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Recovery dynamics and invasibility of herbaceous plant communities after exposure to experimental climate extremes

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1 **Recovery dynamics and invasibility of herbaceous plant**
2 **communities after exposure to experimental climate**
3 **extremes**

4
5 **Freja E. Dreesen, Hans J. De Boeck*, Joanna A. Horemans, Ivan A. Janssens &**
6 **Ivan Nijs**

7 *Corresponding author. Tel.: 003232652282; fax: 003232652271.

8 E-mail address: hans.deboeck@uantwerp.be.

9 Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology, University of Antwerp,
10 Universiteitsplein 1, 2610 Wilrijk, Belgium

11
12 **Abstract**

13 Do climatic extremes increase the invasibility of plant communities, for example through the
14 creation of gaps and the associated local surplus of available resources? To address this
15 question, small experimental communities consisting of three forb species were first subjected
16 to extreme drought and/or heat treatments in different seasons and species mortality and end-
17 of-season biomass were examined. Then, the establishment of new species and their effects
18 on the productivity of the community were recorded in two subsequent years without
19 additional treatments.

20 The immediate response to the experimentally induced extremes was similar in all three
21 originally planted species, with drought treatments in summer and autumn, especially when
22 combined with heat, inducing the greatest plant mortality. Recovery in terms of end-of-season
23 aboveground biomass was species-specific, however. The dominant species, the N-fixer
24 *Trifolium repens*, recovered poorly from the drought and drought + heat treatments.
25 Differences in community biomass between treatments and to the controls were no longer
26 significant in the next year. Especially graminoid species successfully invaded the
27 communities, possibly because of functional dissimilarity with the species already present.

1 Invasibility in the year following the extreme events was increased in communities that had
2 been exposed to both a heat wave and a drought, but the number of newly established species
3 did not increase community productivity. The identities of invading species varied distinctly,
4 but had no clear relation with the extreme events the communities had been exposed too.

5 The induced climate extremes greatly affected the survival and productivity of the species and
6 influenced the invasibility of the plant communities. However, none of the community
7 properties seemed to be affected in the longer run, as the induced responses faded out after
8 one or two years.

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10 *Keywords:* biomass; colonization; drought; experiment; gap; heat wave; legacy effects; plant
11 ecology

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13 *Running head:* Recovery and invasibility after climate extremes

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1 **Introduction**

2 Extreme climate events have become a key issue in global change research, in view of their
3 increasing frequency and intensity and their potential impact on ecosystems (IPCC 2012). In
4 plant communities, intense drought and heat events can cause major disturbance, including
5 loss of productivity (Ciais et al. 2005; De Boeck, Dreesen, Janssens & Nijs 2011) and
6 increased die-off (Breshears et al. 2005; Kreyling, Wenigmann, Beierkuhnlein & Jentsch
7 2008b). Lagged responses include higher mortality, slow recovery or increased sensitivity to
8 pests or future events (Arnone et al. 2008; Reichstein et al. 2013). This might even turn CO₂
9 sinks into sources, creating a positive feedback for climate warming (Reichstein et al. 2013).
10 An additional effect of extreme events is that they may render communities more sensitive to
11 invasion by new species since disturbance, by creating gaps in the original community, is a
12 major driver of invasibility (Burke & Grime 1996). This imposes additional pressures on the
13 persistence of plant communities besides the direct effect of the events themselves.

14 According to the fluctuating resource availability theory (Davis, Grime & Thompson 2000), a
15 community becomes more susceptible to invasion when the amount of unused resources is
16 increased. This occurs when resource uptake by the resident community is diminished (e.g.
17 following plant mortality) or when an increase in resources exceeds the sequestration rate of
18 the resident plants (e.g. following improved water supply or eutrophication) (Davis, Grime &
19 Thompson 2000). Several studies have indeed reported enhanced invasibility after disturbance
20 events, including droughts (Belote, Jones, Hood & Wender 2008; Jiménez et al. 2011;
21 Kreyling, Beierkuhnlein, Ellis & Jentsch 2008a). However, invasibility could also be reduced
22 by disturbance if the events create suboptimal conditions, allowing only few, disturbance-
23 tolerant species to colonize and establish (Davis, Thompson & Grime 2005). Several studies
24 have suggested that communities containing more species would generally lower invasibility
25 as more niches are occupied and the amount of unused resources is decreased (e.g. Dukes
26 2001; Frankow-Lindberg 2012; van Ruijven, De Deyn & Berendse 2003). This relationship is
27 not ubiquitous and is also related to scale (Fridley et al. 2007). Even so, disturbance can
28 influence the diversity of communities through mortality, diversity can affect invasibility and
29 invasibility can in turn determine diversity through newly incoming species, suggesting that

1 diversity, disturbance (i.e. changes in available resources) and invasibility all co-vary (Clark
2 & Johnston 2011).

