



# Climate drivers of seed rain phenology of subtropical forest communities along an elevational gradient

Liu Yang<sup>1</sup> · Zehao Shen<sup>1</sup> · Xuejing Wang<sup>1</sup> · Shaopeng Wang<sup>1</sup> · Yuyang Xie<sup>1</sup> · Markku Larjavaara<sup>1</sup> · Jie Zhang<sup>1</sup> · Guo Li<sup>2</sup>

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## Abstract

Seed rain phenology (the start and end date of seed rain) is an essential component of plant phenology, critical for understanding population regeneration and community dynamics. However, intra- and inter-annual changes of seed rain phenology along environmental gradients have rarely been studied and the responses of seed rain phenology to climate variations are unclear. We monitored seed rain phenology of four forest communities in four years at different elevations (900 m, 1450 m, 1650 m, 1900 m a.s.l.) of a subtropical mountain in Central China. We analyzed the spatiotemporal patterns of seed rain phenology of 29 common woody plant species (total observed species in the seed rain), and related the phenological variations to seed number and climatic variables using mixed-effect models with the correlation matrix of phylogeny. We found that changes in the period length were mainly driven by the end rather than the start date. The end date and the period length of seed rain were significantly different between the mast and non-mast seeding years, while no significant elevation-related trend was detected in seed rain phenology variation. Seed number, mean temperature in spring ( $T_{\text{spr}}$ ), and winter ( $T_{\text{win}}$ ), summer precipitation ( $P_{\text{sum}}$ ) had significant effects on seed rain phenology. When  $T_{\text{spr}}$  increased, the start date of seed rain advanced, while the end date was delayed and the seed rain period length was mainly prolonged by a higher seed number,  $T_{\text{win}}$  and  $P_{\text{sum}}$ . Forest canopy might have a buffering effect on understory climatic conditions, especially in precipitation that lead to difference in seed rain phenology between canopy and shrub species. Our novel evidence of seed rain phenology can improve prediction of community regeneration dynamics in responding to climate changes.

**Keywords** Seed rain · Phenology · Spatiotemporal patterns · Mast and non-mast seeding · Elevational gradient · Climate change

## Introduction

Phenology is an important part of species life history, population dynamics, and ecosystem functions such as carbon and nutrient cycles (Fitchett et al. 2015; Liu et al. 2016; Piao et al. 2019). Phenology can also act as a limiting factor of species distribution (Wolkovich et al. 2013; Clark et al. 2014), being critical in particular for plant-pollinator coevolution and sympatric speciation (Taylor and Friesen 2017).

Moreover, plant phenology is commonly applied to reflect ecosystem responses to climate changes (Gordo and Sanz 2010; Vitasse et al. 2018; Rosbakh et al. 2021).

Seed production and dispersal is central to the life history of plants (Nathan and Muller-Landau 2000). Seed rain occurs when a large number of seeds are scattered from the parent plants at a specific time (Wagner 1965), thus contains essential phenological information on the start and end of seed dispersal process, and also on the composition, abundance and biomass of seeds produced by particular species and the community as a whole (Shen et al. 2007). Changes in seed rain phenology affect the seed yield and population regeneration, which in turn indicate species life history strategies and community dynamics in response to environmental changes (Ganesh and Davidar 2005; Arruda et al. 2018).

Seed rain dynamics shows strong seasonality, exhibiting unimodal (Zang et al. 2007; Garcia-del-Rey et al. 2011; Piotto et al. 2019) or bimodal patterns (Marques and Oliveira 2010; Li et al. 2012). Interannual variations of seed rain

✉ Zehao Shen  
shzh@pku.edu.cn

✉ Guo Li  
liguo@craes.org.cn

<sup>1</sup> MOE Laboratory for Earth Surface Processes, Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

<sup>2</sup> Institute of Ecological Environment, Chinese Research Academy of Environmental Sciences, Beijing 100012, China

are typically characterized by the alternance of mast and non-mast seeding years. For example, Houle (1998) found a difference of more than one order of magnitude in seed rain density for *Betula alleghaniensis* between different years. In ten-year monitoring of forest seed rain, a 3–4 years periodic fluctuation in density and species richness of seed rain was detected for a species rich, subtropic forest community (Xu et al. 2012). Just like the timing of leaf onset and offset, seed production phenology is also dominated by climate dynamics at both intra- and interannual scales (Yin and Shen 2016). The occurrence of mast seeding year was found to respond to both temperature and precipitation, and show correlation with leaf phenology in the spring (Wang et al. 2017). Climate as a primary driver generally forces interspecific synchrony of seed rain phenology both seasonally and yearly, but asynchrony interspecific feedback of seed rain to climate changes has also been reported (Herbison et al. 2015; Wang et al. 2022). Meanwhile, biotic factors such as interspecific competition and seed predation by frugivores can also regulate temporal variations of seed production, with both synchronizing and asynchronizing effects observed (Mckone et al. 1998; Martínez-Garza et al. 2011, Rossi et al. 2016), but a general understanding remains lack for their contributions and interactions (Li et al. 2012; Shepherd et al. 2008; Xu et al. 2015).

