RESEARCH PAPER

Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China

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ABSTRACT

Aim The phylogenetic constraint hypothesis of flowering phenology states that closely related species flower at similar times of the year. We test this hypothesis for the Chinese angiosperm flora and assess additional effects of growth form, deciduousness, pollination mode and fruit type. We further examine whether the phylogenetic conservatism of flowering phenology tends to increase from tropical to temperate latitudes.

Location China.

Methods The midpoint of flowering time for 19,631 angiosperm species present in China was compiled. The phylogenetic signal for flowering time was evaluated for the whole country using the Blomberg *K*-value (adjusted for circular data). We then regressed the phylogenetic signal for 28 provinces as a function of their latitude. An analysis of variance for circular data was conducted to test the differences among growth forms. Watson–Williams tests for circular flowering data were used to compare flowering dates between deciduous and evergreen species, animal-pollinated and wind-pollinated species, and fleshy and non-fleshy fruits.

Results The results support the phylogenetic constraint hypothesis. The phylogenetic signal at the whole country scale was lower than that at the province scale. Phylogenetic signal was also lower at tropical latitudes than at temperate latitudes. Flowering dates were associated with biological traits, with growth form having the largest effect.

Main conclusions Flowering phenology was constrained by phylogeny, and so one should account for phylogeny when studying the underlying drivers of phenology. The strength of phylogenetic conservatism appears weaker at larger scales and becomes stronger towards temperate regions. Flowering phenology also varies predictably according to biological traits such as growth form, suggesting that both phylogeny and traits could be used to inform the flowering times of species for which no phenology data are available. It remains to be tested whether the phylogenetic signal for other functional traits putatively related with flowering time also increases with latitude.

Keywords

Chinese flora, deciduousness, fruit type, growth form, phylogenetic conservatism, pollination type.

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INTRODUCTION

The phenology, or timing of the life cycle or seasonal events, of plants is key to the reproductive success of individuals and the long-term persistence of populations (Rathcke & Lacey, 1985; Craine *et al.*, 2012). Flowering time in particular is highly sensitive to environmental cues such as photoperiod, temperature and water stress (Rathcke & Lacey, 1985; Ollerton & Lack, 1992), resulting in a highly variable and apparently flexible trait (Chuine, 2010). Despite this apparent variation and flexibility, a recent large-scale meta-analysis from the European and North American floras demonstrated a significant effect of evolutionary history on flowering phenology, i.e. more closely related species flowered at similar times (Davies *et al.*, 2013). In this paper we provide an independent test of this hypothesis with the much larger diverse angiosperm flora of China. In addition, we extend the analysis to ask whether phylogenetic conservatism of phenology varies by latitude.

Given that many organisms depend on access to resources such as water, nutrients or light, to ensure survival and reproduction, it is of no surprise that they use these resources, or cues to their imminence, as drivers of their life cycles. Examples with both clear environmental cues and evolutionary causes are (1) wind-pollinated trees that flower early in the growing season before leafing has occurred, allowing greater dispersal of pollen (Whitehead, 1969; Heinrich, 1976; Faegri & van der Pijl, 1979) and (2) many woodland herbaceous plants that also flower prior to the decrease in availability of light following leafing of the tree canopy (Kudo *et al.*, 2008). Many long-term observational studies have demonstrated strong correlations of flowering and leafing phenology with abiotic cues (Fitter & Fitter, 2002), including clear effects of recent anthropogenic climate change (e.g. Miller-Rushing & Primack, 2008; Calinger *et al.*, 2013).

Moreover, the two previous examples illustrate the importance of species attributes or traits in determining or mediating their phenology (Calinger *et al.*, 2013). For example, wind-pollinated trees are likely to have divergent flowering phenology from animal-pollinated trees, as do animal-pollinated trees from herbs. Thus, the phenology of angiosperms is constrained by biological, ecological or developmental traits such as growth form, pollinator type, fruit type or seed size, over and above the resource requirements and abiotic cues to these resources (Rabinowitz *et al.*, 1981; Primack, 1985; Kochmer & Handel, 1986; Bolmgren & Lönnberg, 2005).

