged in a changed latin square. The plots measure 1 m<sup>2</sup>, whereby the different treatments are randomly distributed over the site. The temperature manipulation took place 24 hours a day from April to

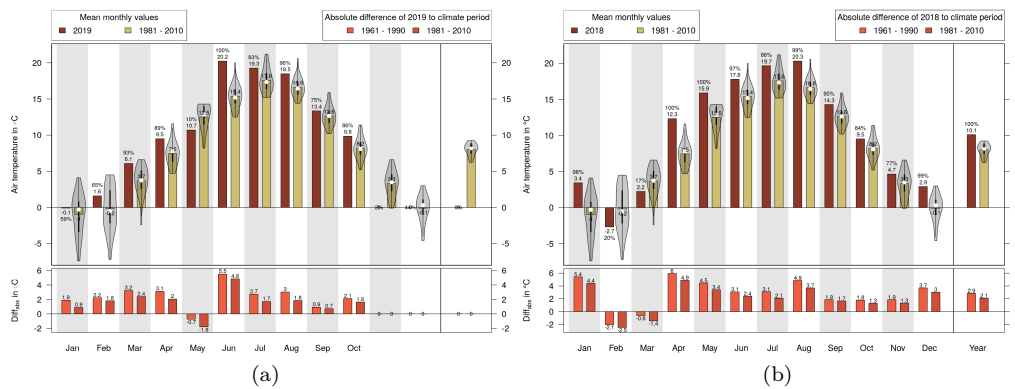


Figure 2: Air Temperature 2018 & 2019  
source: Micrometeorology University of Bayreuth

May for Summer warming and from November to March for the winter warming and was conducted by overhead infrared heaters with reflector domes (IOT/90 250 W Elstein, Northeim, Germany) and installed at 0.8 m aboveground. Both soil and air temperature were significantly increased. The Air temperature by 1,3 ° in summer and 0.9 °C in winter, whereby the soil temperature at 2 cm below ground was increased by 0.6 °C in summer and 1.5 °C during the winter (Grant et al. 2017). The plots with the temperature manipulation have been created in the period of 2009/10, whereas the control plots were already created in 2008. Therefore our analysis will comprise the data from 2010 until today.

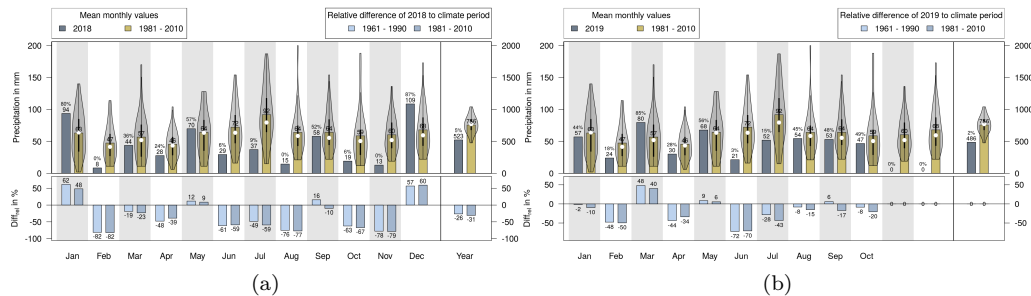


Figure 3: Precipitation 2018 & 2019  
source: Micrometeorology University of Bayreuth

## Productivity

As an indicator of the productivity of the system the biomass was measured, after Grant et al. 2017. Therefore, the plots were harvested every year between June and the beginning of July. Thereby, 0.1 m<sup>2</sup> (20\*50 cm) frames were used and randomly placed within the plots, to harvest samples at 3 cm aboveground. The cut vegetation was getting sorted by its functional groups, namely woody species, herbaceous, legumes and grasses, dried at 60 °C and weighted (Grant et al. 2017). The data was analysed with R version 3.6.1 (R Core Team 2019) by using the package "pgirmess" (Giraudoux P. et al. 2018). We conducted a Shapiro.Test to control assumptions of data being normally distributed. As our data is not normally distributed we log transformed our data to the base of 10 and computed

the exponential function, to conform our data into a normal distribution. We conducted a One-way Analysis of Variance (ANOVA) to test the differences in productivity within our treatments. Further we conducted a Tukey's HSD Post Hoc-Test to investigate where there are significant differences between the treatments. To be able to link productivity changes according precipitation rate we further compared the precipitation-rich 2017 with the year 2019, as this year and the previous year were very low in precipitation (Wetterstadion Bayreuth). Further, we tested our data on differences in productivity between the functional groups, to see which one is more affected by the different treatments than the others. Therefore, we conducted a multivariate Anova (Manova) within the 'stats' package (R Core Team 2019).

### **Biodiversity**

To analyse changes in the abundance of species, species cover estimation were conducted. Thereby, species were recorded and their ground cover estimated. This is a very simple method, however one need to take into account that variability within the data might exist, according to different teams recording the data (Kercher et al. 2003). For the statistical analysis we were using the "vegan" package (Oksane et al. 2019), to conduct an ordination. Therefore we transformed our dataset to to a community data matrix by using the reshape-package (Wickham 2018). In the following, we conducted a Principal Component Analysis (PCA), as we in addition to necessary pre-conditions do not include environmental variables. Therefore, we conducted a de-trended correspondence analysis to see if our data meets the requirements of the PCA. Further, we conducted a RDA, as part of the vegan package for the redundancy analysis.

