



Plants with lengthened phenophases increase their dominance under warming in an alpine plant community

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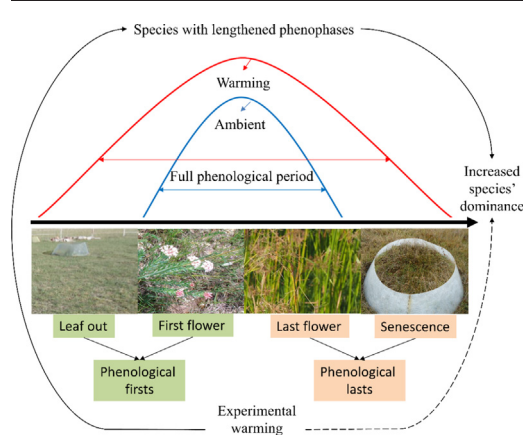
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HIGHLIGHTS

- Warming advanced phenological firsts (leaf-out and first flower dates).
- Warming had variable effects on phenological lasts (leaf senescence and last flower).
- Warming reduced community evenness and differentially affected species dominance.
- Species with lengthened phenological periods under warming increased their dominance.
- Species-specific phenophases may be related to changes in community structure.

GRAPHICAL ABSTRACT



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ABSTRACT

Predicting how shifts in plant phenology affect species dominance remains challenging, because plant phenology and species dominance have been largely investigated independently. Moreover, most phenological research has primarily focused on phenological firsts (leaf-out and first flower dates), leading to a lack of representation of phenological lasts (leaf senescence and last flower) and full phenological periods (growing season length and flower duration). Here, we simultaneously investigated the effects of experimental warming on different phenological events of various species and species dominance in an alpine meadow on the Tibetan Plateau. Warming significantly advanced phenological firsts for most species but had variable effects on phenological lasts. As a result, warming tended to extend species' full phenological periods, although this trend was not significant for all species. Experimental warming reduced community evenness and differentially impacted species dominance. Shifts in full phenological periods, rather than a single shift in phenological firsts or phenological lasts, were associated with changes in species dominance. Species with lengthened full phenological periods under warming increased their dominance. Our results advance the understanding of how altered species-specific phenophases relate to changes in community structure in response to climate change.

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1. Introduction

Studies of shifts in plant phenology as influenced by changes in environmental conditions provide some of the most compelling, but understudied, indications that plant phenology and species dominance may be intimately linked (CaraDonna et al., 2014; Fridley et al., 2016). Changes in plant phenology may determine the biotic and abiotic environmental conditions experienced during each developmental phase (Augspurger, 2013; Forrest and Miller-Rushing, 2010; Parmesan, 2006). For example, species with advanced leaf-out dates may either increase their dominance due to enhanced competitive ability for light and nutrients (Ovaskainen et al., 2013; Rollinson and Kaye, 2012) or reduce their dominance due to increased risk of frost and/or insect damage (Richardson et al., 2018). Shifts in plant phenology could also affect facilitative interactions among species, which could potentially reshape plant community composition (Callaway et al., 2002; Choler et al., 2001). Indeed, the impacts of rising temperatures on both plant phenology and species dominance are well documented (Root et al., 2003; Thuiller et al., 2005). However, investigations into plant phenology and species dominance have largely proceeded independently (Diez et al., 2012; Rudolf, 2019). Thus, accurate predictions of the relationship between plant species-specific phenology and species dominance under climate warming remain challenging.

Current understanding of warming impacts on plant phenology and its linkages with species dominance stems mainly from a focus on 'phenological firsts' (e.g., leaf-out and first flower) (Dunne et al., 2003; Leblans et al., 2017; Sherry et al., 2007). However, several recent studies have shown that 'phenological lasts' (e.g., leaf senescence and last flower) respond asymmetrically or even contrastingly to climate warming as compared to phenological firsts (Dorji et al., 2020; Ensing and Eckert, 2019; Gallinat et al., 2015; Prev y et al., 2019), leading to unpredicted changes in full phenological periods. Consequently, the impacts of shifts in full phenological periods on species dominance remains unresolved. In addition, species have consistently shown divergent phenological responses to climate warming, rather than shifting unidirectionally (Sherry et al., 2007). These highly differentiated species-specific phenological responses to warming may have substantial, but underexplored, impacts on species turnover (Fridley et al., 2016; Kraft et al., 2015; Post et al., 2016; Zohner et al., 2018). Therefore, it is critical to integrate impacts of species-specific phenological firsts and phenological lasts to better understand phenological responses to

climate warming and the consequences this may have for plant species turnover.

Plant phenology is highly sensitive to climate warming and finely tuned to the changing environment (Cleland et al., 2007; Nicotra et al., 2010; Parmesan, 2006). However, the underlying factors associated with shifts in species phenology in response to climate warming remain unclear (Chmura et al., 2019; Petitpierre et al., 2012; Tang et al., 2016), thereby hindering an improved understanding of the potential links between plant phenology and species dominance (Forrest and Miller-Rushing, 2010; Godoy et al., 2018). Rising temperatures could advance the leaf-out date of some species due to faster accumulation of growing-degree days (Cayton et al., 2015; Marchin et al., 2015; Suonan et al., 2017), or could delay leaf-out for other species due to delayed or even failed fulfillment of winter chilling requirements (Guo et al., 2019). Apart from the direct effects of rising temperatures, changes in soil moisture and soil nutrient availability could also significantly affect plant phenology (Estiarte and Pe uelas, 2015; Gill et al., 2015; Peaucelle et al., 2019). For example, reductions in soil moisture have been found to delay reproductive phenology (Dorji et al., 2013; Sherry et al., 2007) or reduce flowering duration (de Valpine and Harte, 2001), whereas higher soil moisture may lengthen flowering duration and seed production (Dorji et al., 2020). Furthermore, phenological firsts and lasts are likely controlled by different environmental factors even for the same species (Bahuguna and Jagadish, 2015; Ernakovich et al., 2014; Gill et al., 2015), further heightening the challenge of predicting the impacts of warming on species-specific phenology, species dominance, and ecosystem structure.

