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The effects of increased snow depth on plant and microbial biomass and community composition along a precipitation gradient in temperate steppes

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4

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26   **ABSTRACT**

27   Shift in precipitation regime could greatly alter plant and microbial activity, and

28   thus the contemporary and future ecosystem dynamics in grasslands. We investigated

29   how changes in snow depth affect plants, microbes and their relationships after 10

30   consecutive years of snow treatments in different steppes. We selected 8 snow fences

31   along a mean annual precipitation (MAP) gradient from 225 to 375 mm in Inner

32   Mongolia. For each snow fence, study plots were set up at 7 transects with different

33   levels of snow depth. We found that ecosystem properties, including soil moisture, the

34   biomass and nitrogen (N) pools of microbes and plants, the fungi: bacteria ratio and

35   the grass: forb ratio, increased with increasing snow depth at the drier sites with lower

36   MAP, but not at the wetter sites with higher MAP. At any given site, the sensitivity of

37   these ecosystem properties to changes in snow depth was determined by the slopes of

38   these variables against snow depth. The results showed that the sensitivity of these

39   ecosystem properties to changes in snow depth decreased linearly with increase in

40   MAP levels. In addition, we also found that increased snow depth shifted the

41   relationship between microbial and plant biomass from positive to negative. Our work

42   reveals the importance of snow water in regulating plant and microbial processes in

43   temperate steppes, especially under lower MAP conditions. The greater plant and

44   microbial biomass and the shift of community toward greater fungi: bacteria and grass:

45   forb ratio imply that increased snowmelt input alleviated water limitation in temperate

46   steppes and altered plant and microbial communities. Our study helps to better predict

47 that how changes in winter precipitation could affect the biomass and composition of

48 plants and soil microbes in grasslands.

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1. Introduction

Numerous studies have assessed how changes in precipitation regimes influence ecosystem structure and functioning using manipulation experiments (Bachar et al., 2010; Estiarte et al., 2016). Most of these studies focused on the effects of annual or summer precipitation on plant and microbial processes, and often with site-level data (Vicente-Serrano et al., 2013; Estiarte et al., 2016). Climate change is expected to alter the amount of precipitation falling as snow in Northern Hemisphere (Peng et al., 2010; IPCC, 2014). In addition, the changes in wind patterns or vegetation cover will also alter snow redistribution by wind drifting, especially in ecosystems with short-status plants such as grasslands (Ayres et al., 2010). Snow could greatly affect water and nutrient cycles, especially during winter and early growing season (Schimel et al., 2004). However, we know very little about how changes in snow depth or redistribution will affect the productivity and communities of plants and soil microbes, as well as their relationship across the precipitation gradient.

Changes in snow depth can affect soil microbial activity and plant growth through abiotic or biotic mechanisms (Buckeridge et al., 2010; Sorensen et al., 2016). Greater snow accumulation elevates soil temperature by insulating soils from cold winter air (Brooks et al., 2005; Natali et al., 2011), and increases soil moisture (Groffman et al., 2001). Aside from increasing water availability (Groffman et al., 2001), greater snow depth stimulates nitrogen (N) mineralization (Schimel et al., 2004; Freppaz et al., 2007; Freppaz et al., 2012) and increases N availability during spring, especially in N limited ecosystems (Buckeridge et al., 2010; Leffler and Welker,

5

75   2013). Together these mechanisms can increase water and nutrient supply for soil

76   microbes and plants (Groffman et al., 2006; Buckeridge et al., 2010). In addition,

77   greater snow accumulation could also alter both plant and microbial community

78   compositions (Zinger et al., 2009; Kreyling et al., 2012; Bokhorst et al., 2013;

79   Morgado et al., 2016; Semenova et al., 2016).

80   The sensitivity of ecosystem productivity to changing precipitation, defined as the

81   slope of the precipitation-productivity relationship, have often found to be related to

82   local precipitation conditions (Knapp et al., 2017). How rainfall changes will affect

83   the sensitivity of plant productivity to precipitation has been studied in various

84   ecosystems using rainfall manipulative experiments (Estiarte et al., 2016; Knapp et al.,

85   2017). However, currently there are limited experimental evidences on how changes

86   in snow depth will affect the productivity and communities of plants and microbes

87   along precipitation gradients, and whether long-term changes in snow amount will

88   modify the patterns of plant-microbe interactions at a landscape scale. Coordinated

89   distributed experiments (CDEs) (Fraser et al., 2013) involving snow gradients offer a

90   tractable approach for addressing these questions. For example, in Inner Mongolia,

91   China, snow fences have been built to reduce snow accumulation on roads during

92   winter. The redistribution of snow by drifting generates a long-term gradient of snow

93   depth on both sides of the snow fences, and eventually alters the amount of snow

94   water input to soils. Those snow fences can be treated as CDEs to test how variation

95   in snow depth affects plant and microbial biomass and communities.

96   In the current study, we selected 8 snow fences that were built in 2003 across a

97   precipitation gradient from 225 to 375 mm in temperate steppes in Inner Mongolia.

98   We analyzed the biomass and composition of plants and microbes 10 years after the

99   fences were built. Therefore our study includes snow depth variation driven by snow

100   fences within sites and the precipitation gradient across sites. We aimed to test the

101   hypothesis that increased snow depth would increase plant and soil microbial biomass

102   and alter their community compositions. Specifically, increasing snow depth would

103   alleviate water limitation for plants and microbes, and thus increase their biomass.

104   The sensitivity of plant and microbial biomass to increasing snow depth would

105   decrease with the increase in local MAP. In addition, we expected that changes in

106   snow depth will alter plant and microbial community composition, and consequently

107   induce changes in the relationships between plants and microbes.

