Biogeosciences
Discussions

Interactive comment on "Recovery dynamics and invasibility of herbaceous plant communities after exposure to fifty-year climate extremes in different seasons" *by* F. E. Dreesen et al.

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We are grateful to both reviewers for reading our manuscript and providing us with constructive comments and very helpful suggestions. The statistical analysis has been reworked with the help of a statistician, while major conclusions are upheld. The focus of our paper will be readjusted to conform better to the Biogeosciences scope by adding analysis and discussion on nutrient cycles and biomass production and linking the paper more closely to an earlier paper on the direct effects of the induced climate extremes (De Boeck et al. 2011, New Phytologist).

Referee 1

Comment: The authors focus on the recovery dynamics in the first two years after the events. These recovery dynamics are not restricted to the resident plant species, but also to naturally colonizing species, which were allowed to establish for two years. This approach is potentially interesting, because it may shed light on the long-term effects of extreme events on the functional composition of natural communities, which may have consequences for ecosystem functioning. However, the approach is also a bit tricky, because it depends on the available species pool. In this case, the experiment has been performed on the campus of the university, which raises the question whether the species pool present accurately reflects the pool of potential colonizers of the natural communities the experiment is mimicking.

Answer: Our campus is located outside of the city and is surrounded by hay meadows which are mown twice yearly and horse-grazed fields. Pots were placed in the open, so seed input should have been plentiful. Moreover, the soil we used was a local, homogenized soil which had not been sterilized, and which should therefore contain plenty of seeds of locally common grassland species. Figure 1 below shows a satellite picture of our site and the surroundings.

Comment: Another problem of natural colonization, particularly in small pots and over short timespans, is the potentially high variability of colonization: the species that eventually establish in the experiment may be greatly affected by the chance that its seeds actually reach a pot. This is clearly illustrated in Table S1, which shows several examples of species being highly successful in a particular pot, but absent from most others (e.g. Trifolium pratense, Lotus corniculatus, Achillea millefolium). Most probably, this is due to a relative low density in the local seed rain, making the chance that it reaches a pot rather small (as the authors acknowledge). Again, can this be considered to reflect what would happen in natural communities? Probably not. To avoid this problem, one could actively add seeds to each pot. I think the authors should briefly mention why they did not do this, and also discuss how this alternative approach may have changed their results.

Answer: As illustrated above, we believe that both the surroundings and the soil used reflect relatively closely the seeds that would be present in local grasslands. All pots were kept together during the two years following the extreme events, so the seed rain should have been very similar, and the soil used in all pots was homogenized prior to planting, so the historical seed bank should also have been near-identical in all pots. We were therefore convinced that manually adding seeds was not necessary. We will add a similar description in the manuscript. A consideration not made in the original manuscript is the fact that, under a natural climate extreme, the landscape would also have been affected, which may have resulted in a different composition of the seed rain (reflecting differences in phenology, mortality, etc. in response to the extreme event) and different seed characteristics (e.g. affected via epigenetics). We will devote a few lines in the discussion on this issue.

Comment: An additional problem of the high variability in colonization is that it makes it difficult to reach clear conclusions. If there are no effects of extreme events on community composition after colonization, is this due to inherently high variability in invasion probability among species or does it mean that extreme events have little impact on community composition? This problem is illustrated by the conclusions of the authors. For example, in the abstract, they first conclude that the observed change in composition was independent of the extreme event (l19-20), but later, they conclude that extreme events modified species composition (l22). This should be improved.

Answer: While we did see different colonization after the extreme event between treatments, this was a temporary phenomenon and had disappeared by year two. With the altered statistical analysis (see comments referee 2), we will rephrase certain parts of the discussion and will address the nuance suggested by the referee more clearly. We will furthermore correct conflicting statements in the abstract.

Comment: The introduction is clear and well structured. Perhaps the part about recurring events (l26) can be removed because the experiment does not include recurring events.

Answer: This will be edited as suggested.