Additionally, we calculated the Simpson Diversity Index, to to get an estimate for biodiversity for each treatment and tested it for variance with an ANOVA. This index determines the probability of one species to be found again at another place and therefore the species richness in an area (Smith & Smith 2009).

### **Competition**

As an indicator for competition we measured the height of the vegetation in our plots as well as the Photosynthetic Active Radiation (PAR) above, within and below the vegetation . Furthermore we used the data to calculate the asymmetry of light availability within the vegetation. DeMalach et al. 2017 proposed, that light asymmetry may function as an indicator for competition between the different species. We conducted the measurements in the beginning of June, whereby the measurements for the control data were conducted ten days after the other plots. For the height measurements we conducted five measurements per plot. Four at the edges, 30 cm within the plot to avoid edge effects, and one additional measurement for the maximum height of the vegetation. To measure the PAR we used a ACCUPAR LP-80. For each plot we measured a transect each time on the right and on the left side. Alternating, we measured above the vegetation or within the vegetation at 40cm, 25cm, 10cm and on the ground at 0cm. To calculate the light asymmetry by the slope of linear regression between height and PAR data. Therefore, we average the PAR data from the right and left side of each plot at each height. Further, we calculate the ratio between PAR above the vegetation and within. We implement a regression model for each plot, to test for a relationship between height and light and tested for a significant difference between the treatments by conducting the Kruskal-Wallis-Test. As the light ratio

will always equal one, when there is no vegetation, we include data on the maximum height per plot, to know where to stop the regression.

## Results

### Productivity

A significant difference in productivity (at  $P = 0.0101^*$ ) exist between all the treatment plots. Specifically, the significant difference (at  $P < 0.05$ ) exist between the control and winter warming plot as well as between the winter warming and summer warming plot (Fig. 4 a). In addition, Figure 4 b shows the variation in productivity between the different functional groups namely legumes, herbs, woody and grasses and how they differ within the treatment plots. The highest proportion of biomass is produced by grasses followed by legumes, herbs and woody plants in a descending order. Whereas the highest proportion of biomass is produced during the winter warming scenario for all the functional groups.

No significant difference exists in biomass (at  $P > 0.05$ ) between treatments for each functional group. Although legumes and herbs produce more biomass in the winter warming than in the summer warming and control, grasses produce more biomass in the winter warming and control than in the summer warming while for woody species, the differences in biomass between treatments are very similar. Overall in most of the functional groups, we have more biomass being produced in the winter warming simulation (Fig. 4 b)

The difference in productivity or biomass between the summer warming of 2017 and 2019 are displayed below. We can observe a higher quantity of biomass in the summer warming of 2019 than in the summer warming of 2017 (Fig. 5 a). Similarly, for the winter warming scenario, productivity or biomass quantity was higher in 2019 than 2017. (Fig. 5 b)

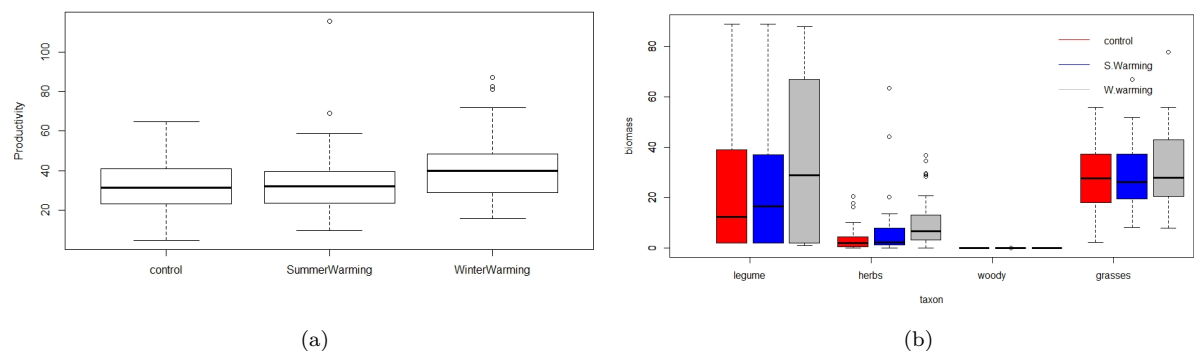


Figure 4: a: Differences in productivity between different functional groups. Significant difference exist between all the treatment plots (at  $P < 0.05 = 0.0101^*$ ). No significant difference ( $P > 0.05$ ): Control – Summer Warming. Kruskal-Wallis test ( $p < 0.05$ ) and Kruskal Posthoc Multiple Comparison test b: i. Difference in productivity between functional groups within treatments. ii. Difference in productivity between treatments in each functional group. No significant difference exists between treatment in each functional group. For woody species however, the differences are similar and not clear. Multivariate analysis of variance test MANOVA ( $P > 0.05$ ).