The Tibetan Plateau is warming at a faster rate than the global average due to its high elevation (Deutsch et al., 2008; You et al., 2016). To increase knowledge of the links between species phenology and dominance, a three-year field-manipulative warming experiment using open top chambers (OTCs) was conducted in an alpine meadow grassland on the Tibetan Plateau. To assess and compare species-specific responses of plant phenology and species dominance to warming, eight common plant species were monitored across three growing seasons. These were the only species observed in all experimental plots at the study site. Two key questions motivated our work: (1) what are the species-level impacts of warming on plant phenology? and (2) do species-level impacts of warming on plant phenology scale up to affect species dominance?

2. Materials and methods

2.1. Study site

A manipulative warming experiment was performed in the field at the Haipei Grassland Ecological Monitoring Station (Xihai Town, Qinghai province, 100°51'E, 36°57'N, 3140 m a.s.l.). The study site has been used as a winter grazing grassland since 1976, with moderate grazing intensity during the non-growing season. Based on meteorological records from 1995 to 2013, the mean annual precipitation is 408 mm, and the mean annual temperature is 1.3 °C (Chen et al., 2018; Chen et al., 2019). Relatively high air temperatures and rainfall occur from mid-April to mid-October (growing season), while low rainfall (< 5% of annual) and low temperatures occur during the non-growing season. Additional long-term, detailed information about the study site can be found in Guo et al. (2018) and Li et al. (2019) (Fig. S1). The dominant species are *Stipa krylovii*, *Poa crymophila*, *Koeleria cristata*, *Medicago ruthenica*, and *Kobresia humilis* (Fig. S1 and Table S1).

2.2. Experimental design

The study site (200 m × 400 m) was fenced off for three years before the initiation of experimental warming to exclude disturbance by herbivores. All mammalian herbivores were completely removed for the duration of the experiment. In August 2010, the study site was divided into six blocks with 10-m buffer zones between the edges of adjacent blocks. Each block was then divided into two plots (5 m × 10 m), one of which was randomly selected for experimental warming. In each of the six experimental warming plots, one OTC (with a base area of 2.1 m²) was installed to achieve a passively warmed environment (Fig. S1). All plots, especially the paired ambient-warming plots, were carefully selected to minimize vegetation heterogeneity. Protocols for the OTCs used in this study are described in detail for previous studies at this site (Chen et al., 2017a; Chen et al., 2017b), as well as at other sites (Baruah et al., 2017; Dorji et al., 2013).

2.3. Measurements

The main objective of this study was to investigate species' phenological responses to warming, as well as their shifts in dominance. To meet this objective, eight species were selected and monitored across three growing seasons. These species represented all plant functional groups at the study site (three grasses, one sedge, one legume, three forbs). Based on our preliminary field investigations, those eight species were the only common species observed in all experimental plots at the study site (Fig. S1 and Table S1). The total aboveground biomass of these eight species comprised >85% of the total community biomass, and the total cover of these eight species occupied >90% of the total community cover (Table S1) (Chen et al., 2017a).

To avoid edge effects caused by the OTCs, a quadrat (0.5 m × 0.5 m) was placed in the center of each OTC and of each ambient plot for all phenology and dominance measurements. To reduce the heterogeneity and uncertainties associated with variations among individual plants, six individuals of each focal species were randomly selected and marked in each quadrat after the first leaf-out. These marked individuals were monitored every 2 to 4 days during the whole growing season. Phenological observations of each species in each quadrat were calculated as the mean of the marked individuals, and individuals were not replaced if they died during the growing season. The first flower dates were documented when flower buds had broken and anthers/stigmas were visible for the marked plants (Suonan et al., 2017). The last flower dates were documented when all petals had dropped off (CaraDonna et al., 2014; Iler et al., 2013). Leaf senescence was defined as >50% of a plant's leaves having changed color (Marchin et al., 2015). The duration of the growing season was calculated as the difference between leaf-out and leaf senescence dates, and the length of flower duration was calculated

as the difference between first and last flower dates. Phenological observations for each species in each quadrat were recorded from 2011 to 2013. All phenological observations were transformed into Julian days for further analysis.

Height, abundance, and cover for each species within the quadrats in ambient and warming plots were recorded during the peak biomass period, which was in mid-August for all species except *Gentiana squarrosa*, which peaks in mid-July. Height for each species was calculated as the mean of the marked individuals in each quadrat. Species abundance was calculated as the total number of individuals of each species within the quadrat. A grid frame (0.5 m × 0.5 m) with 25 grid cells (0.1 m × 0.1 m) was placed in each quadrat to help estimate the total areal cover of each focal species in each plot (Damgaard, 2014; Penuelas et al., 2004).

Soil temperature during the whole year and soil volumetric moisture during the growing season (frozen during the non-growing season) for each plot were documented using HOBO data loggers at a depth of 10 cm (Onset Computer Company, USA) (Chen et al., 2016). For each plot, three soil cores (0–10 cm) adjacent to each quadrat were collected and combined to make a composite soil sample in mid-August. Soil inorganic nitrogen (N) content was measured from water solutes extracted from the soil samples using a flow injection auto-analyzer (FIAstar 5000 Analyzer, Denmark).

2.4. Data analyses

All data analysis and plotting was performed in R 3.5.1 (R Core Team, 2019). Relative height (RH), relative abundance (RA) and relative cover (RC) were calculated by normalizing the species-specific absolute height, abundance and cover against the total height, abundance and cover for the eight focal species in each plot. Simpson's evenness index (*E*) (Simpson, 1949) was adopted to evaluate community evenness. Species' importance value (IV) was used to assess species-specific dominance, which is quantified as the mean of relative height, relative abundance, and relative coverage (Whittaker, 1965).

$$RH = \frac{\text{Height of a species}}{\text{Height of all species}} \times 100\% \quad (1)$$

$$RA = \frac{\text{Abundance of a species}}{\text{Abundance of all species}} \times 100\% \quad (2)$$

$$RC = \frac{\text{Coverage of a species}}{\text{Coverage of all species}} \times 100\% \quad (3)$$

$$E = D' / S \quad (4)$$

$$D' = 1 / \sum_{i=1}^S RA_i^2 \quad (5)$$

$$IV = \frac{RH + RA + RC}{3} \quad (6)$$

where *D'* is Simpson's reciprocal index of diversity (Simpson, 1949), *S* is the total number of species included in this study (eight) and *RA_i* is the relative abundance for each species in each plot. Experimental warming-induced changes in each variable were calculated from the paired plots within each block in each year:

$$\text{Warming induced changes} = \frac{W_v - A_v}{A_v} \times 100\% \quad (7)$$

where *W_v* and *A_v* were observed values from warming and ambient treatments, respectively.