The effect of climate change on plant reproduction phenology has become an active theme in last two decades; one of the focuses was climate drivers for mast seeding (Mutke et al. 2005; Davi et al., 2016; Pesendorfer, et al. 2020; Clark et al. 2021). In fact, seed rain dynamics has been addressed with regards to climate factors and local scale processes (Yin and Shen 2016), such as vegetation disturbance, plant-animal relationships and community succession (Ceccon and Hernandez 2008; Norghauerand Newbery, 2015; Arruda et al. 2018). Among which, studies based on long-term seed rain observations along environment gradients (such as elevation) have been rare. Indeed, apart from a few cases (Xu et al. 2012; Chang-Yang et al. 2016; Wang et al. 2022), there is little knowledge about the elevational patterns of seasonality of seed rain phenology, and the role of climate factors and extreme climate in regulating seed rain phenology is elusive. Taking advantage of improvements and applications of remote sensing technologies in the last decades, leaf phenological studies have been used to estimate the effects of global changes on ecosystem functions (Vitasse et al. 2018; Piao et al. 2019), but substantial knowledge gaps remain for seed rain phenology.

The present study was based on 4 years (2011–2014) monitoring of seed rain phenology in four species-rich forest communities along an elevational gradient of a mountain in Central China. We explored the variations of seed rain phenology in the forest communities with regards to the elevational climate gradient, and evaluated the contributions of

seed number and climate factors on the community level seed rain phenology. Specifically, we addressed the following questions: (1) How do seed rain phenology of the forests respond to the elevation related climatic gradient? (2) What are the limiting climatic factors of seed rain phenological indices (i.e., start and end dates, period length)? (3) Can forest structure buffer the effect of climate on seed rain phenology, such as the effect on understory plant species?

## Materials and methods

### Study area

The study area is located in Dalaoling Nature Reserve, Hubei Province in Central China (110°52′–111°01′E, 31°01′–31°08′N). The region has a subtropical humid climate dominated by monsoon, with synchronic seasonality in temperature and precipitation. The records of meteorological station (75 m a.s.l.) in the south slope of Dalaoling Mountain indicate that the annual mean temperature is 16.7°C, the mean temperatures in January and July are 5.5°C and 27.3°C, respectively. The annual precipitation is 1215.6 mm, with 80% occurring from April to September. The zonal soil type below 800 m a.s.l. is red soil, which is replaced by yellow–brown soil at higher elevations (Xu et al. 2012). The zonal vegetation below 900 m a.s.l. is originally evergreen broadleaved forests, but is mostly replaced by degraded shrubs, coniferous forests and farmland. The mixed coniferous and evergreen broadleaved forests dominate at 900–1700 m a.s.l., and a mosaic of temperate coniferous forests and deciduous forests comprise the majority of vegetation from 1700 m up to 2008 m at the mountain summit (Shen et al. 2000).

### Experimental design and data collection

Seed rain was monitored in the Dalaoling Mountain from 2011 to 2014, in four 100 m × 100 m forest plots set at 900 m, 1450 m, 1650 m and 1900 m a.s.l., respectively (Table 1). A total of 81 seed traps (of 1 m<sup>2</sup> area) were set within each plot, locating at each corner (except those on the boundary) of the 10 m × 10 m quadrats. To prevent rodents from feeding on collected seeds, each seed trap was set in a frame made of iron wire, held up to 1 m high by four bamboo poles with frame surfaces kept horizontal. We began seed collection each year from the first week of August, checked seed traps weekly and collected seeds and fruits trapped. Collection stopped when no new seed was found in all traps for four consecutive observations. Based on the seed collections from all 81 seed traps within each plot, we obtained the seed rain phenology information of four forests. This information was summarized by community and by species,

**Table 1** Characteristics of plant communities for seed rain monitoring in Dalaoling

Sites	Elevation (m)	Geographic coordinates	Dominant species
Tanjiaya	900	N30.979906°; E110.921735°	<i>Platycarya strobilacea</i> , <i>Bothrocaryum contro-</i> <i>versum</i>
Liangya	1450	N31.065761°; E110.948223°	<i>Fagus lucida</i>
Zhucaogou	1650	N31.078946°; E110.881153°	<i>F. lucida</i> , <i>Castanea henryi</i>
Hentianshi	1900	N31.084395°; E110.941484°	<i>F. lucida</i>

including the start date and the end date of seed rain in each year. The phenological dates were converted into the number of days from January 1st. We selected woody species seeds harvested in more than one plot of different elevations, in at least one of the four years of seed rain monitoring. During the monitoring, a total of 27,448 seeds, belonging to 29 common woody species, were collected in seed traps set at four elevations. The yearly seed harvest during 2011–2014 was 7031, 5359, 11,069 and 3989 seeds, respectively, indicating that 2013 was a mast seeding year, and the other three years were non-mast seeding years. We classify the species with seed rain records as understory species and canopy species according to their growth forms that corresponding to shrub and tree species (Table S2), based on taxonomic literature of this region (Zheng 1993).