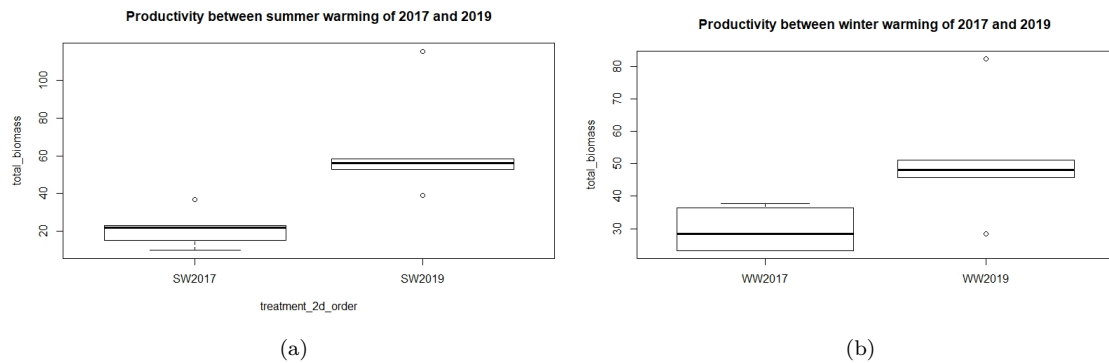


Figure 5: Differences in productivity between the winter warming of 2017 and 2019. Kruskal-Wallis test ( $p < 0.05$ ). (b) Differences in productivity between summer warming of 2017 and 2019. Kruskal-Wallis test ( $p < 0.05$ ) (a), according to years with different precipitation rates. 2017 was known as very rich in precipitation and 2019 was low in precipitation

## Biodiversity

Warming significantly caused a difference in biodiversity (at  $P < 0.05$ ) between the control plot and summer warming plot as well as between the control plot and the winter warming plot (Fig. 6). The mean values of the Simpson diversity index calculated for the control, winter warming, and summer warming plots are 0.939, 0.937, and 0.931 respectively. In addition, species diversity for each treatment was visualized using ordination plots generated from principle component analysis (Fig. 7 a, b & c). We chose the first and second principle component for each treatment and plotted the species on these axes because they explain the largest variation in our species dataset.

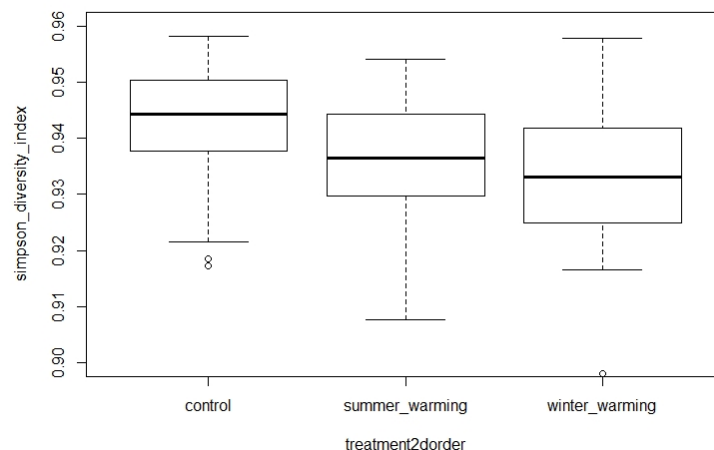
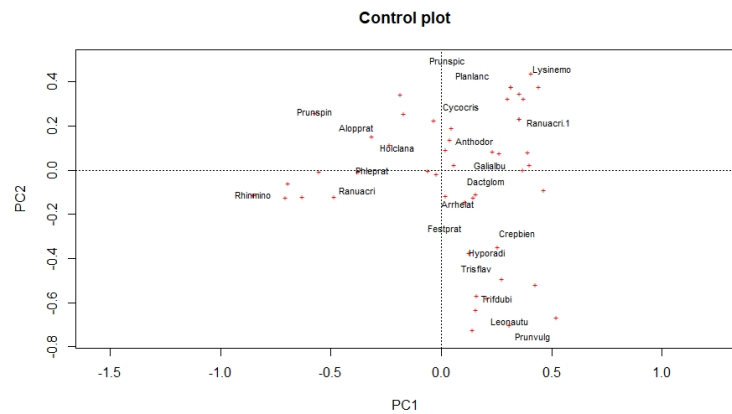
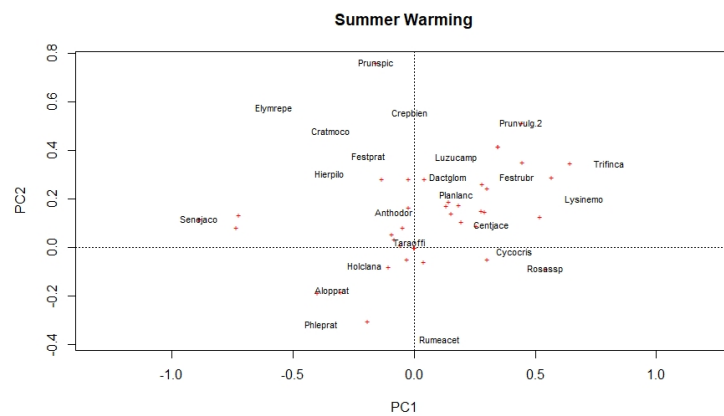