108   **2. Materials and methods**

109   *2.1. Study sites and experimental design*

110   Snow fence sites were located in Inner Mongolia in Northern China (Table 1).

111   Average maximum winter snow depth has ranged from 8.3 to 13 cm over the past 20

112   years, with an increasing trend over the past 20 years (Peng et al., 2010). Snow fences

113   with a height of 2 m were installed parallel to highways and perpendicular to the

114   prevailing winter wind direction by the Inner Mongolia Department of Transportation.

115   Fences were located 150-200 m from the highways (Figs. S1 and S2).

116   We selected 8 snow fences built in 2003 along a precipitation gradient (225 to

117   375 mm/yr) from west to east in Inner Mongolia. These sites included typical and

118   meadow steppe ecosystems and the details were listed in Table 1. For all fences, there

119   was a consistent pattern of snow accumulation, with early accumulation and deeper

120   snow near the fence to late accumulation and shallower snow away from the fence

121   (Fig. S1). Specifically, we established 6 sampling transects parallel to each of the

122   snow fences, located at 3, 7, and 10 m on either side. We also established another

123   transect 100 m away from the snow fence as an ambient snow treatment. This resulted

124   in 7 snow depth transects in each site. On each transect, we established 3 replicate

125   sampling plots separated by 50 m, resulting in 21 sampling plots total per site (Fig.

126   S2).

127   Soil samples were collected from all plots during August 1-15, 2013. Sampling

128   was timed to coincide with maximum aboveground biomass in each site. In each plot,

129   four soil cores (5 cm depth and 5 cm diameter) were taken at random and combined

130   into a composite sample. After removing roots and stones by sieving (2 mm mesh),

131   the samples were stored on ice and transferred to the lab for inorganic N concentration

132   and microbial analyses within one week. Subsamples were taken to measure

133   gravimetric water content and soil chemical properties (air-dried, finely ground, and

134   sieved to < 250μm).

135   *2.2. Snow depth calculation*

136   During February 15-28, 2016, we measured snow depth using poles to push

137   through the snow to the soil surface at each transect in each site. We measured 3

138   replicates to get a mean snow depth for each transect.

139   We used a model based on wind tunnel testing to simulate the maximum snow

140   depths on the windward and leeward sides of each fence for 2013 (Zhao, 2012). The

141   model was validated and calibrated with the snow depth measured in 2016. Snow

142   depth at WUL could not be measured because the access road was temporarily closed

143   to vehicles. For WUL, we used the average of measured snow depth in the two nearby

144   sites (BAY and XIL) to validate modeled snow depth. Prior to calibration, the model

145   was reasonably accurate at predicting the snow depth for most sites, although there

146   was a tendency to overestimate snow depth at AER. To account for any site-level bias,

147   we calibrated the model outputs from 2013 based on a regression of modeled versus

148   measured snow depth in 2016 (Fig. S3). At each site i, we calculated snow depth for

149   2013 as $D_i^* = (D_i - b_i)/m_i$, where D_i is the modeled 2013 snow depth, and b_i and m_i

150   are the regression intercept and slope for each site in 2016.

151   Based on the calibrated model outputs, we calculated the cross-site mean snow

152   depth for each of the snow fence transects. Among the 7 transections, there was 1

153   snow-reduced transect (Snow-R) with 48% reduction in ambient snow depth, 1

154   ambient snow depth transect (Ambient), and 5 snow-increased transects (Snow-In1,

155   Snow-In2, Snow-In3, Snow-In4 and Snow-In5), which were equivalent to 1.8, 2.3,

156   3.3, 3.7 and 4.8 mean folds of increase in ambient snow depth, respectively (Table

157   S1).

158   *2.3. Plant and soil properties*

159   Aboveground plant biomass was estimated by clipping live biomass at the same

160   time as soil sampling. All living plant tissues were harvested from a 1×1 m quadrat in

161 each plot, and plant litter in the same quadrat was also collected. All plant samples

162 were oven-dried at 70 ℃ for 48 h and weighed to determine biomass.

163   Soil bulk density was measured by calculating the ratio of the oven-dried mass

164 (105°C) of soil to bulk soil volume. Soil C, soil N, and plant N were determined using

165 elemental analysis (Analysensysteme, Germany).

166   The biomass and structure of the soil microbial community was assessed by

167 phospholipid fatty acids (PLFA) analysis using the method described by Frostegard &

168 Baath (1996). The resultant fatty acid methyl esters were separated, quantified, and

169 identified using capillary gas chromatography (GC). Qualitative and quantitative fatty

170 acid analyses were performed with an Agilent 6890 gas chromatograph (Agilent

171 Technologies, Palo Alto, CA) and the MIDI Sherlock Microbial Identification System

172 (MIDI, Newark, DE, USA). The concentration of each individual phospholipid fatty

173 acid (PLFA) (among the 25 most abundant PLFAs) was expressed as nmol g $^{-1}$ dry

174 soil in a given sample based on an internal standard (methyl ester C19:0,

175 Sigma-Aldrich). Using bulk density values, these concentrations were expressed in

176 units of mol m^{-2}. Total fatty acids were used to represent total soil microbial biomass.

177 The fatty acids i-14:0, i-15:0, a-15:0, i-16:0, 16:1ω9, i-17:0, a-17:0, 17:0-cyclo,

178 18:1ω9 and 19:0-cyclo were pooled to represent bacterial PLFA biomass; 18:2ω6 was

179 used as an indicator of fungal biomass (representing decomposer fungi, but not

180 arbuscular mycorrhizal fungi) (Frostegard and Baath, 1996), and 16:1ω5c was used as

181 an indicator of arbuscular mycorrhizal fungal (AMF) biomass. The ratio of fungal to

182 bacterial PLFA was taken to represent the relative abundance of these two groups.

