

ENSO and frost codetermine decade-long temporal variation in flower and seed production in a subtropical rain forest

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Summary

1. Flower and seed production of plants can be greatly influenced by both natural climatic oscillations and local weather extremes. However, owing to the rarity of long-term monitoring studies conducted at a sufficient temporal scale to capture climatic oscillations and the unpredictability of extreme weather events, evidence that demonstrates how these two external forcings act in concert to drive plant reproduction remains scarce.

2. In addition, considerable variation in species' phenological responses to the external climatic forcings was often observed. Phylogenetic relationships may mediate this interspecific variation, but previous studies yielded inconsistent results when testing this hypothesis.

3. We monitored the flower and seed production in a subtropical rain forest, Fushan, Taiwan (24°45'N, 121°35'E), for over 10 years (since September 2002). In March 2005, a record low temperature (−1.3 °C) occurred at Fushan and caused great frost damage to plants. We used weekly phenological records and long-term meteorological data to assess the effects of climatic fluctuations and extreme weather event on plant reproductive output.

4. We show that the El Niño Southern Oscillation (ENSO) indices, which integrated local climatic variables at Fushan over several months, were strongly associated with flower and seed production. The 2005 spring frost also had long-lasting effects on the flower and seed production of several species.

5. In particular, we detected phylogenetic signals in the relationships between phenological responses of flowering production and several climatic variables (maximum temperature, irradiance and ENSO34 index). By contrast, the relationships between seed production and climatic variables, as well as phenological responses to the frost event, did not exhibit a phylogenetic signal.

6. *Synthesis.* Our findings add to the growing evidence that together the natural climatic oscillation (ENSO) and the extreme weather event (frost) determined the temporal variation in flower and seed production. In addition, phylogenetically closely related species resembled each other in their flowering responses to abiotic variation in this subtropical rain forest. Improved understanding of these abiotic and biotic interactions may help predicting population- and community-level phenological responses under future climate changes.

Key-words: El Niño Southern Oscillation, extreme weather events, frost, Fushan Forest Dynamics Plot, phenology, phylogenetic signal, reproductive ecology

Introduction

Understanding interannual variation in flower and seed production is key to predicting dynamics of terrestrial ecosystems

in response to environmental changes. Temporal variation in plant reproductive production not only has great influence on the recruitment of plant population themselves (Shibata & Nakashizuka 1995; Connell & Green 2000; Norden *et al.* 2007), but also can create large resource pulses in an ecosystem, initiating trophic cascades of ecosystem

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effects (Wright *et al.* 1999; Curran & Leighton 2000; Ostfeld & Keesing 2000). Large-scale climatic oscillations, such as the El Niño Southern Oscillation (ENSO), influence plant reproduction through altering local climatic variation (Wright *et al.* 1999; Kelly & Sork 2002; Schaubert *et al.* 2002; Post 2003; Wright & Calderón 2006). Local weather extremes, such as spring frost, also have great impact on plant reproduction (Inouye 2008; Augspurger 2009; Wipf, Stoeckli & Bebi 2009). As climate change may alter the frequency and intensity of the ENSO and spring frost (Collins *et al.* 2010; Augspurger 2013; IPCC, 2013), there is a growing concern regarding how these changes will affect ecosystem functions through changing plant life-history events (e.g. Schaubert *et al.* 2002; Wright & Calderón 2006).

The El Niño Southern Oscillation (ENSO) is one of the prominent large-scale climate patterns and has profound effects on both aquatic and terrestrial ecosystems (Holmgren *et al.* 2001; Stenseth *et al.* 2002; McPhaden, Zebiak & Glantz 2006). Climatic anomalies caused by the ENSO affect plant metabolism and, as a result, influence plant reproduction. In temperate ecosystems, temperature anomalies related to the ENSO trigger mast flowering or seeding in plant communities (Koenig & Knops 1998; Schaubert *et al.* 2002). In tropical moist forests, heavy flower and fruit production are significantly associated with unusually high irradiance or dry conditions caused by El Niño events (van Schaik 1986; Wright *et al.* 1999; Numata *et al.* 2003; Sakai *et al.* 2006; Wright & Calderón 2006). However, assessing the effect of (either local or large-scale) climatic fluctuations on ecological processes is challenging, due to the noisy and complex interactions in environmental and ecological systems (Wood 2010).

Extreme weather events, though unpredictable, often are ecologically more important than natural fluctuations in climate (Easterling *et al.* 2000; Meehl *et al.* 2000; Parmesan, Root & Willig 2000). Frost, heat waves, drought or heavy rainfall can have serious negative impacts on plant growth, survival and reproduction (Inouye, Morales & Dodge 2002; Rich, Breshears & White 2008; Jentsch *et al.* 2009; Piessens *et al.* 2009; Wipf, Stoeckli & Bebi 2009). For example, spring frost could damage developing leaves and flowers and even kill a plant (Inouye 2000). Because plant species exhibit different susceptibility to frost damage, frost damage may differentially affect plant vital rates and thus change population demography, forest regeneration and relative species abundance in plant communities (Inouye 2000, 2008; Augspurger 2009). The loss of flowers and therefore seeds also has profound effects on trophic interactions. In deciduous forests of south-eastern Ohio, a spring frost in 1966 resulted in no fruit production of *Quercus* and *Fagus* trees, causing populations of squirrels, which depended on acorns as their major food items, declined sharply due to a cessation of breeding, plus higher emigration and/or mortality (Nixon & McClain 1969). Nonetheless, only a limited number of studies have documented the effects of frost damage on plant reproduction at the community level (Augspurger 2009).

While there are prominent effects of climatic fluctuations on plant reproduction at the community level, considerable

interspecific variation was frequently observed in phenological responses to the external forcings (Fitter & Fitter 2002; Davis *et al.* 2010; CaraDonna, Iler & Inouye 2014). Phylogenetic relationships between species may mediate the species-specific phenological responses to climatic variation due to shared evolutionary history. Physiological responses to environmental cues may be conserved among phylogenetically closely related species. Many studies based on various scales (from community-level to global scale) showed that closely related species generally have similar phenological schedules (e.g. Kochmer & Handel 1986; Wright & Calderón 1995; Boulter, Kitching & Howlett 2006; Chang-Yang *et al.* 2013; Davies *et al.* 2013; Du *et al.* 2015). However, investigation of phylogenetic relationships in phenological responses to climatic variation yielded inconsistent results. For example, Davis *et al.* (2010) reported that closely related species exhibited similar shifts in first flowering dates as they responded to recent temperature change in two distant plant communities. In contrast, Wolkovich *et al.* (2013) and CaraDonna & Inouye (2015) showed that there was no phylogenetic signal in phenological sensitivity to climate change. Evidence from long-term studies is needed to further verify this phylogenetic hypothesis of phenological sensitivity to climatic fluctuation. If the closely related species exhibit similar responses to climatic variation, phylogenetic relatedness may be used as a surrogate for predicting community- and ecosystem-level changes under expected climate change (Buckley & Kingsolver 2012; Wolkovich, Cook & Davies 2014).