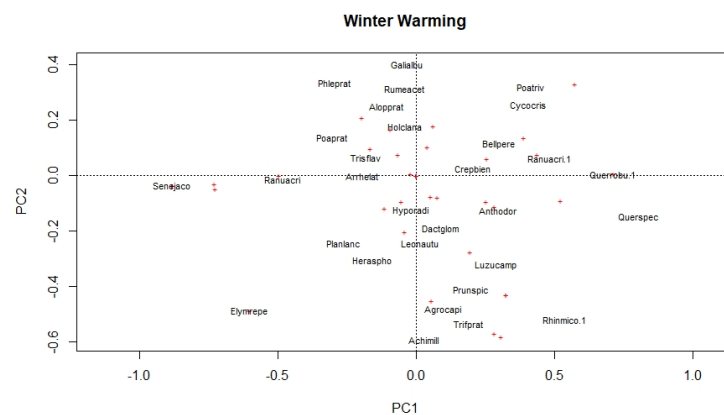
Figure 6: Differences in the Simpson diversity index calculated for each treatment. No significance difference exists between summer warming and winter warming plots. Kruskal-Wallis test ( $p < 0.05$ ) and Kruskal Posthoc Multiple Comparison test



a



b



c

Figure 7: Ordination plots showing differences in species composition between two treatments. PC1 and PC2 explain the largest variation in the species dataset. Names of the most abundant species are displayed while less abundant species are represented by red crosses. Principle component analysis PCA



## Competition

Fig. 8 shows the difference in above ground competition between treatment plots. Here, no statistically significant difference exist (at  $P > 0.05$ ) in above ground competition between all the treatment plots. In other words, neither summer warming nor winter warming significantly increased above ground competition in our experiment.

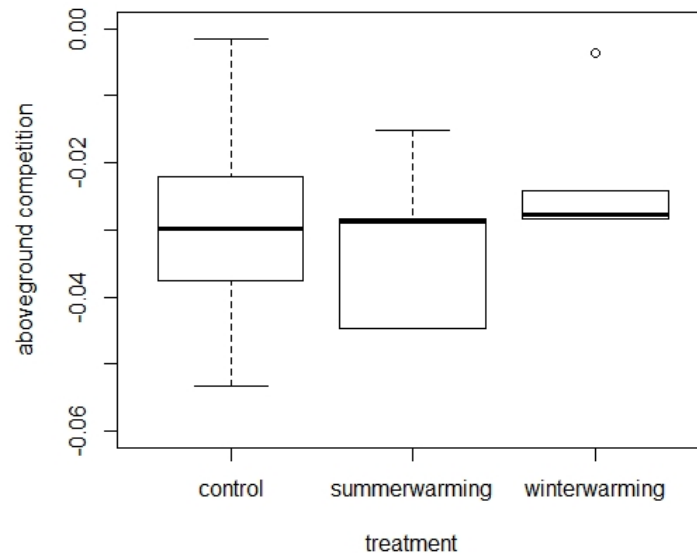


Figure 8: Difference in above ground competition between treatment plots. No significant difference exists in above ground competition between treatment plots. Kruskal-Wallis test ( $p > 0.05$ ) and Kruskal Posthoc Multiple Comparison test

## Discussion

### Productivity

In our experiment we compared the productivity, aboveground competition and biodiversity under winter warming, summer warming and no treatment. Thereby, we found, that the productivity is increased with warming treatments in winter. However, we found no significant changes in productivity with warming treatments in summer, which partly confirms our hypothesis that productivity during winter warming will be increased. However, further investigations are needed weather precipitation rate can be linked to to the productivity under summer warming or not.

In terms of the winter warming manipulation Grant et al. 2017 already proposed, that the increase may be due to a extended growing season. Further, the plants may not acclimate to colder temperatures, as this process is temperature dependent and with higher temperatures in winter the threshold may not be reached. This means, that plants can use the photosynthesis products for further growth, instead of transforming these into soluble sugars to increase their winter hardiness (Pagter & Arora 2013). Even in the case of the plant acclimatising to cold temperatures, temperatures for de-acclimatising

is reached earlier, leading to an earlier onset of photosynthesis and therefore growth and an earlier onset of sprouting events and bud-break (Pagter & Arora 2013; Grant et al. 2017). In addition, the plots with winter warming might be not or at least less negatively affected by late frost events. In general, predictions suggest an increase in air temperature during winter, meaning similar effects on plant communities as shown in our experiment. However, the occurrence of winter warm spells is also predicted to increase, as results of anomalies in the geopotential height and a positive North Atlantic Oscillation. This would mean that plants, during winter dormancy face problems in sustaining their cold acclimatisation and face higher risk of frost damage afterwards (Tomczyk 2019; Beniston 2005). This effect may be increased by elevated CO<sub>2</sub> that increases the risk of frost damage in plants (Woldendorp et al. 2008).