Linear mixed-effects (LME) models were conducted using the "lme" function in "nlme" package (Zuur et al., 2009) to assess the effects of

warming on soil temperature, soil moisture, soil inorganic N, species-specific phenology, Simpson's evenness index and species dominance. All of these variables were observed from 2011 to 2013. In the LME models, we set warming, year, and their interactions as fixed effects and plot nested within block as a random effect. We assessed the impacts of warming on plant phenophases and species dominance separately for each species. Residuals and residual variances for all variables satisfied the assumptions of normality and homogeneity.

Linear mixed effects models were also used to explore the relationship between shifts in species-specific plant phenology and the corresponding changes in species dominance. The R-squared value of the LME models was calculated by using the "r.squaredGLMM" function in the "MuMIn" package. Experiment block, year, and species were considered as random effects when examining the relationships between plant phenology and species dominance in LME models. To explore the potential factors affecting species phenology and dominance, redundancy analysis (RDA) was conducted with the "vegan" package, with treatment (ambient and warm) and environmental factors (soil temperature, soil moisture, and soil inorganic N) as explanatory variables. The importance of each explanatory variable was calculated by forward selection with 999 unrestricted permutations. The RDAs were performed separately for each plant phenological event and for species dominance.

2.5. Data availability

The data associated with this paper are available from the online supplementary file and from figshare (<https://figshare.com/s/4e7061a904f66d1a4504>).

3. Results

3.1. Climate and soil N availability

The total annual precipitation was 447, 472, and 454 mm for 2011, 2012, and 2013, respectively. The mean annual air temperature was 1.5, 1.4, and 2.0 °C, and the mean soil temperature was 5.6, 5.3, and

6.0 °C for 2011, 2012, and 2013, respectively (Fig. S2). Averaged across the three consecutive years, experimental warming by OTCs significantly increased upper layer (0–10 cm) soil temperature by 1.1 ± 0.1 °C (mean \pm standard error for six replicates; same below), increased soil inorganic N by $10.9 \pm 1.0\%$, and significantly decreased soil volumetric moisture by $2.8 \pm 0.1\%$ (Figs. 1 and S3). The interactive effects of warming and year on soil temperature and soil inorganic N were not statistically significant (Table S2). However, the warming effect on soil volumetric moisture differed significantly among years, with reductions in soil moisture of $4.8 \pm 0.2\%$ in 2011, $2.6 \pm 0.1\%$ in 2012, and $1.2 \pm 0.2\%$ in 2013 (Table S2).

3.2. Leaf-out, leaf senescence and growing season length

The effects of warming on leaf-out, leaf senescence, and growing season length differed significantly among species (Table S3 and Fig. S4). Warming significantly advanced leaf-out dates for six of the eight species, by 4.7 ± 0.6 to 7.4 ± 0.5 days, but had no effect on the leaf-out date of *Artemisia scoparia* and *Heteropappus altaicus* (Table 1 and Fig. 2). Warming significantly delayed leaf senescence for *Kobresia humilis* (3.2 ± 1.0 days), *Artemisia scoparia* (4.2 ± 0.5 days), and *Heteropappus altaicus* (5.7 ± 0.5 days), while warming advanced leaf senescence for *Gentiana squarrosa* by 6.7 ± 0.7 days. Warming significantly extended growing season length by 5.4 ± 1.1 to 9.0 ± 1.1 days for five of the eight species, while warming did not affect growing season length for *Artemisia scoparia*, *Heteropappus altaicus*, and *Gentiana squarrosa*.

When soil temperature, soil moisture, soil inorganic N, and the warming treatment were used to constrain the ordination of species-specific phenology with RDA, the full RDA model accounted for 57% of variation in leaf-out, 70% in leaf senescence, and 66% in growing season length (Fig. S5).

3.3. First flower, last flower and flower duration

Warming significantly advanced first flower dates for six of the eight species, by 3.8 ± 0.6 to 7.3 ± 0.5 days, while warming significantly