3 The species that enter the community after an extreme climatic event can influence carbon,
4 water and nutrient cycling through species-specific impacts on productivity, above- and
5 belowground nitrogen storage, etc. For example, grasses invading a semiarid shrubland have
6 been found to increase carbon and nitrogen storage while the opposite was found for woody
7 plants invading wet grasslands (Jackson, Banner, Jobbagy, Pockman & Wall 2002;
8 Wolkovich, Lipson, Virginia, Cottingham & Bolger 2010). Meta-analysis of plant invasion
9 studies revealed that invading woody and N-fixing species usually had a greater impact on
10 carbon and nitrogen cycles than those by herbaceous and non-N-fixing species (Liao et al.
11 2008). Knowledge on how extreme events would affect community composition after an
12 extreme event is therefore relevant when assessing elemental cycles of ecosystems over
13 longer periods. Which species invade communities would not only depend on the amount of
14 unused resources and gaps, but also on the characteristics of species that were already present.
15 It is often speculated that species that are functionally different from resident species have a
16 higher invasion success (see the meta-analysis of Price & Pärtel 2012). The fact that no
17 graminoid species were originally present in our communities enables us to test this
18 assumption.

19 In this study, we subjected constructed plant communities consisting of three common
20 herbaceous species to experimentally induced drought and/or heat events in different seasons.
21 In the following two years, other species were allowed to invade the plant communities. We
22 hypothesized that (i) the climate extremes would cause different amounts of stress depending
23 on the type and timing of the extreme and on plant-specific characteristics, giving rise to
24 different patterns of mortality and productivity; (ii) invasibility would subsequently be higher
25 in the treatments which lost more biomass, as the amount of unused resources is increased;
26 (iii) because the communities originally contained only forbs, graminoids would be more
27 successful colonizers as they are functionally more dissimilar, while invasion by forbs would
28 be slower and dependent on mortality of the originally present species. Our principle
29 objective was thus to determine how a disturbance in the form of a climate extreme affected

1 community composition and productivity immediately after the extreme and in the following
2 two years.

3

4 **Materials and Methods**

5 **Study site, plant material and treatments**

6 This study was conducted from April 2009 until October 2011 at an experimental field site on
7 the Drie Eiken Campus of the University of Antwerp (Belgium, 51°09' N, 4°24' E). Details
8 on the experimental set-up can be found in Appendix A. In short, 216 experimental plant
9 communities in cylindrical containers (20 cm diameter, 40 cm depth) with three species in
10 equal proportions (*Plantago lanceolata* L., *Rumex acetosella* L. and *Trifolium repens* L.) were
11 subjected to experimental climate extremes (drought, D; heat, H or both combined, DH)
12 corresponding to events that would occur approximately once per 50 years regionally. The
13 treatments were imposed in different seasons (spring, summer and autumn) by means of
14 rainout shelters and infrared heaters. After the biomass harvest in the year of the imposed
15 extremes (October 2009), 72 communities (6 per treatment and 18 controls) were removed
16 from the set-up and subjected to ambient air temperature and precipitation. From then on, new
17 species were allowed to naturally invade the communities. The two following years (2010 and
18 2011), communities were clipped at 4 cm on 19-20 June and 26-30 October, in order to
19 simulate local mowing practices. After each harvest, the spatial arrangement of the
20 communities was changed. No fertilizer was added. We assume that natural seed influx was
21 adequate because of the open nature of the field site and the nearby presence of several
22 grasslands. Edge effects should have been similar as we placed all communities per treatment
23 in a 2×3 arrangement (i.e. without core zone). The propagule pressure was likely highly
24 comparable in all communities because they all were set up close together (in a 3×4 m area)
25 and the soil was homogenised (i.e. comparable seed bank). Fig. S1 shows the mean monthly
26 air temperature and monthly precipitation during the experimental years, along with the
27 monthly averages (period 1981-2010).