The climate data for the four forest plots was collected from one formal meteorological stations at 75 m a.s.l., and three other temporary automatic meteorological stations set up since 2010, located at 1280 m, 1600 m and 1990 m a.s.l., respectively, within the Dalaoling Reserve. Due to the close horizontal distance between meteorological stations and the monitoring plots, the climate condition differences between stations reflected mainly the elevational differences. Therefore, we used a linear model between climate factors and elevation to interpolate the values of climate factor at all elevations of the sample plots. We selected summer (June–July–August) precipitation of last year ( $P_{1\text{-sum}}$ ), winter (December–January–February) minimum temperature ( $T_{\text{win}}$ ), spring (March–April–May) temperature ( $T_{\text{spr}}$ ), and summer precipitation ( $P_{\text{sum}}$ ) of current year as climate factors.

### Statistical analysis

R programming environment software (R Development Core and Team, 2022; version 4.1.3) software was used for data statistics, analysis and figure drawing.

We used a linear regression model to explore the correlations between the start date, end date, and period length of the seed rain phenology based on species-level data. To test for an elevational trend of seeding phenology variation, we calculated the differences of start dates of seed rain records across all elevational pairs of four plots for each species, obtained slopes of start date differences on

elevational differences, aggregated slopes across all species in all monitoring years and tested the significance of differences between the mean slope and zero. The same analytical procedure was applied for the end date and the period length of seed rain. We also calculated the differences of species-specific seed rain phenological indices between all pairs of mast versus non-mast seed years, and tested the statistical significance of differences.

To test for the effects of seed number, precipitation of the previous and current summers, previous winter and current spring temperatures on the start date, the end date and the period length of seed rain on species-level, we fitted a mixed effect model, using “lme4” function in the “coxme” package (Therneau et al., 2018). The “lme4” function of the “coxme” package is developed based on the “lmer” function of the “lme4” package, which can solve the problem that the phylogenetic matrix effect cannot be calculated in the mixed effects model (Kubelka et al. 2018). The start date, the end date and the period length were used as response variables. The fixed factors were seed number and climate variables. However, as  $T_{\text{win}}$  and  $T_{\text{spr}}$  were strongly correlated ( $r_{\text{spearman}} = 0.74$ ,  $p < 0.05$ ), they could not be reliably combined in the same model (Dormann et al. 2013).  $T_{\text{spr}}$  was hence included in the model as the residual variation in  $T_{\text{spr}}$  after removal of  $T_{\text{win}}$  variation. The residual was extracted from a simple linear regression with  $T_{\text{spr}}$  as the dependent variable and  $T_{\text{win}}$  as the predictor variable only. The fixed factors were seed number,  $P_{1\text{-sum}}$ ,  $P_{\text{sum}}$ ,  $T_{\text{win}}$  and  $T_{\text{spr\_res}}$ . All data were standardized to ensure their comparability. The random factor was species, and the correlation matrix of species phylogeny was simultaneously considered because the phylogenetic relationship among species may affect the difference of their phenological indices (Lorts et al. 2008; Kubelka et al. 2018). The phylogenetic tree was constructed for the 29 common woody species with seed rain records in four plots, using the “phylo.maker” function in the “V.PhyloMaker” package (Jin and Qian 2019). We constructed a phylogenetic matrix based on the clade branch length of the phylogenetic tree using the “vcv.phylo” function in “ape” package (Paradis et al. 2004).  $R^2_m$  represents the marginal variance explained by fixed factor in the mixed-effects model, obtained by dividing

the variance of the fixed factor in the mixed-effects model by the variance of the total model.  $R^2_c$  represents the conditional variance explained by random effect with phylogeny in the mixed-effects model, obtained by dividing the variance of the random factor with phylogeny in the mixed-effects model by the variance of the total model. The mixed effect model was fitted as follows:

*lasiocarpa* and *Decaisnea insignis* in 2011) and the latest on day 310 (*Viburnum betulifolium* in 2014); seed rain stopped earliest on day 214 (*C. myrsinifolia* in 2011) latest on day 390 (*L. erythrocarpa*, *Paulownia fortune*, *Lindera communis*, *B. controversum* and *Platycarya strobilacea* in 2014); the period length of species specific seed rain phenology ranged from 1 (only one record) to 171 days, and the period

$$\text{Model} = \text{lme}(\text{seed rain phenology} \sim \text{Seed number} + P_{1-\text{sum}} + P_{\text{sum}} + T_{\text{win}} + T_{\text{spr\_res}}(1|\text{species}), \text{varlist} = \text{list}(\text{phylogeny}))$$