Despite the significant impact of natural climatic fluctuations and extreme weather events, studies that simultaneously evaluate the roles of these two external forcings on plant reproduction remain scarce. Moreover, evidence of how climatic forcings regulate plant reproductive output largely comes from studies focusing on a single or a few species (e.g. Inouye, Morales & Dodge 2002; Richardson *et al.* 2005; Övergaard, Gemmel & Karlsson 2007; Drobyshev *et al.* 2010; Smaill *et al.* 2011). Documentation is rare for entire communities because both community-wide phenological observations and frost events are rare. In this study, we monitored flower and seed production weekly from 2002 to 2012 in a subtropical rain forest of northern Taiwan. During the study period, a rare frost event occurred in March 2005 and caused great damage to flowers, flower buds and new leaves of many plant species. This provided a unique opportunity to evaluate the effects of rare weather extreme and natural climatic fluctuations on temporal variation in plant reproduction. We used long-term meteorological data and quantitative flower/seed records to quantify the association among flower (or seed) production, local climatic factors and regional climatic fluctuation (*i.e.* ENSO) and to assess the impact of the frost event on flower (or) seed production. We expected that both climatic fluctuations (local and regional) and the rare frost event significantly influence the temporal variation in plant reproductive output. In addition, we expected that the species' responses to climatic variation would exhibit significantly phylogenetic signal because physiological responses may be evolutionarily conserved among closely

related species. In sum, our study aimed to test whether the climatic factor (ENSO) and the extreme weather event (frost) together determined the interannual or decadal variation in flower and seed production, and whether phylogenetically closely related species responded similarly to these climatic factors.

Materials and methods

STUDY SITE AND CLIMATE

This study was conducted in the 25-ha Fushan Forest Dynamics Plot (FDP; 24°45' N, 121°35' E; 600–733 m asl) in north-eastern Taiwan. A total of 114 354 individuals belonging to 110 woody plant species were recorded in the plot (Su *et al.* 2007). Fushan has a very moist and seasonal climate (Fig. S1) (Lu *et al.* 2000; Lu, Hwang & Huang 2009), and supports a subtropical rain forest, according to the Holdridge's life-zone system (Holdridge 1947). The climate of Fushan is strongly influenced by north-eastern monsoon in winter and by typhoons in summer and autumn. Between 1990 and 2012, the annual precipitation ranged from 2740 to 7440 mm, with a mean of 4100 mm. The monthly average of relative humidity exceeds 90% throughout the year. The mean annual temperature is 18.3 °C, ranging from 11.9 °C in January to 24.5 °C in July. Solar irradiance is highly correlated with temperature, exhibiting a peak in July and a trough between November and December. Weather data were collected at the Fushan meteorological station, which is 3 km from the study plot. A detailed plot description can be found in Su *et al.* (2007, 2010).

QUANTITATIVE PHENOLOGICAL RECORDS

We used a sampling network of 87 traps in the Fushan FDP to collect quantitative flower and fruit records, following the protocol used in the FDP on Barro Colorado Island, Panama (Wright & Calderón 1995, 2006). Each trap consisted of a 1.6-mm nylon-mesh net hung at 0.8 m above the ground on a 0.5-m² PVC frame. The average distance between nearest traps was 18.2 ± 2.5 m (mean \pm SD). All traps were censused weekly from 1 September 2002 until present (2015). In each weekly census, all plant reproductive parts received in the traps were collected and identified to species. The presence of flowers, including part of flowers (such as corollas or stamens), was recorded. Mature seeds and fruits (with filled endosperm) were counted. For species with more than one seed per fruit, the number of seeds within each fruit was also counted. We identified most samples to the species level with a few exceptions (Table S1). Throughout the paper, we loosely refer to all taxa with the term 'species'.

In this study, we used data from 1 September 2002 to 29 August 2012, a total of 516 weekly censuses (five censuses were discarded due to missing data). To ensure that multiple individuals were sampled, only species with ten or more flower/seed records encountered in five or more traps in at least 1 year were included in the analysis. A total of 44 and 28 species met this criterion for flower and seed fall, respectively (Table S1).

ENSO INDICES

The monthly sea surface temperature (SST) indices (ENSO34, ENSO4) and the Southern Oscillation Index (SOI) were obtained from the Climate Prediction Center, NOAA ([http://](http://www.cpc.ncep.noaa.gov/data/indices)

www.cpc.ncep.noaa.gov/data/indices). The ENSO SST indices are negatively correlated with the SOI. El Niño and La Niña events were identified when the 5-month running average of the monthly SST anomalies (differences between monthly average and the long-term mean of the 1981–2010 base period) was $> +0.4$ °C and < -0.4 °C for at least 6 months, respectively (Trenberth 1997).

COMMUNITY RESPONSE TO INTERANNUAL CLIMATIC VARIATION

We examined cross-correlations of time series between the number of species flowering (or fruiting) each month and monthly climatic variables. We created two phenological time series, the number of species flowering and fruiting each month, by pooling 516 weekly censuses into 120 months. When census week spanned two consecutive months, it was assigned to the month with more census days. The effects of five local climatic variables (mean temperature, maximum temperature, minimum temperature, irradiance and rainfall) and three ENSO indices (ENSO34, ENSO4 and SOI) (Fig. S2) were investigated with time-lags of 0–18 months. We used stationary bootstraps for hypothesis testing in correlation analysis in order to account for serial correlation in time-series data (Politis & Romano 1994; Hsieh *et al.* 2009; Patton, Politis & White 2009; Tsai *et al.* 2014). The bootstrap procedure starts from randomly drawing a number X_1 from the original time series. Then, with probability p , the next number X_2 is selected randomly, and with probability $(1-p)$, X_2 is chosen as the next observation from original time series following X_1 . The probability p is determined based on the autocorrelation structure of the original time series (Patton, Politis & White 2009). The resampling procedure was carried out 5000 times to compute the 95% confidence limits of the correlation coefficient for hypothesis testing. The accelerated bias correction method was used to adjust confidence limits (Efron & Tibshirani 1993). Seasonality was removed from each monthly time series using a seasonal-trend decomposition procedure (Cleveland *et al.* 1990) before performing the correlation analysis. Since some of the local climatic variables are correlated with each other (Fig. S3), the results of correlation should be interpreted with caution.