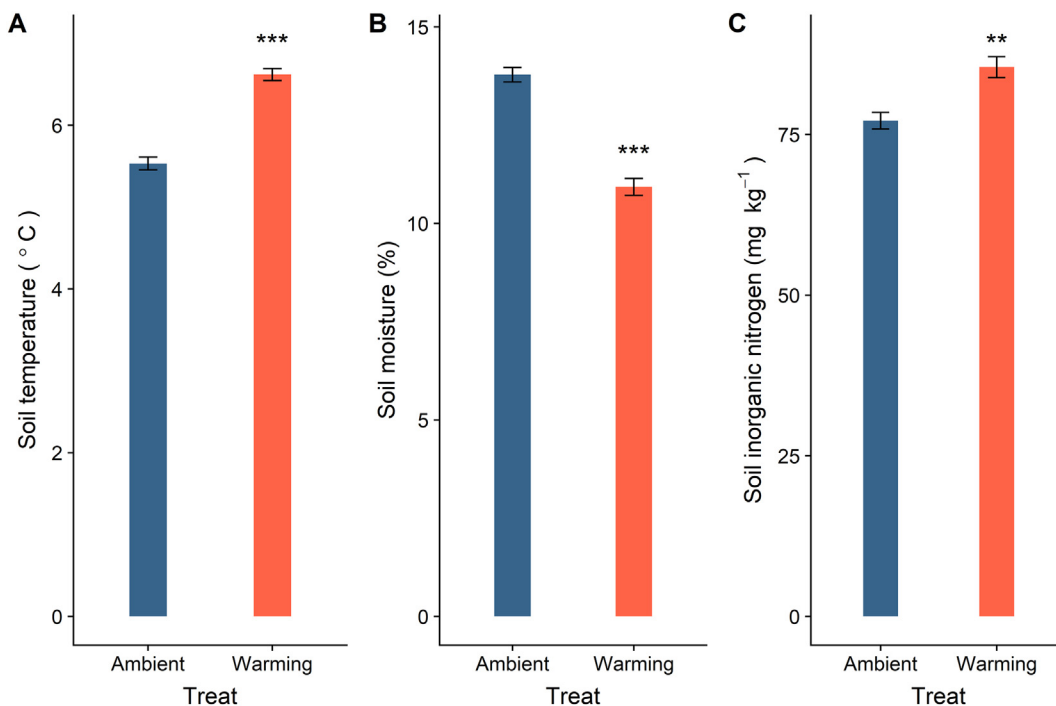


Fig. 1. Effects of the warming treatment on (A) soil temperature, (B) soil volumetric moisture and (C) soil inorganic nitrogen content. Asterisks indicate significant difference at $P < 0.01$ (**) and $P < 0.001$ (***). Values are mean \pm standard errors across years.

Table 1

F values for linear mixed-effects models of warming (W), year (Y) and their interactive (W × Y) effects on plant phenology for each species.

Species	Treat-ment	numDF	denDF	Leaf out	Leaf senescence	Growing days	First flower	Last flower	Flower duration
Sk	W	1	5	22.78**	4.29	24.54**	28.55**	2.75	31.34**
	Y	2	20	0.36	8.79**	5.09*	0.83	0.51	1.42
	W * Y	2	20	0.16	0.25	0.50	0.20	0.05	0.19
Pc	W	1	5	61.87***	0.75	18.11**	25.49**	7.39*	28.89**
	Y	2	20	0.30	1.03	1.07	1.61	2.14	1.87
	W * Y	2	20	0.04	0.07	0.10	0.41	0.27	0.62
Kc	W	1	5	21.68**	0.03	9.23*	10.28*	15.22*	52.03***
	Y	2	20	0.66	0.79	0.75	1.40	4.79*	4.42*
	W * Y	2	20	0.66	0.04	0.48	0.86	0.38	2.59
Mr	W	1	5	27.32**	0.23	14.92*	41.53**	0.14	30.05**
	Y	2	20	2.69	0.35	1.73	2.90	1.89	3.13
	W * Y	2	20	0.36	0.07	0.05	0.22	0.33	0.56
Kh	W	1	5	25.67**	9.89*	42.02**	45.98**	0.20	12.70*
	Y	2	20	7.09**	12.44***	1.78	5.43*	1.48	4.64*
	W * Y	2	20	0.10	0.44	0.17	0.03	0.60	0.36
As	W	1	5	0.75	11.65*	2.01	4.50	16.60**	1.14
	Y	2	20	0.57	0.78	1.05	1.26	0.68	0.28
	W * Y	2	20	0.12	0.10	0.16	0.18	0.04	0.03
Ha	W	1	5	3.96	32.63**	5.22	8.97*	39.56**	2.03
	Y	2	20	5.18*	0.39	3.49*	2.20	12.58***	2.73
	W * Y	2	20	0.32	0.34	0.53	0.14	0.47	0.03
Gs	W	1	5	41.92**	34.75**	0.26	47.43**	39.98**	0.06
	Y	2	20	3.04	5.69*	0.45	5.27*	0.24	2.08
	W * Y	2	20	0.12	1.42	0.40	0.92	1.61	0.22

numDF: numerator degrees of freedom. denDF: denominator degrees of freedom. Linear mixed-effects models were conducted separately for each species for each phenological observation. Warming (W), year (Y) and their interaction (W * Y) were considered as fixed factors, while plot nested within block was considered as a random factor. Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Sk: *Stipa krylovii*. Pc: *Poa crymophila*. Kc: *Koeleria cristata*. Mr.: *Medicago ruthenica*. Kh: *Kobresia humilis*. As: *Artemisia scoparia*. Ha: *Heteropappus altaicus*. Gs: *Gentiana squarrosa*.

delayed first flowering by 3.9 ± 0.9 days for *Heteropappus altaicus* (Table 1 and Figs. 3 and S4). Warming significantly delayed last flower dates for *Poa crymophila* (3.0 ± 0.9 days), *Koeleria cristata* (3.7 ± 0.4 days), *Artemisia scoparia* (4.8 ± 0.7 days) and *Heteropappus altaicus* (6.3 ± 0.4 days), while last flower was significantly advanced for *Gentiana squarrosa* by 7.7 ± 0.8 days. Warming significantly lengthened flower duration for five of the eight species, by 5.0 ± 1.1 to 8.8 ± 1.0 days, while it did not significantly affect flower duration for *Artemisia scoparia*, *Heteropappus altaicus*, and *Gentiana squarrosa* (Fig. 3).

The RDA analysis showed that soil temperature and soil moisture played more important roles than soil inorganic N in driving flowering

phenology. Soil temperature and soil moisture together explained 54% of the variation in first flower, 64% in last flower, and 62% in flower duration, respectively (Fig. S6).

3.4. Plant species dominance

Warming significantly decreased plant community evenness when calculated for the eight common species, and it had differential impacts on species dominance (Fig. 4, and Tables S4 and S5). Specifically, warming significantly increased the dominance of *Stipa krylovii*, *Poa crymophila*, *Koeleria cristata*, *Medicago ruthenica* and *Kobresia humilis*,