Recent work has also highlighted the role of phylogenetic constraints on flowering phenology – how the evolutionary relationships between species determine their biological characteristics (Wright & Calderon, 1995; Boulter *et al.*, 2006; Chang-yang *et al.*, 2013; Davies *et al.*, 2013). Because of their shared evolutionary history, closely related species share similar genetic constraints that limit their potential evolutionary response to their environment (Rathcke & Lacey, 1985). Thus, closely related species are likely to be more similar than those species that are less closely related, leading to non-independence of data and violation of the assumptions of statistical tests in comparative analyses that do not account for this autocorrelation (Revell *et al.*, 2008).

The strength of any phylogenetic signal (i.e. the degree of phylogenetic constraint or conservatism) may also vary, depending on the trait in question. Some traits (such as seed mass and woody density) are more constrained than others (such as leaf size and specific leaf area) (Kraft & Ackerly, 2010). The signal strength may also vary as a function of similar climatic or environmental cues to phenology, which will be strongly determined by latitude (e.g. variation in day length decreases as one approaches the equator) or because there are fewer cues to use (e.g. there is no frost in the tropics). Furthermore, latitude is also a strong driver of community structure and composition, through its influence on climate (Pau *et al.*, 2011). Most angiosperm lineages originated in tropical environments prior to the Eocene (50–35 Ma; Davies *et al.*, 2013), and as the planet cooled these lineages had to evolve cold tolerance in order to invade the new, less benign ecosystems (Wiens *et al.*, 2006). Thus, because these extra-tropical ecosystems such as the boreal zone are younger than tropical ecosystems, and because cold appears evolutionarily difficult to overcome, species in colder regions tend to be more closely related to each other than expected by chance and clades tend to be younger (Qian *et al.*, 2013). For all these reasons, we would expect any phylogenetic signal in angiosperm phenology to be stronger in plant communities further from the equator.

Apart from highlighting the non-independence of species values, the inclusion of biological traits and phylogeny in analyses of phenology not only permits a greater understanding of the proximate and ultimate drivers of phenology (e.g. Panchen *et al.*, 2014) but also creates a useful framework whereby we can generate predictions of phenological events for species for which we have only trait data and/or phylogenetic information (Brooks *et al.*, 1992; Mazer *et al.*, 2013), especially in the face of climate change (Bolmgren & Lönnberg, 2005).

Here we tested the phylogenetic constraint hypothesis of flowering phenology for the Chinese angiosperm flora (19,631 species), both in geographical range and phylogenetic relationships, and assessed variation in phenology as a function of four traits – growth form, deciduousness, pollination mode and fruit type. Other functional traits are also likely to affect flowering date, such as seed size (Primack, 1987) and dispersal mode (Bolmgren & Cowan, 2008); however, these data are not available, so we did not include them in our study. We further examined whether the phylogenetic conservatism of flowering phenology tended to increase from tropical to temperate latitudes. Our flowering phenology study uses the largest taxon sampling dataset compiled to date and incorporates a rigorous phylogenetic framework to clarify flowering patterns in Northern Hemisphere angiosperms, ranging from 19° N (tropical) to 46° N (temperate climate).

METHODS

Phenology data

We compiled the flowering dates of angiosperms listed in *Flora Reipublicae Popularis Sinicae* (FRPS, i.e. Flora of China in Chinese version; Editorial Committee of Flora Reipublicae Popularis Sinicae, 1959–2004; 125 volumes, a result of the work of more than 450 well-qualified Chinese taxonomists over the past 50 years). Native species with incomplete flowering information and alien species, including cultivated and introduced naturalized species, were removed from the dataset. A total of 19,631 species belonging to 2284 genera and 181 families were included in the final analysis. Family, genus, start and end date of flowering by month, growth form, fruit type (fleshy/not fleshy), pollination mode (animal and wind pollinated) and deciduousness (deciduous/evergreen) were compiled for each species. We used five growth form categories: annual herb, perennial herb, shrub, tree and woody vine (liana). The pollination type for each species was based on FRPS, the published literature or was judged from the morphology of the flowers. According to the pollination syndrome, showy flowers with conspicuous perianths were categorized as animal pollinated and flowers without obvious attractants were categorized as wind pollinated (Proctor & Yeo, 1972; Faegri & van der Pijl, 1979). Despite the shortcomings of basing the pollination syndrome on flower morphology, the distinction between animal and wind pollination is useful, especially in large comparative analyses (Fenster *et al.*, 2004).