The risks of losing their cold adaptation are the plants under no and summer warming treatments already facing. As the productivity of these treatments is not different to each other this may indicate that plants are temperature limited during the winter time and less during the summer time under non extreme condition. However Grant et al. 2017 already proposed, that the temperature difference of the summer warming treatment may be too low to show sufficient effects. Higher temperatures will increase evaporation rates and may lead to an increased drought stress in plants. Grant et al. 2017 found a correlation between precipitation variability and a decrease in biomass. However our comparison between the productivity in a year with high and low precipitation shows an increase of productivity in the year with less precipitation within all treatments. However, this might be due to the relatively small data set. Further, showed the weather data (Wetterstation Bayreuth), that the precipitation in 2019 was in general low, but not in March which might have been favourable for plant growth. Moreover, it was found that heavy precipitation in winter has less of an effect than in summer and that a drought in spring significantly reduces biomass, which suggests that precipitation in winter/spring is important for plant growth (Zeppel et al. 2014; Zhang et al. 2012 et al.) Furthermore, it should be mentioned that 2019 had less frost days in Spring than the year 2017 (Wetterstation Bayreuth), which may indicate, that the plants in 2017 were affected by frost damage during spring. However, for drawing sufficient conclusions, more investigations into the correlation between warming and precipitation need to be done (for example by increasing the temperature difference between the control and the manipulation).

Our results also showed differences in productivity between the functional groups within the different treatments. In general, it was shown that all functional groups had an increase in productivity under the influence of winter warming, which we already discussed above. In comparison show the plots under summer warming a more variable influence on the functional groups. These differences are as already mentioned less likely a result of higher temperatures in summer but more likely due to winter effects, which is supported by the fact, that no significant differences are existing between the control and summer treatment for legume species, woody species and grasses. Only herbs show an increase in comparison to the control plot. Increased temperatures, seemed not severe enough to increase the productivity in general, however elevated temperatures are known to effect the accumulation of secondary phytochemicals, as well as the enzyme activity, by maintaining their growth (Yuan et al. 2011). Here, the accumulation may be reduced, whereby it caused an increase in growth of the plant species. Admittedly, it is not known if the temperature increase was sufficient to promote such an effect.

## Biodiversity

Our hypothesis was biodiversity would remain unchanged in both winter warming and summer warming scenarios. Our hypothesis of no changes in biodiversity by either warming treatment was only partly supported by our results. Although we found no significant difference between winter warming and control plots, there was a significant difference between summer warming and control plots. The difference among the control, winter warming, and summer warming values was extremely low, and likely not very significant, at 0.939, 0.938, 0.932, respectively. The high biodiversity value associated with the control plots (0.939), since it is closest to +1, indicates that it had the highest probability of having many individuals not of the same species; contrarily, the lowest diversity mean, for summer warming (0.932), indicates that it had less species diversity, though more than likely by only a small amount. Similar to what we observed with productivity values during winter warming, a possible explanation for our results is late frost events may not affect species as severely in the treated winter plots due to the warming effect of the heat lamps (Grant et al. 2017).

Isbell et al. 2015 found that biodiversity increased ecosystem productivity resistance to change. The slight increase in productivity we observed in winter warming could be correlated to the increase in biodiversity value observed in winter warming. The lowest mean of biodiversity in summer warming is further supported by the data in Grant et al., whose study found a decrease in above ground net primary production (ANPP) by 17% for a spring drought scenario, though it should be noted that the warming scenario in summer in our study did not produce conditions dry enough to be considered drought for this geographical area. The study additionally found an increase of 12% ANPP for winter warming. Further, their results revealed summer warming to decrease species richness (but have no effect on biomass). However, it should be noted that this difference between means of winter warming and summer warming is only 0.0058. A case for a limited overall response of biodiversity to the experimental conditions can also be observed in Jentsch and Beierkuhnlein 2010, in which total biomass did not respond as strongly as expected. The study further found biodiversity to both buffer extremes in some cases and accelerate stress in others. A case for a slow environmental response of biodiversity can also be made from the study by Essl et al. 2015. Limitations of the study can be viewed as potentially low overall number of sample plots, and more observations of the effects of precipitation rate and trends could be useful information. Gonzalez et al. 2016 posits that the evidence for patterns of species loss at local scales is mixed, and that richness estimates can be inherently biased if species gains during recovery are not also examined in conjunction with species losses that occurred during the disturbance.

## Future directions:

Similar to our hypothesis about productivity being highly variable and more controlled by outside factors, such as precipitation, outside factors could also be an explanation for our results with relation to biodiversity. Although the EVENT experiments do not focus on microbial communities, future interdisciplinary studies on the interplay of winter and summer warming on microbial communities may yield interesting data. A study by Vogel et al. 2013, at the Jena Experiment in Germany, found plant diversity loss and summer drought separately impeded soil processes, such as rates of decomposer communities and microbial properties. The study also found decomposers functioned better decomposing community-specific plant litter and in more diverse plant communities. These results are further supported by Jentsch et al. 2011, who found drought to severely reduce below

ground microbial performance. In addition, measuring how microbial communities in EVENT plots react to both community-specific and non-native plant litter may intrigue researchers.

Observing trends at a longer scale is important, as it will yield valuable insights that can be incorporated into wider studies on crop systems. For example, in one study, a meta-examination of > 7,000 productivity experiments with a mean length of 13 years, revealed strong biodiversity to be as effective in promoting productivity of some biomass crops as fertilization (Tilman et al. 2012). The study also found a loss of biodiversity to have potentially as much impact on ecosystem functioning as other anthropogenic drivers of climatic change, such as changes in nitrogen, CO<sub>2</sub>, herbivores, drought, or fire.