183   Soil microbial C and N were estimated using the chloroform

184   fumigation-extraction method (Vance et al., 1987). Briefly, fresh soil samples were

185   transferred to the lab, and field moist samples (15 g dry weight equivalent) were

186   fumigated for 24 h with ethanol-free $CHCl_3$. The fumigated and unfumigated samples

187   were then extracted with 60 ml of 0.5M K_2SO_4 for 30 min on a shaker. K_2SO_4 extracts

188   were filtered through 0.45 μm filters and frozen at –20°C prior to analysis for

189   extractable C and N by an elemental analyzer (liquid TOC, Analysensystem,

190   Germany) and Kjeldahl digestion, respectively. Microbial C and N were calculated as

191   the difference between extractable C and N in the fumigated and the unfumigated

192   samples using a conversion factor of 0.45 (Liu et al., 2016). MBC in the BAY and

193   AER sites was not determined due to instrument failure.

194   *2.4. Statistical analysis*

195   We used univariate linear regression to assess how the measurements of

196   ecosystem properties, including soil moisture (0-10 cm), plant aboveground biomass,

197   microbial PLFA biomass, plant and microbial community composition varied along

198   with the snow depth for each site. To assess whether those ecosystem properties were

199   more sensitive to changes in snow depth at the drier sites, we extracted the regression

200   slopes from each sites and used linear model to evaluate whether the slopes decreased

201   along with the increase in MAP across sites. We also used linear model to explore the

202   relationships between soil moisture and soil microbial or aboveground biomass at

203   each site.

204   To determine how changes in snow depth affect plant-microbe relationship, we

205   conducted linear regressions between total microbial PLFAs and plant biomass across

206   sites for each snow transect. We took the slopes from these regressions as an index of

207   the plant-microbial relationship (i.e. positive slope = positive relationship) and

208   compared the differences in slopes among the 7 snow depth transects by one-way

209   ANOVA. All statistical analyses were performed with R 3.2.2 (R Development Core

210   Team). Significance was accepted at P value <0.05 level of probability.

211

212   **3. Results**

213   *3.1. Soil moisture*

214   Soil moisture increased significantly with increase in snow depth for 5 sites with

215   lower MAP (225, 247, 280, 283, 314 mm), but no significant pattern was observed at

216   the other 3 sites with higher MAP (301, 368 and 375 mm, Fig. 1a). When pooling all

217   sites together, the slopes between soil moisture and snow depth decreased linearly

218   with MAP levels (Fig. 1b).

219   *3.2. Biomass and N pools of soil microbes and plants*

220   Total PLFAs and plant biomass increased with increase in snow depth, although

221   such correlations were significant only at the low MAP sites (Figs. 2a and 3c). The

222   responses of both soil microbial and plant biomass N pools were consistent with the

223   responses of total PLFAs and plant biomass at each site, respectively (Figs. 3a and 3c).

224   Except for soil microbial biomass N pool, the slopes of those variables against snow

12

225 depth negatively correlated with MAP levels (Figs. 2b, 2d, 3b and 3d). Changes in

226 snow depth did not affect soil N pool across all sites (Figs. 3e and 3f).

227 *3.3. Community composition of soil microbes and plants*

228 Similarly, fungi:bacteria ratio (Fig 4a), AMF abundance (Fig 4c), grass biomass

229 (Fig 5a) and grass: forb ratio (Fig 5e) tended to increase with increase in snow depth,

230 but the significant correlations were only found at the low MAP sites. When pooling

231 all sites together, the slopes of F:B ratio (Fig 3b), AMF abundance (Fig 3d), grass

232 biomass (Fig 4b) and grass: forb ratio (Fig 4f) against snow depth all declined along

233 with the increase in MAP (Figs. 2b and 2d). No significant pattern was observed for

234 forb biomass (Fig 4c and 4d)

235 *3.4. Plant-microbe correlations*

236 We also pooled data for each snow transect and assessed whether changes in

237 snow depth will alter the relationships between plants and microbes across the

238 precipitation gradient. Microbial PLFA biomass correlated positively with plant

239 biomass at the snow-reduced and the ambient snow transects (Figs. 6a and b).

240 However, the regression slopes declined with increasing snow depth, becoming

241 negative at the transect with deepest snow (Figs. 6c-g). The regression slopes were

242 significantly different among the 7 snow transects (Fig. 6h).

243

244 **4. Discussion**

245 Our findings indicate that increasing snow depth stimulated plant and soil

246 microbial growth, and altered their community composition in temperate steppes, but

247   these effects diminished with increasing MAP levels. The stimulation in plant and

248   microbial biomass at the low MAP sites could be due to alleviation of water stress

249   from increased snowmelt (Loik et al., 2013). In Inner Mongolia, plant growth during

250   spring highly relied on snow water, especially in the dry steppes (Peng et al., 2010).

251   The greater sensitivity of plant and microbial productivity to increase in snow depth

252   under lower MAP levels is similar to the more pronounced plant productivity

253   responses to rainfall in the drier regions (Haverd et al., 2017). In addition, we found

254   that soil moisture during summer time was significant higher at transects with deeper

255   snow at five low MAP sites (Fig.1a), implying that the effects of snow on soil

256   moisture could persist until the summer. This could be due to that increasing winter

257   snow amount enhanced soil water holding capacity by increasing litter layer thickness

258   and root density (Loik et al., 2013). Our findings indicated that the amount of winter

259   snow direct or indirectly regulated soil water availability in temperate steppes, and

260   this effect can even last till summer. How winter snow contributes to ecosystem water

261   use efficiency should be assessed in future studies.