28

1 **Measurements**

2 Apparent mortality of plants (no green tissues visible) was recorded on the last day of
3 experimental treatments, i.e., on 13 May, 31 July or 9 October 2009 by counting all plants in
4 6 replicate communities per treatment. Note that complete loss of green tissue does not
5 necessarily mean that a plant died completely, as regrowth is possible from meristems. At the
6 end of each growing season (October), the aboveground biomass was separated by species
7 and weighed after drying for 72 hours at 70 °C.

8

9 **Data Analysis**

10 To establish whether the end-of-season aboveground biomass of the individual original
11 species (2009, 2010 and 2011), the total plant biomass (2009, 2010 and 2011) and the
12 biomass of invading species (2010, 2011) were affected by the type of treatment (C, D, H and
13 DH) and the season in which the treatment was imposed (spring, summer or autumn), separate
14 analyses of variance (ANOVA) were performed. We adapted the general linear model (GLM)
15 to take into account binomially distributed responses (based on the chi-square test) when
16 analysing mortality of the individual original species at the end of the year of treatment
17 application (2009). Additional ANOVAs were performed to study whether responses to the
18 treatments (type and season) were different among invading species. We therefore assigned
19 species to functional groups. Other classifications, such as annual/perennial or native/non-
20 native did not allow for statistical analysis because of insufficient occurrences across
21 treatments and/or years (cf. Table S1). We distinguished between graminoids, nitrogen fixing
22 species and non-N-fixing forbs (this included rare seedlings of two tree species, cf. Table S1).
23 Where needed, post-hoc tests were performed with the Tukey-Kramer correction. Pearson's
24 correlation was used to test the influence of N-fixers on the number of newly established
25 species (as increased nitrogen availability could facilitate invasion). The biomass of N-fixing
26 species (sampled in autumn) was compared to the number of species in the next year because
27 their establishment usually occurs in early spring. These statistical tests were performed using
28 SAS (version 9.1, SAS Institute Inc., Cary, NC, USA) with a significance threshold of 0.05.

1 The effects of the extreme events and their timing (season) on community composition of the
2 invading species were studied by a non-parametric, permutational, multivariate analysis of
3 variance (PERMANOVA), which was preferred over standard multivariate methods because
4 of its flexibility and lack of assumptions (often not met for ecological multivariate datasets).
5 The method allows a direct additive partitioning of the variance and provides a pseudo F-
6 statistic calculated from the distance matrix. In the overall analysis and for each of the two by
7 two comparisons, 7999 permutations were made to obtain sufficient precision in p-value
8 calculation. Bray-Curtis distances were used in the analysis since they account for abundances
9 as well as species composition. Since this measure is susceptible to outliers and high zero
10 response abundances, the data were first transformed by the formula $(\log(y + 1))$. We used
11 the ADONIS function in R for this analysis.

12

13

14 **Results**

15 **Short-term effect: species mortality**

16 Fig. 1A shows the apparent plant mortality per species on the last day of the seasonal
17 extremes, i.e. on day of year 133, 212 and 282 for spring, summer and autumn, respectively.
18 Among the treatments applied in spring, only the DH extreme had an impact. This extreme
19 led to substantial apparent mortality in *T. repens* (23% mortality, $P = 0.004$), but not in the
20 other two species. When occurring in summer, the DH extreme affected all three species,
21 causing more than 80% mortality ($P < 0.001$ for *P. lanceolata*, *T. repens* and *R. acetosella*).
22 The summer D extreme reduced the number of living plants of *T. repens* and *R. acetosella* by
23 32% and 30%, respectively ($P < 0.001$ and $P = 0.03$), but did not induce mortality in *P.*
24 *lanceolata*. In autumn, the DH extreme also caused significant mortality in all three species,
25 ranging from 45% in *P. lanceolata* to 67% in *R. acetosella* ($P < 0.001$), while the autumn D
26 treatment had an impact only on *R. acetosella* (mortality of 20%, $P = 0.03$). The H extremes
27 never caused loss of living plants, in any of the seasons.

