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1 **Joint forcing of heat waves and mowing poses a threat to grassland ecosystems: Evidence**  
2 **from a manipulative experiment**

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21 **Key words:** Climatic extremes; steppe; clipping; plant community; phenology

22  
23 **Running Head:** Joint forcing of heat waves and mowing effects on grassland ecosystem

24 **Abstract**

25 The frequency and intensity of heat waves (HWs) have increased in recent years, but it remains  
26 unclear how grassland ecosystem respond to such extreme weather. A 3-year manipulative field  
27 experiment was conducted to simulate HWs under different mowing intensities in a *Stipa krylovii*  
28 steppe on the Mongolian Plateau to examine their effects on plant morphology, phenology and  
29 community. At the species level, the morphology and phenology of the three main herb species  
30 (*Stipa krylovii*, *Melilotoides ruthenica* and *Potentilla tanacetifolia*) showed species-specific  
31 responses to the HW and mowing treatments. The major dominant species *Stipa krylovii* shed  
32 ~50% of the tiller outer layer to protect the internal tiller from HW stress, thereby directly  
33 decreasing the heat load and water loss from green plant tissue and indirectly increasing the litter  
34 biomass. HWs also caused increases of community index (richness, diversity, and evenness), but  
35 associated with a 30% decrease in the importance value of *Stipa krylovii*, whereas mowing  
36 enhanced this value by 27%. When HWs were combined with mowing, the joint forcing of  
37 mechanical damage and low C accumulation aggravated negative effects of stress on plant health  
38 and growth, which further decreased community index. We constructed a framework to fully  
39 describe the effects of HWs and mowing and their interrelationship on different ecological levels  
40 and explain how short-term effects, such as extreme climate, produce long-term effects on  
41 ecosystems. In conclusion, we found that synergisms between climate extremes (HWs) and  
42 human activities (mowing) can reduce ecosystem stability, posing a threat to the grasslands.

43

## 44 **Introduction**

45 Heat waves (HWs) are naturally occurring hazards characterized by sudden anomalously high  
46 (absolute or relative) temperatures which last for a relative short period, that can cause negative  
47 effects on ecosystem function and stability (Chen, Hu, Yang, & Qian, 2017; Reichstein et al.,  
48 2013). Mounting evidence points to an increase in the frequency and intensity of HWs, which  
49 have affected more than 73% of the global terrestrial area since the mid-20<sup>th</sup> century (IPCC, 2013;  
50 Perkins-Kirkpatrick et al., 2016), and have caused large and widespread impacts at all ecological  
51 scales from the species level to the ecosystem level. Severe HW events not only rapidly reduce  
52 plant photosynthesis and respiration (Crous Kristine et al., 2018), decrease aboveground and  
53 belowground biomass accumulation (Qu, Chen, Dong, & Shao, 2018) and alter the (re)allocation  
54 of carbon and nitrogen within a plant (Li et al., 2017), but also result in a decrease in ecosystem  
55 gross primary productivity (GPP) and net ecosystem carbon exchange (NEE) (Ciais et al., 2005;  
56 Qu et al., 2018; Tatarinov et al., 2016). However, these studies mostly concentrate on HWs  
57 effects on plant growth (photosynthesis system) or ecosystem carbon exchange, but how plant  
58 morphology, phenology and community structure respond to such extreme events remains poorly  
59 understood.

60 Compared with gradual temperature increases, the sudden high temperatures associated with  
61 HWs have a greater and more rapid impact on plant health and ecosystem carbon exchange, and  
62 are associated with an increased risk of fire (Sanz-Lázaro, 2016; Xia, Niu, & Wan, 2009). Such  
63 conditions cause increases in plant mortality (Teskey et al., 2015; Wang, Heckathorn, Mainali, &

64 Tripathee, 2016), resulting in the elimination of individuals that are unsuited to the new  
65 environment, thus altering the community and ecosystem structure (Gutschick & BassiriRad,  
66 2003; Li et al., 2017; Zinta et al., 2014). Legacy effects of HWs are associated with changes in  
67 plant species and trophic interactions (Kreyling et al., 2017) that lead to complex responses at the  
68 community level (Elst et al., 2017; Sentis, Hemptinne, & Brodeur, 2013). However, until now,  
69 direct evidence on the effect of HWs at the community level has been lacking because prior  
70 research on HWs usually did not focus at this level. Early observational research on naturally  
71 occurring HW events primarily focused on ecosystem responses (e.g., carbon and water cycles),  
72 and fewer studies focused on the responses at the scale of plant communities because natural  
73 HWs occur at random and control groups are lacking (Ciais et al., 2005; Yuan et al., 2016).  
74 Meanwhile, laboratory-based studies of HWs have mainly focused on the characteristics and  
75 phenological variations among individual plant species, with plant communities being relatively  
76 ignored (Ameye et al., 2012; Bauweraerts et al., 2013). Plants may respond very differently to  
77 climate change when growing in a community because of the occurrence of interspecific  
78 interactions (De Boeck et al., 2018; Isbell et al., 2015), such as the presence of nitrogen-fixing  
79 legumes can increase the speed at which neighbouring plants recover after an extreme climate  
80 event (Hoekstra, Suter, Finn, Husse, & Lüscher, 2014; Kreyling et al., 2017). Here, we  
81 acknowledge the importance of such community-scale effects in this study and focus on the  
82 mechanisms underlying the effects of HWs on different ecological levels and how these are  
83 connected.

84       Beside direct HW effects on plant health, plant phenology may also be affected by such an  
85       extreme. Phenology refers to the seasonal timing of phenomena (e.g., flowering and fruiting),  
86       and it is regulated by environmental factors and sensitive to climate change (Chen, Hu, & Yu,  
87       2005; Dunnell & Travers, 2011; Liu & Sun, 2011; Wolkovich et al., 2012). When plant  
88       phenology changes, it will eventually alter the plant community structure, inter-species  
89       interactions (Xia et al., 2015), and ecosystem CO<sub>2</sub> and water exchange (Musolin, Tougou, &  
90       Fujisaki, 2010). Cremonese *et al.* (2017) reported that a HW was responsible for the observed  
91       reduction of canopy greenness in a mountain grassland, but did not measure the responses of the  
92       individual species. Several manipulative field experiments observed advancements in the timing  
93       of flowering phenology under warmer conditions (Lambrecht, Loik, Inouye, & Harte, 2007;  
94       Wolkovich et al., 2012), likely caused by warming-accelerated spring biomass growth  
95       (Carbognani, Bernareggi, Perucco, Tomaselli, & Petraglia, 2016; Whittington, Tilman, Wragg, &  
96       Powers, 2015), but these phenological studies have mostly focused on responses to general  
97       warming. High absolute temperatures usually occur during summer rather than during spring,  
98       and do not last for the whole growing season, indicating that the mechanisms underlying plant  
99       phenological responses to general warming and HWs may be different. However, due to the lack  
100       of field experiments evaluating the phenological response of individual plant species to HWs, a  
101       critical unknown is whether short, hot periods (i.e. HWs) can affect plant phenology. The answer  
102       to this question is fundamental in assessing plant resistance to HW stress and in identifying  
103       future community composition and structure under elevated and frequent HW events.

104 In addition to the HW effect caused by global change, land use changes caused by human  
105 activities also deserve attention on the Mongolian Plateau, especially if there are interactive  
106 effects on grassland ecosystem. The Mongolian Plateau covers an area of 2.73 million km<sup>2</sup>,  
107 with >60% composed of grassland, and because of this relatively simple vegetation type,  
108 nomadism represents the main land-use practice on the plateau. However, with the increasing  
109 settlement of herdsman, mowing for hay has become a widely practised pasture management  
110 method in recent decades (Chen, John, Zhang, et al., 2015). Although increases in mowing  
111 intensity have economic benefits, they significantly alter the carbon flux and energy budgets by  
112 changing the photosynthetic activity and stimulating compensatory growth (Niu *et al.*, 2013;  
113 Shao *et al.* 2014). They also influence the microclimate (Shao et al., 2016) and associated plant  
114 traits, such as plant height and specific leaf area (Reisch & Poschlod, 2011), which in turn will  
115 affect plant reproductive phenology (Benot et al., 2014). More importantly, increases in mowing  
116 intensity not only have profound consequences for grassland ecosystems (Shao, Chen, & Li,  
117 2013) but can also increase the sensitivity of grassland ecosystems to climate change (Chen,  
118 John, Shao, et al., 2015). Here, we hypothesize that mowing may interact with global warming  
119 and reduce ecosystem resilience to extreme weather (Benot et al., 2014), thereby further  
120 exacerbating the effects of HWs on ecosystem carbon and water fluxes (Gourlez de la Motte et  
121 al., 2018; Qu et al., 2018). However, significant knowledge gaps remain regarding the  
122 interactions between HWs and land use, especially their joint influences on plant morphology,  
123 phenology, community structure, and the underlying processes responsible for ecosystem

124 functions.

