



# Apple phenology occurs earlier across South Korea with higher temperatures and increased precipitation

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## Abstract

This study examined relationships between temperature, precipitation, geo-topography, and the spring phenology of Fuji and Hongro apple cultivars along spatial gradients across South Korea. Phenology data was gathered from 2011 to 2014 in 42 uniformly managed research orchards which span a range in climate, latitude, and elevation. We used linear models and spatially explicit forecasts to study apple phenology under climate change scenarios. Given dry winters and complex terrain in South Korea, we hypothesized that, in addition to temperature, precipitation and geo-topographic factors influence apple phenology. We also expected responses to climate variation to be similar between (spatial) and within (temporal) orchards, given the controlled conditions and the use of apple clones in this study. With other factors held constant, phenological sensitivity ranged from  $-3.2$  to  $-3.4$  days  $^{\circ}\text{C}^{-1}$  for air temperature and  $-0.5$  to  $-0.6$  days  $\text{cm}^{-1}$  for March precipitation in a combined model. When modeled without temperature, phenology changed by up to 10 days over the full range in March precipitation. Spring temperatures and precipitation in March had very little cross-correlation ( $r < 0.05$ ), suggesting these patterns are independent; however, in a combined model including temperature, predicted changes in precipitation over the next 80 years have only a small impact on future apple phenology. Combining the best models with climate forecasts for South Korea, spring phenology continues to occur earlier over the next 80 years, mostly due to warming temperatures but with strong variation between regions. This suggests regionally specific climate change adaptation strategies are needed for future apple production in South Korea.

**Keywords** Apple phenology · Climate change · Precipitation · Topography · Temperature

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## Introduction

Plant phenology is a fundamental bioindicator of climate change (Cleland et al. 2007; Zhao et al. 2013; Schmidt 2014; Schröder et al. 2014). Long-lived woody plants are especially valuable given their long residence times, providing an integrated record of past and current climate on the same organism. Indeed, long-term trends in tree phenology are widely consistent with warming temperatures evident in weather records (Menzel 2003; Menzel et al. 2006), and trends in tree phenology are similar across natural forests, orchards, and ornamental settings (Chmielewski et al. 2004; Schröder et al. 2014). Orchards are an important resource for the study of phenology as individual trees are closely monitored and records are often decadal in length.

Various approaches are used to study and forecast tree phenology, including theoretical, experimental, and empirical approaches (Cleland et al. 2007; Chuine et al. 2013; Zhao et al. 2013; Chiou et al. 2015). In all approaches, the most important factor is air temperature, as seen in many studies

(Menzel 2003; Badeck et al. 2004; Menzel et al. 2006; Gordo and Sanz 2010; Carroll et al. 2017). In a recent study in Lithuania, for example, temperature in March–April had a strong influence on the date of tree leaf elongation (Juknys et al. 2016). Likewise, increasing temperatures are projected to accelerate flowering in peach and pear trees in South Korea (Hur and Ahn 2015), and spring air temperatures are highly correlated with budding and flowering of apples in Japan (Fujisawa and Kobayashi 2010), Germany (Chmielewski et al. 2011), and South Africa (Grab and Craparo 2011). Temperature, especially in spring, is clearly the main determinant of tree phenology in temperate latitudes in natural and agricultural settings.

Secondary environmental factors, like precipitation, photoperiod, and solar radiation, can also influence tree phenology in addition to or independently of temperature (Badeck et al. 2004; Cleland et al. 2007; Gordo and Sanz 2010). Phenology has been correlated with spring precipitation (Gordo and Sanz 2010; Juknys et al. 2016), and Grab and Craparo (2011) found spring precipitation is significantly and positively correlated with bloom dates in apples. In some cases, rainfall has a stronger influence than temperature on phenology, especially in arid and semiarid areas (Wielgolaski 1974; Peñuelas et al. 2004), and rainfall generally can influence phenology by providing needed moisture in regions with dry springtime conditions (Seghieri et al. 2009; Zhao et al. 2013; Laube et al. 2014). In addition, geo-topographic influences like slope, aspect, and elevation can alter phenology above and beyond direct climatic effects (Fisher et al. 2006; Eccel et al. 2009)—e.g., by changing the partial pressure of trace gases, altering the angle of incoming sunlight, and influencing the residence time of moisture in the soil—and by capturing microclimatic conditions not evident in basic weather data (Böhner and Antonić 2009).

Varieties of domesticated apple trees (*Malus domestica* Borkh.) demonstrate a clear relationship between phenology and warming temperatures across the world. Apple is widely studied for its economic importance as the most productive fruit tree species in temperate zones, for example, producing 84.6 million tons of fruit globally in 2014 from orchards covering 5 million ha (FAO 2014). Phenology studies from apple orchards span the Northern Hemisphere—in Europe (e.g., Rea and Eccel 2006; Gordo and Sanz 2010; Hoffmann and Rath 2013; Schröder et al. 2014; Legave et al. 2015; Funes et al. 2016), north Africa (Legave et al. 2015), North America (Wolfe et al. 2005), and Asia (Fujisawa and Kobayashi 2010; Asakura 2011)—and the Southern Hemisphere in South Africa (Grab and Craparo 2011), South America (Legave et al. 2015), and Oceania (Darbyshire et al. 2013, 2014; Logan et al. 2016). These studies document a broad and substantial shift in apple phenology, with flowering advancing by 2.2 days decade<sup>-1</sup> in Germany (Chmielewski et al. 2004), 2.1–3.5 days decade<sup>-1</sup> in Japan (Fujisawa and

Kobayashi 2010), and 1.6 days decade<sup>-1</sup> in South Africa (Grab and Craparo 2011).

Shifts in apple tree phenology have important implications. On a basic level, optimal areas for a crop are determined by its phenology, and species and varieties can become poorly suited to an area as climate changes (Chmielewski 2013; Schröder et al. 2014). The risk of fruit loss in a late spring freeze increases as phenology occurs earlier, as newly emerged tissues are highly vulnerable to frost damage (Chmielewski et al. 2004; Eccel et al. 2009; Hoffmann and Rath 2013). Concurrent shifts in the phenology, distribution, and populations of tree diseases and insects are also important implications of warmer temperatures (Thomson et al. 2010; Schröder et al. 2014). Finally, changing phenology risks asynchronies between plants and pollinators, especially in heterozygous species like apples (Cleland et al. 2007; Donoso et al. 2016).