1 **Long-term effect: productivity**

2 By the end of the growing season, much of the observed plant mortality had been
3 compensated by regrowth (Fig. 1B). For example, although more than 20% of *T. repens*
4 plants were deprived of all aboveground green tissues after the DH spring extreme, end-of-
5 season production was not affected. A similar effect was observed after even stronger initial
6 responses to the summer D and DH treatments by *P. lanceolata* and *R. acetosella* (Fig. 1B). *T.*
7 *repens*, on the other hand, did not recover from these summer extremes, resulting in a reduced
8 biomass after the summer D extreme (-34%; $P = 0.05$) and nearly no biomass after the
9 summer DH extreme ($P < 0.001$). In response to the autumn D and DH extremes, *T. repens*
10 likewise had much less biomass than in controls (-37% and -73%; $P = 0.05$ and $P < 0.001$,
11 respectively). Furthermore, the autumn DH extreme was the only treatment from which *P.*
12 *lanceolata* and *R. acetosella* could not recover, resulting in a biomass decline of 41% and
13 92%, respectively ($P < 0.001$ and $P = 0.004$). Note that the much shorter recovery period after
14 the autumn extremes compared to the summer and spring extremes influenced the amount of
15 aboveground biomass that was harvested.

16 The aboveground community biomass in the year in which the extremes were applied (Fig. 2),
17 reflected the response of *T. repens* (see Fig. 1B, middle panel), with strong decreases after the
18 summer and autumn D and DH treatments. One year later, differences in community
19 aboveground biomass had disappeared (Fig. 2), also in the communities that experienced
20 substantial plant mortality and biomass decrease. This was still the case in 2011, although the
21 standard errors increased relative to 2010, indicating greater within-treatment differences
22 (Fig. 2). Aboveground productivity was in general markedly lower in the two years following
23 the extreme events with biomass in controls dropping by 50% and more. When looking how
24 the three originally planted species performed in 2010 and 2011, treatments did not differ
25 from controls anymore (no significant effect of treatment type, season or their interaction).
26 Between treatments, some differences remained, however. For *P. lanceolata*, productivity
27 was lower in 2010 in the DH treatment compared to both the D ($P = 0.002$) and the H
28 treatment ($P = 0.004$) (see also Table S1). For *T. repens*, no significant differences between
29 treatments or their timing were found for 2010. In 2011, the season in which the extremes had
30 been imposed had an effect, with reduced aboveground productivity in the communities

1 exposed to a climate extreme in summer two years earlier compared to one in spring ($P =$
2 0.03) or autumn ($P = 0.009$). For *R. acetosella*, no significant differences were found in any
3 year.

4 **Long-term effect: invasibility and changes in community composition**

5 Since the various extreme events induced mortality and lowered productivity to different
6 degrees, we expected these differences to be reflected in diverse rates and patterns of
7 invasion. One year after the climate extremes (in 2010), more newly established species were
8 found in the DH treatments (Fig.3a; $P = 0.005$, only a main effect of the type of extreme
9 event, no interaction with season). However, per species, these newly established species only
10 produced little biomass (Fig. 3b). Although not statistically significant ($P = 0.09$), the biomass
11 of the newly established species tended to be higher in the control treatments, despite the fact
12 that the number of invading species was lower than in the DH treatments. In 2011, two years
13 after the applied extremes, no differences in the number of newly established species, nor in
14 newly established biomass between the treatments remained (Figs. 3A and B).

15 Because the extreme events had substantial effects on the N-fixing species in the original
16 communities, we tested whether differences in the presence of a functional group able to
17 facilitate establishment and productivity of other species through its effect on N availability
18 would have significant effects. We found no significant correlation between N-fixer
19 productivity and the number of species that established in the community, however (Fig. S2).

20 Table S1 lists all the species found in the plant communities as well as their aboveground
21 biomass, including the three originally planted species. More than 30 species were identified
22 across all communities during 2010 and 2011. The list shows major variation in species
23 composition and biomass among treatments, but also among replicates within the same
24 treatment. Analysis of the composition of the species that invaded the different communities
25 after the imposed climate extremes, indicated significant interactions between year and season
26 ($P = 0.009$) and between year and type of extreme event ($P = 0.02$) when analyzing the
27 dataset as a whole. In other words, the effect of the treatments on species composition
28 changed in time. Analysis of the two years separately showed that in 2010, the interaction
29 between season and type of extreme event was marginally insignificant ($P = 0.057$), with the

1 season in which the extreme events occurred significantly affecting the species composition
2 ($P = 0.04$). More specifically, summer events had a different impact on the composition of
3 invading species compared to spring and autumn events ($P = 0.04$ and $P = 0.05$).