## Results

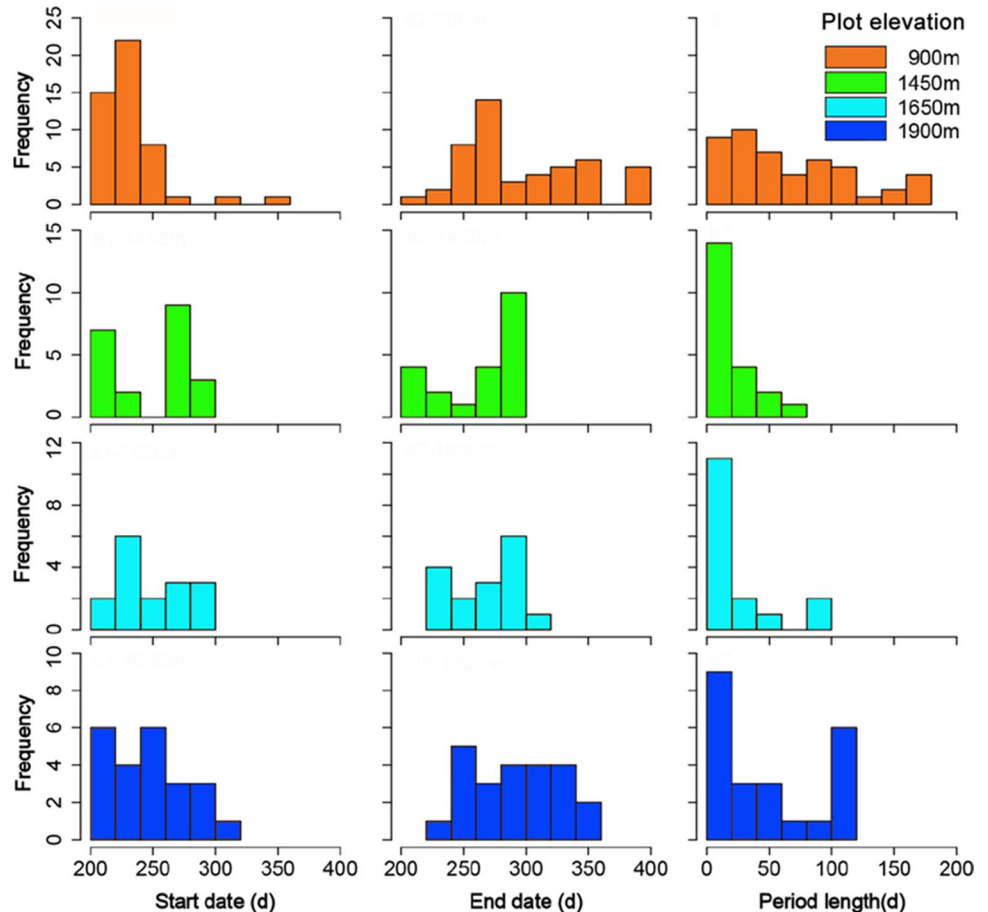
### Seed rain phenological indices and their correlations

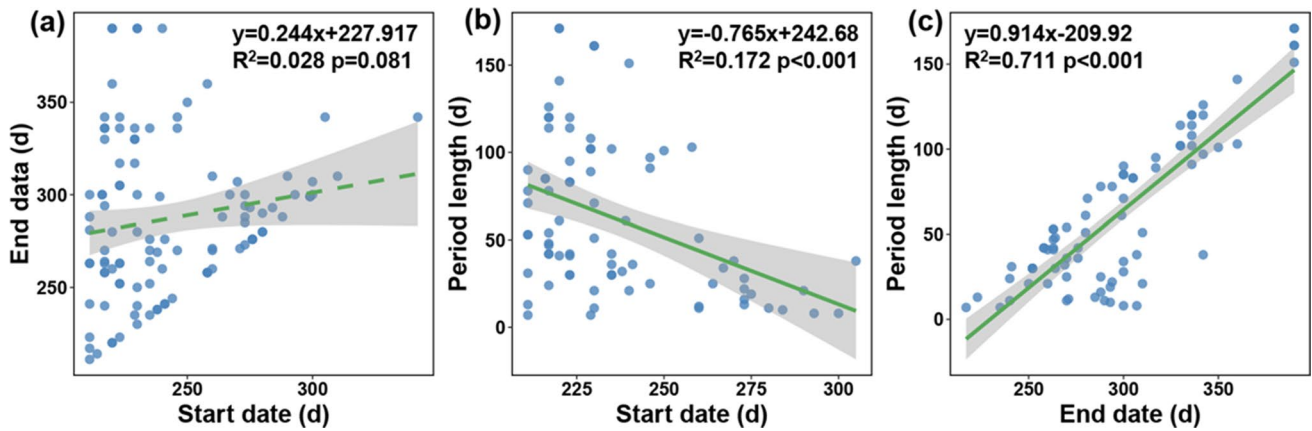
The phenology of seed rain differs remarkably among species. According to the records of field seed collection during the period from 2011 to 2014, the earliest seed rain began on day 214 of the year (*Castanea seguinii*, *Lindera erythrocarpa*, *Quercus glandulifera*, *Cyclobalanopsis myrsinifolia*, *Bothrocaryum controversum*, *Euscaphis japonica*, *Populus*

length for four forest communities at the elevation of 900 m, 1450 m, 1650 m and 1900 m a.s.l. were 1 – 171, 1 – 61, 1 – 85 and 1 – 120 days, respectively, within the 4 years of seed rain monitoring (Fig. 1).