125 The main aim of this study was to assess the responses of a natural ecosystem to climate  
126 extremes (HWs) and human activity (mowing) and determine their interactions at the plant and  
127 community level. For this purpose, a 3-year field experiment was designed on a Mongolian  
128 Plateau grassland ecosystem to determine plant morphology, phenology, and community  
129 structure responses to imposed HWs in conjunction with different mowing practices. We  
130 hypothesized that: (1) HWs and mowing have significant effects on each species, including  
131 changes in plant morphology and phenology, and suggest that plants might prolong the flowering  
132 of fruit phenology due to decreased carbon accumulation; (2) diversity may decline because  
133 species sensitive to HWs, mowing or their combination perish, thus causing additional variation  
134 in community structure.

## 135 **Materials and Methods**

### 136 *Study site*

137 The manipulative experiment was conducted in a semi-arid area in Duolun County (42°02' N,  
138 116°17' E), Inner Mongolia, China. The mean annual precipitation at this site is 385 mm, the  
139 mean annual air temperature is 2.1 °C, and the monthly mean temperatures range from -17.5 °C  
140 in January to 18.9 °C in July (data from 1965-2013). The soils are classified as chestnut soils in  
141 the Chinese classification or Haplic Calcisols using the FAO classification, and they are  
142 composed of 62.75±0.04% sand, 20.30±0.01% silt, and 16.95±0.01% clay. The mean soil bulk



143 density is  $1.31 \text{ g cm}^{-3}$ , and the pH is  $7.12 \pm 0.07$ . The plant community is dominated by perennial  
144 species, including *Stipa krylovii* Roshev, *Artemisia frigida* Willd., *Potentilla acaulis* L.,  
145 *Cleistogenes squarrosa* (Trin.) Keng, *Allium bidentatum* Fisch.ex Prokh., and *Agropyron*  
146 *crisatum* (L.) Gaertn. A total of 36 species were recorded at the end of the experiment, and they  
147 fell into four functional groups (Table S1): Perennial Bunchgrass (PB, 4 species), Perennial Forb  
148 (PF, 26 species), Perennial Rhizome grass (PR, 4 species), and Shrub and Semi-shrub (SS, 2  
149 species). Three common species were chosen for continuous observation: one PB species (*Stipa*  
150 *krylovii*), which is a perennial tussock-forming C3 grass and the dominant species in the  
151 community, and two PF species, *Melilotoides ruthenica*, a perennial legume species widely  
152 distributed in high-quality pasture on the Mongolian Plateau, and *Potentilla tanacetifolia*, a  
153 perennial Rosaceae species that is mainly distributed as a common auxiliary species in typical  
154 meadow steppes on the plateau.

### 155 *Experimental design*

156 A fully factorial experimental design with two factors, HW and mowing, was implemented. The  
157 HW treatment included two levels (HW and no HW), while the mowing treatment had three  
158 levels: no mowing, light mowing (to a plant height of 7 cm, M<sub>7</sub>), and heavy mowing (to a plant  
159 height of 2 cm, M<sub>2</sub>). This experimental design yielded six treatments: C (control, no HW+no  
160 mowing), HW (HW+no mowing), NM<sub>7</sub> (no HW+7 cm stubble), NM<sub>2</sub> (no HW+2 cm stubble),  
161 HM<sub>7</sub> (HW+7 cm stubble) and HM<sub>2</sub> (HW+2 cm stubble). The study site had not been mowed

162 since it was fenced in 2001 (Shao, Li, Dong, & Chen, 2014). The M<sub>7</sub> and M<sub>2</sub> treatments were  
163 used to simulate local grassland harvesting; the 7 cm treatment was the common plant height  
164 after normal mowing, whereas the 2 cm treatment simulated the plant height after over-mowing.  
165 The mowing treatments were conducted using a field mower (Yard-Man 160CC, USA) at the end  
166 of August, when local harvesting normally occurs. Each treatment had four replicates, yielding a  
167 total of 24 plots (2 m × 2 m). We randomly allocated the treatments among the plots, which were  
168 laid out in a total area of 308 m<sup>2</sup>, with a 2 m buffer zone between any two neighbouring plots.  
169 The same experimental design has been used to investigate the effects of HWs and mowing on  
170 ecosystem carbon sink strength and carbon and water fluxes (Qu et al., 2018).

#### 171 *Heat wave treatment*

172 The effects of HWs were simulated using octagonal open-top chambers (OTCs; diameter, 2.0 m;  
173 height, 1.5 m) that were constructed using steel tubes. A heater (0.20 m × 0.15 m × 0.15 m) was  
174 installed within each OTC at 1.5 m above the ground and powered with a 3500 W power supply  
175 (Fig. S1). During the implementation of the HW treatments, the OTCs were covered with  
176 transparent PVC film that had a light transmittance of >90% based on measurements of the  
177 photosynthetically active radiation (PAR) inside and outside. OTCs have been reported to  
178 exacerbate temperature peaks under sunny conditions (Hans J De Boeck, De Groote, & Nijs,  
179 2012), which made them suitable for our HW simulation. The OTCs were open for 1 h per day at  
180 05:00-06:00 h to avoid large inconsistencies between the internal and external environment

181 (apart from temperature). The non-heated plots were also covered with a similar chamber to  
182 ensure comparable conditions. Our simulated HWs were carried out to ensure similarity to  
183 naturally occurring HWs (Qu et al., 2018). According to local historical climate data  
184 (<http://cdc.cma.gov.cn/>), HWs predominantly occur in July, which is when we carried out our  
185 heat simulation experiments. Dry sunny days were selected for the heating periods, which is in  
186 accordance with the conditions of natural HWs. The simulated HW intensity (canopy  
187 temperature increased by ~6-10 °C during the day and by ~4 °C at night) and duration (3-5 days)  
188 were also similar to the local historical conditions. The HW treatments were carried out during  
189 three consecutive years: over 3 days in 2012 during a preliminary experiment and over 5 days in  
190 2013 and 2014 (Fig. S2).

#### 191 *Biomass & measurement*

192 The peak aboveground biomass was estimated by harvesting the vegetation within a 0.15 m ×  
193 0.50 m quadrat in each plot in late August one day before the mowing treatment. After the  
194 aboveground plant residue was removed, one soil core (10 cm diameter) was collected from each  
195 plot to estimate the belowground biomass in the 0-15 cm and 15-30 cm soil layers. The soil cores  
196 were transported to the laboratory on the day of collection and carefully washed on a 60-mesh  
197 sieve to separate the roots from the soil. The plant samples and washed roots were oven dried at  
198 65 °C for 72 h before weighing. The results were treated as the aboveground and litter biomass  
199 for the current year.