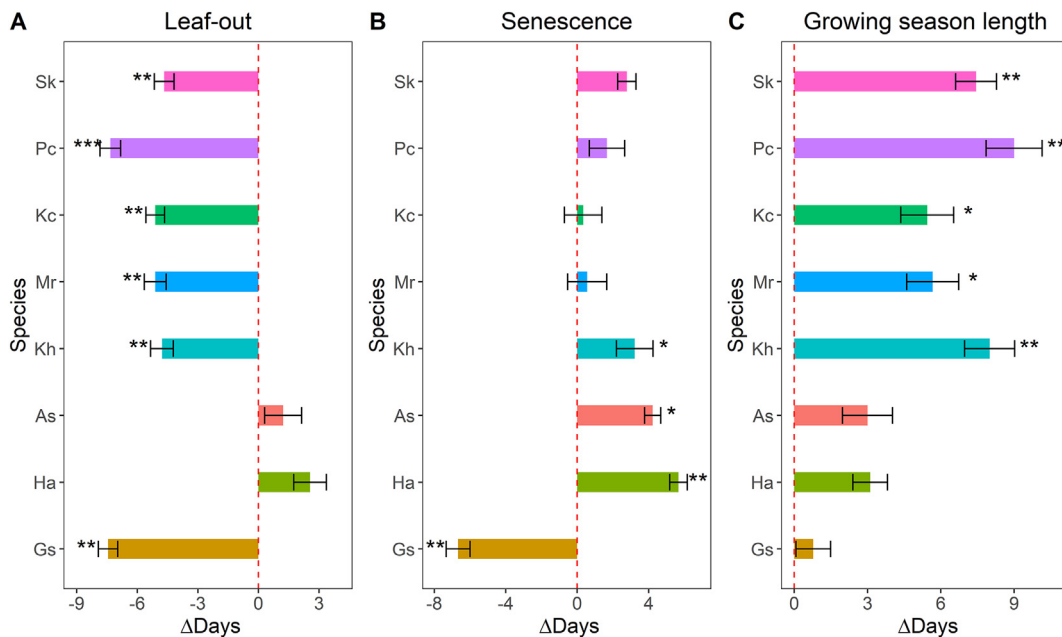


Fig. 2. Effects of warming on (A) leaf-out, (B) leaf senescence and (C) growing season length for each species. Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values show mean \pm standard errors. Sk: *Stipa krylovii*. Pc: *Poa crymophila*. Kc: *Koeleria cristata*. Mr.: *Medicago ruthenica*. Kh: *Kobresia humilis*. As: *Artemisia scoparia*. Ha: *Heteropappus altaicus*. Gs: *Gentiana squarrosa*.

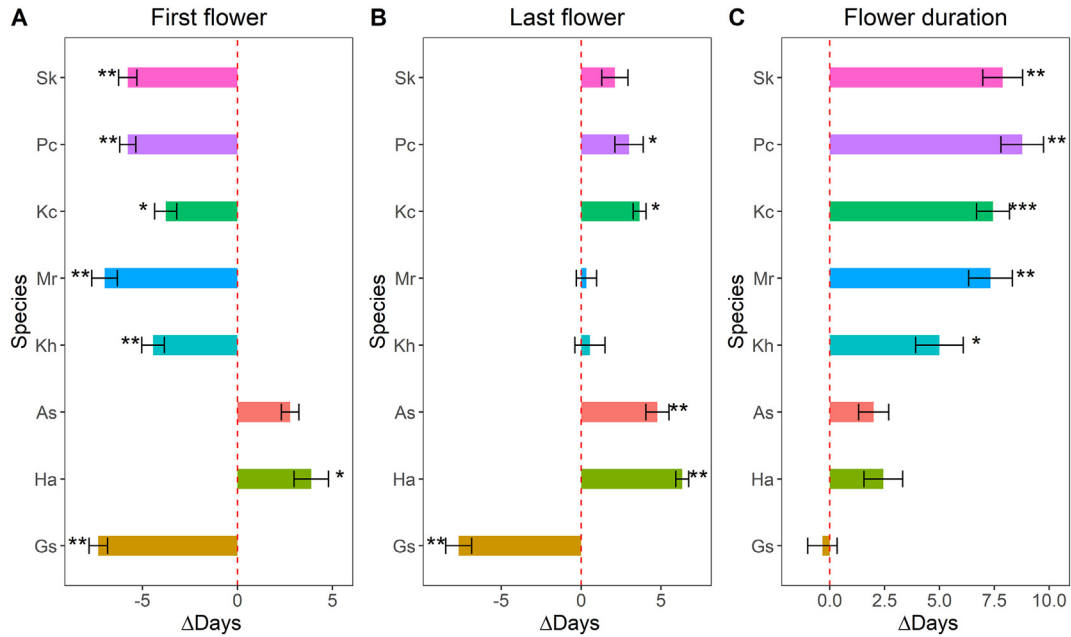


Fig. 3. Effects of warming on (A) first flower, (B) last flower and (C) flower duration for each species. Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values show mean \pm standard errors. Sk: *Stipa krylovii*. Pc: *Poa crymophila*. Kc: *Koeleria cristata*. Mr.: *Medicago ruthenica*. Kh: *Kobresia humilis*. As: *Artemisia scoparia*. Ha: *Heteropappus altaicus*. Gs: *Gentiana squarrosa*.

while warming decreased the dominance of *Artemisia scoparia*, *Heteropappus altaicus* and *Gentiana squarrosa*. The five species with increased dominance under warming exhibited negative relationships between community evenness and dominance (Fig. S7). The RDA analysis with treatment and environmental variables accounted for 41% of the variation in species dominance (Fig. S8). In general, species with a greater extension in growing season length and flower duration tended to increase their dominance, at the expense of community evenness (Fig. 5). Specifically, changes in growing season length and flower duration explained 27% and 22% of the variance in changes in species dominance, respectively. By contrast, there was no relationship between changes in phenological firsts or phenological lasts with changes in species dominance (Fig. 5).