4 We determined whether characteristics of the invading species interacted with the type of
5 treatment and season in which they occurred to alter the establishment success. No
6 interactions between treatment type and season were observed, neither in 2010 ($P = 0.56$) and
7 2011 ($P = 0.48$). The type of climate extreme imposed in 2009 did lead to differences in the
8 aboveground biomass of invading graminoids in 2010, which was significantly higher in
9 controls than in communities subjected to drought ($P = 0.007$), heat ($P = 0.009$) or drought
10 and heat ($P = 0.02$) (Table 1). These differences had disappeared in 2011. The biomass of
11 invading non-N-fixing forbs did not differ between control and treatments in 2010, although it
12 was higher in DH compared to D ($P = 0.007$) and H ($P = 0.01$), but these differences also
13 disappeared in 2011. Treatment type and season did not affect biomass of invading N-fixing
14 species significantly in any year. In general, invader biomass was significantly different
15 between the three functional groups ($P < 0.001$). Graminoids, not present in the original
16 communities, were the most productive invaders both in 2010 and 2011 (73% of total invader
17 biomass in 2010, 56% in 2011). Newly arrived non-N-fixing forbs made up only 8% of
18 invader biomass in 2010, but this rose to 32% in 2011, coinciding with a biomass decrease of
19 similar magnitude of *P. lanceolata*, originally present in the communities (Table S2). N-
20 fixing species contributed 19% and 12% of invader biomass in 2010 and 2011, respectively,
21 and also here, the biomass proportion of new to originally present N-fixers increased in 2011
22 (Table S2).

23

24 **Discussion**

25 Earlier analysis of the impact of seasonal climate extremes on community level demonstrated
26 that community biomass strongly declined in response to severe drought (an effect that was
27 exacerbated by high temperatures) and that immediate responses to seasonal extremes not
28 only depended on the drought severity reached in the different treatments but also on the

1 developmental stage of the plants (De Boeck, Dreesen, Janssens & Nijs 2011). We here
2 showed that species differed in their sensitivity to the imposed extreme events, especially
3 regarding their resilience. The event with the largest short-term impact (the combination of
4 drought and a heat wave in summer) led to aboveground die-off of more than 80% in all three
5 species present, but this large impact was no longer detected in the end-of-season
6 aboveground biomass for two of the three species. Several other studies have indeed found
7 high recovery rates for grassland species after an extreme event (Dreesen, De Boeck, Janssens
8 & Nijs 2014; van Ruijven & Berendse 2010). However, the third species, *Trifolium repens*,
9 hardly recovered from the harshest extremes, where the soil water content reached values
10 below wilting point (DH in summer and autumn). This species is known to be drought-
11 sensitive due to its shallow root system and inefficient stomatal control, resulting in
12 accelerated leaf wilting and die off (Hart 1987). In general, *T. repens* is capable of making
13 osmotic adjustments in the stolons to allow conservation of and regrowth from these organs
14 once water availability increases again (Turner 1990). Given the poor regrowth, the stress in
15 our treatments was likely too intense to maintain this adjustment.

16 The strong decline of *T. repens* clearly dominated the response of the community biomass. A
17 single dominant can thus significantly affect the stability of an entire community, something
18 also observed in other studies (Buckland, Grime, Hodgson & Thompson 1997; Sasaki &
19 Lauenroth 2011). Changes in dominance patterns can have important implications for the
20 functioning of an ecosystem, since species have different traits that can influence elemental
21 cycles. Our dominant species was an N-fixer, which can play an important role as a facilitator
22 (e.g. Maron & Connors 1996), especially in nutrient-poor soils such as the one used here. The
23 large effects of the climate treatments on the survival and production of *T. repens* were not
24 reflected in the community productivity of 2010, however (Fig. 2). This apparent
25 contradiction may be due to the overall decline of *T. repens* across all treatments and controls
26 in 2010 and 2011, so that differences between the treatments generally disappeared. Although
27 interannual differences in climatic conditions may have played a role, we assume that this
28 decline was mostly related to nutrient depletion in the (unfertilized) communities. Especially
29 low phosphorus concentrations (13 mg kg^{-1} dry soil was present at the start of the experiment)

1 would have been relevant for N-fixing species, whose poor performance would in turn have
2 further increased nitrogen limitation.