200 *Importance value (IV) and vegetation diversity*

201 The number of seedlings ( $N_s$ ) of all plant species was measured in a subplot of 0.2 m × 1.0 m in  
202 each plot four times a year: twice before the HW treatment (6 and 24 July 2013, 10 and 27 July  
203 2014) and twice after HW treatment (15 and 30 August 2013, 16 and 30 August 2014). The  
204 number of tillers ( $N_t$ ), nutritive plant height ( $H_p$ ), plant species cover ( $C_p$ ) and crown width ( $C_w$ )  
205 were measured. The percent cover of each plant species was estimated by a 1 × 1 m frame with  
206 100 equally distributed cells (10 cm × 10 cm) held above the canopy. Crown width was  
207 calculated as the product of the measured north-south and east-west trending lengths. The species  
208 importance value (IV) was calculated based on the relative height ( $H_r$ , the ratio of a single  
209 species height to all species height), relative cover ( $C_r$ , the ratio of a single species coverage to  
210 all species coverage) and relative abundance ( $A_r$ , the ratio of a single species abundance to all  
211 species abundance) according to Peet (1974), Curtis and McIntosh (1951):

212 IV  
213 
$$= \frac{H_r + C_r + A_r}{3}$$

214 Various indices of vegetation diversity were calculated for the plant community in each  
215 treatment. The Margalef richness index ( $D_{ma}$ ), Simpson diversity index ( $D$ ) and Pielou's  
216 evenness index ( $J$ ) were calculated using Equations 2-4.

217 Margalef richness index:

218 
$$D_{ma} = \frac{(S - 1)}{\ln(N)} \quad (2)$$

219 Simpson diversity index:

220 
$$D = 1 - \sum p_i^2 \quad (3)$$

221 Pielou's evenness index:

222 
$$J = \left( - \sum p_i \ln(p_i) \right) / \ln S \quad (4)$$

223 where  $S$  represents the number of species;  $p_i = n_i / N$  indicates the relative number of species  $i$ ;  $n_i$   
224 represents the individual number of species  $i$ ; and  $N$  represents the total individual number of all  
225 species in the community.

## 226 *Phenology*

227 At the beginning of the growing season, we tagged five mature individuals of *Stipa* and three  
228 mature individuals of *Melilotoides* and *Potentilla* in each plot as soon as any of the species had  
229 produced obvious buds, and we then recorded the timing and duration of the flowering and  
230 fruiting of the three studied species (*Stipa*, *Melilotoides*, and *Potentilla*) from early May to early  
231 September. The changes in plant reproductive phenology over time followed a logistic growth  
232 curve (Sadras, Bange, & Milroy, 1997), and the reproductive phenology of both the graminoid  
233 (grass) and non-graminoid (forb and semi-shrub) species was divided into several stages (Dunne,  
234 Harte, & Taylor, 2003; Sherry et al., 2007). We divided the phenology of the grasses into the  
235 following stages: plants with flower stalks (stage 0), most culms in the boot visible (stage 0.5),  
236 spikelets present (stage 2), dried and broken off anthers and styles (seed development; stage 3),  
237 and disarticulated seeds (stage 4). For the forbs and semi shrubs, plant phenology was divided  
238 into 6 stages: non-flowering plant (stage 0), unopened buds (stage 1), open flowers (stage 2), old

239 flowers or post-anthesis (stage 3), initiated fruit (stage 4), expanding fruit (stage 5) and dehisced  
240 fruit (stage 6). In addition, we continuously monitored the current stages of all individuals every  
241 3-4 days. If a plant had more than one flower, we recorded the current stage for each flower and  
242 then calculated an average score for each plant as the mean stage number across all flowers.  
243 Based on these values, we obtained a single ‘phenological score’ for the individuals in each plot  
244 and recorded the observation date.

245 Based on the phenological observations, we fitted the observed scores to the Richards growth  
246 equation (Richards, 1959), which is thought to be very flexible in describing different shapes of  
247 growth data distributions and has been successfully applied in the study of plant phenology in the  
248 Inner Mongolian steppe of North China (Xia & Wan, 2013). We applied the Richards growth  
249 equation with the contraction-expansion algorithm (Gu, Hui, & Bian, 1998) to fit the  
250 phenological scores ( $Y$ ) of each species against the Julian day ( $X$ ) for each plot. The equation is  
251 as follows:

$$252 \quad Y = \frac{K}{(1 + a * e^{-b*X})^m} \quad (5)$$

253 where  $Y$  is the phenological stage score (0–6 for forbs and 0–4 for grasses),  $K$  is the maximum  
254 growth (here the final phenological stage, 6 for forbs and 4 for grasses),  $a$  is an empirical  
255 coefficient representing the first observation date,  $b$  is the growth rate (change in phenological  
256 stage per day) over time  $X$  (days since the first observation date), and  $m$  is a parameter reflecting  
257 the shape of the curve. The timing of each phenological event is calculated as follows:

$$X = -\frac{1}{b} \ln\left(\frac{m\sqrt{K/Y} - 1}{a}\right) \quad (6)$$

258  
 259 We calculated the timing and duration of reproduction using the following steps. First, the  
 260 sequences of calculated phenological scores from a species in each plot for each season were  
 261 fitted to Eq. 5. The best parameter estimates of  $K$ ,  $a$ ,  $b$ ,  $X$ , and  $m$  were obtained for individuals by  
 262 plot and by year ( $r^2 > 0.95$ ,  $P < 0.05$ ). Second, based on Eq. 6, the flowering time was calculated as  
 263  $Y=2$  for all species and the fruiting time was calculated as  $Y=2.5$  and  $Y=3.5$  for grasses and  
 264 forbs/semishrubs, respectively. The phenological duration was calculated as  $X$  between stages 0.5  
 265 ( $Y=0.5$ ) and 3 ( $Y=3$ ) for grasses and between stages 1 ( $Y=1$ ) and 5 ( $Y=5$ ) for forbs/semishrubs  
 266 (Gu et al., 1998). Finally, the calculated flowering and fruiting times as well as the phenological  
 267 duration were used in further statistical analyses for treatment effects. The scoring of phenology  
 268 was performed following the modified method described by Dunne, Harte, and Taylor (2003),  
 269 Sherry et al. (2007), and Xia and Wan (2013).

#### 270 *Data analysis*

271 A repeated-measures ANOVA was applied to examine the effects of HWs, mowing and their  
 272 possible interactions on  $N_s$ ,  $C_p$ ,  $N_t$ ,  $H_p$ ,  $W_c$  and IV value of *Stipa*, *Melilotoides* and *Potentilla* in  
 273 2013 and 2014 together. Two-way ANOVA was used to examine the effects of HWs, mowing  
 274 and interactions on flowering time, fruiting time and phenology duration of 3 species in 2013.  
 275 Subsequently, the two-way ANOVAs were used again to examine the treatment effects on  
 276 community structure (richness, diversity and evenness index) and biomass (aboveground and

277 litter) separated per year (2013 and 2014), and also used to examine differences in mean IV  
278 values across both years. Finally, one-way ANOVA was used to examine the differences of  $N_s$   
279 and  $C_p$  among the six treatments in 2013 (15 August) and 2014 (16 August) ( $P < 0.05$ , Duncan's  
280 post hoc test). Multiple one-way ANOVAs were also used for  $N_t$ ,  $H_p$ , and  $W_c$  (2014), the  
281 phenology of the three species (2013) and their 2-year mean IV value, and aboveground, litter  
282 biomass, and community structure (2013 and 2014). Prior to the ANOVA, all data were tested to  
283 satisfy the assumptions of normality ( $P > 0.05$ ) and homogeneity of variance ( $P < 0.05$ ). All  
284 statistical analyses were conducted using SPSS 22.0 for Windows (SPSS Inc., Chicago, Illinois,  
285 USA).