4. Discussion

Our results support the emerging trend that species-specific phenological firsts (leaf-out and first flower) and lasts (leaf senescence and last flower) are differentially sensitive to climate warming (Figs. 2-3) (Dorji et al., 2020). Some studies have reported no relation between shifts in plant phenology and community properties, but such studies have focused solely on linking phenological firsts with community dynamics (Block et al., 2019; McLean et al., 2016). Our results advance understanding of the relationship between plant phenology and community composition by linking full phenological periods (growing season length and flower duration) with species dominance (i.e., the average of species relative height, abundance and cover). These processes

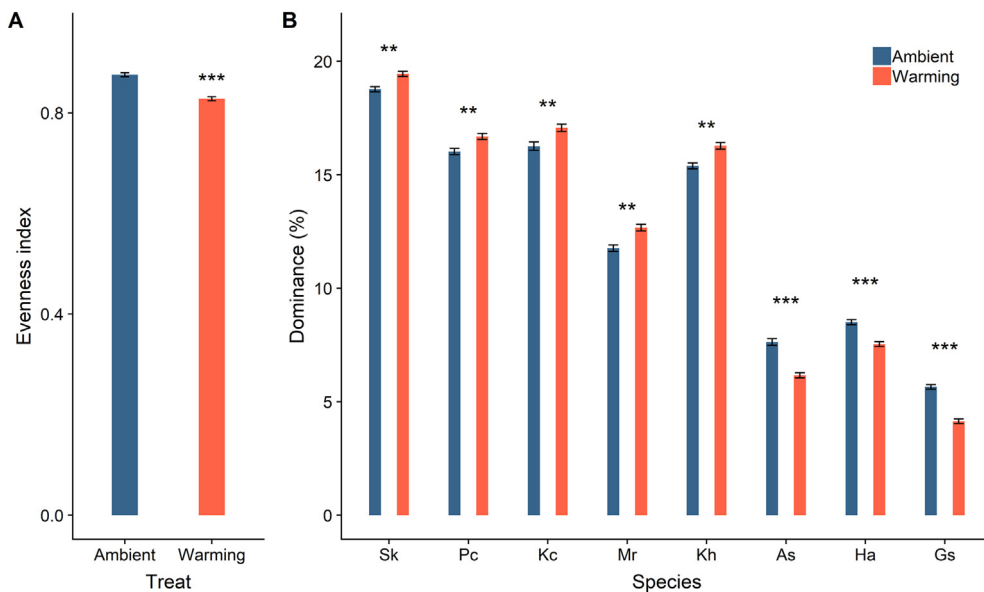


Fig. 4. Warming effects on (A) Simpson evenness index and (B) species dominance. Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values show mean \pm standard errors. Dominance was calculated as the mean of relative height, relative abundance, and relative coverage; see the methods section for detailed information. Sk: *Stipa krylovii*. Pc: *Poa crymophila*. Kc: *Koeleria cristata*. Mr.: *Medicago ruthenica*. Kh: *Kobresia humilis*. As: *Artemisia scoparia*. Ha: *Heteropappus altaicus*. Gs: *Gentiana squarrosa*.

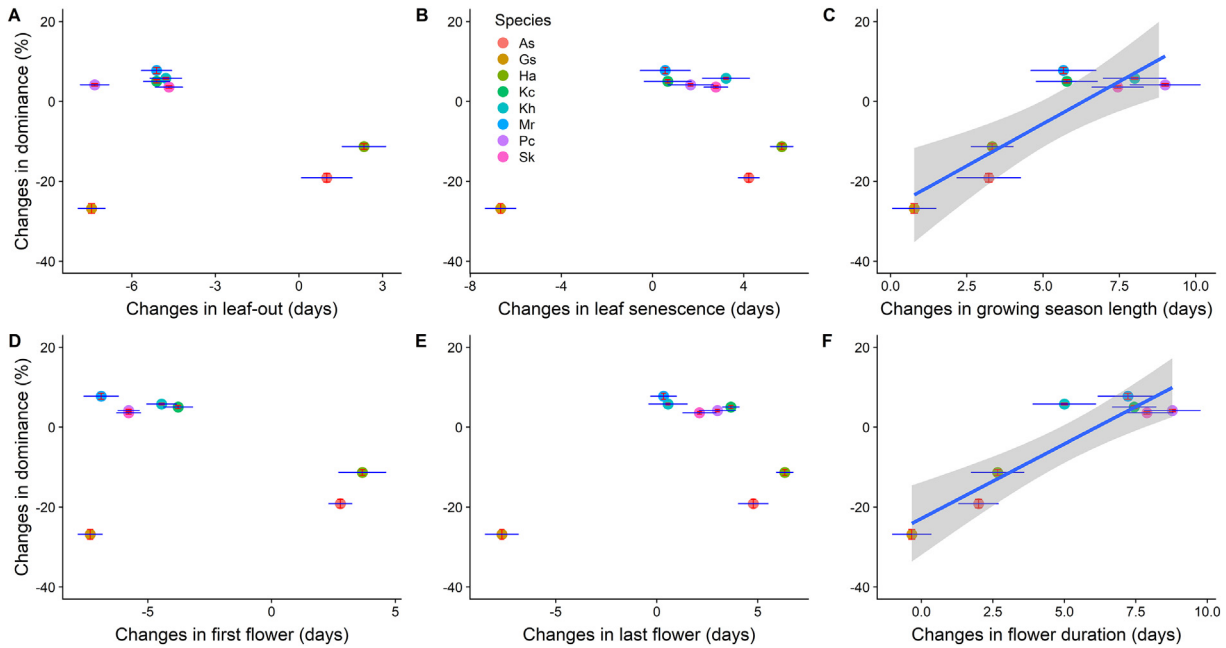


Fig. 5. Relationships between changes in species dominance and shifts in species (A) leaf-out, (B) leaf senescence, (C) growing season length, (D) first flower, (E) last flower and (F) flower duration. Positive relationships were observed between changes in species dominance and flower duration ($Y = 0.037 X - 0.228, R^2 = 0.832, df = 6, F = 35.730, P = 0.001$) and growing season length ($Y = 0.042 X - 0.267, R^2 = 0.784, df = 6, F = 21.800, P = 0.003$). The solid lines denote significant model slopes of the linear mixed effects models, and shaded areas show the 95% CI for slopes. Data is averaged by species across the three years. Sk: *Stipa krylovii*. Pc: *Poa crymophila*. Kc: *Koeleria cristata*. Mr.: *Medicago ruthenica*. Kh: *Kobresia humilis*. As: *Artemisia scoparia*. Ha: *Heteropappus altaicus*. Gs: *Gentiana squarrosa*.

and their linkages have rarely been explored. Importantly, we find that shifts in full phenological periods, rather than single phenological firsts or phenological lasts, are associated with changes in species dominance (Fig. 5). Although longer-duration studies are needed to fully assess long-lived species turnover under warming in this alpine community, our results stress that (1) the sole observation of phenological firsts provides an incomplete picture for assessing and predicting response of plant phenology and plant species turnover to climate warming, and (2) shifts in full phenological periods provide useful indicators of how climatic warming may affect species dominance, and by extension, community structure.