262   Plant and microbial communities are expected to respond and adapt to

263   environmental changes in the long-term (Walker and Wardle, 2014). Grassland

264   productivity in Inner Mongolia is co-limited by water and N (Bai et al., 2004; Niu et

265   al., 2010). When water limitation is alleviated via greater snowmelt inputs, plants and

266   microbes would require more nutrients to support their growth. Indeed, we found that

267   increasing snow depth increased the size of plant and microbial N pools at the low

268   MAP sites (Figs. 3a and 3c), but soil N pool did not change at any site (Fig. 3e). In

14

269 this situation, species with higher capacity to acquire nutrients or with higher nutrients

270 use efficiency could become more dominant (Gong et al., 2011; Yang et al., 2011).

271 Indeed, we found that grass biomass, which have higher C:N ratios (Fig. S4) and

272 denser root systems than forbs, increased with greater snow at the low MAP sites. The

273 high fine root biomass of grasses could reduce nutrient leaching during snow melt

274 (Kreyling et al., 2012). Furthermore, the denser root systems could increase AMF

275 infection as we found AMF increased with snow depth (Fig. 4c), which should

276 facilitate nutrient transfer from soils to plants (Hodge et al., 2000; Phillips et al.,

277 2013).

278　　There is a great interest in exploring how environmental change-induced shift of

279 community will alter the pattern of ecological processes (Estiarte et al., 2016; Knapp

280 et al., 2017). Our study showed that increasing snow amount generally stimulated

281 plant and microbial biomass at the low MAP sites, but did not alter them at the high

282 MAP sites. The differential responses to snow amount could alter the relationship

283 between plants and microbes. Indeed, we found that there were positive relationships

284 across sites between plant and microbial biomass at the two shallow snow transects

285 (Fig. 6), which is consistent with previous predictions that plant productivity

286 positively correlates with microbial biomass because plants and microbes trade C and

287 nutrients with each other (Zak et al., 1994). However, with the increase in snow

288 amount, the plant-microbe relationship shifted from positive to negative. Although

289 our study could not fully reveal the mechanisms that govern the relationship between

290 plants and microbes under increasing snow depth, we demonstrated that the current

291   relationships of plants and microbes could not be used to predict their relationship in

292   future climate scenario.

293   Compared to rainfall manipulation studies that have been extensively conducted

294   across biomes, few long-term studies have been done to explore how snow regime

295   changes affect ecosystem processes. Our study, although with a relative narrow range

296   of MAP (225 - 375 mm), provides initial evidence on the importance of snow and

297   rainfall regimes jointly regulating the patterns of plant and microbial processes.

298   Future researches spanning over a wider range of MAP gradient are needed to

299   improve our understanding of the legacy effects of winter snow on ecosystem

300   processes during growing season. In addition, future researches are also needed to

301   improve the techniques to better simulate snow regime changes caused by climate

302   changes. Currently, snow fence is the most widely used method in snow manipulation

303   experiments. However, because snow is redistributed by drifting to create different

304   level of treatments, snow fences could not accurately simulate the changes in the

305   depth and duration of snow cover caused by a real climate change scenario.

306

313

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418

Table 1. Mean annual temperature (MAT), precipitation (MAP), snow depth (measured in 2016), soil properties and the dominant plant species in the 8 sites.

Sites	Coordinates	MAT (^{o}C)	MAP (mm)	Snow depth (cm)	Steppe type	Soil type	Soil C (g kg^{-1})	Soil N (g kg^{-1})	C:N	Soil pH	Dominant plant species
AER Aershan	44.73 N 115.78 E 994 m a.s.l.	1.9	225	10.9±0.76	Typical	Chestnet (China) Kastanozem (FAO)	7.0±0.75	0.8±0.05	8.7±0.5	7.49±0.08	*Aneurotepidimu chinense* *Cleistogenes squarrosa* (Trin.) Keng. *Stipa krylovii* Roshev.
BAY Bayanbaolige	44.05 N 115.94 E 1022 m a.s.l.	2.1	247	6.2±0.58	Typical	Chestnet (China) Kastanozem (FAO)	13.3±0.82	1.5±0.07	9.0±0.5	7.88±0.08	*Aneurotepidimu chinense* *Stipa krylovii* Roshev.
WUL Wulagai	45.68 N 117.46 E 965 m a.s.l.	0.4	280	NA	Typical	Chestnet (China) Haplic Calcisols (FAO)	13.6±0.80	1.3±0.05	10.3±0.5	7.11±0.08	*Aneurotepidimu chinense* *Cleistogenes squarrosa* (Trin.) Keng. *Stipa krylovii* Roshev.
XIL Xilinhot	43.93 N 116.28 E 1230 m a.s.l.	1.5	283	14.7±1.10	Typical	Chestnet (China) Haplic Calcisols (FAO)	15.4±0.68	1.5±0.05	10.0±0.5	7.36±0.08	*Aneurotepidimu chinense* *Carex korshinskyi* *Cleistogenes squarrosa* (Trin.) Keng.
BAI Baiyinxile	43.62 N 116.65 E 1187 m a.s.l.	1.6	301	21.6±0.71	Typical	Chestnet (China) Haplic Calcisols (FAO)	6.6±0.07	0.8±0.07	8.2±0.4	7.15±0.04	*Aneurotepidimu chinense* *Stipa krylovii* Roshev. *Agropyron cristatum* (L.)Gaertn.
DAL Dalinuoer	43.46 N 116.75 E 1257 m a.s.l.	1.5	314	18.8±3.40	Typical	Chestnet (China) Haplic Calcisols (FAO)	7.5±0.06	0.9±0.05	8.6±0.5	7.38±0.08	*Aneurotepidimu chinense* *Artemisia annua* L. *Carex korshinskyi*
HAL Halagaitu	45.83 N 119.43 E 908 m a.s.l.	0.3	368	13.0±0.54	Meadow	Chernozem (China) Chernozem (FAO)	19.2±0.91	1.7±0.05	11.0±0.5	6.86±0.08	*Leymus chinensis* (Trin.) Tzvel. *Carex korshinskyi* *Cleistogenes squarrosa* (Trin.) Keng.
GAN Ganqiaobao	45.69 N 119.52 E 980 m a.s.l.	0.2	375	16.3±0.86	Meadow	Chernozem (China) Chernozem (FAO)	12.9±0.82	1.1±0.09	11.6±0.6	6.95±0.18	*Leymus chinensis* (Trin.) Tzvel. *Agropyron cristatum* (L.)Gaertn. *Cleistogenes squarrosa* (Trin.) Keng.