Apples are an important crop in South Korea, but studies of apple responses to climate change are lacking. South Korea has warmed over the last century at double the global average as mean annual temperatures have risen 1.5 °C (Kwon 2005), and models predict regional temperatures will increase by another 3–5.7 °C by the end of the twenty-first century (KMA 2012). Precipitation is also predicted to increase by 16–18% in this period, 3–4 times higher than the global average (KMA 2012). Such systemic change is having a fundamental effect on fruit tree biology in the region and provides a strong model to study the effects of pronounced climate change on fruit tree phenology. The primary objective of this study is to explore relationships between temperature, precipitation, and geo-topography with the spring phenology of two important apple cultivars—‘Fuji’ and ‘Hongro’—along spatial gradients across South Korea, using research orchards which span a wide range in climate, latitude, and elevation. Spatial gradients can be helpful in assessing phenological responses to warming, especially when long time series are not available or poorly replicated (Jochner et al. 2013), and studies with both temporal and spatial data can evaluate how phenology responds to climatic variability in temporal time series vs. spatial gradients. With these data, we used linear models and spatially explicit forecasts to study apple phenology under climate change scenarios for South Korea. We expected the magnitude and direction of phenological response to climate variation to be similar between (spatial) and within (temporal) orchards, given the carefully controlled conditions and the use of identical apple varieties (i.e., apples are clones, propagated asexually) in this study. We expected along with temperature, increased precipitation in winter and spring—when it is dry in South Korea (Seghieri et al. 2009; Zhao et al. 2013)—causes earlier

phenology. We also expected strong regional patterns in South Korea, given the wide area where apples are grown. Finally, by altering local conditions, we expected topography to effect phenology on top of climate (Böhner and Antonić 2009).

## Materials and methods

**Phenological data** We recorded phenology in 2011–2014 in 42 research orchards that span the full range of conditions where apples are grown in South Korea (Fig. S1), from 35.23° N–38.17° N latitude to 126.59° W–129.09° W longitude, and 11–661 m in elevation. All orchards were directly operated or supervised by Agricultural Research and Extension Services (ARES) fruit tree scientists and managed with cultivation methods standardized by the Rural Development Administration (RDA 2003a). A single planting system (the slender spindle) and the same apple clones—Fuji and Hongro—were used in all orchards. By carefully standardizing conditions, the orchards serve as common gardens for the study of apple biology across South Korea and, unlike in studies of phenology on observational gradients, allow external forcing factors to be better isolated. ARES teams were trained annually to uniformly apply the RDA’s phenology protocol (RDA 2003b). Budburst (defined as the date when the first green leaf tips are visible and ~50% of a tree’s bud scales are elongated 1–2 mm) and flowering (the date when ~10% of a tree’s flowers have opened) were observed each year on 3 designated trees per orchard. These are equivalent to stage 53 for budburst and stage 61 for flowering in the BBCH scale for pome fruit (Meier 2001).

**Phenology drivers** We examined the role of temperature, precipitation, and geo-topography in apple phenology. We obtained the monthly mean air temperatures and monthly total precipitation data from 2010 to 2014 from 90 weather stations (Fig. S1) operated by Korea Meteorological Administration (KMA 2016). We estimated climate for an orchard by spatially interpolating temperature and precipitation with raster functions in ArcGIS (ESRI, Redlands, CA, USA), a common step in phenology research as study sites are often distant from weather stations (Schmidt 2014). We used an inverse distance weight method to create a continuous coverage of temperature data (Yun 2004), with a lapse rate correction factor of 0.0065 °C m<sup>-1</sup> for elevation, obtained from a 30 × 30 m DEM (Tachikawa et al. 2011). Monthly precipitation data was extracted for each orchard using a kriging interpolation method (Goovaerts 2000). Latitude, elevation, slope, and aspect were extracted from the DEM. Slope and aspect were generated from the DEM using R (R Core Team 2017) and “raster” package (Hijmans 2015). For statistical analyses, aspect was transformed to a linear north–south gradient

(northness) by the cosine function, ranging from -1 (south-facing) to 1 (north-facing).

**Statistical analysis** We developed independent models of the budburst and flowering dates with multiple linear regressions for both apple varieties. As budburst and flowering occur in spring, we focused our analysis on winter and spring climate summaries: air temperatures in monthly, 2-month, and 3-month running averages from January through April and monthly precipitation in January through April. To build candidate models, we first examined each variable individually against phenology with Pearson correlations, and we examined multicollinearity among predictors, calculating cross-correlations and variance inflation factors (VIFs) to avoid regression pitfalls (Neter 1990). Precipitation can covary with temperature, for example, but can be positively or negatively associated depending on region and season (Trenberth and Shea 2005). Variables with a cross-correlation >0.40 or a VIF >1.5 were not used in the same model. Latitude and elevation had VIFs >1.5 and were highly cross-correlated with temperature (Table S1), and so were not used in the full models, but slope and northness were retained in models with climate. We used an information-theoretic approach (i.e., to avoid overfitting models; Burnham 2010) using 2-unit support intervals  $\Delta AIC_c < 2$  (approximately equivalent to a 95% support limit; Hilborn and Mangel 1997) to choose among the best models. To assess potential omitted-variable bias from restriction to this set of predictors, we also compared the magnitude and direction of modeled effects in the selected full models to those models which included latitude and elevation. Finally, we compared the representativeness of the climate during our study to the prior 30 years of climate in South Korea.

**Temporal and spatial patterns in phenology** Using linear regressions, we compared patterns in phenology within each orchard for 4 years (temporal) to the patterns between orchards along the climate gradients in a given year (spatial), and contrasted these results to a full spatiotemporal model which used all 4 years of data from all orchards. For the temporal models, 4 years of data is sufficient replication to consider just one predictor variable, so only temperature was evaluated. For the spatial models, we evaluated temperature and precipitation, and assessed the rigor of the models by comparing phenology between each of the 4 years individually and against the full model.