3 The presence of more N-fixers did not facilitate the arrival of more species, perhaps because
4 increased N availability was canceled out by limitations of other nutrients or because higher
5 N-fixing biomass and therefore cover meant that fewer gaps were available for establishment.
6 On the other hand, local mortality after the imposed climate extremes would have led to both
7 more available nutrients and more space and/or light, conditions which have been reported to
8 increase susceptibility to invasion (Davis, Grime & Thompson 2000). Indeed, we observed
9 that invasibility was increased in the communities that had been exposed to those treatments
10 (DH) that caused the greatest mortality. However, this effect only lasted for one year,
11 suggesting that the amount of unused resources declined again rapidly.

12 In several invasion studies the identity of the invading species determined their establishment
13 success after a disturbance event (Kreyling, Beierkuhnlein, Ellis & Jentsch 2008a; Stampfli &
14 Zeiter 2004). We found that graminoids were the most successful invaders in general, which
15 was expected on the basis of their functional dissimilarity with the herbaceous species making
16 up the original communities. Their vertical leaf structure would for example enable them to
17 capture more light through spatial complementarity than most invading herbaceous species
18 (cf. Spehn et al. 2000). Indeed, both N-fixing and non-N-fixing forbs established to a lesser
19 extent, only increasing their success once the two most productive original species (*P.*
20 *lanceolata* and *T. repens*) decreased in productivity in the second year after the extremes. The
21 fact that the success of invading forb species seemed to be inversely related to the biomass of
22 already present forbs reflects findings of Price & Pärtel (2012). However, when *P. lanceolata*
23 biomass decreased in the DH treatment in 2010 compared to D and H, non-N-fixing forb
24 biomass increased (Table 1 and Table S1), which is contrary to the general effect we found.

25 This is not the only instance in which we found effects that seemed stochastic rather than
26 deterministic, as we generally observed high variation in invading species within the same
27 treatment. The fact that stochastic processes can play an important role during early stages of
28 community assemblage, which may reflect our communities that originally consisted of only
29 three species, has been suggested before (Bakker, de Graaf, Ernst & van Bodegom 2005; Del

1 Moral & Lacher 2005). The later the successional stage, the more compositional changes are
2 expected to be driven by competition and to follow deterministic rules (MacDougall, Wilson
3 & Bakker 2008). In our plant communities, results suggest an influence on invasibility and
4 species composition of both stochastic processes and competitive interactions. Competitive
5 interactions played a role not only in the aforementioned (dis)similarity, but also in the
6 finding that while more species invaded into communities with the highest apparent rates of
7 mortality following the extreme (the DH treatments), the contribution of these species to
8 community biomass was modest. It has been shown that competitive species with high
9 photosynthetic uptake rates benefit most when establishing in small gaps with low light
10 conditions (Seidlova, Verlinden, Gloser, Milbau & Nijs 2009), which in our case would be in
11 those communities with low mortality and high productivity. In the communities with high
12 mortality and decreased aboveground biomass production in 2009, on the other hand, the
13 larger, brighter gaps would not favour such species. This can result in more, but less
14 productive new species in communities that had been exposed to high-impact extreme events,
15 and less but more productive new species in controls. Again, differences in invasive biomass
16 between treatments and controls had disappeared by 2011.

17 In conclusion, resistance to the imposed climate extremes in terms of apparent mortality was
18 similar for all species and lowest when drought effects were exacerbated by a heat wave.
19 However, recovery and resilience differed greatly among species, which led to significant
20 differences in end-of-season biomass on both the species and the community level. Especially
21 graminoid species were successful invaders, possibly because of their functionally
22 dissimilarity from the already available (forb) species. The harshest extreme events
23 accelerated the invasion of new species, likely mostly through space created by higher
24 mortality of the plants originally present, but differences between the treatments levelled out
25 fairly quickly. The composition of invaded communities was different only in the first year
26 after the climate extremes, but differences were small and could not be clearly related to the
27 extreme the communities had been exposed to. Two years after the extremes, both the
28 communities' susceptibility to invasion as well as their biomass stabilised in all treatments.

29

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6 **Appendix A. Supplementary data**

7 Supplementary data associated with this article can be found, in the online version, at
8 XXXXX.

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1 **Table 1.**

2 Average aboveground biomass per community for species grouped per functional group (FG)
 3 invading plant communities that had been subjected climate extremes in different seasons. C
 4 = control, D = drought extreme, H = heat extreme, DH = drought + heat extreme.