Figure captions

423   Figure 1. The relationships between snow depth and soil moisture (0-10 cm) under

424   each MAP level (225 mm,247 mm,280 mm,283 mm, 301 mm, 314 mm, 368 mm, and

425   375 mm) (a) and the changes in their slopes with increased levels of MAP (b). Solid

426   lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate

427   non-significant relationships.

428

429   Figure 2. The relationships between snow depth and soil microbial biomass as total

430   PLFAs (a), plant biomass (c) under each MAP level (225 mm,247 mm,280 mm,283

431   mm, 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their slopes with

432   increased levels of MAP (b and d), respectively. Solid lines indicate significant

433   relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

434

435   Figure 3. The relationships between snow depth and the N pools of soil microbial

436   biomass (a), plant biomass (c), and soils (e) under MAP level (225 mm,247 mm,280

437   mm,283 mm, 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their

438   slopes with increased levels of MAP (b, d and f), respectively. Solid lines indicate

439   significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant

440   relationships.

441

442   Figure 4. The relationships between snow depth and fungi to bacteria ratio (a), and the

443   percentage of arbuscular mycorrhizal fungal (AMF.c) under each MAP level (225

21

444 mm,247 mm,280 mm,283 mm, 301 mm, 314 mm, 368 mm, and 375 mm) and the

445 changes in their slopes with increased levels of MAP (b and d), respectively. Solid

446 lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate

447 non-significant relationships.

448

449 Figure 5. The relationships between snow depth and grass biomass (a), forb biomass

450 (c), and grass:forb ratio (e) under each MAP level (225 mm,247 mm,280 mm,283 mm,

451 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their slopes with

452 increased levels of MAP (b, d and f), respectively. Solid lines indicate significant

453 relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

454

455 Figure 6. The relationship between soil total PLFAs versus plant aboveground

456 biomass across sites for each snow depth transect (a-g), and the comparison of the