Hillebrand et al. 2017, has even argued that biodiversity is uncoupled from species richness, and that species turnover, both in presence (identity) and dominance (abundance), is a more accurate parameter. They argue in favor of new measurements of biodiversity, as their meta analyses reveal little observed change in local species richness through time. In a similar manner, Jones et al. 2017 also promote the idea that species reordering, not richness, primarily drives long term grassland community dynamics. In conclusion, more research on the dynamics of biodiversity gains and losses in response to treatments will yield valuable data for climate change planning and management measures. Determining the true present and future impact globally of humans on biodiversity change is critical to implementing proper planning measures, and dictating reactions to modelled scenarios (Gonzalez et al. 2016).

## **Competition**

We measured available light above and within the canopy as a measure for aboveground competition. Thereby we found no significant effect of warming on light competition and thus cannot confirm our hypothesis that winter warming, and summer warming simulations will contribute to more above ground competition.

In other words, above ground competition is facilitated to a greater extent by light availability within the canopy rather than warming. However, in relation to the observed differences in productivity of functional groups within treatments, grasses have the highest biomass in the control and summer warming simulation while legumes dominate in the winter warming simulation. This emphasizes the importance of warming in facilitating competition between the functional groups.

Warming influences the rate of aboveground biomass produced. Generally, warming contributes to an increase in evapotranspiration that significantly reduce the amount of water available to plants, this leads to an increase in below ground competition for soil water and a decrease in above ground competition. As confirmed by Boeck et al. 2006, warming predominantly leads to a decrease in above-ground productivity and even a higher decrease in below-ground grassland productivity which is synonymous to lower soil water content. However, as mentioned above it is questionable if the warming of our plots increase evaporation sufficiently.

Decreases in species richness or biodiversity earlier observed for the winter and summer warming simulations is influenced by the degree of light competition. Light asymmetry is also proven to have a negative effect on species richness in a grassland habitat (DeMalach et al. 2017). As light asymmetry becomes stronger, light competition is transferred from below ground to above ground competition thereby leading to a loss of biodiversity.

The figure below (Figure 8) shows a negative relationship between photosynthetic active radiation (a

measure of light intensity) and plant heights within the canopy suggesting a negative light asymmetry as light interception decreases with increasing plant heights. In other words, shorter plants intercept more light than taller plants and as a result competition for light at the canopy level becomes weak. This phenomenon is observed when there is a high proportion of light available to underground plants than taller plants due to increased light penetration onto the soil surface (Borer et al. 2014). Therefore, shorter plants derive high benefits from light penetration and more above ground biomass is produced at the shrub level. Among the parameters that significantly influence the amount of light that is penetrated to the ground surface are canopy heights and within-canopy light gradients (De Malach et al. 2017).

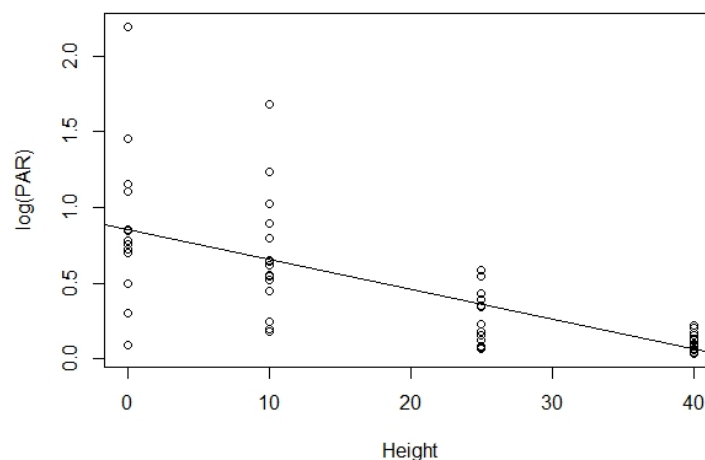


Figure 9: Relationship between photosynthetic active radiation (as a measure of light) and Height of plants. Negative relationship exists between light and height (at  $P < 0.05$ ). The slope of the line is a measure of above ground competition. Simple linear regression ( $P < 0.05$ )

A negative light asymmetry or light penetration would be a result of several plant physiological and chemical traits which predominantly enhances the proportion of light harvested at subcanopy levels and significantly alters light incidence at canopy levels. Some of these traits include the structural characteristics of plant leaves and shoot, light-driven plastic modifications in traits, chlorophyll content in leaves, stand age and size as well as variations in plant functional types (Niinemets 2010). A negative size light asymmetry would occur where plants of greater heights possess structural features that do not hinder the penetration of a significant amount of light into the stand. For example, taller plants may possess significantly lower leaf sizes than underground plants, and this may contribute to light intercepted by underground plants. A scenario where taller plants possess genetic traits that alters light interception while shorter plants absorb more lights would also enhance light penetration. Chemical traits such as leaf chlorophyll content determines the proportion of light being harvested through the process of photosynthesis. There are shade-intolerant and shade-tolerant species in the upper and lower canopy of a grassland habitat respectively. Light penetration would be enhanced when shade tolerant species possess higher chlorophyll content in their leaves than shade intolerant

species. However, it has been proven for specific ecosystems that foliage chlorophyll content increases with decreasing light availability (Hallik et al. 2009). Within a stand, total leaf area index and stand biomass varies among different plant functional types. Plant species with high leaf area and high biomass investment in leaves such as herbs and shrubs will intercept more light than plants with relatively lower leaf area and biomass investment. In situations where there are few gaps penetrating the upper canopy, understory environments usually contain plant functional groups that require high light availabilities for high foliar area and biomass production (Niinemets 2010).