## 286 **Results**

### 287 *Effects of HWs and mowing on the species level: number, coverage, morphology and phenology*

288 The daily mean air temperature during the growing season (May-September) in 2012, 2013 and  
289 2014 was 15.7 °C, 16.6 °C and 15.6 °C, respectively, while the total precipitation over the  
290 growing season was 307 mm, 418 mm and 286 mm, respectively. The mowing treatment was  
291 conducted at the end of August in 2012; thus, our analysis began in 2013. *Stipa*, *Melilotoides*,  
292 and *Potentilla* responded differently to the HWs, mowing treatments, and their interaction effects  
293 (Table 1). The effects of HWs and mowing on *Stipa* were most evident through changes in  $H_p$ ,  $C_p$   
294 and  $N_s$ . HWs resulted in a significant increase in the  $N_s$  of *Stipa* in the heavily mown plots in  
295 2013 but not in the unmown plots, and this effect did not persist into 2014 (Fig. 1c, d). HWs



296 lowered the  $C_p$  in both the unmown and heavily mown plots in both 2013 and 2014 (Fig. 1a, b)  
297 and restricted the growth ( $H_p$ ) of *Stipa* (Fig. 2a). Compared with the HWs, mowing significantly  
298 decreased the  $N_s$ ,  $C_p$ , and  $H_p$  of *Stipa* and a significant D×HW×M interaction was observed for  
299  $H_p$  ( $P=0.018$ , Table 1). Based on the comparison of the C and HM<sub>2</sub> treatments, HWs and mowing  
300 significantly increased the  $N_t$  of *Stipa* in 2013 ( $P<0.05$ ) but not in 2014 ( $P>0.05$ , Fig. 1c, d),  
301 significantly decreased the  $H_p$  and  $C_w$  ( $P<0.05$ ), and did not significantly affect the  $N_t$  ( $P>0.05$ ,  
302 Fig. 2a).

303 The response of *Melilotoides* to the HW and mowing treatments was characterized by  
304 significant changes in  $C_w$  and  $H_p$  (Fig. 2b). HWs, mowing, and their combination had significant  
305 effects on  $C_w$ , while  $H_p$  was significantly affected by mowing and the HW×M interaction (Table  
306 1). For the  $N_s$  and  $C_p$  of *Melilotoides*, the only significant difference over the two years was in  
307 terms of the  $N_s$  in 2014, when it was higher in the light mowing treatment (NM<sub>7</sub>) compared to the  
308 control (C) (Fig. 1e-h). While HWs had no significant effect on *Potentilla*, mowing alone had  
309 significant effects on  $C_p$  ( $P=0.038$ , Table 1). No significant effects of the treatments on the  $N_s$   
310 and  $C_p$  of *Potentilla* were observed at the end of the experiment (Fig. 1i-l). However, light  
311 mowing increased the  $H_p$  of *Potentilla*, while heavy mowing had the opposite effect ( $P>0.05$ , Fig.  
312 2c).

313 HWs significantly affected the timing of the flowering and fruiting of *Stipa*, while mowing led  
314 to significant changes in all phenological characteristics (Table 2). Specifically, HWs advanced  
315 the timing of flowering and fruiting by approximately 2 days (unmown plots), and the interactive

316 effect with mowing delayed these phenological stages by ~3 days (light and heavy mowing plots)  
317 (Table 3). Interestingly, HWs had no significant effect on the phenology of *Melilotoides*, while  
318 mowing significantly affected the timing and duration of flowering and fruiting (Table 2). In  
319 general, HWs extended the phenological durations of the different stages under all mowing  
320 levels (Table 3), with the changes ranging from no significant effect of HWs in the unmown and  
321 lightly mown plots to significant delays in the heavily mown plots (5-6 days). Unlike *Stipa* and  
322 *Melilotoides*, HWs and mowing did not independently affect the phenology of *Potentilla*,  
323 although their interaction significantly affected the timing of duration and fruiting (Table 2). Of  
324 the 3 species, the phenology of *Potentilla* appeared to be the most sensitive to the combination of  
325 HWs and mowing. In the heavily mown plots, HWs delayed fruiting by 7 days and increased the  
326 phenological duration by 14 days (Table 3). Overall, the phenological duration of *Stipa* and  
327 *Melilotoides* and the flowering time of *Potentilla* seemed stable under the main effect of HW or  
328 mowing. However, HWs delayed the flowering time of all species and showed an interactive  
329 effect with mowing (Table 3).

### 330 *Effects of HWs and mowing on the community level: IV, diversity and functional group biomass*

331 The time series of IV values for the three species over the 2013-2014 growing seasons provided  
332 direct evidence of both instantaneous and delayed responses to the HW treatments under the  
333 different mowing conditions (Table 1). Generally, *Stipa* was confirmed to be the dominant  
334 species in the grassland and had a mean IV of 47.90 across all treatments in 2013 and 2014,

335 whereas *Melilotoides* and *Potentilla* were co-dominants, with mean IV values of 9.26 and 4.34,  
336 respectively (Fig. 3). From a long-term perspective (2 years mean IV value), mowing  
337 significantly affected *Stipa* ( $P = 0.006$ ) and *Potentilla* ( $P = 0.029$ ), but there was no significant  
338 effect of HWs and their interactions (Table 4), and none of these effects changed the dominance  
339 ranking of the species (Fig. 3). We noticed that the IV of *Stipa* began to decrease in the unmown  
340 plots after the first HW event in 2013 and continued to decline in 2014 (Fig. 4a), this  
341 phenomenon was more obvious in the heavy mowing treatment (Fig. 4c). For the mown  
342 treatments, the IV values of *Stipa* in 2013 were nearly identical in the plots with or without HWs,  
343 whereas in 2014, the IV values were higher under the HW treatments. On average, HWs  
344 significantly decreased the mean IV of *Stipa* in the unmown plots, while mowing significantly  
345 increased the mean IV of *Stipa* (Fig. 3a). In contrast, the mean IV values for *Melilotoides*  
346 increased after the first HW events and continued to increase in 2014 (Fig. 4d). Light mowing  
347 (NM<sub>7</sub>) resulted in a decreased IV for *Melilotoides* in both 2013 and 2014, while heavy mowing  
348 had no effect in either year (NM<sub>2</sub>, Fig. 4e, f). In conclusion, HWs caused a significant increase in  
349 the IV of *Melilotoides* in the unmown plots, but a significant decrease in the lightly mown plots  
350 (comparison of NM<sub>7</sub> and HM<sub>7</sub>), and had no significant effects in the heavily mown plots (Fig.  
351 3b). For *Potentilla*, HWs had nonsignificant effects on the IV values, but mowing decline its IV  
352 since the first treatment (Fig. 4h, i), which caused a significant decrease in the mean IV (Fig. 3c).

353 The variation of species IV actually indicated changes in community structure, with mowing  
354 causing significant effects on the community diversity index and evenness index, and HWs

355 having interactive effects with mowing on evenness (Table 5). Under the combination of HWs  
356 and heavy mowing (HM<sub>2</sub> plots), the community diversity and evenness indices significantly  
357 decreased in both 2013 and 2014 while the richness index values presented nonsignificant  
358 decreases (Table 6). The community richness in the control plots in 2013 was identical to that in  
359 2014 (2.29 vs 2.25), indicating stable conditions throughout the study period, which is  
360 inconsistent with the richness in the HM<sub>2</sub> plots, which decreased by 14% between 2013 (2.16)  
361 and 2014 (1.86).

362 Mowing led to a significant decrease in the aboveground and litter biomass in both 2013 and  
363 2014 (Fig. 5). HWs accelerated the accumulation of litter biomass in 2013, although the effect  
364 did not last into 2014 (Fig. 5c, d), and HWs did not have a significant effect on aboveground  
365 biomass in either year (Table 5). Of the four plant functional groups, PB and PF were the main  
366 components of the ecosystem biomass and composed ~90% of the aboveground biomass (Fig. 5a,  
367 b). Compared to the unmown plots, heavy mowing decreased the percentage of PF in the  
368 aboveground biomass (44.5% to 31.5% in 2014). Moreover, the effects of HWs on the biomass  
369 composition were affected by the mowing level. In 2013 and 2014 combined, HWs alone  
370 increased the PF percentage in unmown plots from 44.9% (C) to 60.6% (HW) and from 47.3% to  
371 54.1% under light mowing (NM<sub>7</sub>), but no significant change was observed in the heavy mowing  
372 treatments (38.8% in NM<sub>2</sub> and 38.0% in HM<sub>2</sub>).