The period length of seed rain was significantly negatively correlated with the start date ( $p < 0.001$ ), and was positively correlated with the end date ( $p < 0.001$ ). However, there was no significant correlation between the start date and the end date ( $p > 0.05$ ). The results indicate that the period length was mainly restricted by the end date (Fig. 2).

**Fig. 1** The histogram of frequency distribution of the start date, the end date and the period length of seed rain phenology of forest community plots being monitored at 900 m, 1450 m, 1650 m, and 1900 m a.s.l., respectively, during 2011–2014





**Fig. 2** The relationships among the phenological indices of seed rain of forest communities, putting together the observations of all species in four years. (a) the start date vs. the end date, (b) the start date vs. the period length, (c) the end date vs. the period length

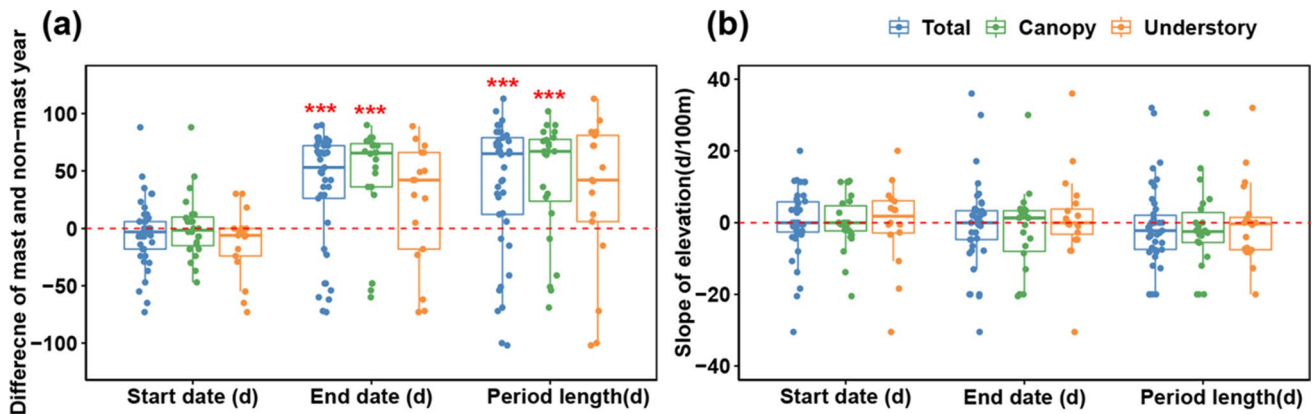
**Spatiotemporal variations of seed rain phenology indices**

Considering all communities together for the difference of seed rain phenology between the mast and non-mast seeding years, the *t*-test of the start date detected no significant difference for all species, canopy species, or understory species. In contrast, the end date showed a significant delay in the mast seeding year for all species ( $p = 6.204 \times 10^{-5}$ ) and canopy species ( $p = 1.033 \times 10^{-4}$ ), but no significant delay ( $p = 0.114$ ) for understory species. A significantly prolonged seed rain period length in the mast seeding year was also confirmed by the *t*-test for total species ( $p = 1.761 \times 10^{-4}$ ) and canopy species ( $p = 4.214 \times 10^{-4}$ ), but not for understory species ( $p = 0.091$ ) (Fig. 3a). Meanwhile, the *t*-tests rejected a significance of elevational slope for the start date, the end date or the period length ( $p > 0.05$ ) of seed rain phenology

for either canopy species, understory species, or total species (Fig. 3b).