The flowering date for each species was calculated using the start and end dates of flowering listed in the FRPS. We calculated the midpoint for each species between the start and end dates of flowering. This method often results in a conservative estimate of mean flowering time because right-skewed flowering curves are common (Rabinowitz *et al.*, 1981), but it is widely used in studies of reproductive phenology (e.g. Kochmer & Handel, 1986; Johnson, 1993; Wright & Calderon, 1995).

Phylogenetic tree

Species classification was matched to the Angiosperm Phylogeny Group III classification system (APG III (Angiosperm Phylogeny Group III), 2009). For the 19,631 species, a supertree was constructed using the software Phylomatic (Webb *et al.*, 2008) and the branch length was calculated using the 'bladj' module in Phylocom. The phylogenetic backbone was based on the APG III tree (R20120829, http://phylodiversity.net/phylomatic/). This method of phylogenetic reconstruction often leaves many polytomies at the genus level unresolved, because current molecular phylogenies are lacking or have not been incorporated yet into the software. Nevertheless, this method has been used in many other studies (e.g. Queenborough *et al.*, 2009; Lavergne *et al.*, 2013; Amano *et al.*, 2014).

Data analyses

The phenology data (date of the midpoint of flowering) were transformed onto a circular scale using the 'as.circular()'

function in the package 'circular v.0.4-7' (Agostinelli & Lund, 2013) in R v.3.0.2 (R Development Core Team, 2009). Thus, the difference between day 365 (final day of the year) and day 1 (first day of the year) is equivalent to 1 day on the circular scale, rather than 364 in absolute terms.

We quantified the strength of phylogenetic conservatism in flowering phenology based on the circular Blomberg *K*-value as implemented in the 'picante 1.6–2' package (Kembel *et al.*, 2010) in R. Specifically, we adapted the function for calculating the significance test of the *K* statistic to account for the circular nature of the phenological data. The test for phylogenetic signal using *K* involves randomization of the data from the tips of the phylogeny to create new pseudo-data that lack phylogenetic structure. From these data phylogenetically independent contrasts (PICs) were computed. The variance of these is then compared with that of the PICs from the original data. The method for calculating contrasts was simply adapted to account for the circular scale, specifically by calculating the differences for contrasts using circular distances rather than absolute.

In order to study whether there was a latitudinal gradient in the strength of phylogenetic conservatism in flowering, we calculated the *K*-value in each of the 28 provinces in China, and then regressed the *K*-value as a function of the latitude of each province (latitude of its geometric centroid).

The broad-scale strength of phylogenetic conservatism is likely to be spatially autocorrelated, which may inflate the Type I error rate (Diniz-Filho *et al.*, 2003) and thus bias regression coefficients (Dormann, 2007) in hypothesis testing. Accordingly, we used the Moran *I* statistic to assess the presence of spatial autocorrelation in residuals of regression models. We found that ordinary least squares (OLS) regression did not have significant spatial autocorrelations in model residuals (Blomberg's *K*: Moran's $I = -0.078$, $P = 0.69$). Therefore, we performed OLS directly.

We conducted an analysis of variance for circular data to test for differences in flowering time among growth forms, and then applied the function 'TukeyHSD' to get adjusted *P*-values for all comparisons. Watson–Williams tests were performed by comparing the effects of deciduousness (deciduous versus evergreen), fruit type (fleshy versus non-fleshy fruits) and pollination syndrome (animal versus wind pollination) on flowering date, using the 'watson.williams.test()' function. To test whether these correlations between biological traits and flowering dates varied among growth forms, we performed the 'aov.circular()' function in the package 'circular' for each growth form. Because the sample size was small for annual herbs and perennial herbs (for example, there were no deciduous annuals, only 18 evergreen perennials and only three fleshy-fruited annuals), here we did not separate herbs into annuals and perennials.

To account for the potential effect of species' shared evolutionary history, we calculated the effects of growth form on flowering time using the 'phylANOVA' function in the package 'phytools' (Revell, 2012) in R.

Table 1 Phylogenetic signal for flowering phenology in each of 28 provinces in China. The *K*-value is the circular Blomberg *K*-value which was adapted for calculating the significance test of the *K* statistic to account for the circular nature of the phenological data.