SPECIES RESPONSE TO INTERANNUAL CLIMATIC VARIATION

To investigate whether the flowering (or fruiting) intensity tracked climatic variation, we examined the Pearson correlation coefficients between flower (or seed) production and climatic variables at the interannual scale for each species. We investigated the effects of the above-mentioned five local climatic variables and the ENSO indices. Because all three ENSO indices yielded similar results and the ENSO34 index generally showed higher correlations with flower (or seed) production, we report only the results of the ENSO34 index for simplicity. Annual flower production was measured as the number of times flowers were present (*i.e.* the total number of trap-census combinations that received flowers) in 1 year. Annual seed production was measured as the total number of seeds collected in 1 year. Annual flower and seed production were assigned to meteorological years using mean flowering and fruiting dates, respectively (Wright & Calderón 2006). We defined meteorological years as beginning on 1 March to capture the climate seasonality at Fushan (Chang-Yang *et al.* 2013). Annual mean of each climatic variable was computed for each meteorological year. Annual flower and seed production were natural log-transformed (after adding 1) prior to the analyses to improve normality.

Because plants might only respond to climate conditions of a certain season, we also considered the correlations between annual flower (or seed) production and seasonal means (four quarters are MAM, JJA, SON and DJF) of each climatic variable. The mean values of each climatic variable in the previous autumn (SON) and winter (DJF) were also included. A total of seven different time periods were investigated for each climatic variable. The quarter with the highest correlation with flower (or seed) production was considered to be the quarter whose climate best predicted reproductive output.

FROST EFFECT

To evaluate whether the frost event in 2005 had a long-lasting impact on plant reproduction, mean annual flower (or seed) production before and after the frost event were compared for each species using 95% confidence limits of the means obtained from 1000 bootstraps. Significantly higher or lower production after frost was considered as a positive or negative effect of frost, respectively. The frost effects were then coded as 1, 0 and -1 for positive, neutral and negative effects, respectively, for further phylogenetic signal testing.

PHYLOGENETIC SIGNAL IN PHENOLOGICAL RESPONSES TO CLIMATIC FORCINGS

To evaluate whether phylogenetically closely related species have similar phenological responses to climatic variation, we quantified phylogenetic signal in correlations between flower (or seed) production and climatic variables (irradiance, rainfall, mean temperature, maximum temperature, minimum temperature and ENSO34 index) using the Blomberg's *K*-statistic. *K* values represent the observed degree of ecological similarity among phylogenetically related species compared with expectations from a Brownian motion model of trait evolution (Blomberg, Garland & Ives 2003). *K* values close to zero imply that closely related species are ecologically distinct. We assessed the significance of the phylogenetic signal by comparing the observed *K* values with a null distribution of *K* values generated from 999 randomizations. In each randomization, we randomly shuffled the species' identities across the tips of the phylogenetic tree and then calculated a new *K* value each time.

The hypothesized phylogeny for the studied species was constructed by using the Phylomatic software (Webb & Donoghue 2005) with the most recent angiosperm phylogeny hypothesis available at the time of analysis (R20120829, archived at <http://phylodiversity.net/phyloomatic/>). The branch lengths of the phylogenetic tree were assigned by using Phylocom's BLADJ algorithm (Webb, Ackerly & Kembel 2008) with the age estimates from fossil plants in Wikström, Savolainen & Chase (2001).

All analyses were performed using the statistical programming language R version 3.2.0 (R Core Team, 2015). The stationary bootstrap was computed using the code provided by Patton, Politis & White (2009). The Blomberg's *K*-statistic was calculated using the R package 'phytools' (Revell 2012).

Results

COMMUNITY RESPONSE TO INTERANNUAL CLIMATIC VARIATION

Our results clearly showed that local climate variations exhibited strong influence on plant reproduction in the Fushan

subtropical rain forest (Table 1, Fig. S5). Seven of the ten cross-correlations between the number of reproductive species and the local climatic variables were significant. Both the number of species flowering and fruiting were positively correlated with maximum temperature and irradiance, and negatively correlated with rainfall (Table 1, Fig. S5). Only the number of species flowering was correlated with mean temperature (Table 1). Neither the number of species flowering nor fruiting was correlated with minimum temperature (Table 1). In general, the time-lags between the number of species fruiting and the local climatic variables were greater than those between the number of species flowering and the local climatic variables (Table 1, Fig. S5).

Our results also showed that the number of species flowering and fruiting tended to increase in El Niño events and decrease in La Niña events during the 10-year study period (Fig. 1). All six cross-correlations between the number of reproductive species and ENSO indices were significant. This indicates a strong influence of ENSO on the number of species flowering and fruiting. Plant reproduction was positively correlated with the SST indices and negatively correlated with SOI (Table 1). The number of species flowering peaked 5–7 months after ENSO indices (Table 1, Fig. S5). The number of species fruiting peaked 0–2 months after ENSO indices (Table 1, Fig. S3). In addition, the correlation coefficients between plant reproduction and ENSO indices were higher than those between plant reproduction and local climatic variables (Table 1).

The effect of the ENSO on plant reproduction might be mediated by its influence on the Fushan climate. Mean

Table 1. The highest cross-correlation coefficients of climatic variables vs. phenological time series and the corresponding time-lags. The phenological time series is the number of species flowering or fruiting in the Fushan subtropical rain forest. The climatic variables are the local climatic variables recorded in the Fushan weather station (irradiance, rainfall, mean temperature, maximum temperature and minimum temperature) and three indices of the El Niño Southern Oscillation (ENSO34, ENSO4 and SOI) at a monthly scale. Seasonality was removed from each time series before performing cross-correlations. Correlation coefficients are reported as significant or not significant (n.s.) based on the stationary bootstrap analysis with $\alpha = 0.05$. The lag correlation was tested up to 18 months

	Number of species flowering		Number of species fruiting	
	<i>r</i>	Lag (months)	<i>r</i>	Lag (months)
Irradiance	0.256	0	0.252	13
Rainfall	-0.252	1	-0.182	10
Temperature				
Mean	0.225	6	n.s.	
Maximum	0.272	6	0.286	15
Minimum	n.s.		n.s.	
ENSO34	0.474	5	0.467	0
ENSO4	0.481	6	0.438	2
SOI	-0.337	7	-0.493	0