In addition, we conducted tests of the time-space interchangeability of phenological responses to climate to determine if apple phenology along the spatial gradient responds consistently to variation in climate. We hypothesized the patterns in a given year across orchards on the spatial gradient are

interchangeable with the temporal patterns within an orchard over the course of the study. We tested this by comparing models with “split” temperature predictors, the remaining predictors from the full model, and a latitude\*temperature interaction—which tells us if there is temperature sensitivity across orchards locations—to a “basic” model with simple temperature data, the remaining predictors from the full model, and no interaction. We split temperature into two variables: a constant mean temperature for each orchard as predicted by latitude and elevation, and a residual of this prediction and the observed temperature for the orchard. If the model using the split temperature is significantly better than the basic temperature model, this is evidence that the response to annual fluctuation in temperature is different from the response to geographic variation due to location. For each outcome, two models were fit using generalized estimating equations with an exchangeable error structure (Halekoh et al. 2006) to account for multiple measures within orchards.

Using a forward selection modeling process, we also addressed the linearity of the phenology response to temporal temperature variation and whether the phenological response to temperature fluctuation varies by location. For each cultivar, separate models of budburst and flowering were made which included the split temperature variables, the variables from the full model, and a forward selection screen of the following additional variables: the square of residual temperature (to detect a nonlinear response), latitude, the square of latitude (to detect a nonlinear response), and the interaction of latitude and residual temperature to test for location sensitivity. The forward selection process compares models using the likelihood ratio with  $P \geq 0.05$  as the stopping criterion.

**Future climate scenarios** We used the best, full model to project changes in apple phenology under the future climate scenarios, RCP4.5 and RCP8.5. Mean air temperatures and monthly precipitation for these scenarios were provided by the Korea Meteorological Administration (KMA 2017) in a spatially explicit 1-km grid using ensemble methods from five regional climate models (Suh et al. 2012; KMA 2017). These downscaled scenarios include the main regional trend of warming temperatures and increasing precipitation, as well as annual cycles and fluctuations in weather. Topographic effects were held as constants in the prediction models. For each phenophase, we calculated a 30-year moving average from annual patterns for 2020 to 2100. To examine regional variation in climate change effects, we mapped projected changes in phenology across South Korea from 2021 to 2050 and 2071 to 2100 with spatially explicit “difference” maps between current and future phenology. These maps highlight portions of the country most resistant and most sensitive to future climate change, depending on phenophase, cultivar, and spatially explicit (1-km) variation in predicted climate change (KMA 2017).

## Results

**Spring phenology and explanatory variables** The weather conditions during the 4-year study remained consistent with the range experienced in South Korea in the 30 years preceding our study, and mean values of temperature and precipitation between the two periods were very similar (Table S2). Likewise, precipitation was similar to previous patterns, though the 4-year period does not capture the entire range of past precipitation. Finally, 2011 was a very dry year in South Korea, but such conditions also occurred in 1984, 1994, 2000, 2001, and 2006 (Fig. S2).

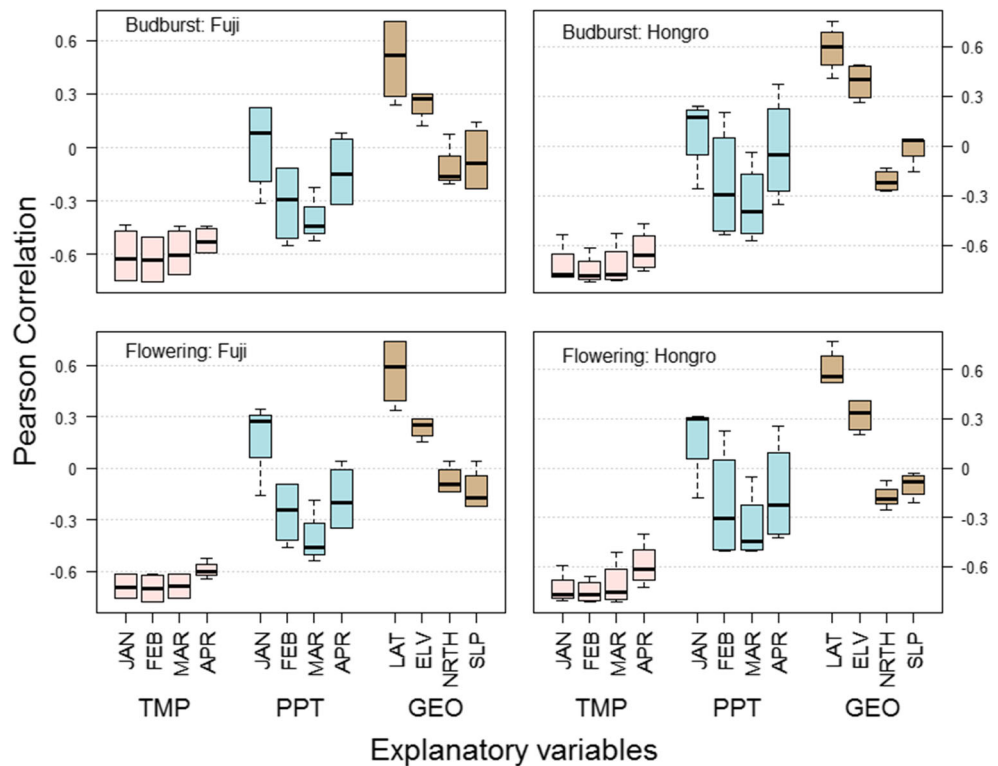
Table S3 reports mean phenology in each orchard including a summary of temperature, precipitation, and geotopographic features. Overall, there was a strong latitudinal pattern in the timing of apple phenology (Fig. S3), which occurred earlier in the warmer southern and coastal areas than in the cooler upland and northern sites. Over the full study, for Fuji, mean budburst occurred on April 3 (day of year; DOY = 93.4, range 87–102) and mean flowering on April 28 (DOY = 118.2, range 111–131); for Hongro, mean budburst occurred on March 31 (DOY = 90.4, range 79–101) and mean flowering on April 25 (DOY = 115.8, range 104–128).

Phenology consistently began earlier in warmer years and warmer sites; both cultivars had highly negative Pearson correlations with mean monthly temperatures in January through April, ranging from  $-0.38 < r < -0.79$  ( $P < 0.001$  for all correlations; Fig. 1, Table S4). Precipitation also was negatively correlated with phenology—precipitation in March consistently showed the strongest correlation ( $-0.39 < r < -0.48$ ,  $P < 0.001$ )—but the correlations were weaker and less consistent than temperature. Latitude and elevation had positive correlations with phenology (e.g., phenology began later in northern and higher sites), ranging from  $0.32 < r < 0.5$  ( $P < 0.001$ ) for latitude and  $0.19 < r < 0.28$  ( $P < 0.1$  to  $0.001$ ) for elevation. Correlations with northness were marginally significant for flowering, while slope was not significant for either cultivar.