## Conclusion

As extreme events, such as milder winters, and warmer, more drought afflicted summers, become more commonplace in today's world and our future, determining the effect those events may have on grassland species becomes crucial. These data are needed to inform how to protect these areas and the ecosystem services they provide for both humans and flora and fauna. Our results show only slight effects of warming on biodiversity and likely unimportant difference between summer warming and control plots. This small significant result could be due to a small difference in composition. Further, we found a significant difference between the control and winter warming treatments for productivity measurements, leading our findings to support our hypothesis in this instance. This could be due to an extended growing period from the heat lamp. Finally, for above ground competition, we found no significant relationships. This goes against our prediction that above ground competition would increase, along with productivity, during winter warming. We believe this missing relationship could be due to an increase in below ground competition, however more studies are needed to test this theory. Our study will provide valuable insights for future studies and management practices. Testing whether or not our results hold up in future studies would provide more evidence to support or reject our findings and could even help refine models. Carrying out further research on potential effects of future climate extremes and trends will help us develop the most complete and informed mitigation and adaptation strategies to ensure the highest likelihood of positive results.

## Literature

**Beniston M.** (2005) Warm Winter Spells in the Swiss Alps: Strong heat waves in a cold season? A Study focusing on climate observations at the Santis high mountain site, *Geophysical Research Letter* Vol 32, L01812

**Blüthgen N.**, Simons N. K., Jung K., Prati D., Renner S. C., Boch S., Fischer M., Hölzel N., Klaus V. H., Kleinebecker T., Tschapka M., Weisser W. W., Gossner M. M. (2016) Land Use Imperils Plant and Animal Community Stability through Changes in Asynchrony Rather than Diversity, *Nature Communications*, vol. 7, no. 1, 10697, doi:10.1038/ncomms10697

**Borer E.T.**, Seabloom E.W., Gruner D.S., Harpole W.S., Hillebrand H., Lind E.M. et al. (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508, 517–520

**Craven D.**, Isbell F., Manning P., Connolly J., Bruelheide H., Ebeling A., Roscher C., Van Ruijven J., Weigelt A., Wilsey B., Beierkuhnlein C., De Luca E., Griffin J. N., Hautier Y., Hector A., Jentsch A., Kreyling J., Lanta V., Loreau M., Meyer S. T., Mori A. S., Naeem S., Palmour C., Polley H. W., Reich P. B., Schmid B., Siebenkäs A., Seabloom E., Thakur M. P., Tilman D., Vogel A., Eisenhauer

- N. 2016 Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Phil. Trans. R. Soc. B* 371: 20150277. <http://dx.doi.org/10.1098/rstb.2015.0277>
- DeMalach N.**, Zaady E., Kadmon R. (2017), Light asymmetry explains the effect of nutrient enrichment on grassland diversity, *Ecological Letters*, 20, 60-69
- Essl F.**, Dullinger S., Rabitsch W., Hulme P.E., Pyšek P., Wilson J.R.U., Richardson D.M. (2015). Delayed biodiversity change: no time to waste. *Cell Press Forum. Trends in Ecology and Evolution*, 2016, 1-4.
- Giraudoux P.**, Antonietti J-P., Beale C., Pleydell D., Treglia M. (2018), *pgirmess- Spatial Analysis and Data Mining for Field Ecologists*, R Package Version 1.6.9
- Gonzalez A.**, Cardinale B.J., Allington G.R.H., Byrnes J., Endsley K.A., Brown D.G., Hopper D.U., Isbell F., O'Connor M.I., Loreau M. (2016). Estimating local biodiversity change: A critique of papers claiming no net loss of local diversity, *Ecology*, 97(8), 1949–1960
- Grant K.**, Kreyling J., Beierkuhnlein C. Jentsch A. (2017) Importance of Seasonality for the Response of a Mesic Temperate Grassland to Increase Precipitation Variability and Warming, *Ecosystems*, 20, 1454-1467
- Hallik L.**, Kull O., Niinemets U., Aas A. (2009) Contrasting correlation networks between leaf structure, nitrogen and chlorophyll in herbaceous and woody canopies. *Basic Appl Ecol*, 10, 309–318
- Hautier Y.**, Niklaus P.A., Hector A. (2009) Competition for Light Causes Plant Biodiversity Loss After Eutrophication, *Science*, vol. 324, no. 5927, 636–638., doi:10.1126/science.1169640.
- Hillebrand H.**, Blasius B., Borer E.T., Chase J.M., Downing J.A., Eriksson B.K., Filstrup C.T., Harpole W.S., Hodapp D., Larsen S., Lewandowska A.M., Seabloom E.W., Van de Waal D.B., Ryabov A.B. (2017) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *Journal of Applied Ecology*, 1-16, DOI: 10.1111/1365-2664.12959.
- Isbell F.**, Craven D., Connolly J., Loreau M., Schmid B. (2015) Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes, *Iowa State University Digital Repository: Ecology, Evolution, and Organismal Biology Publications*
- Jentsch A.**, Kreyling J., Elmer M., Gellesch E., Glaser B., Grant K., Hein R., Lara M., Mirzae H., Nadler S.E., Nagy L., Otieno D., Pritsch K., Rascher U., Schädler M., Schlöter M., Singh B.K., Stadler J., Walter J., Wellstein C., Wöllecke J., Beierkuhnlein C. (2011) Climate Extremes Initiate Ecosystem-Regulating Functions While Maintaining Productivity, *Journal of Ecology*, vol. 99, no. 3, 689–702, doi:10.1111/j.1365-2745.2011.01817.x.
- Jentsch A.** & Beierkuhnlein C. (2010) Simulating the Future – Responses of Ecosystems, Key Species, and European Provenances to Expected Climatic Trends and Events, *Nova Acta Leopoldina NF*, vol. 112, no. 384, 89–98
- Jentsch A.** & Beierkuhnlein C. (2008) Research Frontiers in Climate Change: Effects of Extreme Meteorological Events on Ecosystems, *Comptes Rendus Geoscience*, vol. 340, no. 9-10, 621–628., doi:10.1016/j.crte.2008.07.002.
- Jones S.K.**, Ripplinger J., Collins S.L. (2017) “Species Reordering, Not Changes in Richness, Drives Long-Term Dynamics in Grassland Communities.” *Ecology Letters*, vol. 20, no. 12, 1556–1565., doi:10.1111/ele.12864.
- Kercher S.M.**, Frieswyk C.B., Zedler J.B. (2003), Effects of sampling teams and estimation methods on the assessment of plant cover, *Journal of Vegetation Science*, Volume 14, Issue 6, Pages 899-906