457 regression slopes among the 7 snow depth transects (h). Solid lines indicate

458 significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant
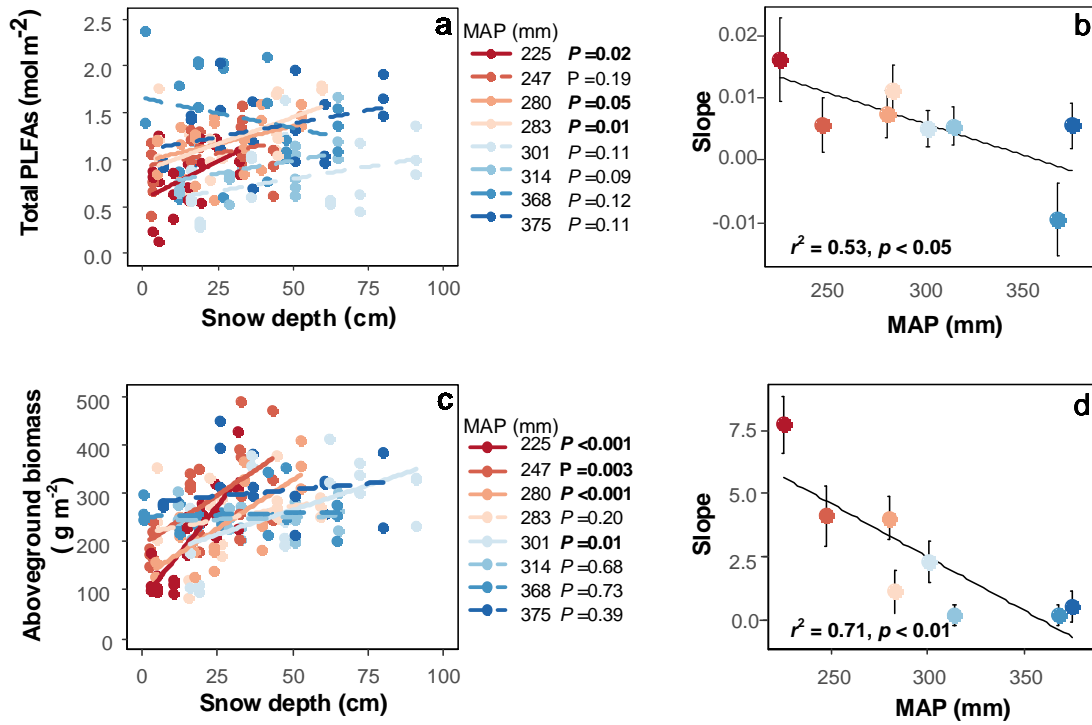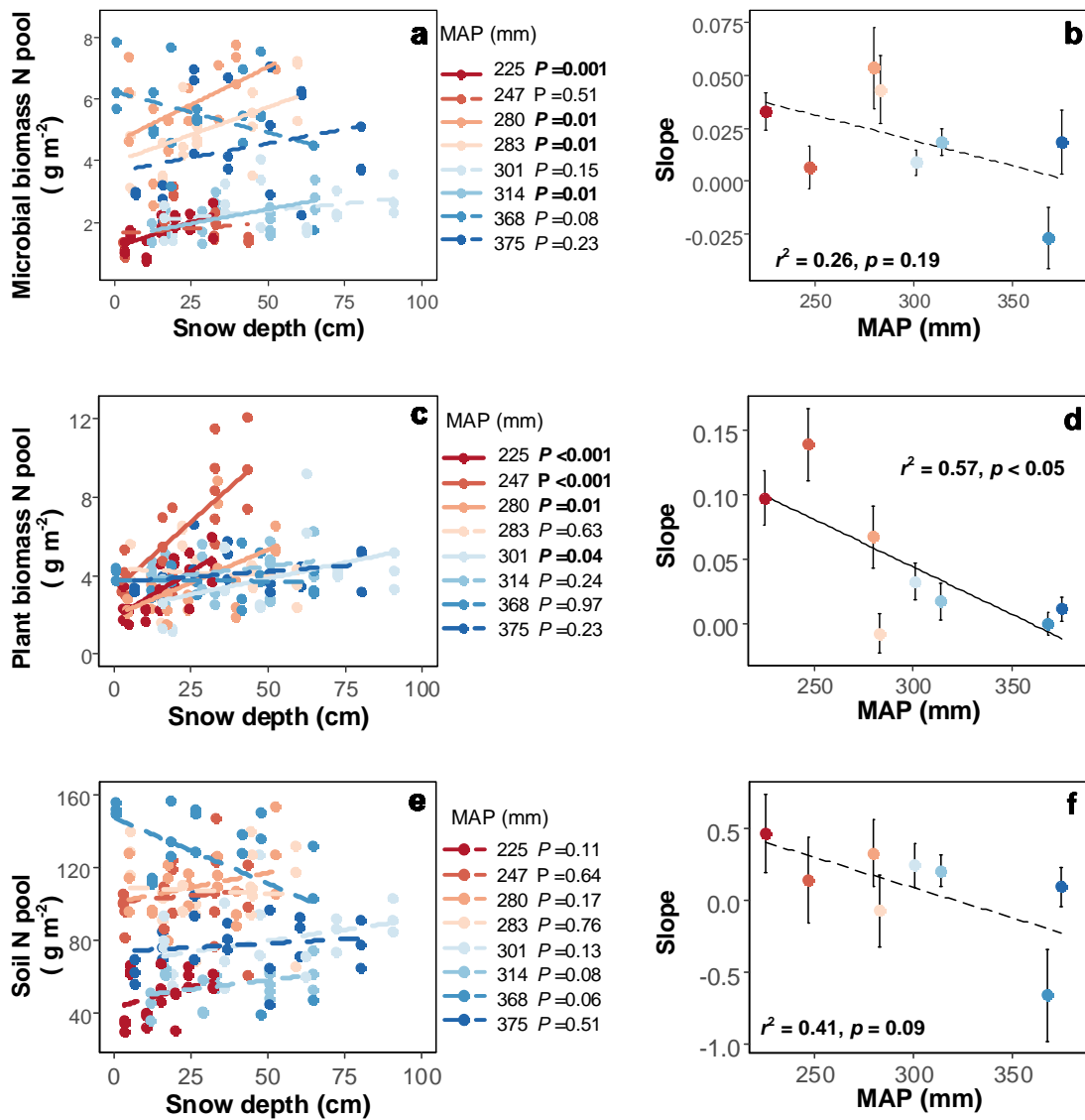