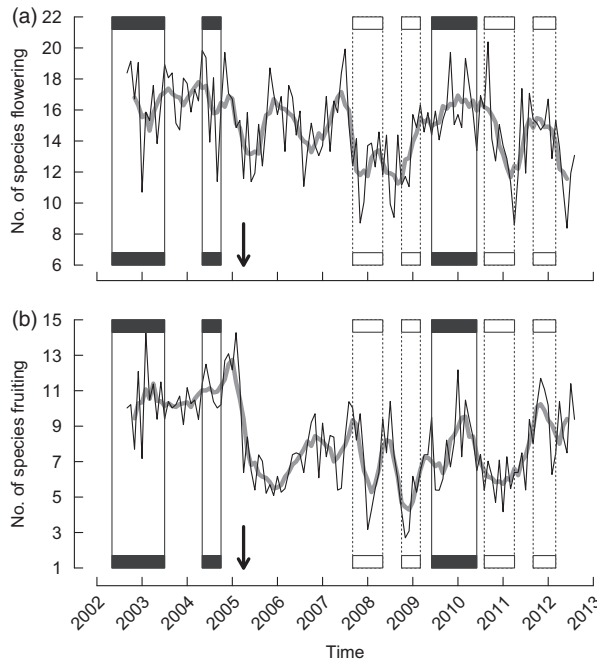


Fig. 1. The number of species flowering (a) and fruiting (b) each month for 10 years in the Fushan subtropical rain forest. Thin solid lines are the number of reproductive species after removing the seasonality (see methods). Thick grey lines are the 5-month moving averages. El Niño and La Niña events are represented by the black boxes with solid vertical lines and the open boxes with dashed vertical lines, respectively. Arrows indicate the frost event in March 2005.

temperature and maximum temperature were positively correlated with SST indices at about 6-month lag, while minimum temperature was negatively correlated at about 8-month lag (Table 2, Fig. S6). Irradiance peaked 0–1 month after ENSO indices (Table 2). Rainfall was only slightly correlated with the SOI index at a 4-month lag (Table 2).

SPECIES' RESPONSES TO INTERANNUAL CLIMATIC VARIATION

Across all studied species, annual flower and seed production peaked in the El Niño years (2003, 2004 and 2009) and fell to low levels in the La Niña years (2008, 2010, except 2011) (Fig. 2). For most species, annual flower and seed production were positively associated with maximum temperature, irradiance and the ENSO34 index and negatively correlated with mean temperature and rainfall (Fig. 3). Flower production was negatively correlated with minimum temperature. On the contrary, seed production was positively correlated with minimum temperature (Fig. 3). As expected, flower and seed production were better predicted by seasonal means of the climatic variables than by annual means (Fig. S7). Among 264 and 168 species-variable pairs for flower and seed production, 247 and 153 pairs showed higher correlations with seasonal means than with annual means for flower and seed production, respectively.

PHYLOGENETIC SIGNAL IN PHENOLOGICAL RESPONSES TO CLIMATIC FORCINGS

We detected significant phylogenetic signal in species' phenological responses of flower production to some climatic variables at Fushan. Among the six groups of correlations between flower production and climatic variables, one (maximum temperature) had Blomberg's K values significantly higher than expected by chance, and two (irradiance and ENSO34 index) had a marginally significant K value, suggesting that the phylogenetically closely related species resembled each other in their responses to these three climatic variables (Table 3, Fig. S8). By contrast, the relationships between seed production and climatic variables did not exhibit a phylogenetic signal (Table 3, Fig. S9).

FROST EFFECT

The influence of the 2005 frost event was highly significant. The number of species flowering and fruiting was greatly reduced after the frost event in 2005 (Fig. 3). Moreover, compared with the number of species flowering, the number of species fruiting remained at lower levels for a longer period (Fig. 1). A long-lasting impact on flower and seed production was observed for several species (Table S1). Flower and seed production after the frost event were significantly lower than before the frost event for nine and six species, respectively, while three species had significantly higher flower production after the frost event. Species' responses to the frost event do not show significant phylogenetic signal (flower: Blomberg's $K = 0.408$, $P = 0.238$; seed: $K = 0.617$, $P = 0.165$).

Discussion

The fact that all six cross-correlations between the number of reproductive species and ENSO indices were significant indicated plant reproduction in the Fushan subtropical rain forest was greatly influenced by natural climatic oscillations. This positive association was likely mediated by the interannual variations in the local climate. The ENSO events typically reach their mature phases during the boreal winter (Wang & Fiedler 2006) and would interact with the Asian monsoons (Wang, Wu & Fu 2000). Asian monsoon is the predominant force affecting the winter climate of our study site, and the strength of it determined the interannual variation in climatic conditions at Fushan. As the strength of the Asian monsoon decreased during the El Niño events (Wu, Chao & Hsu 2007), mean temperature and irradiance increased, and rainfall decreased at Fushan, which would facilitate plant reproduction.

Relatively higher temperature and irradiance, associated with the El Niño events, enhanced plant reproduction for most species at Fushan. The number of species flowering and fruiting peaked after 6 and 15 months after maximum temperature, suggesting that temperature in previous growing season and winter was critical for floral initiation (development of flower primordia). It has been shown that temperature during

Table 2. The highest cross-correlation coefficients and corresponding time-lags among the local climatic variables recorded in the Fushan weather station (irradiance, rainfall, mean temperature, maximum temperature and minimum temperature) and three indices of the El Niño Southern Oscillation (ENSO34, ENSO4 and SOI) at a monthly scale. Seasonality was removed from each time series before performing cross-correlations. Correlation coefficients are reported as significant or not significant (n.s.) based on the stationary bootstrap analysis with $\alpha = 0.05$. The lag correlation was tested up to 18 months

	Irradiance		Rainfall		Mean temperature		Maximum temperature		Minimum temperature	
	<i>r</i>	Lag (months)	<i>r</i>	Lag (months)	<i>r</i>	Lag (months)	<i>r</i>	Lag (months)	<i>r</i>	Lag (months)
ENSO34	0.181	0	n.s.		0.239	4	0.167	4	−0.124	8
ENSO4	0.191	0	n.s.		0.215	3	0.187	0	−0.160	11
SOI	−0.171	1	−0.094	4	−0.291	5	−0.223	5	0.122	8

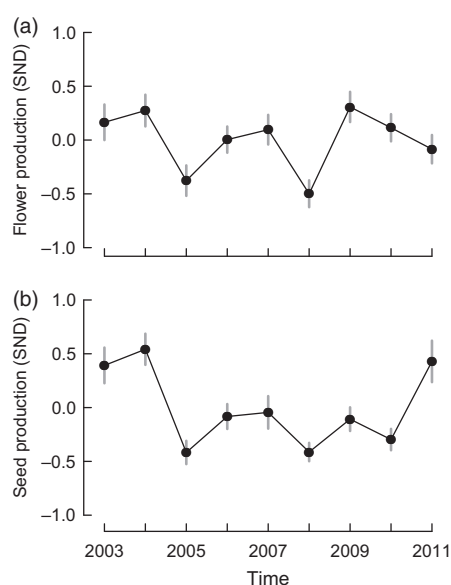


Fig. 2. The quantitative (a) flower and (b) seed production for the species with sufficient sampling size for data analysis over nine phenological years in the Fushan subtropical rain forest. Because our study period did not cover the full phenological years of 2002 and 2012, we excluded these 2 years from this figure. The flower production is defined as the number of traps with flower presence. The seed production is defined as the number of seeds collected. Annual reproductive production of each species was transformed to the standard normal deviates (SND) by subtracting the mean of each species and dividing by 1 standard deviation. Symbols represent the mean standard normal deviates (± 1 SE) among the studied species for each year.