		2010							
Season	FG	C		D		H		DH	
		(g)	se	(g)	se	(g)	se	(g)	se
Spring	Graminoid	2.42	0.22	1.65	0.23	1.90	0.20	1.60	0.20
	N-fixer	1.26	0.68	0.04	0.02	0.00	0.00	0.01	0.01
	Non-N-fixing forb	0.11	0.01	0.24	0.02	0.18	0.03	0.81	0.08
Summer	Graminoid	2.42	0.22	0.74	0.09	0.64	0.11	0.98	0.15
	N-fixer	1.26	0.68	0.16	0.08	0.00	0.00	0.01	0.00
	Non-N-fixing forb	0.11	0.01	0.00	0.00	0.09	0.01	0.05	0.00
Autumn	Graminoid	2.42	0.22	0.96	0.16	0.96	0.17	1.40	0.21
	N-fixer	1.26	0.68	0.02	0.01	0.01	0.00	0.77	0.44
	Non-N-fixing forb	0.11	0.01	0.04	0.00	0.22	0.02	0.21	0.02

		2011							
Season	FG	C		D		H		DH	
		(g)	se	(g)	se	(g)	se	(g)	se
Spring	Graminoid	1.81	0.12	2.52	0.39	2.51	0.39	2.19	0.25
	N-fixer	1.02	0.57	0.03	0.02	0.12	0.06	0.01	0.01
	Non-N-fixing forb	1.65	0.15	4.34	0.61	1.31	0.10	2.45	0.22
Summer	Graminoid	1.81	0.12	2.84	0.38	3.51	0.51	4.55	0.53
	N-fixer	1.02	0.57	0.05	0.01	0.01	0.00	0.00	0.00
	Non-N-fixing forb	1.65	0.15	0.81	0.07	0.50	0.05	0.85	0.08
Autumn	Graminoid	1.81	0.12	2.79	0.44	2.12	0.26	1.74	0.24
	N-fixer	1.02	0.57	0.00	0.00	0.01	0.00	3.47	1.99
	Non-N-fixing forb	1.65	0.15	0.15	0.01	0.54	0.03	1.70	0.11

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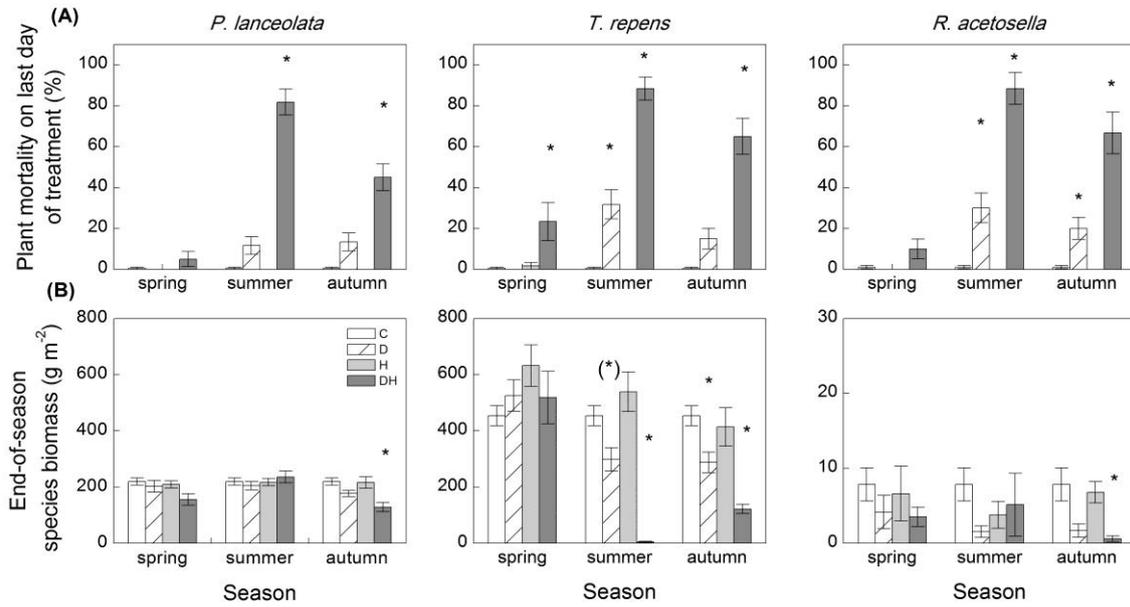
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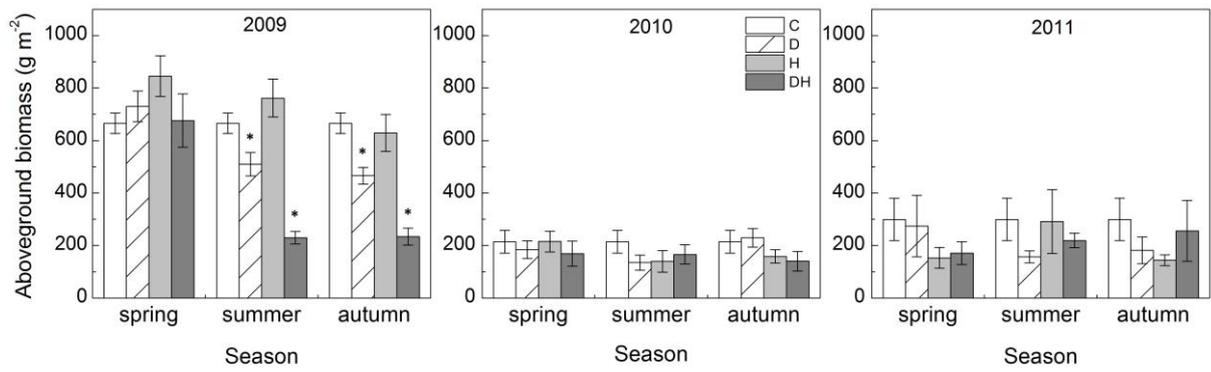
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1 **Fig. 1.** (A) Apparent plant mortality at the end of climate extremes imposed in 2009, and (B)
 2 species aboveground biomass at the end of the 2009 growing season. Asterisks indicate
 3 significant differences from the control ($P < 0.05$), with borderline significances depicted by
 4 asterisks between brackets ($P < 0.06$).