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462   Figure 1.
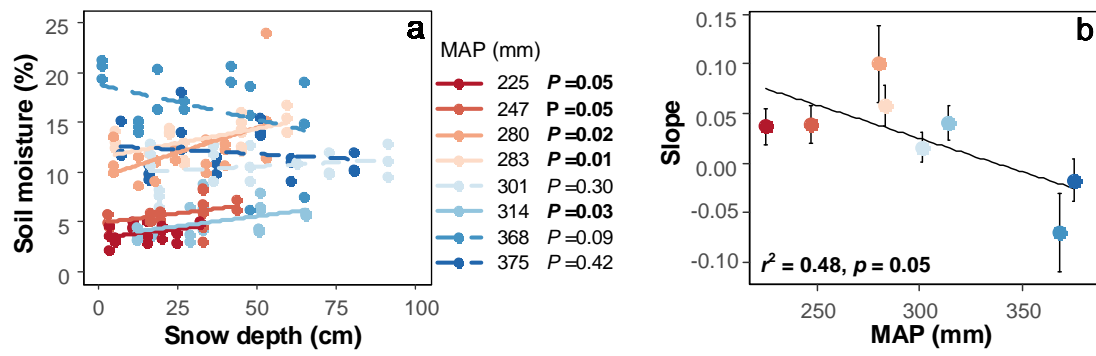
465   Figure 2.
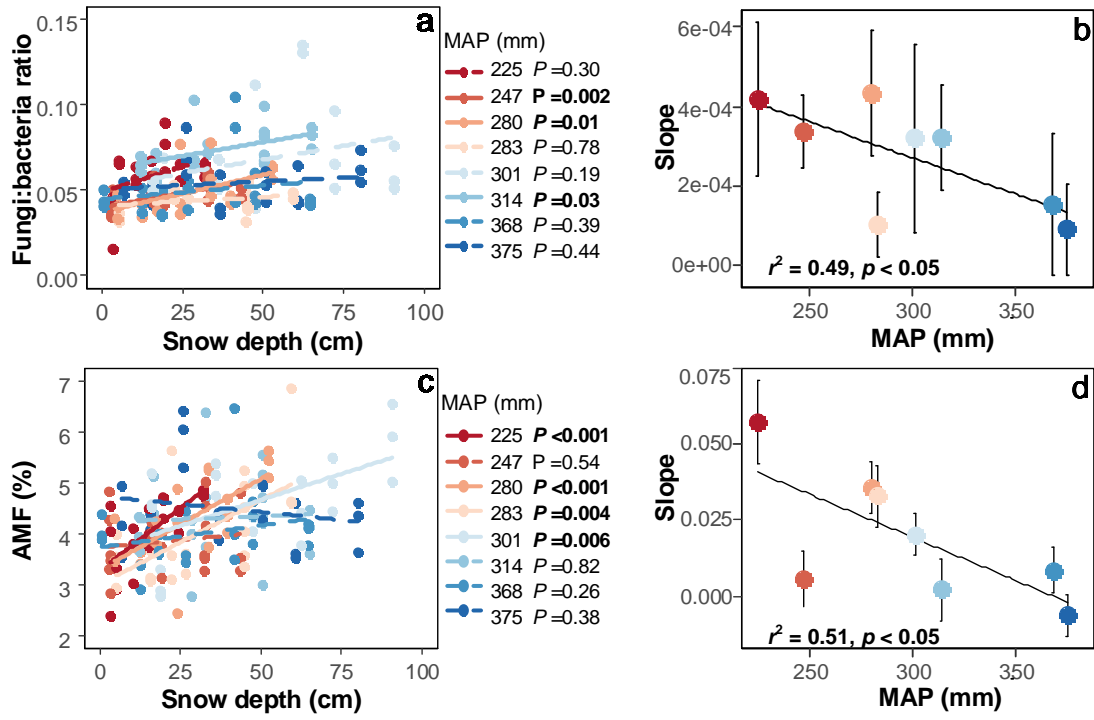
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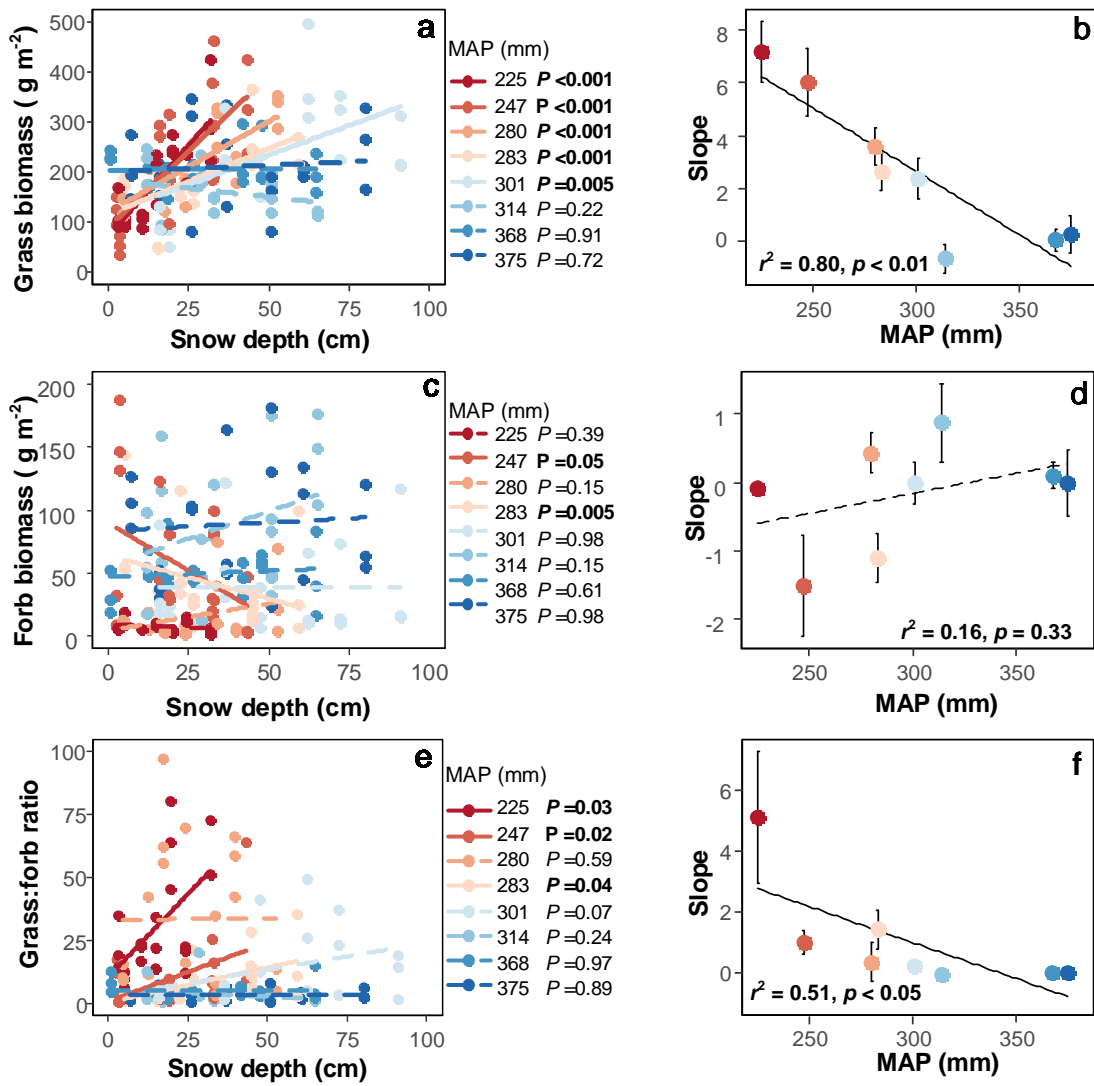469   Figure 3.