floral initiation was linked to subsequent flower or seed production for a variety of taxa (e.g. Matthews 1955; McKone, Kelly & Lee 1998; Schaubert *et al.* 2002; Övergaard, Gemmel & Karlsson 2007; Smaill *et al.* 2011). A possible mechanism for these widely observed patterns is that the initiation and differentiation of flower bud are affected by gibberellins, and production of gibberellins may be controlled by temperature (Pharis & King 1985). We also observed negative effects of temperature on flower or seed production for some species. In these cases, cooler weather conditions might reduce the evapotranspiration demand, promote accumulation of

bioassimilates (Clark *et al.* 2003) and thus benefit plant reproduction. In contrast to temperature, the effect of irradiance on flower and seed production received less attention in previous studies. However, light is a well-known factor that limits net primary production in tropical moist forests (Loescher *et al.* 2003). Graham *et al.* (2003) also demonstrated experimentally that light augmentation during cloudy days increased maximum photosynthetic potentials, realized carbon uptake, numbers of reproductive buds, and fruit mass. Wright & Calderón (2006) argued that moderate El Niño events might relieve light limitations and enhance plant reproduction, which is consistent with our results.

Negative relationships between plant reproduction and rainfall were also observed at Fushan. Rainfall dynamics is linked with the temporal variability in flower and seed production in both tropical and temperate plant species (Ernest, Brown & Parmenter 2000; Piovesan & Adams 2001; Sakai *et al.* 2006). However, the effects of rainfall vary with the rainfall regime. In arid ecosystems, heavy rainfall triggered the explosive production of seeds in plant communities (Lima, Marquet & Jaksic 1999; Ernest, Brown & Parmenter 2000), whereas in high rainfall regions such as Fushan, heavy rainfall may reduce pollinator activities (González *et al.* 2009; Hegland *et al.* 2009), increase the risk of pathogen infection on developing fruits (Anderson *et al.* 2004), thus suppressing plant reproduction. Negative correlations between flower (or seed) production and rainfall could also be an indirect effect of positive correlations between reproductive output and irradiance (Wright & Calderón 2006), since rainfall is negatively correlated with irradiance at Fushan (Fig. S3).

Interannual variation in plant reproduction was better explained by ENSO indices than the local climatic variables (Table 1). Large-scale climatic indices, such as the ENSO and the North Atlantic Oscillation indices, have been associated with many ecological processes (Stenseth *et al.* 2002, 2003) and generally have better predictive power than a single climatic variable (Stenseth & Mysterud 2005). In fact, ecological processes probably are not influenced by a single climatic variable, but rather by a suite of climatic variables. The large-scale climatic indices might serve as ‘weather packages’ that combine appropriate temporal and spatial features

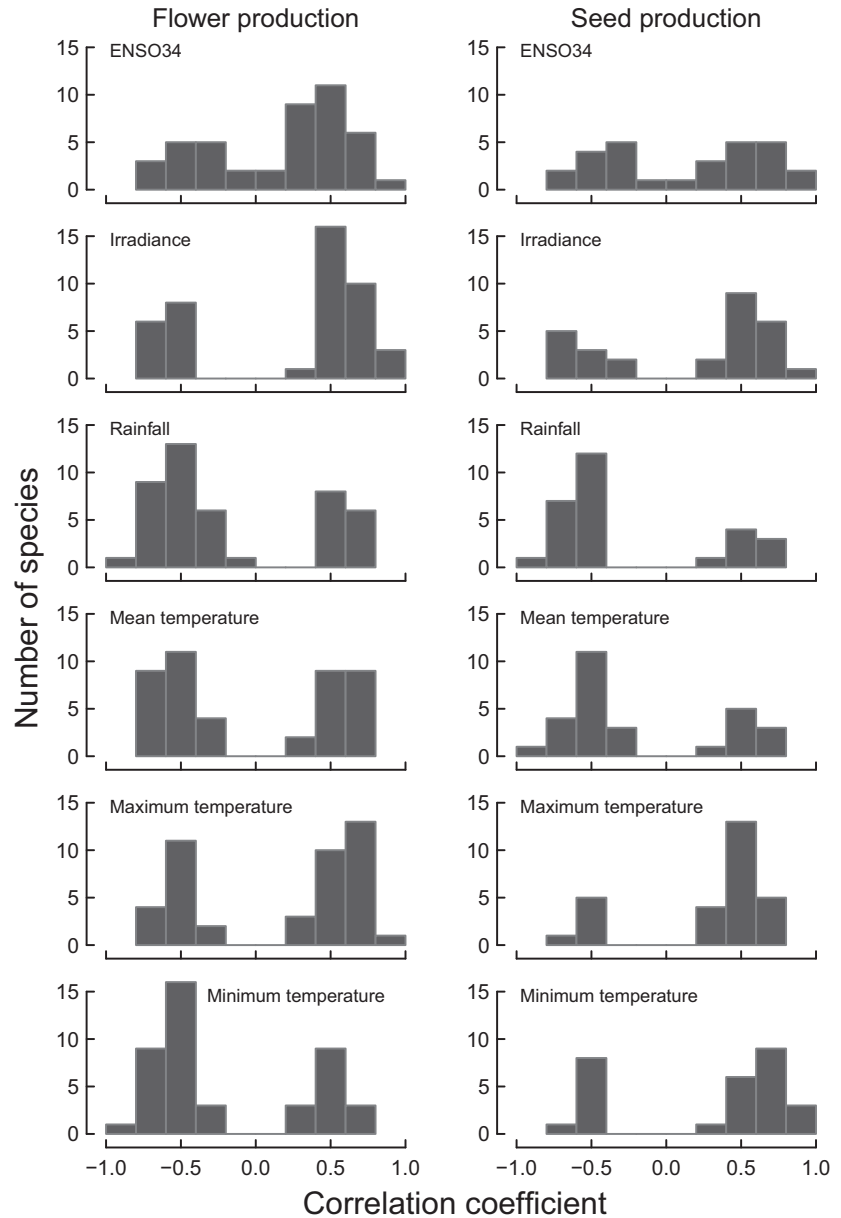


Fig. 3. Frequency distributions of the correlations between the flower (left panel)/ seed (right panel) production and climatic variables (panels from top to bottom: ENSO34 index, irradiance, rainfall, mean temperature, maximum temperature and minimum temperature).

of several local weather components (Hallett *et al.* 2004; Stenseth & Mysterud 2005) and therefore could better predict the interannual variation in flower and fruit production. Another explanation for higher correlations between plant reproduction and the ENSO was that the ENSO reflected the long-term accumulative effects of local weather conditions (Wright & Calderón 2006). Indeed, we found that both the numbers of reproductive species and ENSO indices were significantly correlated with the long-term averages of irradiance and maximum temperature, and the correlation coefficient progressively increased with larger time window (Figs S10 and S11). These results strongly suggest that the interannual variation in the local climatic conditions at Fushan is driven by regional climatic fluctuations, such as the ENSO, to which plant reproduction responds.