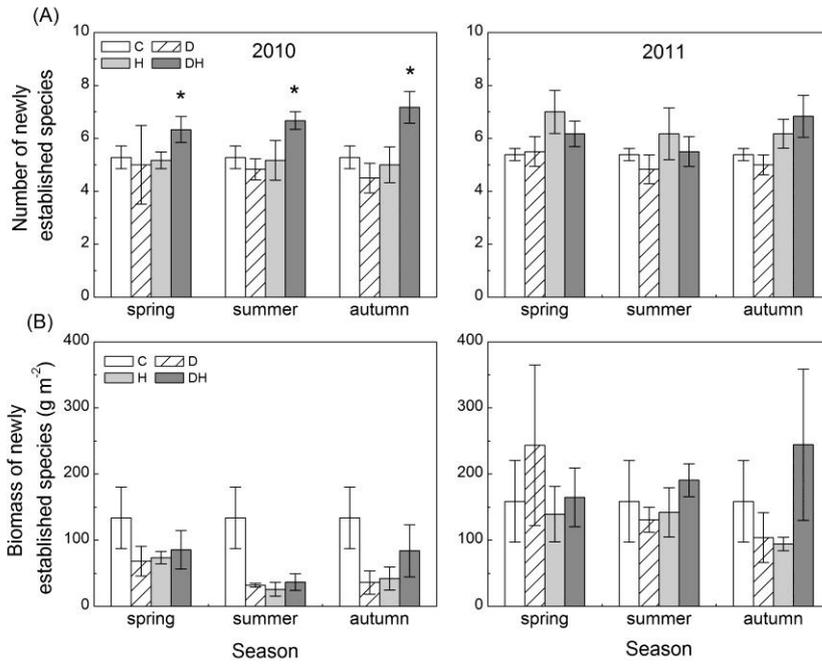
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1 **Fig. 2.** Aboveground community biomass of the different treatments (type of extreme event
 2 and season in which it was applied) collected at the end of the growing season in 2009, 2010,
 3 and 2011. Asterisks indicate significant differences from the control ($P < 0.05$).



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1 **Fig. 3.** (A) Number and (B) aboveground biomass of newly established species in 2010 and
 2 2011, both determined at the end of the growing season in 2010 and 2011. Asterisks indicate
 3 significant differences of the DH treatment from the control ($P < 0.05$).



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