- Linhardt Sven**, Wetterstadion Bayreuth, available at: <https://www.wetter-bayreuth.de> , state: 28.11.2019
- Niinemets Ü.** (2010) A review of light interception in plant stands from leaf to canopy in different functional types and in species with varying shade tolerance. *Ecol Res* 25, 693–714
- Oksanen J.**, Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara R. B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E., Wagner H. (2019) *vegan- Community Ecology Package*, R package version 2.5-6
- Pagter M & Arora R.** (2013) Winter survival and deacclimation of perennials under warming climate: physiological perspective, *Physiologica Plantarum* 147: 75-87
- R Core Team** (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Roberts F.** (2013) What the IPCC Report Says about Extreme Weather Events, Carbon Brief Ltd., <https://www.carbonbrief.org/what-the-ipcc-report-says-about-extreme-weather-events>, state: Jan 2020
- Smith T.M.**, Smith R.L. (2009), *Ökologie*, 6. Auflage, München, Pearson
- Thomas C.**, Micrometeorology University of Bayreuth, available at: [http://www.bayceer.uni-bayreuth.de/meteo/en/klima/gru/html.php?id\\_obj=140009](http://www.bayceer.uni-bayreuth.de/meteo/en/klima/gru/html.php?id_obj=140009), state: 28.11.2019
- Tilman D.**, Reich P.B., Isbell F. (2012) “Biodiversity Impacts Ecosystem Productivity as Much as Resources, Disturbance, or Herbivory.” *Proceedings of the National Academy of Sciences*, vol. 109, no. 26, 10394–10397., doi:10.1073/pnas.1208240109.
- Tomczyk A.M.**, Sulikowska A., Bednorz E., Pórolniczak M. (2019) Atmospheric circulation conditions during winter warm spells in Central Europe, *Natural Hazards*, <https://doi.org/10.1007/s11069-019-03621-4>
- Vogel A.**, Eisenhauer N., Weigelt A., Scherer-Lorenzen M. (2013) “Plant Diversity Does Not Buffer Drought Effects on Early-Stage Litter Mass Loss Rates and Microbial Properties.” *Global Change Biology*, vol. 19, no. 9, 2795–2803., doi:10.1111/gcb.12225.
- Wickham H.** (2018) *reshape-Flexibility reshape data*, R package version 0.8.8
- Woldendorp G.**, Hill M.J., Doran R., Ball M., (2008), Frost in a future climate: modelling interactive effects of warmer temperatures and rising atmospheric CO<sub>2</sub> on the incidence and severity of frost damage in a temperate evergreen (*Eucalyptus pauciflora*), *Global Change Biology*, 14, 294-308
- Yuan Y.**, Liu Y., Luo Y., Huang L., Chen S., Yang Z., Qin S. (2011), High temperatures effect on flavones accumulation and antioxidant system in *Scutellaria baicalensis* Georgi cells, *African Journal of Biotechnology*, Vol 10 (26), 5182-5192
- Zeppel M.J.B.**, Wilks J. V., Lewis J. D. (2014) Impacts of extreme precipitation and seasonal changes in precipitation on plants, *Biogeosciences*, 11, 3083–3093
- Zhang L.**, Xiao J. , Li J., Wang K., Lei L., Guo H. (2012), The 2010 spring drought reduced primary productivity in southwestern China, *Environmental Research Letters*, Vol 7, Nr 4