The number of species fruiting was significantly correlated with ENSO indices with only 0- to 1-month time-lag

(Table 1, Fig. S4); however, the time-lag of local climate and fruiting species was 10–15 months. This might seem counter-intuitive if we assumed that the effect of ENSO was mediated by local climate. One possible explanation for this pattern is that the ENSO indices are likely to integrate the local climatic conditions over several months (Fig. S11); thus, the ENSO indices exhibited a much shorter time-lag with the number of species fruiting than local climate did.

The extreme cold temperature (-1.3°C) recorded in March 2005 was a rare event at Fushan and was very unusual in its timing: this freezing temperature only occurred once in March for the past 24 years from 1991 to 2014 (Lu *et al.* 2000; Lu, Hwang & Huang 2009). This frost event appeared to have a long-lasting effect on plant reproduction of several species at Fushan, especially to those species with new leaves or flowers during the frost. For example, many Lauraceae species that produced new leaves and flowers in early March were greatly

Table 3. Phylogenetic signals in species' responses to the climatic variables at Fushan. The phylogenetic signal was quantified using Blomberg's *K*. *K* values close to zero imply that phylogenetically closely related species are ecologically distinct. The significance of the *K* value was evaluated by the randomization test

Variable	Flower production		Seed production	
	<i>K</i>	<i>P</i>	<i>K</i>	<i>P</i>
Irradiance	0.484	0.051	0.310	0.951
Rainfall	0.363	0.421	0.420	0.585
Temperature				
Mean	0.376	0.320	0.576	0.177
Maximum	0.570	0.012	0.367	0.780
Minimum	0.330	0.627	0.527	0.274
ENSO34	0.458	0.087	0.393	0.679

impacted by this event. In consequence, these species did not produce seeds in the following fall. The disastrous loss of flowers and seeds not only reduced recruitment in these plant populations but also initiated trophic cascades (Inouye 2000). For instance, Formosan rock macaques (*Macaca cyclopis*) that rely heavily on fruits as their main diet suffered from extremely high mortality in 2005 and low birth rates in 2006 at Fushan (Su, Teng & Lai 2010).

The flower and seed production at Fushan did not evince any significant trend during our study period (see Appendix S1), in contrast to a previous study conducted in a tropical wet forest in Panama (Wright & Calderón 2006). This is probably because the temporal patterns in flower and seed production at Fushan were shaped by interactions between the ENSO and the rare frost event. Our data showed that plant reproductive output did increase during El Niño events, but the frost event in 2005 interrupted the increasing trend; furthermore, the weather pattern after 2005 shifted towards La Niña conditions (Fig. 1). Together, this led to poor production in flower and seed of many species. Our findings clearly suggest the necessity of simultaneously considering the effects of natural climatic oscillations and extreme weather events when assessing the impacts of climate changes on phenological responses. Ignoring any of these external forcings may lead to potentially inaccurate conclusions.

Phylogenetically closely related species tended to have similar flowering responses to climatic variation at Fushan. To our knowledge, our findings are the first to identify significant phylogenetic signal in the relationships between flowering intensity and climatic variables. The most striking phylogenetic structure was the negative correlations between flower production and maximum temperature for the species from Eurosids II, contrasting with the positive correlations for the species from Magnoliids and Monocots (Fig. S8). Physiological mechanisms related to flowering intensity may be relatively conserved among some taxonomic groups. For example, *FLOWERING LOCUS T (FT)*, a key flowering gene involving in integrating temperature, photoperiod and autonomous signals for the floral transition or initiation in *Arabidopsis*, is widely conserved in angiosperms (Andrés & Coupland 2012). The orthologues of *FT* and other relevant genes

(*LEAFY* and *APETALA1*) were also identified in a typical masting species, *Fagus crenata*, and the gene expression levels were significantly related to the flowering intensity in *F. crenata* (Miyazaki *et al.* 2014). To what extent this genetic pathway is conserved among different taxonomic groups remains open for investigation.

No significant phylogenetic signals were detected either in the relationships between seed production and climatic variables or in the phenological responses to the frost event. There are several possible explanations for this pattern. First, seed production depends not only on climatic variables, but also on several biotic factors, such as pollinator activity and internal resource level. These ecological factors might outweigh the physiological constraints that underlie seed development that shared by closely related species. Secondly, local adaptation may have a stronger effect than phylogenetic constraints. Species may adapt to the local environmental factors and thus exhibit trait adaptations that are not well predictable by phylogeny (Davis *et al.* 2010). Thirdly, species' responses to some external forcings, such as the frost event, might be independent of taxonomic membership because these extreme events varied in timing and intensity and, more likely, beyond the responsive range of species (*e.g.* out of its maximum freezing tolerance); therefore, it is unlikely to detect significant phylogenetic signal in species' response to these extreme weather events.

Our study demonstrates that both the ENSO and the frost event have great influences on the temporal variation in flower and seed production. By quantifying the phylogenetic signals in species' phenological responses to these external forcings, we have provided evidence that phylogenetically closely related species exhibited similar relationships between their flower production and climatic factors. As many species in Fushan are widely distributed in East and Southeast Asia (such as *Diospyros morrisiana* [Ebenaceae], *Engelhardia roxburghiana* [Juglandaceae] and *Schefflera octophylla* [Araliaceae]), our findings may have implications for assessing the potential impacts of climate change on boundary dynamics of tropical species' range distributions. Further changes in the ENSO and increasing frequency of spring frost are expected under current global warming trend (Collins *et al.* 2010; Augspurger 2013; IPCC, 2013), and this will alter the composition and temporal variability of flower and seed production, which subsequently change the recruitment of plant species and the population dynamics of pollinators and seed consumers. These potential changes inevitably have consequences for forest ecosystems. Drivers and impacts of these changes can only be identified with long-term monitoring on these ecological processes. Future work is needed to elucidate the mechanisms underlying the associations between plant reproduction and climatic variables.

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Data accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.75v7c> (Chang-Yang *et al.* 2015).