4.1. Shifts in plant phenology are associated with species dominance

Across the eight most abundant species in our study area, shifts in full phenological periods were significant predictors of changes in species dominance (Fig. 5). Specifically, species that increased their relative dominance under warming experienced significantly longer full phenological periods. On the other hand, for species that experienced a decrease in dominance under warming, all underwent a directional shift in their phenology (two forbs, *A. scoparia* and *H. altaicus*, shifted later, and one forb, *G. squarrosa*, shifted earlier), without significantly altering their growing season length or flower duration (Figs. 2, 3 and 5).

We propose three non-exclusive hypotheses for how shifts in species-specific plant phenology may impact species dominance. First, a relatively longer full phenological period could mitigate potential phenological mismatches between plant growth and optimal environmental conditions (e.g. temperature and moisture) (Augspurger, 2013; Wheeler et al., 2015). Species with relatively longer growing season lengths and flower durations can better capture favorable growing conditions, potentially increasing their competitive advantages over others (CaraDonna et al., 2014; Ernakovich et al., 2014). For example, shifts in flower duration could affect plant reproduction and plant community composition if these shifts caused significant mismatches with the optimal climate conditions for seed maturation (Forrest, 2015; Høye et al., 2013; Rafferty and Ives, 2011). However, if a longer growing season or flower duration results solely from a unidirectional advance or delay

in either phenological firsts or phenological lasts, this could leave those species vulnerable to adverse conditions at the shoulders of the growing season. For example, substantial advancement of leaf-out and first flower dates of *Gentiana squarrosa* were not accompanied by increased dominance (Figs. 2-4). One explanation might be that a large advance of phenological firsts could increase the likelihood of exposure to spring frost damage or herbivory by spring-active insects (Richardson et al., 2018), which could decrease species dominance in the community.

Second, lengthening of the growing season or flower duration could help species avoid potential trophic mismatches (CaraDonna et al., 2014; Fridley et al., 2016; Renner and Zohner, 2018). For mutualistic plant-animal relationships, for example, phenological mismatches between flowers and pollinators could have crucial effects on plant community composition through reduced plant fitness over time (Elzinga et al., 2007; Schermer et al., 2020; Schmidt et al., 2016). A similar study conducted in three natural deciduous forests in northern Japan showed that species with shortened flower duration could experience pollination failure, leading to lower seed production and consequently reduced dominance within the community (Kudo and Ida, 2013). Conversely, a lengthened growing season or flower duration could help plants remain in sync with their pollinators, despite an advance or delay in the pollinators' own phenology.

Third, a longer growing season would allow for longer periods of photosynthetic activity, nutrient acquisition, and therefore more resource allocation to growth, fecundity, or survival mechanisms, which could eventually increase the relative cover and abundance of a plant species (Ernakovich et al., 2014; Fridley et al., 2016). Similarly, species with prolonged flower duration could support increased seed production and reproductive success, which could also lead to increased abundance (CaraDonna et al., 2014; Craufurd and Wheeler, 2009). Discussion on which mechanisms is more important than others is interesting but a little beyond the scope of this study, for example, because we could not evaluate the pollinators with the current experiment design.

Our results suggest that ongoing climate warming will reshape community structure towards dominance by species with lengthened phenophases (Fig. 5). The species we monitored comprised

most of the plant community biomass (> 85%) and cover (> 90%) under ambient conditions (Table S1). The most dominant of these species increased their dominance further under warming treatments (Fig. 4), which suggests that shifts in plant phenology and concomitant increases in resource use by dominant species could cause gradual biodiversity losses via losses of non-dominant and/or rare species, thereby moving the community towards biotic homogenization (Dawson et al., 2011; McKinney and Lockwood, 1999; Savage and Vellend, 2015; Smith and Knapp, 2003). Previous work in this system and elsewhere on the Tibetan Plateau has shown that warming by OTCs can cause large and rapid species loss (Dorji et al., 2018; Klein et al., 2004; Yang et al., 2018). Our results suggest that shifting dominance could be a mechanism of species loss because community evenness was negatively related to the dominance value of the five most-dominant species (Fig. S7). Such changes in species dominance could also be related to competitive or facilitative interactions between species (Alexander and Levine, 2019; Callaway et al., 2002; Choler et al., 2001). For example, shared mycorrhizal networks among the dominant species could enable them to share resources and outcompete the less-dominant forbs (Li et al., 2018). In addition, other studies have suggested that these dominant species on the Tibetan Plateau are likely more resilient to the phenological mismatches than other less-dominant forbs, for example, they generally rely less on pollinators than do other forbs (Klein et al., 2004; Liu et al., 2014).

4.2. Advanced leaf-out and first flower dates

Warming significantly advanced leaf-out and first flower dates for six of the eight species (Figs. 2-3). Higher temperatures with climatic warming may reduce the number of days required for plants to reach the cumulated thermal requirements for a given phenological event. This is particularly critical in cold environments such as the Tibetan Plateau (Piao et al., 2015; Suonan et al., 2017). Open top chambers were installed year-round across the whole experimental period. During the growing season, increased soil temperature probably stimulated decomposition and nutrient cycling (Estiarte and Peñuelas, 2015). Indeed, we observed that total soil inorganic nitrogen concentrations increased significantly under the warming treatment, which could facilitate plant growth through increased soil N availability (Chen et al., 2017a). At the beginning of the growing season, higher temperatures would prevent soil water from freezing and support both plant and microbial activities (Chen et al., 2017a; Suonan et al., 2017). During the non-growing season, higher temperatures may also advance leaf-out, although a certain period of chilling may also be required prior to initiation of leaf-out (Guo et al., 2019; Marchin et al., 2015; Perry et al., 2020). However, because the mean winter soil temperature was quite low at our study site (Chen et al., 2017b), it is less likely that OTCs raised soil temperatures enough to break the winter chilling requirement threshold (Suonan et al., 2017).