### 373 *Conceptual understanding of HW and mowing effects*

374 Based on our results, we developed a conceptual framework to explain how HWs and mowing

375 affect ecosystems from the cellular to the ecosystem level (Fig. 6). We considered three periods  
376 related to HWs, namely, rapid effects (effects during the HW period), post effects (effects after  
377 the HW period in the same year) and legacy effects (effects after the HW period in the following  
378 years) (Qu *et al.*, 2018). The rapid effects were most evident on the cellular and plant levels,  
379 including changes in photosynthesis and morphology. The impacts on these levels and processes  
380 then fed forward to the community, where responses were observed mostly as post and legacy  
381 effects of HW and mowing. Prior studies have shown that HWs will lead to a less efficient  
382 photosynthetic system, which will further result in the lower availability of nutrients and carbon  
383 starvation and the lowered accumulation of nutrients and carbon. HWs are normally  
384 accompanied by drought, which will lead to hydraulic failure. Mowing then directly removes  
385 part of the plant, causing mechanical damage; moreover, most plant reproductive organs are  
386 located in the top portion of the plant, which is the most likely part to be cut off during mowing.  
387 Moreover, the interaction between HWs and mowing makes these effects more significant; in  
388 association with the mortality of some plants, the community structure is greatly changed. This  
389 altered community structure is usually characterized by low water use efficiency (WUE),  
390 changes to carbon fluxes, etc., which are considered to be the effects of HWs and mowing on  
391 carbon and water fluxes and other processes at the ecosystem level.

## 392 **Discussion**

393 *Species-specific responses of plant number, coverage and morphology to HWs and mowing*

394 Because individual plants represent the basic units of a grassland community, we first focused on  
395 the effects of HWs on plant characteristics, such as seedling abundance, cover, and morphology.  
396 Here, the three main local species (*Stipa*, *Melilotoides*, and *Potentilla*) responded differently to  
397 the HW and mowing treatments, suggesting that they exhibit different species-specific adaptive  
398 strategies to address climate extremes and grazing.

399 In general, HWs caused a reduction in the density of *Stipa* in terms of the number of both  
400 clusters and individuals (as indicated by the decrease in IV). In contrast, mowing represented  
401 mechanical damage to the plants and lowered plant height but enhanced the dominance of *Stipa*  
402 by fragmenting the clusters while increasing its IV. The strategy used by *Stipa* to cope with HWs  
403 involves losing the outer tiller layer to protect the internal tiller. Although we did not formally  
404 quantify the litter fractions, most of the increase in litter biomass seemed to arise from the PB  
405 group, especially the withered biomass of *Stipa*. The strategy of shedding the outer tiller layer  
406 directly decreases the energy loads and moisture consumption of the inner (green) tissues, while  
407 the thicker litter layer does the same for the soil, which in turn stimulates decomposition and  
408 mineralization (Meentemeyer, 1978). These changes in *Stipa* appear to have developed as  
409 necessary adaptive strategies to offset the impacts of HWs (Quesada, Vautard, & Yiou, 2012).  
410 Furthermore, because *Stipa* is the dominant species, these changes are also important in terms of  
411 the adaptation of the community to HW stress (Zhao et al., 2016). Compared to other species,  
412 *Stipa* was the most resistant to mowing, which was likely because mowing has historically been  
413 the major land-use activity in this grassland (Niu, Sherry, Zhou, & Luo, 2013; Shao et al., 2016).

414 As mowing directly removes the green parts of plants from the ecosystem, ecological spatial  
415 niches are created that *Stipa* can occupy (Belsky, Carson, Jensen, & Fox, 1993). When mowing  
416 and HWs occurred simultaneously, the *Stipa* plants decreased in size. However, more *Stipa*  
417 clusters were found and less litter biomass was observed. These effects were observed only in the  
418 first year, which hints at resource exhaustion in the following years and suggests that *Stipa*  
419 exhibits self-survival rather than ecosystem facilitation because it is the dominant species under  
420 the interactive effects of HW and mowing.

421 *Melilotoides* appeared to tolerate both HW and mowing stress, thus maintaining its initial  
422 importance throughout the experiment under both single-factor treatments. Previous studies on  
423 its morphology and anatomy showed that *Melilotoides* has structures that are suitable for  
424 resisting drought stress (Li et al., 2012) and important in the avoidance of the worst heat stress  
425 effects (De Boeck, Dreesen, Janssens, & Nijs, 2011). The procumbent form of *Melilotoides* in  
426 our steppe ecosystem has been shown to be more drought resistant than other forms (Li, Shi, Li,  
427 & Liu, 2010; Shi, Guo, & Li, 2005) due to its small celadon leaves, large stomatal density, small  
428 cell size, compact palisade tissue, hairy epidermal cells, and thick layer of cutin in the leaves  
429 (Shi et al., 2005), which are associated with high water retention capacity, photosynthetic rate  
430 and water use efficiency. In addition to its high drought resistance, *Melilotoides* is a  
431 nitrogen-fixing species (Hoekstra et al., 2014; Isbell et al., 2015) and can enable rapid ecosystem  
432 recovery after HW stress through its fertilization effects (Elst et al., 2017; Kreyling et al., 2017).  
433 It has been reported that *Melilotoides* is resistant to mowing and that light mowing promotes the

434 development of the species (Bouton & Gates, 2003); however, the significant decrease in its IV  
435 (Fig. 3b) in the combined treatment indicates that *Melilotoides* is not well adapted to the  
436 interactive effects of HW and mowing. This finding most likely occurred because the stem of  
437 *Melilotoides* is strong and its leaves mostly occur on the upper ends of branches; thus, the stem is  
438 difficult to repair after mowing. The repair process is further hampered by the lack of leaves and  
439 decreased photosynthetic rate.

440 *Potentilla* has thick, sinuate, anticlinal walls on its leaf cells, which are coupled to nearby  
441 epidermal cells to enhance its resistance to drought, thus supporting our finding that HWs did not  
442 significantly affect *Potentilla*. However, *Potentilla* was less tolerant to mowing and appeared to  
443 adopt a strategy of rapid reproductive phenology and increased seed production to adapt to a  
444 harsh environment (Stinson, 2004). Evidence for this strategy was observed through the  
445 increased seedling abundance in the HM<sub>2</sub> plots, which helped maintain the IV of *Potentilla* under  
446 the HW and mowing conditions in 2013 (Fig. 3c). However, the lower abundance of seedlings in  
447 the same plots in 2014 (Fig. 11) indicated that this species was unable to maintain the production  
448 of more seeds, which was likely because of a nutrient shortage and decreased photosynthesis  
449 caused by continuous HWs and the physical damage resulting from mowing.

#### 450 *HWs and mowing prolong plant phenology*

451 Plant phenology is one of the most effective biological indicators of climate change (Scheffers et  
452 al., 2016) because plants often adjust their phenology according to the weather, including



453 extremes (Wolkovich et al., 2012). In our study, HWs advanced both flowering and fruiting of  
454 the three focal species. We attribute this result to the increased litter biomass in the HW plots,  
455 where the thicker litter layer may have helped accelerate the rate of heat accumulation at the  
456 beginning of the following growing season (Facelli & Pickett, 1991). This litter layer-induced  
457 warming will advance plant phenology in a manner similar to the effects of global warming  
458 (Körner & Basler, 2010; Menzel et al., 2006) while also providing a moister environment for  
459 plant growth (Kelemen, Török, Valkó, Migléc, & Tóthmérész, 2013). This positive effect of  
460 HWs may have benefited the plants emerging in early spring the most by helping them complete  
461 their phenological cycles faster. Indeed, the fruiting time of *Potentilla* advanced by 3 days, and its  
462 phenological duration shortened by 8 days (Table 3). Here, mowing mostly had a negative effect  
463 on plant phenology because mowing removes the top parts of plants, which is where the  
464 reproductive parts of most plant species are abundant (Liu et al., 2017; Yang et al., 2012). When  
465 HWs and mowing occurred together, the litter layer that buffered HWs disappeared due to hay  
466 removal. Furthermore, high temperatures and drought caused by HWs can reduce plant stomatal  
467 conductance and downregulate the quantum yield of photosystem II (Wang et al., 2016). These  
468 changes will affect tissue viability by slowing the transfer of photosynthates to the ear during ovule  
469 fertilization (Suwa et al., 2010), thereby leading to lower kernel sugar content and greater kernel  
470 abortion rates and also decreasing pollen viability (Siebers et al., 2017) because plants need more  
471 time to accumulate the energy and materials necessary to regenerate their reproductive organs.  
472 Taking *Potentilla* as an example, the phenological duration was prolonged by nearly 14 days in

473 the HM<sub>2</sub> treatment relative to NM<sub>2</sub>. Although this strategy might effectively increase plant  
474 survival under severe environmental conditions, it can also increase plant mortality (e.g., if frost  
475 occurs before *Potentilla* completes its fruiting process).