**Models of apple phenology** Phenology was strongly correlated with spring weather. Overall, the direction ( $\pm$ ) and strength of phenological responses to both temperature and precipitation were highly similar in the temporal, spatial, and spatio-temporal models: (1) year-to-year phenology within orchards from 2011 to 2014 (temporal; Tables S5 and S6); (2) within-year phenology across the 42 orchards (spatial; Table 1); and (3) the full model of all years and orchards (spatiotemporal; Table S4).

The analysis of year-to-year phenology within orchards showed strong relationships with temporal variation in temperature—the mean  $R^2$  of simple linear models ranged from 0.69 to 0.77 across budburst and flowering in both cultivars, and despite a comparatively short period of study

**Fig. 1** Box-whisker plots of Pearson correlation coefficients for explanatory variables in each phenological phase of Fuji and Hongro apples. Calculated separately in each year (2011–2014) across the 42 orchards, the plots display interannual variation in the correlations. Climate was evaluated in January, February, March, and April as mean monthly air temperature (TMP) and monthly precipitation totals (PPT), and geo-topography (GEO) as latitude (LAT), elevation (ELV), northness (NRTH), and slope (SLP). In the plots, the black center lines denote the median value, the colored boxes contain the 25th to 75th percentiles of the data, and the whisker bars mark the minimum and maximum values that are 1.5 times the distance of the interquartile range



(4 years of observations), phenology patterns in individual orchards were highly consistent across the population: ~ 80% of orchards were within ± 1 SD of the mean response (Tables S5 and S6). Mean phenology within an orchard was negatively correlated with spring temperatures:  $-4.84 (\pm 0.32 \text{ SE})$  for Fuji and  $-4.55 (\pm 0.31 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  for Hongro budburst (Table S5), and  $-4.32 (\pm 0.32 \text{ SE})$  for Fuji and  $-4.27 (\pm 0.30 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  for Hongro flowering (Table S6). Within-year phenology along the spatial gradient showed similar but slightly weaker patterns (Figs. 2 and 3; Table 1).

Models using generalized estimating equations to evaluate the time-space interchangeability of the predictors provided different results for flowering and budburst phenology. For flowering phenology, the split temperature model was not a significant improvement on the model with a single temperature term for either cultivar:  $P = 0.47$  for Fuji flowering and  $P = 0.57$  for Hongro flowering. Likewise, forward selection models showed linear models of flowering phenology are superior to nonlinear models, and the assumption of time-space interchangeability is robust.

Patterns were more nuanced for budburst phenology in both Fuji and Hongro, as replacing the simple temperature predictor with a two-part temperature predictor improved the models. For Fuji budburst, the best forward selection model retained the split temperature predictors but not any other variables. However, predicted differences in Fuji budburst phenology between models were modest: budburst changed from  $-3.22 (\pm 0.22 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  for the basic model to  $-$

$3.96 (\pm 0.28 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  for the forward selection model. For Hongro budburst, the split temperature predictors and the interaction term (latitude\*residual temperature) were significant, indicating a decrease in the sensitivity of budburst to warmer spring temperatures at higher latitudes in this cultivar:  $-5.34 (\pm 0.45 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  at the minimum latitude,  $-4.32 (\pm 0.26 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  at the median latitude, and  $-2.75 (\pm 0.48 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  at maximum latitude, compared to  $-3.53 (\pm 0.21 \text{ SE})$  days  $^{\circ}\text{C}^{-1}$  in the basic model. Thus, we conclude that the phenology of budburst in both cultivars is sensitive to latitude as well as temperature, but the effects overall are modest. Given the comparable results among models and the more conservative estimates in the basic model, we emphasize below spatiotemporal models based on the basic model.

Table 2 shows the best fits among the evaluated models for the full linear regression models of budburst and flowering (see Tables S7 and S8 for full comparisons). The amount of variation explained by the best models varied from 61.8 to 71.0% (adjusted  $R^2$ ). The effects of temperature and precipitation were statistically significant in all of the full models. With other factors held constant, phenological sensitivity ranged from  $-3.2$  to  $-3.4$  days  $^{\circ}\text{C}^{-1}$  for air temperature and  $-0.05$  to  $-0.06$  day  $\text{mm}^{-1}$  for March precipitation in the combined model. Northness was retained for all models except Fuji flowering, but only marginally improved the models compared to climate alone ( $\Delta\text{AIC}_c = 1.20$ ) (Table S7). Sensitivity to northness was  $0.2$  days  $\text{unit}^{-1}$  to  $1.6$  days  $\text{unit}^{-1}$ ; e.g., for Fuji, it was  $1.25$  days  $\text{unit}^{-1}$ , meaning

**Table 1** Linear regression parameters of phenology modeled by temperature or precipitation along spatial gradients, comparing year-to-year and all-years relationships over the 4-year period of the study. For temperature, budburst was modeled on mean temperature in February–March and flowering was modeled on mean temperature in February–April. Budburst and flowering were both modeled on precipitation in March in a given year

Temperature	2011	2012	2013	2014	All-years
<b>Budburst</b>					
Fuji (day °C <sup>-1</sup> )	-1.553	-1.692	-3.181	-2.925	-3.320
R <sup>2</sup>	0.227	0.260	0.552	0.378	0.557
P value	0.001	0.001	0.000	0.000	0.000
Hongro (day °C <sup>-1</sup> )	-2.436	-2.252	-3.608	-3.509	-3.615
R <sup>2</sup>	0.387	0.401	0.604	0.463	0.620
P value	0.000	0.000	0.000	0.000	0.000
<b>Flowering</b>					
Fuji (day °C <sup>-1</sup> )	-2.308	-2.300	-3.814	-3.730	-3.501
R <sup>2</sup>	0.606	0.635	0.635	0.334	0.655
P value	0.000	0.000	0.000	0.000	0.000
Hongro (day °C <sup>-1</sup> )	-2.645	-2.308	-4.147	-3.910	-3.695
R <sup>2</sup>	0.551	0.617	0.624	0.311	0.636
P value	0.000	0.000	0.000	0.000	0.000
<b>Precipitation</b>					
<b>Budburst</b>					
Fuji (day mm <sup>-1</sup> )	-0.201	-0.085	-0.150	-0.065	-0.091
R <sup>2</sup>	0.049	0.274	0.197	0.195	0.153
P value	0.157	0.000	0.003	0.003	0.000
Hongro (day mm <sup>-1</sup> )	-0.199	-0.094	-0.168	-0.088	-0.098
R <sup>2</sup>	0.034	0.292	0.208	0.303	0.167
P value	0.245	0.000	0.003	0.000	0.000
<b>Flowering</b>					
Fuji (day mm <sup>-1</sup> )	-0.033	-0.062	-0.189	-0.057	-0.094
R <sup>2</sup>	0.002	0.242	0.329	0.092	0.197
P value	0.794	0.001	0.000	0.057	0.000
Hongro (day mm <sup>-1</sup> )	-0.051	-0.065	-0.180	-0.088	-0.110
R <sup>2</sup>	0.003	0.253	0.248	0.159	0.234
P value	0.736	0.001	0.001	0.014	0.000