4.3. Species-specific responses of leaf senescence and last flower dates

The effects of warming on phenological lasts varied among the eight species (Figs. 2-3). Warming effects on leaf senescence and last flower dates were likely jointly controlled by complex interactions of biotic and abiotic factors, such as changes in soil temperature, soil moisture, and soil nutrient availability (Ernakovich et al., 2014; Estiarte and Peñuelas, 2015; Gill et al., 2015). Changes in these factors may advance or delay phenological lasts, depending on their balanced effects. It has been suggested that phenological lasts may be less plastic than phenological firsts to ensure a more stable fruiting period (Jiang et al., 2016). This could help explain why the magnitude of change under warming tended to be smaller for phenological lasts than firsts (Figs. 2-3). The underlying driving mechanisms for plant growth and maintenance of plant metabolic

activities are also highly variable among species (Myers-Smith et al., 2015). For example, some plant species are more sensitive to reductions in soil moisture, while others may be more responsive to changes in soil N availability (Engelbrecht et al., 2007; White et al., 2000). Interactions of the direct and indirect effects of warming on those biotic and abiotic factors can interactively constrain vegetation production in alpine plant communities (Berdanier and Klein, 2011), with potentially differential consequences for species' phenology and dominance.

Species within the same plant functional group varied in how their leaf senescence and last flower dates responded to experimental warming. Among the three forb species, warming advanced leaf senescence and last flower dates for *Gentiana squarrosa* but delayed them for *Heteropappus altaicus* and *Artemisia scoparia* (Figs. 2-3). However, the reasons for the different responses of phenological lasts among the three forbs are unclear. Some recent studies reported that plant functional traits (e.g., leaf morphology and plant height) probably had critical effects on plant phenology even within the same plant functional group (Dorji et al., 2013; Guerin et al., 2012; Kraft et al., 2015). These results call for caution when using plant functional group as a predictor of the effects of warming on plant phenology.

4.4. Uncertainties

Our results highlight the novel links between full phenological periods and species dominance, which help advance understanding of species turnover under warming. However, phenology is a complex plant trait that can be directly and indirectly linked to several biotic and abiotic processes (Cleland et al., 2007; Nicotra et al., 2010; Parmesan, 2006). Thus, to what extent our composition results are driven by phenology is difficult to ascertain. Other mechanisms may also contribute to the changes in species turnover rate under changing climate, such as changes in species competitive and facilitative interactions that affect resource utilization and efficiency (Alexander and Levine, 2019; Callaway et al., 2002; Choler et al., 2001; Germain et al., 2018). Yet, recent work indicates that plant phenology can also be an important mediator of these species interactions under changing climate (Alexander and Levine, 2019).

In addition to the direct effects of warming on vegetation, warming by OTCs could also affect plant phenology and species dominance via indirect pathways, such as the observed OTC-induced changes in soil volumetric moisture and soil inorganic N content (Fig. 1). These indirect impacts to the soil environment likely cause species-specific phenology and dominance responses via particular traits, such as some species' deeper rooting depths that allow them to access limited soil water (Dorji et al., 2013; Marchin et al., 2015; Nicotra et al., 2010). Although additional research would be required to explicitly and systematically explore the direct and indirect effects of climate warming on plant phenology and species interactions, as well as their possible consequences for species turnover rates, it is also unlikely that climate warming will proceed without attendant changes to soil resources. In addition, by focusing only on the eight species that were present across all experimental plots in this study, some uncertainties about community-level phenology and species composition remain. To strengthen our findings, representation of all species from the experimental plots are warranted in future studies.

The OTCs used in this study were carefully constructed following the method developed by the International Tundra Experiment (Marion et al., 1997). We acknowledge some intrinsic drawbacks associated with OTCs, such as large increases in air temperature, reductions in soil moisture, and reduced wind speeds (Chen et al., 2017a; Chen et al., 2017b). Despite those drawbacks, OTCs are widely used in many different ecosystems, especially in remote and harsh regions where electricity is unavailable (Baruah et al., 2017; Dorji et al., 2013). Indeed, every experimental warming method has its own advantages and disadvantages (Chen et al., 2015), thus our results

would be strengthened through comparison with those from other studies using different warming methods. In addition, OTC-induced changes in air temperature were not documented, because the sensors were damaged by the strong radiation on the Tibetan Plateau at that time, limiting our capability to carry out a more detailed assessment of the effects of increased air temperature on phenology and species dominance.

5. Conclusion

Our results from the cold Tibetan Plateau stress that shifts in phenological firsts are inadequate to predict the ecological consequences of climatic warming on plant phenology and plant species turnover. Rather, we find considerable variability among species in how warming impacts the first and last dates of their phenological patterns. As a consequence, it is changes in full phenological periods and phenological lasts, and how these varies among species, that relate most strongly to changes in species dominance. Our results provide novel insights for understanding the effects of climate warming on plant phenology and plant species turnover in a climatically sensitive ecosystem and underscore the need to assess how climatic warming will impact phenological lasts and full phenological periods.

Credit author statement

Ji Chen, Yiqi Luo and Junji Cao: Conceptualization, Methodology. Ji Chen, Yuxin Chen, Kelly A. Hopping, and Yuefang Zhang: Software, Validation, Data curation, Writing- Original draft preparation. Ji Chen, Kelly A. Hopping, Andrew J. Felton, Shuli Niu, Xiaoli Cheng, Jørgen Eivind Olesen, Mathias Neumann Andersen and Uffe Jørgensen: Writing- Reviewing and Editing. All authors contributed substantially to the repeatedly review and revisions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authorship

JC, YQL and JJC designed the study. JC, YXC, KAH, and YFZ analyzed the data.

JC, YXC, KAH, SLN, XLC, YFZ, UJ and JEO collaborated on data synthesis and interpretation. JC, AJF, and KAH wrote the manuscript. All authors contributed substantially to revisions.

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Appendix A. Supplementary data

Additional Supporting Information may be found online in the supporting information tab for this article. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.138891>.

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