476 *Opposite effects of HW and mowing on dominant species and significant negative effects of their*  
477 *interactions on community structure*

478 HWs increased the community diversity and evenness indices, whereas mowing had the opposite  
479 effect. These changes align well with the variation in IV in the dominant plant species, *Stipa*.

480 Specifically, HWs decreased the IV of *Stipa*, thereby creating open niches for other species and  
481 increasing the community richness, diversity and evenness. The higher species richness and  
482 diversity that resulted from the HWs in our study may protect the community from the negative  
483 impacts of other extreme events (Bartelheimer, Poschlod, & Stevens, 2016; Hoekstra et al., 2014;  
484 Isbell et al., 2015), although a reversed effect is also possible (Van Peer, Nijs, Reheul, & De  
485 Cauwer, 2004) because several factors can modulate or confound diversity-stability relationships  
486 in response to extreme events (De Boeck et al., 2018). Compared with the HWs, light mowing  
487 enhanced the dominant species (*Stipa*), which was found to be well tolerant to mowing.

488 Moreover, a comparison of the different mowing intensities indicated that light mowing retained  
489 some of the aboveground green part of the plant, which gave the plant a chance to regenerate;  
490 thus, this treatment had an insignificant effect on community structure over the 3 years of our  
491 experiment (Table 4). Long-term studies have indicated that light mowing offers a better

492 opportunity for some late-growing plants to due to the empty niche caused by mowing, resulting  
493 in an increase of community diversity (Yang et al., 2012). However, heavy mowing nearly cut off  
494 all the aboveground green parts of the plant, and if this mowing occurred before certain plant  
495 species had finished their reproductive phenological development, the plant would experience a  
496 lack of nutritional reproductive capacity, meaning that the species would likely disappear in this  
497 ecosystem (Hart, 2001; Socher et al., 2012). Thus, in a short time, heavy mowing decreased the  
498 community richness, diversity and evenness (Table 4). The same trend was also detected when  
499 HWs and heavy mowing occurred at the same time. The positive effect of HWs on community  
500 structure was no longer apparent in the ecosystems most affected by mowing. Under such  
501 conditions, species with a high carbon sink strength and low tolerance (e.g., leguminous plants)  
502 may disappear, while some low-efficiency forbs will survive, thus causing a further decrease in  
503 nutrient accumulation and productivity. In sum, a spiral of reinforcing negative feedback may  
504 occur if combined disturbances continue, which will ultimately result in profound changes to the  
505 ecosystem.

506 *Conceptual framework explains the rapid effects, post effects and legacy effects of HWs and*  
507 *mowing*

508 The results of this study showed that the HWs and mowing effects on plant individual growth are  
509 just the beginning of a series of effects on the ecosystem (Fig. 6). The short-term (rapid) effects  
510 of HWs and mowing will further lead to changes in population size and community structure,

511 thereby leading to long-term (post and legacy) effects (Qu et al., 2018). As several prior  
512 laboratory-based studies showed, the HW effect was first noticed at the cellular level, which  
513 resulted in a decrease in photosynthetic enzyme activity and low stomatal conductance and had  
514 effects on other eco-physiological characteristics (Wang et al., 2016; Zinta et al., 2014). Recent  
515 findings have confirmed that HWs significantly alter plant photosynthesis and respiration (Qu,  
516 Chen, Bunce, Zhu, & Sicher, 2018; Rashid et al., 2018), reduce CO<sub>2</sub> uptake (Tatarinov et al.,  
517 2016), and lead to the redistribution of carbon and nitrogen in a plant or community (Birami et  
518 al., 2018; Giri, Heckathorn, Mishra, & Krause, 2017). Here, mowing had a similar effect on the  
519 community but directly removed plant parts (photosynthetic product) rather than reducing the  
520 accumulation rate. These were considered as rapid effects, which mainly occurred during the  
521 HW or mowing treatment and over a short period after treatment. The rapid effects, such as a  
522 decrease in plant net photosynthesis, will cause variations in plant morphology due to the  
523 lowered C accumulation (Crafts-Brandner & Salvucci, 2002; Siebers et al., 2017), whereas  
524 mowing also affects plant morphology through physical damage (Benot et al., 2014; Liu et al.,  
525 2017). Most of the variation in plant morphology due to the effects of HWs and mowing,  
526 including mechanical damage, carbon starvation and hydraulic failure, ultimately have a negative  
527 effect on plant health and growth (Li et al., 2017; Zinta et al., 2014), lead to the mortality of  
528 plants with low tolerance and have similar negative effects on plant phenology, and they  
529 eventually cause variation in the community structure (Drake et al., 2018; Elst et al., 2017).  
530 Changes of the species number were indicated that HWs and mowing will cause long-term

531 effects on ecosystem, which was considered as post effects and legacy effects (Fig. 6). Then, the  
532 effects of HWs and mowing on the population extend to the community level as demonstrated by  
533 variations in the community richness, diversity and evenness (Table 4), and they eventually lead  
534 to variations at the ecosystem level, which include changes in the carbon and water flux, LAI  
535 (leaf area index) and biomass (Qu et al., 2016). These alterations ultimately cause changes in the  
536 plant growth environment, especially the soil environment and soil microbes (Bérard, Ben Sassi,  
537 Kaisermann, & Renault, 2015). We further assume that the post and the legacy effects will  
538 become more significant if these disturbances occur repeatedly.

539 In conclusion, our final hypothesis that the ecosystem presents a stress threshold for negative  
540 effects (such as those caused by HWs or mowing) seems to be valid (De Boeck et al., 2018).  
541 When a stressor does not exceed this threshold, the ecosystem can be trained to increase its  
542 tolerance to this particular stress (Gutschick & BassiriRad, 2003). This ‘training’ process can  
543 involve a gradual change in plant community structure (Elst et al., 2017). For example, the  
544 species-specific responses of *Stipa*, *Melilotoides*, and *Potentilla* to HWs and mowing in this  
545 study made the ecosystem less vulnerable when facing future HWs or mowing threats. However,  
546 when the stress exceeded the threshold, such as the stress caused by the interactive effect of HWs  
547 and heavy mowing, the response of the ecosystem became negative, which led to changes that  
548 included a sharp decline in plant or community characteristics. Although some urgent response  
549 strategies were observed (such as the significant increase in cluster number in *Stipa* or the  
550 prolonged phenological duration in *Potentilla*), the studied species were unable to respond

551 consistently when the stress continued to occur, and some strategies will increase the risk of  
552 species inheritance (Teskey et al., 2015). Furthermore, the loss of species actually indicated  
553 reduce the stability of the ecosystem due to the decrease of diversity and evenness, which will  
554 weaken the resilience of the ecosystem to future climate change or human disturbance. Therefore,  
555 we suggest that the conventional means of grassland utilization (heavy mowing) may need to be  
556 revisited, especially in the face of more extreme events, because intensive human activities will  
557 reduce the tolerance of ecosystems to climate change and ultimately cause irreparable damage to  
558 these ecosystems.

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825



826 **Table 1** Outcome of the repeated-measurement ANOVA (*P*-values indicated) for the responses of *Stipa krylovii*, *Melilotoides*  
827 *ruthenica* and *Potentilla tanacetifolia* cluster or seedling number ( $N_s$ ), cover ( $C_p$ ), tiller number ( $N_t$ ), nutritive plant height ( $H_p$ ), crown  
828 width ( $C_w$ ) and importance value (IV) to heat waves (HWs), mowing (M), day (D, including 2 years, 4 days for each year) and their  
829 interactions. *P*-values of <0.05 are in bold.