budburst in north-facing sites was delayed 1.25 days compared to flat sites and 2.5 days compared to south-faced sites.

**Future climate scenarios** Figure 4 shows the effects of projected climate change on phenology, averaged across all of South Korea. Under RCP 4.5, spring phenology occurs progressively earlier until the 2070s, advancing a total of 2.4–13.6 days depending on phenophase and cultivar; under RCP 8.5, phenology occurs progressively earlier through the full forecast, advancing a total of 2.8–14.2 days. Contrasts of the full models with temperature-only models were made for both scenarios. For budburst dates in RCP 4.5, there was no difference in best vs. temperature-only phenology from 2021 to 2050; from 2051 to 2080, best-model apple phenology was 1.4 days earlier on average than in temperature-only, with the gap tapering to 1 day in the final period (2071–2100). Under RCP 8.5, budburst dates were 0.5–0.6 days earlier in the best models in 2021–2050, 1.3 days earlier in 2051–2080, and 0.9 days earlier in 2071–2100. Flowering trends between the two models were similar to budburst.

Figure 5 shows spatially explicit patterns of cumulative days of change in current vs. future in apple phenology across South Korea. Cumulative change was substantial in an inland area north of the southern coast and in mountainous areas, including several major apple cultivation areas in Gyeongbuk and Gyeongnam provinces, while coastal areas and some central inland areas were comparatively resistant. These comparisons show budburst phenology is more spatially variable than flowering, with flowering phenology advancing more uniformly across South Korea in all scenarios. Fuji will retain more area of the country than Hongro where its phenology is less advanced (e.g.,  $< \sim 15$  days), but long-term patterns for both cultivars will ultimately depend on future climate change, with the RCP 8.5 scenario eventually advancing phenology earlier by  $> 25$  days in all instances.

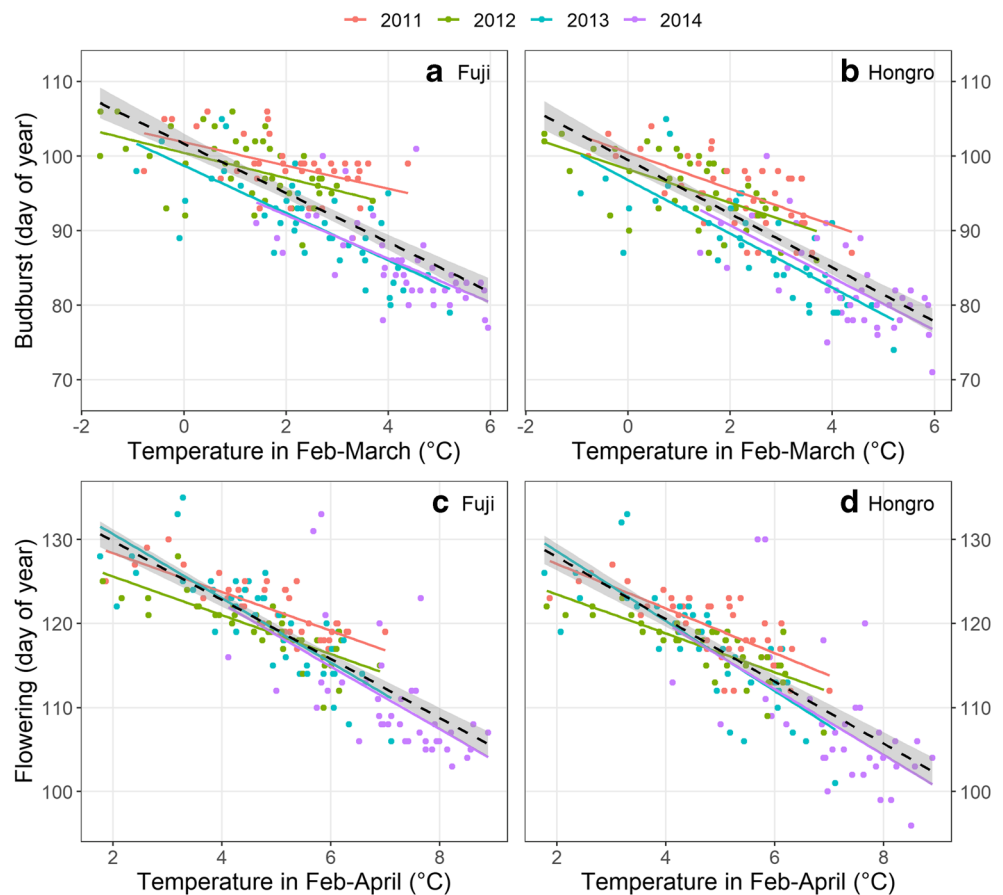
## Discussion

**Apple phenology and climate** Temperature is the primary determinant in temperate and boreal plant phenology, and apple phenology in South Korea is no exception as all models had temperature as the main predictor, with spring temperatures alone explaining 0.58–0.65 (adjusted  $R^2$ ) of variation in phenology. Depending on phenophase and cultivar, apple phenology in South Korea advanced 3.2 to 3.5 days for each degree Celsius of higher temperature, much like the effect of spring temperatures on apples in Japan, Germany, and South Africa, where flowering advanced 3.8 days °C<sup>-1</sup> (Fujisawa and Kobayashi 2010), 4.6 days °C<sup>-1</sup> (Chmielewski et al. 2011), and 2.4 to 4.2 days °C<sup>-1</sup> (Grab and Craparo 2011), respectively.