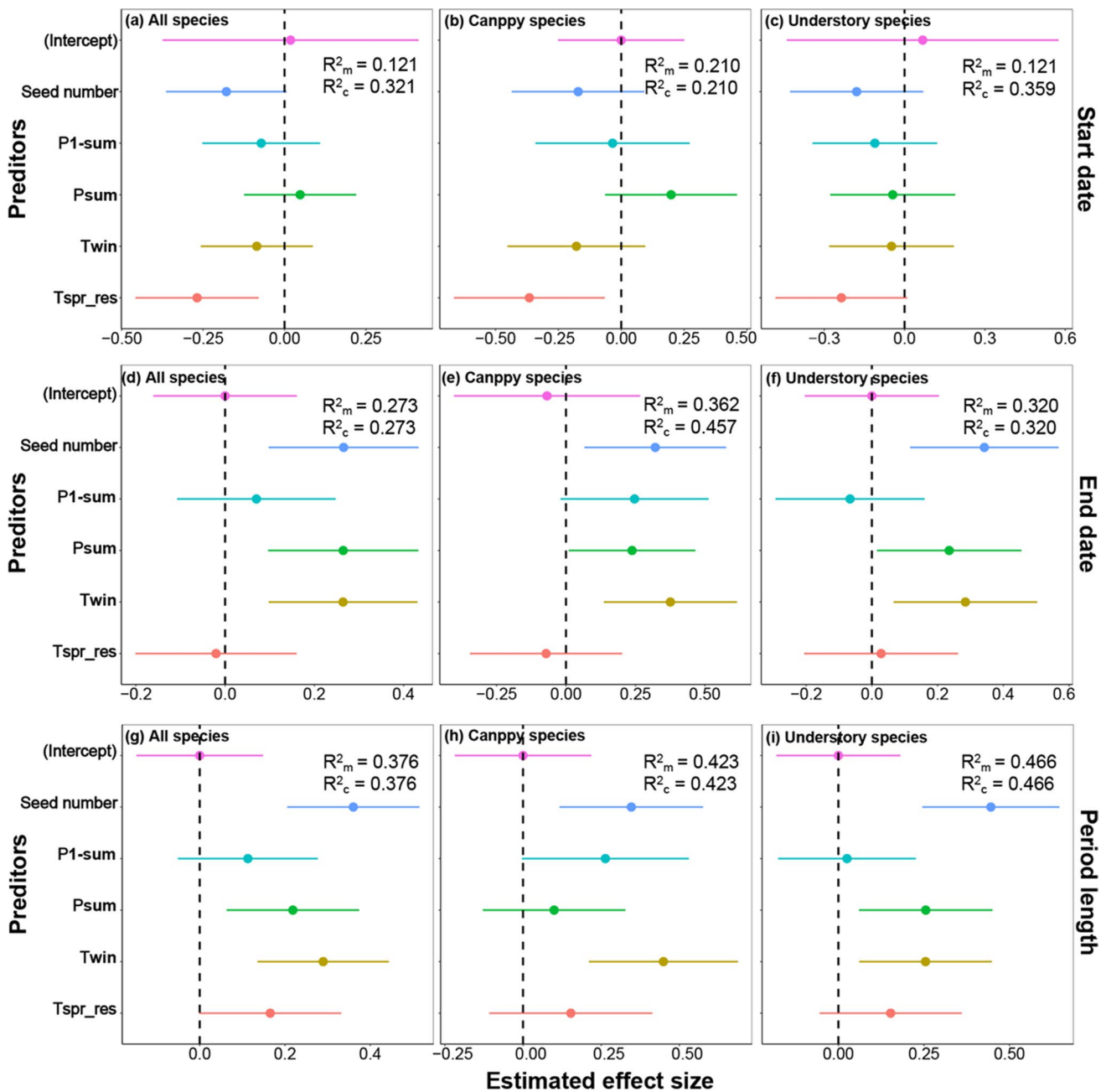
**Influencing factors of phenological indices of seed rain**

For the start date of seed rain,  $T_{spr\_res}$  had significant effects on total and canopy species (Fig. 4a, b; Table S1). The start date of seed rain advanced with  $T_{spr\_res}$  increasing for total and canopy species ( $p < 0.05$ ; Fig. 4a, 4b; Table S1). There was a weak negative correlation between seed number and the start date of seed rain ( $p = 0.059$ ), and the negative relationship was consistent on understory and canopy species (Fig. 4a, b, c; Table S1). The effects of  $P_{sum}$  on the start date of seed rain for canopy and understory species were opposite, although their effects were not significant ( $p > 0.05$ ; Fig. 4b, c, Table S1).



**Fig. 3** *T*-test for the statistical significance of (a) interannual (mast vs non-mast years) variation and (b) elevational trend, in start date, end date and period length of seed rain phenology for total, canopy and

understory species, respectively. Canopy, canopy species; understory, understory species. Total, both canopy and understory species. \*\*\*  $p < 0.001$



**Fig. 4** Interpretation of seed rain phenological indices (start date, end date and period length) based on the phylogenetic mixed-effect models in all species (**a, d, g**), canopy species (**b, e, h**) and understory species (**c, f, i**). Estimated effect sizes represent the slope of fixed factor with 95% confidence intervals. The points represent effect estimate of interpretative variables, and error bars represent 95% confi-

dence intervals.  $R^2_m$ , the marginal variance explained by fixed effects.  $R^2_c$ , the conditional variance explained by fixed and random effects with phylogeny.  $P_{1-sum}$ , summer precipitation of last year;  $P_{sum}$ , summer precipitation of current year;  $T_{win}$ , winter minimum temperature before seed rain;  $T_{spr\_res}$ , spring temperature of current year. Full models outputs can be found in Supplementary information Table S1.

For the end date of seed rain, seed number,  $P_{sum}$  and  $T_{win}$  had significant effects on all species (Fig. 4d, Table S1). The end date of seed rain was delayed when seed number,  $P_{sum}$  and  $T_{win}$  increased for all species ( $p < 0.05$ ; Fig. 4d, Table S1). Compared with the weak positive effect ( $p = 0.07$ ) of  $P_{1-sum}$  on the end date of seed rain in canopy understory

species, while  $P_{1-sum}$  had no significant negative effect ( $p > 0.05$ ) on the end date of seed rain in understory species (Fig. 4e, f, Table S1).