References

- Anderson, P.K., Cunningham, A.A., Patel, N.G., Morales, F.J., Epstein, P.R. & Daszak, P. (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution*, **19**, 535–544.
- Andrés, F. & Coupland, G. (2012) The genetic basis of flowering responses to seasonal cues. *Nature Review Genetics*, **13**, 627–639.
- Augsburger, C.K. (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Functional Ecology*, **23**, 1031–1039.
- Augsburger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology*, **94**, 41–50.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Boulter, S.L., Kitching, R.L. & Howlett, B.G. (2006) Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology*, **94**, 369–382.
- Buckley, L.B. & Kingsolver, J.G. (2012) Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 205–226.
- CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 4916–4921.
- CaraDonna, P.J. & Inouye, D.W. (2015) Phenological responses to climate change do not exhibit phylogenetic signal in a subalpine plant community. *Ecology*, **96**, 355–361.
- Chang-Yang, C.-H., Lu, C.-L., Sun, I.-F. & Hsieh, C.-F. (2013) Flowering and fruiting patterns in a subtropical rain forest, Taiwan. *Biotropica*, **45**, 165–174.
- Chang-Yang, C.-H., Sun, I.-F., Tsai, C.-H., Lu, C.-L. & Hsieh, C.-F. (2015) Data from: ENSO and frost co-determine decade-long temporal variation in flower and seed production in a subtropical rain forest. *Journal of Ecology*, doi:10.5061/dryad.75v7c.
- Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5852–5857.
- Cleveland, R.B., Cleveland, W.S., McRae, J.E. & Terpenning, I. (1990) STL: a seasonal-trend decomposition procedure based on loess. *Journal of Official Statistics*, **6**, 3–73.
- Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F.-F., Jochum, M., Lengaigne, M., Power, S., Timmermann, A., Vecchi, G. & Wittenberg, A. (2010) The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience*, **3**, 391–397.
- Connell, J.H. & Green, P.T. (2000) Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, **81**, 568–584.
- Curran, L.M. & Leighton, M. (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 101–128.
- Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R. *et al.* (2013) Phylogenetic conservatism in plant phenology. *Journal of Ecology*, **101**, 1520–1530.
- Davis, C.C., Willis, C.G., Primack, R.B. & Miller-Rushing, A.J. (2010) The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3201–3213.
- Drobyshev, I., Övergaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M. & Sykes, M.T. (2010) Masting behavior and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. *Forest Ecology and Management*, **259**, 2160–2171.
- Du, Y., Mao, L., Queenborough, S.A., Freckleton, R.P., Chen, B. & Ma, K. (2015) Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. *Global Ecology and Biogeography*, **24**, 928–938.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.
- Efron, B. & Tibshirani, R. (1993) *An Introduction to the Bootstrap*. Chapman and Hall, New York, USA.
- Ernest, S.K.M., Brown, J.H. & Parmenter, R.R. (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, **88**, 470–482.
- Fitter, A.H. & Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.
- González, A.M.M., Dalsgaard, B., Ollerton, J., Timmermann, A., Olesen, J.M., Andersen, L. & Tossas, A.G. (2009) Effects of climate on pollination networks in the West Indies. *Journal of Tropical Ecology*, **25**, 493–506.
- Graham, E.A., Mulkey, S.S., Kitajima, K., Phillips, N.G. & Wright, S.J. (2003) Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 572–576.
- Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, **430**, 71–75.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*, **12**, 184–195.
- Holdridge, L.R. (1947) Determination of world plant formations from simple climatic data. *Science*, **105**, 367–368.
- Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J.R. & Mohren, G.M.J. (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution*, **16**, 89–94.
- Hsieh, C.-H., Chen, C.-S., Chiu, T.-S., Lee, K.-T., Shieh, F.-J., Pan, J.-Y. & Lee, M.-A. (2009) Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. *Fisheries Oceanography*, **18**, 102–117.
- Inouye, D.W. (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457–463.
- Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.
- Inouye, D.W., Morales, M.A. & Dodge, G.J. (2002) Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia*, **130**, 543–550.
- IPCC (2013) Climate change 2013. *The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds T.F. Stocker, D. Qin, G.-K. Plattner, M.M.B. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P.M. Midgley), pp. 1355. Cambridge University Press, Cambridge, UK and New York, USA.
- Jentsch, A., Kreyling, J., Boettcher-Treschkow, J. & Beierkuhnlein, C. (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Global Change Biology*, **15**, 837–849.
- Kelly, D. & Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**, 427–447.
- Kochmer, J.P. & Handel, S.N. (1986) Constraints and competition in the evolution of flowering phenology. *Ecological Monographs*, **56**, 303–325.
- Koenig, W.D. & Knops, J.M.H. (1998) Scale of mast-seeding and tree-ring growth. *Nature*, **396**, 225–226.
- Lima, M., Marquet, P.A. & Jaksic, F.M. (1999) El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. *Ecography*, **22**, 213–218.
- Loescher, H.W., Oberbauer, S.F., Gholz, H.L. & Clark, D.B. (2003) Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. *Global Change Biology*, **9**, 396–412.
- Lu, S.-Y., Hwang, L.-S. & Huang, H.-H. (2009) *Compilation of Meteorological Records for the Stations in the Fushan Research Center (January 2000–June 2009)*. Taiwan Forestry Research Institute, Taipei, Taiwan.
- Lu, S.-Y., Huang, H.-H., Chen, C.-H. & Hwang, J.-L. (2000) *Compilation of Meteorological and Streamflow Records for Fushan Experimental Watershed (1982–1999)*. Taiwan Forestry Research Institute, Taipei, Taiwan.