Precipitation is also an important influence on apple phenology in South Korea, with higher March precipitation associated with earlier budburst and flowering, alone or in combination with temperature. Phenology changed by as much as 10 days when modeled alone over the full range in March precipitation from 2011 to 2014 (6–126 mm; Fig. 3), which is  $\sim 42.5\%$  of the range in phenology associated with February–March temperatures. Spring temperatures and precipitation in March had very little cross-correlation ( $r < 0.05$ , Table S1), suggesting these patterns are largely independent; however, when combined in the full model with temperature, precipitation has only a small cumulative impact on phenology in climate change scenarios (Fig. 5).

Despite the potential importance of environmental effects beyond temperature (Badeck et al. 2004; Cleland et al. 2007; Gordo and Sanz 2010), few studies have evaluated how precipitation can alter the phenology of trees. These studies report similar patterns to our study: higher precipitation accelerates budburst in birch trees (*Betula pubescens*) and the flowering of plums (*Prunus domestica*) (Wielgolaski 2001), and an experimental study in a semiarid ecosystem found higher

**Fig. 2 a–d** Linear regressions of variation in spring phenology with mean temperatures in Feb–March or Feb–April from 2011 to 2014 across 42 research orchards in South Korea. The dashed black lines and shaded 95% confidence intervals show the entire 4-year period modeled at once, and the colored lines show each year modeled individually



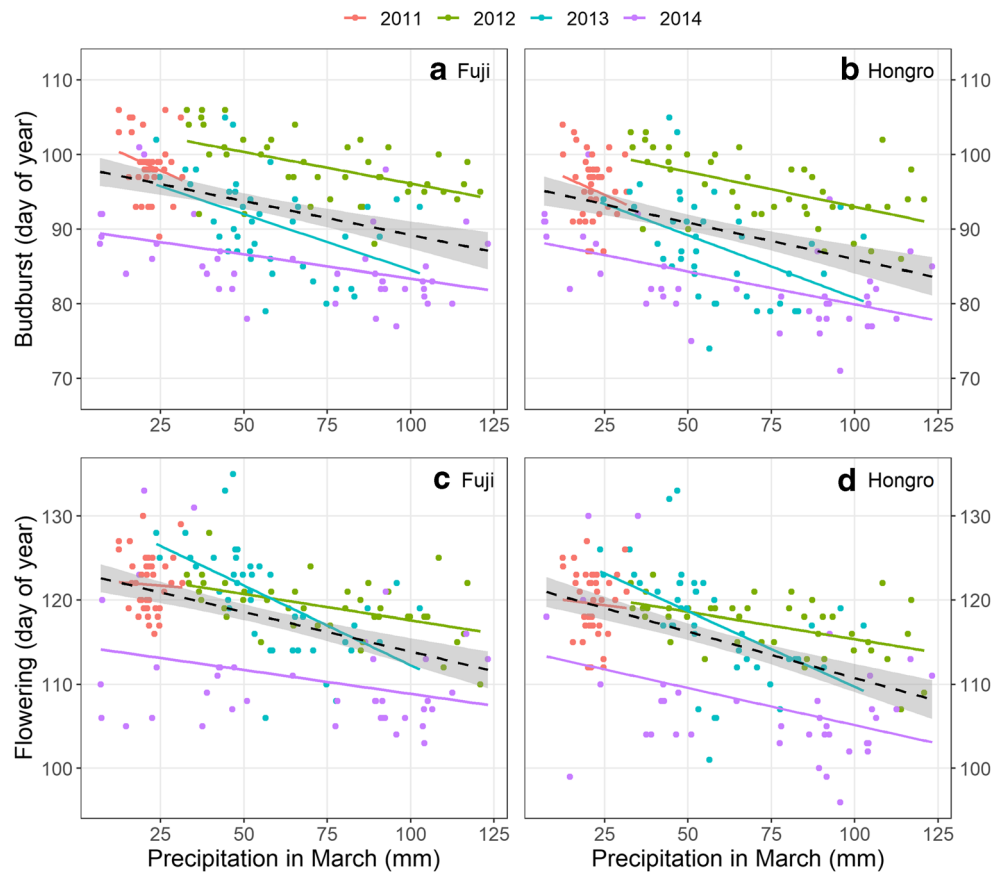
precipitation advanced needle emergence in piñon pine (*Pinus edulis*) (Grossiord et al. 2017). In dry biomes, however, phenology research has incorporated precipitation, where it can play a greater role than temperature (Wielgolaski 1974). It is assumed that the onsets of rains, coincident with appropriate temperatures, are needed to stimulate budburst and flowering in these biomes (Borchert 1994; Tewari et al. 2016). In warm, dry regions of southern Iberia, for example, greenup onset is triggered by autumn rains; even in mesic portions of Iberia, rainfall has a stronger influence than temperature on fruiting phenology (Peñuelas et al. 2004). Similarly, South Korea is dry during most of the dormant season—typically < 10% of total annual precipitation occurs in January–March—making year-to-year variation in precipitation during these months an important influence on spring phenology.

Unlike temperature, the effects of increased precipitation can be ambiguous, having either positive or negative influences on phenology depending on the background climate conditions in a region (Chiou et al. 2015; Ramírez 2015). Extended rainy and heavily cloudy conditions can delay or stop tree flowering altogether, as seen in mango trees (*Mangifera indica*) in the tropics (Ramírez et al. 2010) and delayed bloom dates in apple trees in South Africa (Grab and Craparo 2011). Of course, in tropical latitudes and aseasonal habitats, there is little temperature seasonality and freezing

temperatures generally do not occur except at high elevations (Sherman et al. 2012; Martin and Fahey 2014), so it is unsurprising that tropical phenology is synced with seasonal variation in precipitation (e.g., drought deciduousness in semiarid tropical forests). How phenology might change on tropical mountains with warming—where climate regimes (e.g., the trade-wind inversion; Martin and Fahey 2014) can create conditions similar to both lowland tropical and temperature latitudes—is largely unexplored (Martin and Bellingham 2016). Phenology in aseasonal forests may also be more sensitive to variation in local vegetation structure and composition—which can be highly variable due to ubiquitous natural and human disturbances in many tropical ecosystems (e.g., Crausbay and Martin 2016)—creating strong stand and patch-scale gradients in microclimate.