830

Treatment	<i>Stipa krylovii</i>						<i>Melilotoides ruthenica</i>						<i>Potentilla tanacetifolia</i>					
	$N_s$	$C_p$	$N_t$	$H_p$	$C_w$	IV	$N_s$	$C_p$	$N_t$	$H_p$	$C_w$	IV	$N_s$	$C_p$	$N_t$	$H_p$	$C_w$	IV
HW	0.989	0.935	0.176	0.185	0.423	0.307	0.551	0.340	0.385	0.312	<b>0.005</b>	0.843	0.874	0.630	0.426	0.874	0.862	0.655
M	<b>0.003</b>	<b>0.027</b>	0.496	<b>0.000</b>	0.303	0.201	0.334	0.447	0.768	<b>0.002</b>	0.060	0.257	0.707	<b>0.038</b>	0.803	0.053	0.424	0.206
HW×M	0.225	0.468	0.121	0.471	0.649	0.535	0.158	0.235	0.106	<b>0.082</b>	<b>0.020</b>	0.405	0.291	0.894	0.607	0.989	0.054	0.661
D	<b>0.000</b>	<b>0.006</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.001</b>	0.116	<b>0.008</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.003</b>	<b>0.031</b>	<b>0.002</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.375
D×HW	0.459	<b>0.042</b>	0.409	<b>0.004</b>	0.413	0.537	0.381	0.527	0.880	0.114	<b>0.041</b>	0.316	0.259	0.293	0.111	0.740	0.811	0.590
D×M	0.271	0.242	0.685	0.136	0.373	0.856	0.892	0.972	0.880	0.221	<b>0.027</b>	0.991	0.257	0.810	0.302	0.869	0.431	0.379
D×HW×M	0.571	0.106	0.520	<b>0.018</b>	0.417	0.302	0.730	0.879	<b>0.021</b>	0.161	<b>0.024</b>	0.769	0.145	0.972	0.689	0.410	0.476	0.980

831

832 **Table 2** Outcome of the multivariate ANOVA analysis (*P*-values indicated) on the effects of heat waves (HWs), mowing (M) and  
 833 their interactions on flowering time, fruiting time and phenology duration of *Stipa krylovii*, *Melilotoides ruthenica* and *Potentilla*  
 834 *tanacetifolia* in 2013. *P*-values of <0.05 are in bold, and \*, \*\*, \*\*\* indicate significance at the level of *P*<0.05, 0.01, and 0.001,  
 835 respectively.  
 836

Treatment	<i>Stipa krylovii</i>			<i>Melilotoides ruthenica</i>			<i>Potentilla tanacetifolia</i> <sup>837</sup>		
	Flowering Time	Fruiting time	Phenology duration	Flowering time	Fruiting time	Phenology duration	Flowering time	Fruiting time	Phenology duration
HW	<b>0.027*</b>	<b>0.025*</b>	0.725	0.580	0.307	0.279	0.461	0.496	0.851
M	<b>0.007**</b>	<b>0.011*</b>	<b>0.043*</b>	<b>0.042*</b>	0.073	0.074	0.854	0.558	0.578
HW × M	0.796	0.842	0.438	0.613	0.147	0.756	0.949	<b>0.011*</b>	<b>0.013*</b>

838 **Table 3** Flowering time, fruiting time and phenology duration (mean±SE) of *Stipa krylovii*,  
839 *Melilotoides ruthenica* and *Potentilla tanacetifolia* for different treatments in 2013: C (control,  
840 no heat+no mowing), HW (heat+no mowing), NM<sub>7</sub> (no heat+7 cm stubble), NM<sub>2</sub> (no heat+2 cm  
841 stubble), HM<sub>7</sub> (heat+7 cm stubble) and HM<sub>2</sub> (heat+2 cm stubble). D-values indicate the  
842 difference between the heat and no-heat treatments under the background of no mowing, light  
843 mowing, and heavy mowing. Positive D-values indicate that HWs delay the phenological phase,  
844 and negative values indicate that HWs advance the phenophases. Different letters indicate  
845 significant differences among treatments ( $P<0.05$ , one-way ANOVA, Duncan's post hoc test).  
846

Treatment	Flowering time (day of year)	D-value	Fruiting time (day of year)	D-value	Duration (days)	D-value
<i>Stipa krylovii</i>						
C	227.86±0.78 <sup>bc</sup>	-1.74	233.09±0.78 <sup>bc</sup>	-1.76	28.62±1.14 <sup>a</sup>	-1.04
HW	226.11±0.46 <sup>c</sup>		231.33±0.28 <sup>c</sup>		27.58±0.63 <sup>a</sup>	
NM <sub>7</sub>	231.09±2.02 <sup>ab</sup>	+3.32	235.81±2.01 <sup>ab</sup>	+2.84	25.91±1.01 <sup>a</sup>	-1.54
HM <sub>7</sub>	234.41±0.43 <sup>a</sup>		238.64±1.47 <sup>a</sup>		24.37±1.83 <sup>a</sup>	
NM <sub>2</sub>	227.44±1.57 <sup>bc</sup>	+3.42	232.55±0.29 <sup>bc</sup>	+2.91	28.37±0.87 <sup>a</sup>	-4.15
HM <sub>2</sub>	230.86±2.34 <sup>abc</sup>		235.46±1.67 <sup>abc</sup>		24.21±1.79 <sup>a</sup>	
<i>Melilotoides ruthenica</i>						
C	211.67±0.87 <sup>ab</sup>	-0.81	229.78±0.88 <sup>ab</sup>	-1.00	51.94±1.28 <sup>a</sup>	+3.03
HW	210.86±2.39 <sup>ab</sup>		228.78±2.98 <sup>b</sup>		54.79±1.48 <sup>a</sup>	
NM <sub>7</sub>	210.01±2.18 <sup>b</sup>	+3.42	228.06±1.43 <sup>b</sup>	+1.18	55.40±4.11 <sup>a</sup>	+1.07
HM <sub>7</sub>	213.43±1.12 <sup>ab</sup>		229.24±0.54 <sup>b</sup>		56.47±1.70 <sup>a</sup>	
NM <sub>2</sub>	210.58±0.25 <sup>ab</sup>	+5.43	228.16±0.68 <sup>b</sup>	+5.60	51.04±1.16 <sup>a</sup>	+4.7
HM <sub>2</sub>	216.01±1.12 <sup>a</sup>		233.76±0.72 <sup>a</sup>		55.74±0.71 <sup>a</sup>	
<i>Potentilla tanacetifolia</i>						
C	194.43±1.78 <sup>a</sup>	+1.12	218.73±1.93 <sup>a</sup>	-2.99	71.62±5.25 <sup>a</sup>	-8.07
HW	195.55±1.61 <sup>a</sup>		215.74±2.28 <sup>ab</sup>		63.54±2.31 <sup>ab</sup>	
NM <sub>7</sub>	195.58±1.34 <sup>a</sup>	+0.33	216.01±1.79 <sup>ab</sup>	-1.46	65.73±4.94 <sup>ab</sup>	-4.30
HM <sub>7</sub>	195.90±0.96 <sup>a</sup>		214.54±1.70 <sup>ab</sup>		61.43±2.71 <sup>ab</sup>	
NM <sub>2</sub>	194.61±1.01 <sup>a</sup>	+1.10	212.60±1.59 <sup>b</sup>	+7.47	57.88±3.69 <sup>b</sup>	+14.14
HM <sub>2</sub>	195.71±1.54 <sup>a</sup>		220.08±1.46 <sup>a</sup>		72.02±3.19 <sup>a</sup>	

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848 **Table 4** Outcome of the multivariate ANOVA analysis (*P*-values indicated) on the effects of heat waves (HWs), mowing (M) and their  
 849 interactions on mean important value (IV). *P*-values of <0.05 are indicated in bold, and \*, \*\*, \*\*\* indicate significance at the level of  
 850 *P*<0.05, 0.01, and 0.001, respectively.