Comment: The methods are clear, and sufficiently complete to repeat the experiment. However, for a description of an experiment that has already been published (paragraph 2.1), I think it is too extensive. Hence, I would encourage to substantially shorten this paragraph and refer to De Boeck et al 2011 for details such as the soil composition, the design consisting of 6 boxes (which was not used in the colonization phase, if I understand correctly?), the determination of the length of the extremes, and the detailed data about soil water content (just mentioning if wilting point was reached may be sufficient here).

Answer: We will omit redundant information where possible. In light of the changes that will be made to the manuscript – such as more detail on surrounding area and soil, and a closer link with the findings in the 2011 paper, we will be careful with what information to remove, however, so that the analyses can be understood from the information presented in this paper.

Comment: Other point: I think the three resident species were included in the species composition analyses, but this is not very clear. Please clarify.

Answer: Indeed, the three resident species were included in the analyses in the original manuscript, but this has been adapted in the revised version (see also the comments of referee 2).

Comment: The results are clearly presented, but I think the number of tables and figs can be shortened. For example, Table 1 does not provide a lot of information and can be moved to the supplementary material.

Answer: Referee 2 mentioned that the Relative Euclidean Distance was not a good method for analyzing differences in species composition between treatments. Table 1 will be removed from the new manuscript.

Comment: Fig 1 may also be omitted. A general description of the two years (in terms

of drought-like circumstances, deviations from average climate) may be sufficient. Fig 3c basically shows the same effect as 3a (and 3b) and can be omitted too. Fig 4 puzzled me a bit, see also my previous question about whether the three resident species were also included in the composition data. Fig 4a shows 2009, which is before natural colonization has occurred. Hence, we are actually looking at shifts in abundance of the three experimental species, right? If correct, than this actually repeats the results shown in Fig 2b, which shows strong decline of T. repens in the DH treatment. To what extent does this decline also drive the observed effect in 2010 (Fig 4b)? I think it would be more interesting if you could show that the invader community (rather than the combination of residents and invaders) was different in terms of composition in response to the treatments. In general, I think there is a discrepancy here: for species richness, only invaders are considered (if I understood correctly?), but for composition, the residents were also included. I would only focus on the invaders. In addition, you may want to analyse the response of (a) particular invading species that did actually reach most pots. For example, Holcus lanatus seems to be have reached most pots and become dominant in most treatments (table S1). Personally, I would prefer to have S1 in the main paper, especially because it also contains the biomass of the three resident species in 2010 and 2011, which is lacking from the paper's main figs!

Answer: Figure 1 will be replaced. Fig 3c will be removed and information on the biomass of the invaders instead of only the number of invaders will be added (in response to referee nr. 2). The suggestions of the referee will be taken into account when adapting the other figures of the paper in line with the new analyses that were executed and the increased focus on biomass production and nutrient cycles (see comments referee nr. 2).

Referee 2

Comment: I find the analysis of the invasibility data interesting, but not yet sufficient to back up the conclusion of no major changes in the community composition beyond transient effects: The Euclidian distance within two groups can be exactly the

same yet species compositions can be completely different. The same is true for CSR-scores. A change in species composition sustained over two years following the drought events, however, would be quite important and seems likely when looking at the species biomass of the species initially planted. Ordination techniques can illustrate changes in community composition, and ANOSIM or MRPP can tell if the compositions between groups differ signifcantly. 9/ 1: why Euclidean Distance? It is quite sensitive to rare species. Bray-Curtis is more often used in vegetation science.