Overall, these studies suggest a potentially important role for precipitation in the dynamics of phenology under climate change—while temperature is unambiguously forecast to increase with varying intensities across the planet, climate models show precipitation potentially increasing, decreasing, or unchanging, while also changing in form (snow vs. rain), intensity, and timing, all on a region-by-region basis (e.g., Karl et al. 2009). Hence, in regions where precipitation influences phenology, future precipitation patterns can interact with temperature to alter trajectories and trends in phenology.

**Fig. 3** Linear regressions of variation in spring phenology with monthly precipitation in March from 2011 to 2014 across 42 research orchards in South Korea. The dashed black lines and shaded 95% confidence intervals show the entire 4-year period modeled at once, and the colored lines show each year modeled individually



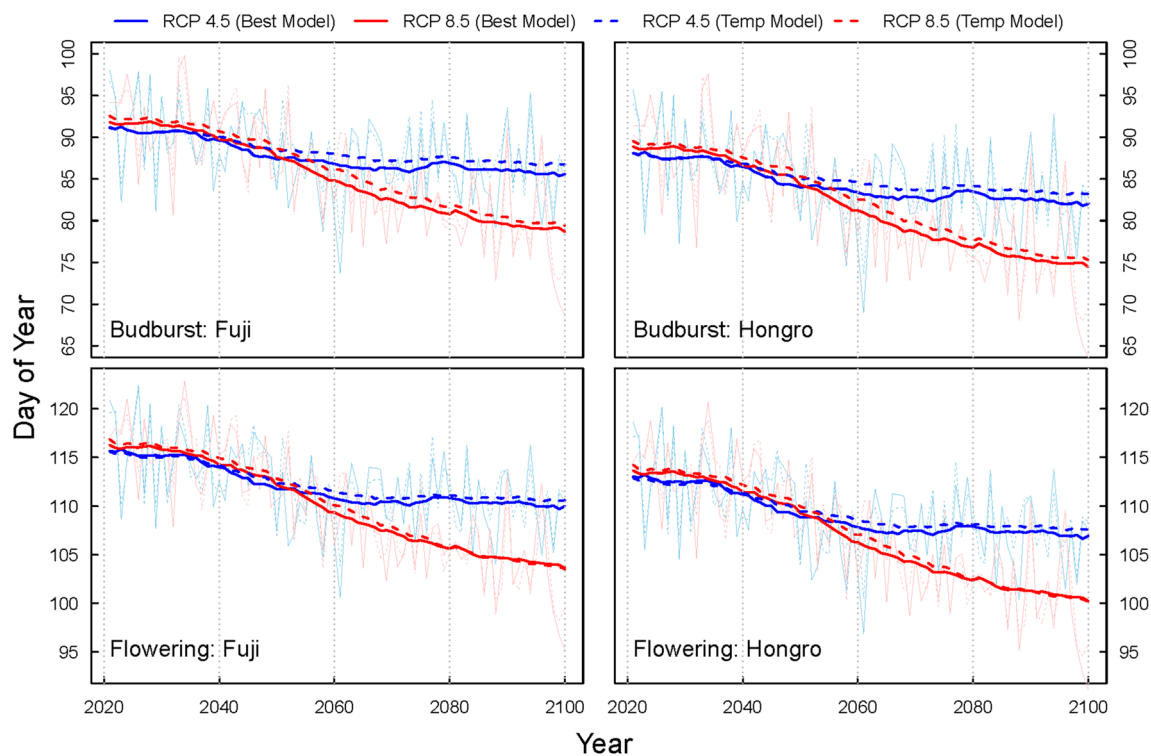
**Table 2** Full linear models of budburst and flowering in Fuji and Hongro cultivars, combining in a single model phenological day of year (DOY), temperature, precipitation, and topographic variables across 42

research orchards over 4 years. All alternate models evaluated are described in Tables S7 and S8

Dependent variable	Predictor (abbr.)	Parameter estimate	P	Partial R <sup>2</sup>	Model				
					Adjusted R <sup>2</sup>	df	F	P	
<b>Fuji apple</b>									
Budburst (DOY)	Mean air temperature across February to March ( $T_{FebMar}$ )	-3.216 (day °C <sup>-1</sup> )	<0.0001	0.555	0.618	3164	91.1	<0.0001	
	Precipitation in March ( $P_{Mar}$ )	-0.056 (day mm <sup>-1</sup> )	<0.0001	0.129					
	Northness ( $N$ )	1.254 (day unit <sup>-1</sup> )	0.0238	0.031					
Flowering (DOY)	Mean air temperature across February to April ( $T_{FebMarApr}$ )	-3.220 (day °C <sup>-1</sup> )	<0.0001	0.644	0.710	2163	203.2	<0.0001	
	Precipitation in March ( $P_{Mar}$ )	-0.053 (day mm <sup>-1</sup> )	<0.0001	0.171					
<b>Hongro apple</b>									
Budburst (DOY)	Mean air temperature across February to March ( $T_{FebMar}$ )	-3.531 (day °C <sup>-1</sup> )	<0.0001	0.638	0.694	3163	126.2	<0.0001	
	Precipitation in March ( $P_{Mar}$ )	-0.061 (day mm <sup>-1</sup> )	<0.0001	0.167					
	Northness ( $N$ )	1.592 (day unit <sup>-1</sup> )	0.0023	0.056					
Flowering (DOY)	Mean air temperature across February to April ( $T_{FebMarApr}$ )	-3.412 (day °C <sup>-1</sup> )	<0.0001	0.619	0.710	4158	100.1	<0.0001	
	Precipitation in March ( $P_{Mar}$ )	-0.058 (day mm <sup>-1</sup> )	<0.0001	0.167					
	Northness ( $N$ )	0.177 (day unit <sup>-1</sup> )	0.0170	0.001					

Northness: aspect of the north (1)–south (-1) gradient





**Fig. 4** Moving 30-year averages (bold lines) of future budburst and flowering dates for Fuji and Hongro apples across South Korea. Forecasts were made using the full model (Table 2) and temperature-