For the period length of seed rain, seed number,  $P_{sum}$  and  $T_{win}$  had significant effects on all species (Fig. 4g, Table S1). The period length of seed rain was prolonged when seed

number,  $P_{\text{sum}}$  and  $T_{\text{win}}$  increased for all species ( $p < 0.05$ ; Fig. 4g, Table S1).  $P_{1\text{-sum}}$  had weak positive effect on the period length of seed rain in canopy species ( $p = 0.053$ ), while no effect on the period length of seed rain in understory species ( $p > 0.05$ ; Fig. 4h, 4i, Table S1).  $P_{\text{sum}}$  had significant positive effect on the period length of seed rain in understory species ( $p < 0.05$ ), while no effect on the period length of seed rain in canopy species ( $p > 0.05$ ; Fig. 4h, i, Table S1).

For the start date, values of  $R^2_c$  were 0.20 and 0.24 greater than values of  $R^2_m$  of total and understory species, respectively (Fig. 4a, c), while  $R^2_c$  and  $R^2_m$  of canopy species were roughly equal (Fig. 4b). The results suggested that phylogenetics had stronger influences on the start date of seed rain in understory species, while no effect in canopy species. For the end date, value of  $R^2_c$  was 0.12 greater than  $R^2_m$  of canopy species (Fig. 4e), while values of  $R^2_c$  and  $R^2_m$  of total and understory species were roughly equal (Fig. 4d, f). The results showed that phylogenetics had an influence on the end date of seed rain in canopy species, while no effect in understory species. For the period length,  $R^2_c$  and  $R^2_m$  of all species were roughly equal (Fig. 4g, h, i), indicating that phylogenetics had weak influences on the period length of seed rain.

## Discussion

Understanding the determinants of plant phenology is essential for estimating species sensitivity to environmental variability, and useful for predicting ecosystem responses to global climate changes (Garonna et al. 2016; Vitasse et al. 2018). Seed production and dispersal phenologies are regulated by weather events (Herbison et al. 2015), climate seasonality and inter-annual variations (Fletcher, 2015; Chang-Yang et al. 2016; Wang et al. 2022). There have been a lot of predictions and discussions about the risks of climate changes for ecosystem functioning and biodiversity loss through plant phenology shift (Vitasse et al. 2018; Piao et al. 2019; Zhao et al. 2020), mostly focusing on leaf phenology that is more easily detected and estimated by remote sensing approach (Zhang et al. 2016; Chen 2017). In contrast, monitoring seed rain phenology at a large spatial or temporal scale is far more difficult, in terms of either equipment or standardized technique protocol.

Based on a 4-year monitoring of seed rain phenology in four forests along an elevational gradient, we found that increasing  $T_{\text{spr}}$  advanced the start date of seed rain, and prolonged the period length of seed rain season at the community level (Fig. 4, Table S1). This is in agreement with the observations that the leaf-out date significantly advances with the increasing spring temperature (Du et al. 2017; Dai et al. 2021). It has been explained that increasing spring temperature promotes photoenzyme activity, advancing the whole

growing season and the accumulation of photosynthesis products needed for offspring reproduction, which in turn leads to earlier seed maturity. The increasing  $T_{\text{win}}$  delayed the end date of seed rain, for which the possible reason is that increasing  $T_{\text{win}}$  leads to a decrease in the chilling accumulation of the plant, which delays the greening of the plant and the maturity period of seed reproduction (Li et al. 2019). Our observations also indicated that increasing  $P_{\text{sum}}$  did not advance the start date, but delayed the end date and prolonged the seed rain season. This phenomenon is also similar to the effect of summer precipitation on leaf phenology (Fan et al. 2014). Higher rainfall in summer is generally related to a larger gross primary productivity (Han et al. 2015), a prolonged growing season and higher total biomass (Singh and Kushwaha 2006; Borchert et al. 2010; Chimner et al. 2010), and probably also higher seed yield. Moreover,  $P_{1\text{-sum}}$  showed a marginal effect on the end date and period length of seed phenology for canopy species compared to understory species, as a marginally significant legacy effect, indicating differences in climate impacts on leaf versus seeding phenology. The former begins in spring and is directly influenced by winter climate or even the lagged climate effect of the previous year (Wang et al. 2022); while seed deposition of subtropical forests mainly begins in summer and continues into winter, the buffering effect of the spring climate seems to be crucial for seed rain phenology. Researches showed that the forest canopy functions as a thermal insulator and buffers sub-canopy microclimatic conditions (Heasen et al., 2021). During the growing season, maximum temperature under at least 50% forest canopy were 5.3 °C lower on average compared to areas without canopy cover across a climate gradient in the northwestern United States (Davis et al. 2019). Zhang et al (2006) found that about 15% of annual precipitation was intercepted by the top-canopy, and 9% of throughfall was retained by the sub-canopy in a subtropical evergreen mixed forest in central-south China. Seed number, as an indicator of difference between mast vs no-mast seeding year, affected the end date and period length, but not the start date of seed rain (Fig. 4). This also highlighted the critical role of climate conditions during, rather than before, the growing season in determining the eventual process of seed production and release.