- Matthews, J.D. (1955) The influence of weather on the frequency of beech mast years in England. *Forestry*, **28**, 107–116.
- McKone, M.J., Kelly, D. & Lee, W.G. (1998) Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology*, **4**, 591–596.
- McPhaden, M.J., Zebiak, S.E. & Glantz, M.H. (2006) ENSO as an integrating concept in earth science. *Science*, **314**, 1740–1745.
- Meehl, G.A., Karl, T., Easterling, D.R., Changnon, S., Pielke, R., Changnon, D. et al. (2000) An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bulletin of the American Meteorological Society*, **81**, 413–416.
- Miyazaki, Y., Maruyama, Y., Chiba, Y., Kobayashi, M.J., Joseph, B., Shimizu, K.K., Mochida, K., Hiura, T., Kon, H. & Satake, A. (2014) Nitrogen as a key regulator of flowering in *Fagus crenata*: understanding the physiological mechanism of masting by gene expression analysis. *Ecology Letters*, **17**, 1299–1309.
- Nixon, C.M. & McClain, M.W. (1969) Squirrel population decline following a late spring frost. *Journal of Wildlife Management*, **33**, 353–357.
- Norden, N., Chave, J., Caubère, A., Châtelet, P., Ferroni, N., Forget, P.-M. & Thébaud, C. (2007) Is temporal variation of seedling communities determined by environment or by seed arrival? *Journal of Ecology*, **95**, 507–516.
- Numata, S., Yasuda, M., Okuda, T., Kachi, N. & Noor, N.S.M. (2003) Temporal and spatial patterns of mass flowerings on the Malay Peninsula. *American Journal of Botany*, **90**, 1025–1031.
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.
- Övergaard, R., Gemmel, P. & Karlsson, M. (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry*, **80**, 555–565.
- Parnesan, C., Root, T.L. & Willig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.
- Patton, A., Politis, D.N. & White, H. (2009) Correction to “Automatic block-length selection for the dependent bootstrap” by D. Politis and H. White. *Econometric Reviews*, **28**, 372–375.
- Pharis, R.P. & King, R.W. (1985) Gibberellins and reproductive development in seed plants. *Annual Review of Plant Physiology*, **36**, 517–568.
- Piessens, K., Adriaens, D., Jacquemyn, H. & Honnay, O. (2009) Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia*, **159**, 117–126.
- Piovesan, G. & Adams, J.M. (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*, **79**, 1039–1047.
- Politis, D.N. & Romano, J.P. (1994) The stationary bootstrap. *Journal of the American Statistical Association*, **89**, 1303–1313.
- Post, E. (2003) Large-scale climate synchronizes the timing of flowering by multiple species. *Ecology*, **84**, 277–281.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. Version 3.2.0. R Foundation for Statistical Computing, Vienna, Austria.
- Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–233.
- Rich, P.M., Breshears, D.D. & White, A.B. (2008) Phenology of mixed woody-herbaceous ecosystems following extreme events: Net and differential responses. *Ecology*, **89**, 342–352.
- Richardson, S.J., Allen, R.B., Whitehead, D., Carswell, F.E., Ruscoe, W.A. & Platt, K.H. (2005) Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology*, **86**, 972–981.
- Sakai, S., Harrison, R.D., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., Chong, L. & Nakashizuka, T. (2006) Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany*, **93**, 1134–1139.
- van Schaik, C.P. (1986) Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology*, **2**, 327–347.
- Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., Payton, I.J., Wilson, P.R., Cowan, P.E. & Brockie, R.E. (2002) Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology*, **83**, 1214–1225.
- Shibata, M. & Nakashizuka, T. (1995) Seed and seedling demography of four co-occurring *Carpinus* species in a temperate deciduous forest. *Ecology*, **76**, 1099–1108.
- Smaill, S.J., Clinton, P.W., Allen, R.B. & Davis, M.R. (2011) Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, **99**, 870–877.
- Stenseth, N.C. & Mysterud, A. (2005) Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology*, **74**, 1195–1198.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.S., Yoccoz, N.G. & Ådlandsvik, B. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 2087–2096.
- Su, H.-H., Teng, Y.-L. & Lai, Z.-J. (2010) Long-term study of Formosan rock macaques (*Macaca cyclopis*) in the Fushan Experimental Forest. *Review and Future Prospects of Long-Term Ecological Research at Fushan Experimental Forest* (ed. H.-H. Wang), pp. 105–124. Taiwan Forestry Research Institute, Taipei, Taiwan.
- Su, S.-H., Chang-Yang, C.-H., Lu, C.-L., Tsui, C.-C., Lin, T.-T., Lin, C.-L., Chiou, W.-L., Kuan, L.-H., Chen, Z.-S. & Hsieh, C.-F. (2007) *Fushan Subtropical Forest Dynamics Plot: Tree Species Characteristics and Distribution Patterns*. Taiwan Forestry Research Institute, Taipei, Taiwan.
- Su, S.-H., Hsieh, C.-F., Chang-Yang, C.-H., Lu, C.-L. & Guan, B.-T. (2010) Micro-topographic differentiation of the tree species composition in a sub-tropical submontane rainforest in northeastern Taiwan. *Taiwan Journal of Forestry Science*, **25**, 63–80.
- Trenberth, K.E. (1997) The definition of El Niño. *Bulletin of the American Meteorological Society*, **78**, 2771–2777.
- Tsai, C.-H., Miki, T., Chang, C.-W., Ishikawa, K., Ichise, S., Kumagai, M. & Hsieh, C.-H. (2014) Phytoplankton functional group dynamics explain species abundance distribution in a directionally changing environment. *Ecology*, **95**, 3335–3343.
- Wang, C. & Fiedler, P.C. (2006) ENSO variability and the eastern tropical Pacific: A review. *Progress in Oceanography*, **69**, 239–266.
- Wang, B., Wu, R. & Fu, X. (2000) Pacific-East Asian teleconnection: How does ENSO affect East Asian climate? *Journal of Climate*, **13**, 1517–1536.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.
- Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.
- Wikström, N., Savolainen, V. & Chase, M.W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 2211–2220.
- Wipf, S., Stoeckli, V. & Bebi, P. (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, **94**, 105–121.
- Wolkovich, E.M., Cook, B.I. & Davies, T.J. (2014) Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. *New Phytologist*, **201**, 1156–1162.
- Wolkovich, E.M., Davies, T.J., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E., Willis, C.G. & Davis, C.C. (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, **100**, 1407–1421.
- Wood, S.N. (2010) Statistical inference for noisy nonlinear ecological dynamic systems. *Nature*, **466**, 1102–1104.
- Wright, S.J. & Calderón, O. (1995) Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology*, **83**, 937–948.
- Wright, S.J. & Calderón, O. (2006) Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*, **9**, 35–44.
- Wright, S.J., Carrasco, C., Calderón, O. & Paton, S. (1999) The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.
- Wu, C.-R., Chao, S.-Y. & Hsu, C. (2007) Transient, seasonal and interannual variability of the Taiwan Strait current. *Journal of Oceanography*, **63**, 821–833.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Main climatic variables at the Fushan subtropical rain forest.

Figure S2. Monthly time series of the local climatic variables.

Figure S3. Correlation matrix for the five local climatic variables.

Figure S4. Cross-correlations between the number of species flowering/fruiting and the local climatic variables.

Figure S5. Cross-correlations between the number of species flowering/fruiting and the ENSO indices.

Figure S6. Cross-correlations between the local climatic variables and the ENSO indices.

Figure S7. Frequency distributions of the best predictive time window of six climatic variables for flower and seed production.

Figure S8. Phylogenetic distribution of correlations between flower production and climatic variables on the phylogenetic tree for 44 studied species.

Figure S9. Phylogenetic distribution of correlations between seed production and climatic variables on the phylogenetic tree for 28 studied species.

Figure S10. Cross-correlations between the number of species flowering/fruiting and the local climatic variables with different moving-average windows.

Figure S11. Cross-correlations between the local climatic variables recorded with different moving-average windows and the ENSO indices.

Table S1. The flower and/or seed production of 49 studied species before and after the frost event.

Appendix S1. Linear mixed-effects models for assessing linear trends in flower and seed production.