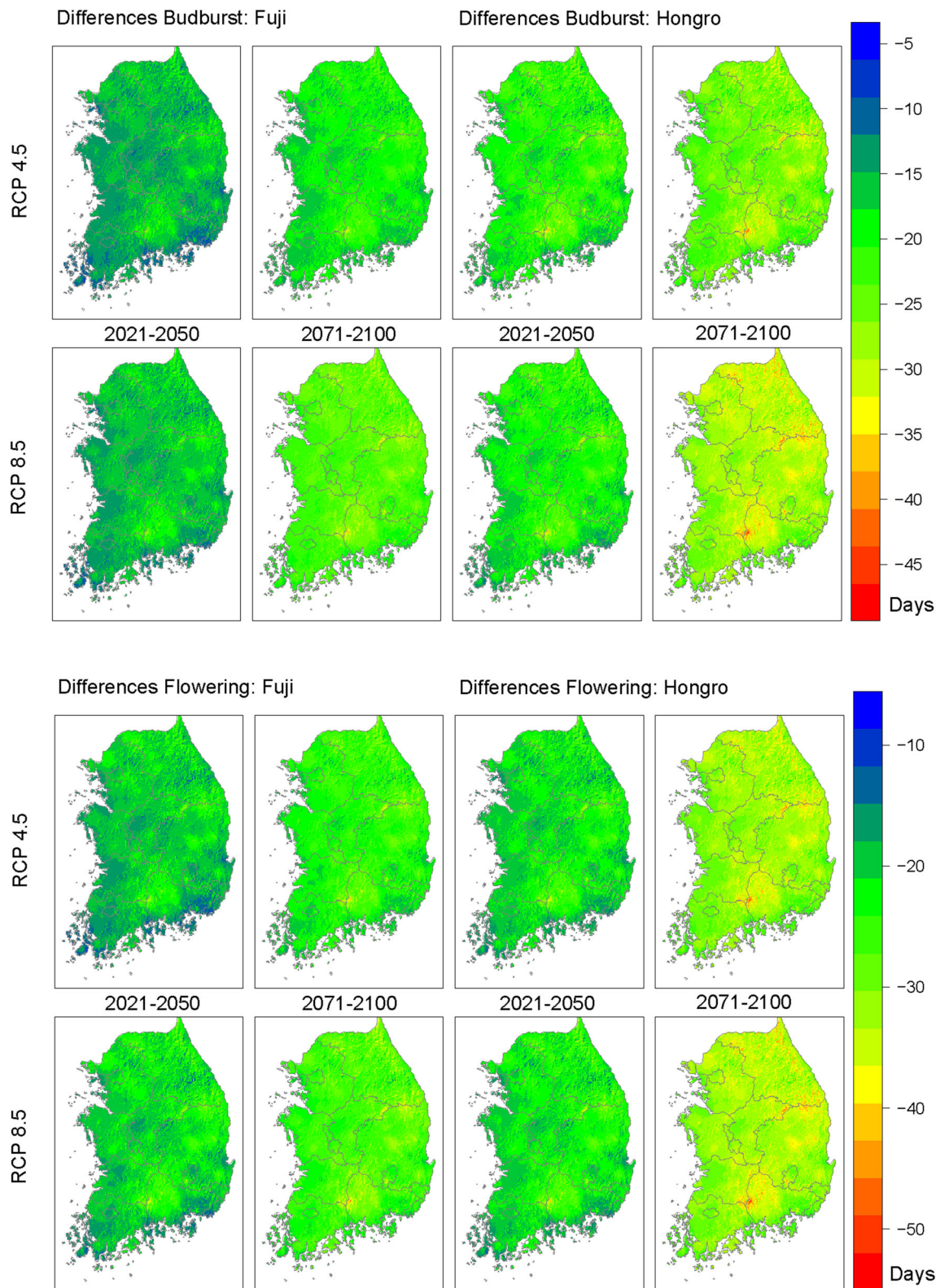
only models for future scenarios RCP4.5 and RCP 8.5. Moving 30-year averages highlight the main trend by averaging short-term fluxes in phenology (thin lines) resulting from annual fluctuations in weather

In particular, deleterious effects of higher temperatures on phenology in such regions could be buffered or amplified by shifts in precipitation in unexpected ways, highlighting the need to consider precipitation in phenology models.

**Spatial and temporal patterns** Spatial gradients are useful in assessing phenological responses to climate, especially when long time series are not available or are poorly replicated (Jochner et al. 2013), and studies with both temporal and spatial data can help elucidate how phenology responds to climatic variability both within and between populations of species. Our analysis found the effect of temperature on phenology was highly comparable between the temporal and spatial datasets, although year-to-year temporal variation in temperature within an orchard on average caused a stronger response (mean  $-4.41 \pm 2.25$  (SD) days  $^{\circ}\text{C}^{-1}$ , Tables S5 and S6) than variation in temperature along spatial gradients (mean  $-2.89 \pm 0.82$  (SD) days  $^{\circ}\text{C}^{-1}$ , Table 1). Given the controlled conditions across the orchards and use of clones as the organism of inquiry, the similarity of temporal and spatial phenology patterns in our study are likely higher than phenological variation would be when studied across natural settings (e.g., Jochner et al. 2013), as local adaptation and local differentiation between populations can modify the response of trees to climate variation along spatial gradients (Buechling et al. 2017). There is evidence, however, that apple clones can physiologically acclimate their heat requirements to changing

conditions between orchards (Eccel et al. 2009), suggesting even the phenology of trees in apple orchards may be dynamic over time as temperatures change.

**Conclusions** Our research has important implications for the apple and fruit tree industries. Based on our phenology models and forecasted climate change in the region, budburst and flowering will continue to occur progressively earlier over the coming decades. Such changes may create problems for apple production or even tree vigor, as earlier phenology increases the risks of damaging spring frosts. Increasing temperatures and shorter winters may reduce frost risks as phenology advances (Legave et al. 2015), but some research has found that spring frost risk remains stable or only slightly decreases in the future (Eccel et al. 2009). Problems also could develop for varieties that are cross-pollinated with another apple or crabapple variety, and there is an increasing risk of phenological mismatches between apple flowering and pollinators. For wild apples and some commercial orchards, pollination is mostly carried out by insects whose phenology is also shifting with climate change (Hodgson et al. 2011; Bartomeus et al. 2011; Bartomeus et al. 2013). More experimental work is needed on phenology, especially to address the role of nontemperature effects. Finally, our study highlights how regional influences on local climates (e.g., coastal areas) should be considered when developing policies and adaptation strategies for apple production in future climates.



**Fig. 5** Spatial patterns of cumulative change in current vs. future in apple phenology across South Korea under two climate scenarios, RCP4.5 and RCP8.5. Phenology was projected using 30-year averages (Fig. 4).

Spatial variation in the projections originates from fine-scale, spatially explicit variation in predicted climate change for South Korea

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## Compliance with ethical standards

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

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