Answer: As we did not have prior knowledge of and experience with the proposed techniques (ANOSIM & MRPP), we collaborated with a statistician (Joanna Horemans, who will be added as a co-author) to improve upon the statistical methods. She echoed the concerns of the referee in that Euclidean distance methods depend greatly on the abundances of the species, and not so much on which species are shared. Bray-Curtis and Kulczynski distances would both incorporate abundances and the species composition of community. ANOSIM and MRPP are interesting tools to compare species compositions but these methods do not give the possibility to differentiate eventually confounding effects of the two explanatory variables present (the type of extreme event and the season in which this stress factor was applied). Therefore she suggested applying a method that additionally allows distinguishing between treatment factors. Her suggested method using Bray-Curtis distances is ADONIS, which is a permutational multivariate analysis of variance using distance matrices. We used year (2010 and 2011), timing of stress (spring, summer or autumn) and the type of extreme event (drought, heat, drought + heat and control) as explanatory factors in the model. In addition, in the revised version, we only considered the invaders and not the combination of invaders and residents (as suggested by referee 1). Using this method on the plant species level, we found two significant interactions when running the model for the two years together, namely an interaction between year and season and one between year and type of extreme event. This indicates that both factors did not have the same effect on the species composition in the two years. When analyzing the two years separately, we found for the year 2010 a significant effect of the season when the extreme events

was applied. The type of extreme event did not have a significant influence. For 2011, there were no significant effects of any explanatory factor on the species composition. These results are in line with the conclusions of our original manuscript.

Comment: Page 4/ Line 8: I recommend Hughes et al. 2007 Ecology Letters for further reading. In general, references should be sorted chronologically.

Answer: These suggestions will be implemented.

Comment: 4/ 26: What would be the opposite event? Grasses dropping out our shrubs invading a grassland?

Answer: We will clarify this sentence: "For example, grasses invading a semiarid shrub-land have been found to increase carbon and nitrogen storage while woody plants invading into wet grasslands caused a decrease in carbon and nitrogen storage (Jackson et al., 2002; Wolkovich et al., 2010)."

Comment: 7/ 2: The shelters appear small and high, what about rain coming in from the side?

Answer: The shelters were high to ensure full air exchange with the surroundings and avoid the build-up of heat. However, the shelters slanted down towards the sides and sticked out 1 m at each side of the boxes. Therefore, rain coming in from the side could not reach the plants in the boxes (unless during very stormy conditions, but did this not occur during our experiment). This information will be added to the manuscript.

Comment: The reduction in biomass by the second year is interesting, yet I have the impression that it cannot be related to the drought in the previous year but rather to overall growing conditions in 2010 as all plots, even the controls, show a similar reduction in biomass. A discussion of the differences in ambient growing conditions would also be helpful for the evaluation of seasonal differences in drought effects.

Answer: We have added a part in the discussion to address this suggestion. Climate conditions in 2010 were close to average overall (slightly cooler and wetter than nor-

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mal), with a dry period in spring and early summer followed by a wetter second part of the summer. For 2011, conditions were in general significantly warmer than average, although summer temperatures were cooler than normal, with a lot of days with precipitation. We cannot rule out that climate played a role in reducing biomass in 2010-2011 compared to 2009 overall, but we do think that it is more likely that the nutrient poor sandy soils used in this experiment (fertilizer was only added at beginning of the experiment in 2009 to help establishment of the communities) combined with the overall decline of the N-fixer species was the primary factor in the declining productivity. We discuss this in greater detail in the revised paper. By adding a discussion on nutrient cycles, we also address in part the concern about the relevance for Biogeosciences. Furthermore, we will explicitly compare the differences in biomass production between 2009 and 2010/2011, as this should more clearly connect the short-term (resistance & immediate resilience) and longer-term responses (colonization) to climate extremes. An increased focus on nutrient cycles and biomass production should improve the study's appeal to Biogeosciences.

Comment: I miss a discussion if the developmental stage is leading to different responses among seasons, or if it is simply a difference in realized drought severity (e.g. comparison of outside weather conditions and the soil moisture availability).

Answer: We will provide a short wrap-up of the most relevant conclusions of the paper that dealt directly with immediate consequences of the extreme events (De Boeck et al., 2011, New Phytologist), including the importance of season, absolute drought/heat wave conditions and interactions.

Comment: Fig. 1: Information for the treatment year should be added here.

Answer: Referee nr.1 suggested to replace fig. 1 by a general description of the climate during the experimental years. Information for the treatment year will be added as well.

Comment: Fig. 3: In addition, the total biomass of invaders would be interesting, as the number of species does not give information on the importance.

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Answer: This information will be added in the revised manuscript.

Fig. 1.