As the result of a higher  $T_{\text{spr}}$ ,  $T_{\text{win}}$  and a larger  $P_{\text{sum}}$ , the advance of the start date and/or delay of the end date of the seed rain records, separately or together, led to a prolonged seed rain season and a mast seeding year, which occurred consistently for four forest communities in 2013, across an elevational range of 1000 m. This showed a spatial synchrony of fecundity at a community level, under the constraint of inter-annual climate variability (Fig. S1). In contrast, the interspecific asynchrony of species level fecundity has been reported by an earlier study of the same study site (Xu et al. 2015), and other cases (Lasky, et al., 2016; Wang et al. 2017). In contrast to the interannual synchrony of seed phenology across elevations,

no significant elevational trend of seed rain phenology was observed, for all data pooled (Fig. 3b), or for data separated by mast or non-mast seed years (Fig. S2). This pattern meant that, although the temperature (including  $T_{\text{spr}}$ ) decreased and precipitation increased with increasing elevation in Dalaoling, it did not lead to a significant delay of the start or the end date of the seed rain season, or a consistent change of seed rain season length. This is distinct from the change of leaf phenology observed in various studies (such as Vitasse et al. 2018), but was in accord with a fruiting phenology analysis of elevational pattern of angiosperm species across China (Du et al. 2020). The insignificant elevational patterns of seed rain phenology indices may be caused by contrasting effects of elevational changes of climate indices, that is, the increase of rainfall and decrease of temperature with increasing elevation might more or less offset their impacts on seed rain phenology, and result in an uncertain pattern, although more observations are required for confirming a general rule.

Differences in seed rain phenology between the mast and non-mast seeding years were significant for both canopy and understory species (Fig. 3a). Actually, an earlier report on ten-year seed rain dynamics in one of the four monitored forests found little correlation in the yearly seed yield between canopy species and understory species (Xu et al. 2012). Comparisons of leaf phenology between the canopy and understory of forests have also been reported in many studies with inconsistent results (Maeno and Hiura 2000; Sun et al. 2006; Liu et al. 2016; Donnelly and Yu 2019), and the proposed mechanisms were multifaceted. Canopy density and dynamics change the light environment on the ground, and lead to adaption in understory species (Valladares 2003); daily and seasonal variations in temperature and precipitation are also buffered by the canopy, which regulates their temporal rhythms (Brauman et al. 2010; Frenne et al. 2019). Seed rain comprised only a part of the total seed yield, for a particular species or the community as a whole. A considerable proportion of seeds are normally consumed by pre-dispersal predation (Ganesh and Davidar 2005; Xu et al. 2015) or removed by animals (Nathan et al. 2008; Yang et al. 2020), and thus are not recorded as seed rain. Therefore, seed rain phenology is a useful indicator of plant reproduction phenology, but has limitations. In addition, our data of seed rain phenology records were based on a sample of seeds harvested in the 81 seed traps of 1 m<sup>2</sup> area in each one hectare forest plot. The 0.81% sampling intensity entails considerable uncertainty, although such sampling intensity is very large compared with many similar studies. Finally, the interannual changes of plant phenology (including fluctuations and trends) exist at multiple temporal scales. A monitoring period of 4 years is not long, left uncertainty regarding the response of seed production phenology to climatic variation, especially the extreme climates. However, our results were based on a proper use of analyzing methods with statistic tests, which support the reliability of our results for

understanding the climate-phenology relationship in our study context. Nevertheless, more observations in a longer term are undoubtedly necessary for comprehensive disentangling the responses of seed rain phenology to climate changes, and for a better understanding of underlying mechanisms driving seed production and dispersal.

## Conclusions

Seed rain phenology is critical for community composition and regeneration dynamics. The 4-year dynamics of seed rain phenology in four forests along an elevational gradient in Dalaoling Mountain showed significant differences between mast and non-mast seeding years, but no consistent response to the elevational climate change. The period length of seed rain was mainly determined by the end date. As prominent determinants of seed rain phenology, when seed number,  $T_{\text{spr}}$ ,  $P_{\text{sum}}$  and  $T_{\text{win}}$  increased, the start date of seed rain advanced, the end date was delayed and the period length was prolonged. Forest canopy has a prominent effect in moderating understory climatic conditions, especially in precipitation, and lead to difference in seed rain phenology of shrub species. The understanding of dominant effects of summer precipitation and the winter freezing on the start and end of seed rain phenology, respectively, would be helpful for predicting plant community dynamics, and its responses to climate changes.

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**Data availability** All data analysed during this study are included in this published article.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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