Treatment	Mean important value (IV)		
	<i>Stipa krylovii</i>	<i>Melilotoides ruthenica</i>	<i>Potentilla tanacetifolia</i>
HW	0.663	0.560	0.568
M	<b>0.006**</b>	0.119	<b>0.029*</b>
HW×M	0.264	0.719	0.140

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875 **Table 5** Outcome of the multivariate ANOVA analysis (*P*-values indicated) on the effects of heat waves (HWs), mowing (M) and their  
876 interactions on community structure (richness, diversity and evenness index) and biomass (aboveground and litter biomass) in 2013  
877 and 2014. *P*-values of <0.05 are indicated in bold, and \*, \*\*, \*\*\* indicate significance at the level of *P*< 0.05, 0.01, and 0.001,  
878 respectively.

Treatment	Community structure			Biomass	
	Richness Index (Margalef index)	Diversity Index (Simpson index)	Evenness Index (Pielou's index)	Aboveground biomass	Litter biomass
<hr/> 2013 <hr/>					
HW	0.713	0.719	0.684	0.862	0.302
M	0.845	<b>0.003**</b>	<b>0.003**</b>	0.734	<b>0.000***</b>
HW × M	0.752	0.168	0.085	0.776	<b>0.032*</b>
<hr/> 2014 <hr/>					
HW	0.871	0.408	0.576	0.683	0.665
M	0.345	<b>0.016*</b>	<b>0.017*</b>	0.057	<b>0.000***</b>
HW × M	0.850	0.407	0.318	0.564	0.946

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890 **Table 6** Richness, diversity and evenness index values (mean  $\pm$  SE) under the six experimental treatments in 2013 and 2014. Different  
891 letters indicate significant differences ( $P < 0.05$ , one-way ANOVA, Duncan's post hoc test) among the treatments. See Table 3 for the  
892 abbreviations.

Treatment	2013			2014		
	Richness Index (Margalef index)	Diversity Index (Simpson index)	Evenness Index (Pielou's index)	Richness Index (Margalef index)	Diversity Index (Simpson index)	Evenness Index (Pielou's index)
C	2.293 $\pm$ 0.30 <sup>a</sup>	0.747 $\pm$ 0.04 <sup>ab</sup>	0.748 $\pm$ 0.03 <sup>ab</sup>	2.251 $\pm$ 0.12 <sup>a</sup>	0.750 $\pm$ 0.02 <sup>a</sup>	0.769 $\pm$ 0.03 <sup>abc</sup>
HW	2.336 $\pm$ 0.23 <sup>a</sup>	0.799 $\pm$ 0.03 <sup>a</sup>	0.815 $\pm$ 0.03 <sup>a</sup>	2.143 $\pm$ 0.14 <sup>a</sup>	0.790 $\pm$ 0.03 <sup>a</sup>	0.823 $\pm$ 0.02 <sup>a</sup>
NM <sub>7</sub>	2.198 $\pm$ 0.34 <sup>a</sup>	0.729 $\pm$ 0.01 <sup>ab</sup>	0.744 $\pm$ 0.02 <sup>ab</sup>	1.991 $\pm$ 0.21 <sup>a</sup>	0.743 $\pm$ 0.03 <sup>a</sup>	0.785 $\pm$ 0.04 <sup>ab</sup>
HM <sub>7</sub>	2.471 $\pm$ 0.05 <sup>a</sup>	0.720 $\pm$ 0.05 <sup>ab</sup>	0.713 $\pm$ 0.05 <sup>bc</sup>	2.094 $\pm$ 0.28 <sup>a</sup>	0.668 $\pm$ 0.07 <sup>ab</sup>	0.711 $\pm$ 0.07 <sup>abc</sup>
NM <sub>2</sub>	2.250 $\pm$ 0.29 <sup>a</sup>	0.686 $\pm$ 0.02 <sup>bc</sup>	0.697 $\pm$ 0.03 <sup>bc</sup>	1.937 $\pm$ 0.16 <sup>a</sup>	0.652 $\pm$ 0.07 <sup>ab</sup>	0.681 $\pm$ 0.06 <sup>bc</sup>
HM <sub>2</sub>	2.157 $\pm$ 0.07 <sup>a</sup>	0.615 $\pm$ 0.02 <sup>c</sup>	0.631 $\pm$ 0.02 <sup>c</sup>	1.863 $\pm$ 0.22 <sup>a</sup>	0.590 $\pm$ 0.03 <sup>b</sup>	0.641 $\pm$ 0.02 <sup>c</sup>

893 **Figure Captions:**

894 **Fig. 1** Heat wave and mowing effects on the number of clusters or seedlings ( $N_s$ ) and cover ( $C_p$ )  
895 (mean $\pm$ SE) of *Stipa krylovii* (a, b, c, d), *Melilotoides ruthenica* (e, f, g, h) and *Potentilla*  
896 *tanacetifolia* (i, j, k, l) in 2013 and 2014. C (control, no heat+no mowing), HW (heat+no  
897 mowing), NM<sub>7</sub> (no heat+7 cm stubble), NM<sub>2</sub> (no heat+2 cm stubble), HM<sub>7</sub> (heat+7 cm stubble)  
898 and HM<sub>2</sub> (heat+2 cm stubble). The grey columns indicate the heat wave treatment, and the  
899 hatched columns indicate the mowing treatment. Different letters indicate significant differences  
900 among treatments ( $P<0.05$ , one-way ANOVA, Duncan's post hoc test). Based on data of 15  
901 August (2013) and 16 August (2014).

902 **Fig. 2** Morphological characteristics of *Stipa krylovii* (a), *Melilotoides ruthenica* (b) and  
903 *Potentilla tanacetifolia* (c) under different treatments based on data from 16 August 2014.  
904 Number of plant tillers ( $N_t$ ) is plotted on the x-axis, nutritive plant height ( $H_p$ ) is plotted on the  
905 y-axis, and the circular area indicates the plant crown width ( $C_w$ ); the grey circles denote the heat  
906 wave treatment; the hatched circles denote the mowing treatment. See Fig. 1 for the treatment  
907 abbreviations. Different letters indicate significant differences among treatments ( $P<0.05$ ,  
908 one-way ANOVA, Duncan's post hoc test), with 'abc' representing differences in nutritive plant  
909 height, 'ABC' representing differences in number of tillers and 'xyz' representing differences in  
910 crown width.

911 **Fig. 3** Mean importance values (IV, mean $\pm$ SE) of *Stipa krylovii* (a), *Melilotoides ruthenica* (b)  
912 and *Potentilla tanacetifolia* (c) under different treatments in 2013 and 2014. The grey columns  
913 indicate the heat wave treatment and the hatched columns indicate the mowing treatment. See  
914 Fig. 1 for the treatment abbreviations. Different letters indicate significant differences among  
915 treatments ( $P<0.05$ , one-way ANOVA, Duncan's post hoc test).

916 **Fig. 4** Time series comparing the importance values (IV, mean $\pm$ SE) of *Stipa krylovii* (a, b, c),  
917 *Melilotoides ruthenica* (d, e, f) and *Potentilla tanacetifolia* (g, h, i) in 2013 and 2014 under

918 different treatments. The grey arrow and HW denote the timing of the heat wave treatment; the  
919 black arrow and M indicate the timing of mowing treatment. See Fig. 1 for the abbreviations.

920 **Fig. 5** Aboveground biomass and litter biomass (mean±SE) of different functional groups (see  
921 appendix) under the different treatments in 2013 (a, c) and 2014 (b, d). See Fig. 1 for the  
922 treatment abbreviations. Different letters indicate significant differences in the total aboveground  
923 biomass among treatments ( $P < 0.05$ , one-way ANOVA, Duncan's post hoc test). Aboveground  
924 biomass was separately collected by plant functional groups, the litter biomass was not  
925 separated.

926 **Fig. 6** Conceptual framework of the cell-plant-community-ecosystem feedback to heat waves  
927 (HWs) and mowing (M) on the grassland ecosystem (see text). H and red letters indicate the  
928 effect of heat waves, M and blue letters indicate the effect of mowing. '+' and '-' indicate the  
929 respective positive or negative impacts, '±' indicates the impacts were different for different  
930 plant species, and '?' indicates uncertain impacts. The solid box shows the reported results with  
931 data support, the dashed box shows the results that are mentioned in prior studies but lack data  
932 support and the effect was uncertain. Solid arrows show the connection between different  
933 indications.  
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