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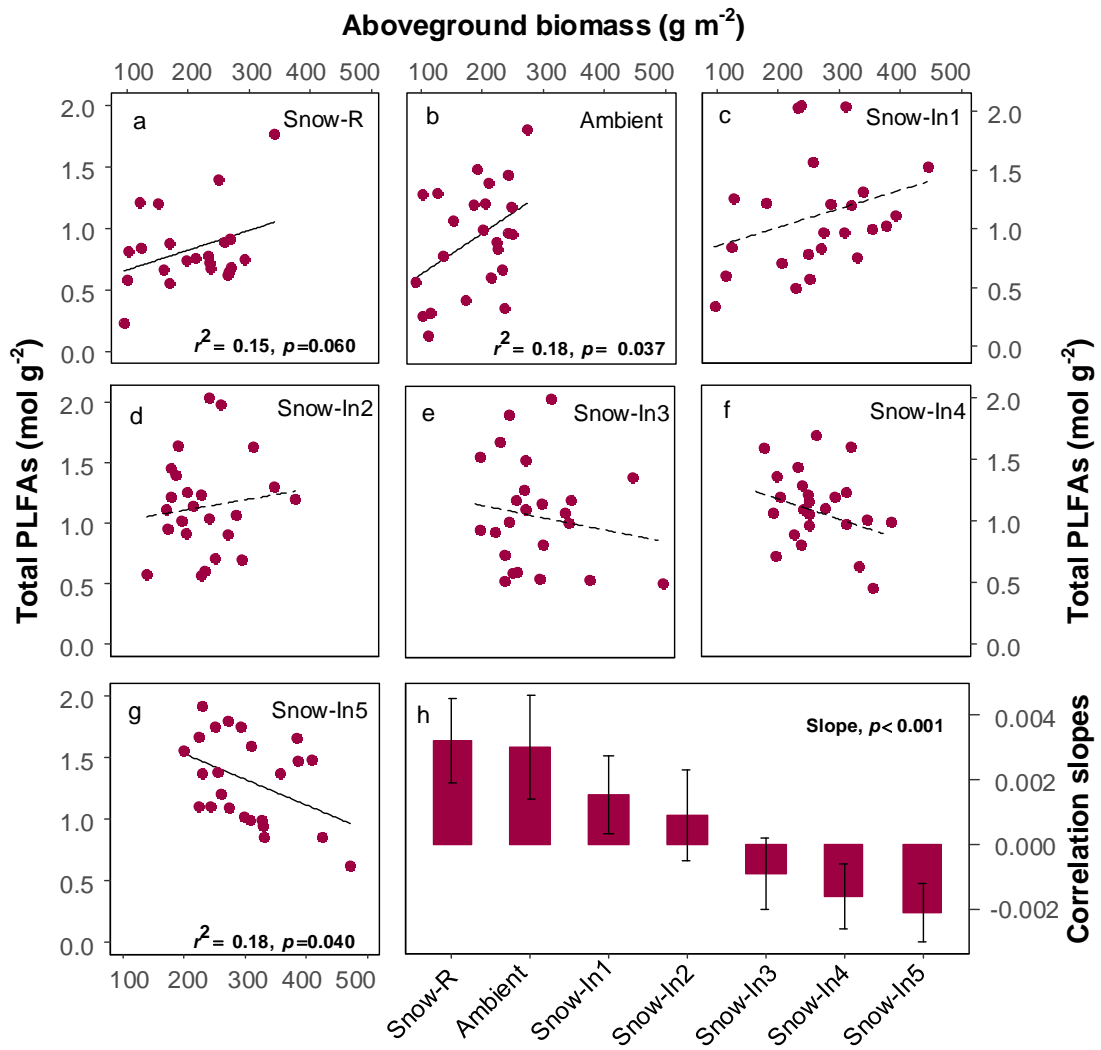472   Figure 4.

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481   **Supporting Information**

482   Table S1. Cross-site mean snow depth level for each transect across all sites.

483

484   Figure S1. Images of snow fences in winter (a) and the growing season (b). Yellow

485   circles represent approximate sampling locations.

486

487   Figure S2. Soil sampling design for each site with sampling locations indicated by

488   circles.

489

490   Figure S3. The correlations between model-predicted and measured snow depth for

491   sites excluding the site of WUL in Feb 2016. Snow depth at site WUL was not

492   measured due to access road closure. For each site, the snow depth was modeled using

493   empirical functions of fence height and the angle between the snow fence and the

494   prevailing wind direction developed by wind tunnel testing. Snow depth at the

495   windward side of the fence was simulated by a 3nd order polynomial function; the

496   leeward side was simulated by a 2nd order polynomial function. Details of the

497   empirical functions were given by Zhao (2012).

498

499   Figure S4. The tissue N concentration and C/N ratio in grasses versus forbs at the

500   regional scale. Differences between forb and grass are statistically significant (P

501   <0.05, t-test).