Province	Latitude (°N)	No. of species	*K*-value	*P*-value
Hainan	19.22	1436	0.150	<0.001
Guangxi	23.01	3572	0.153	<0.001
Guangdong	23.27	2638	0.176	<0.001
Taiwan	23.65	1441	0.185	<0.001
Yunnan	24.14	7467	0.157	<0.001
Fujian	26.00	1729	0.182	<0.001
Guizhou	26.66	3127	0.190	<0.001
Jiangxi	27.73	1813	0.218	<0.001
Hunan	28.02	2226	0.215	<0.001
Zhejiang	29.11	1534	0.215	<0.001
Sichuan	30.27	6190	0.232	<0.001
Hubei	30.90	2305	0.227	<0.001
Xizang	31.10	4257	0.233	<0.001
Anhui	32.01	1327	0.250	<0.001
Jiangsu	32.47	917	0.235	<0.001
Henan	33.80	1601	0.264	<0.001
Shaanxi	34.11	2229	0.297	<0.001
Qinghai	35.72	1824	0.285	<0.001
Gansu	35.94	2515	0.316	<0.001
Shandong	36.17	679	0.355	<0.001
Ningxia	37.36	852	0.279	<0.001
Shanxi	37.69	1138	0.336	<0.001
Hebei	38.22	1248	0.324	<0.001
Neimenggu	41.38	1428	0.213	<0.001
Liaoning	41.47	1032	0.360	<0.001
Xinjiang	42.00	2375	0.155	<0.001
Jilin	43.50	1122	0.304	<0.001
Heilongjiang	46.77	1113	0.288	<0.001

Figure 1 Regression between the strength of phylogenetic conservatism in flowering phenology (Blomberg's *K*) and latitude, and the geographical patterns of the *K*-values in China estimated at the province scale. Each point in the regression represents a province of China. The line is the polynomial regression line with a quadratic term. The blank area in the map in the middle of China is a municipality directly under the control of the central government for which we do not have data.

quadratic terms with the *K*-value (Fig. 1; with r^2 0.48 and 0.57 respectively, $P < 0.001$).

RESULTS

Evaluating phylogenetic conservatism

The midpoint of flowering for all 19,631 species pooled was day 187 (6 July) (SD = 1.02, range 1–349). Over 57% of species flowered in June, July or August. Less than 4% of species flowered in November, December or January.

At the country scale for the full phylogeny of all species, flowering date showed a significant phylogenetic signal ($K = 0.149$, $P < 0.001$) indicating that more closely related species tended to flower at more similar times. Further, there was a significant phylogenetic signal in flowering date in all 28 provinces (Table 1). However, the phylogenetic signal strength at the country scale was lower than the signal in all 28 provinces (Table 1).

In line with our prediction, latitude was positively correlated with phylogenetic signal, and was highest around 40° N (Fig. 1). The regression between the strength of phylogenetic conservatism and latitude was significantly improved by including
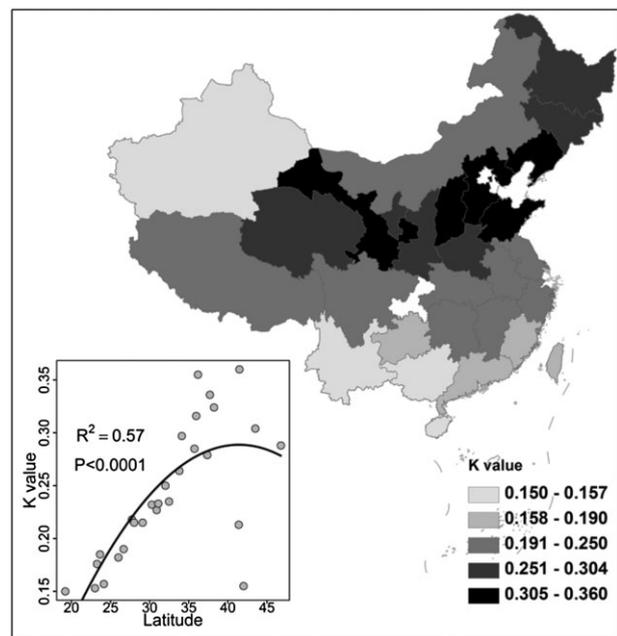
Effect of biological traits

Growth form

The five major growth forms had significantly different flowering times when accounting for the potential effect of species shared evolutionary history ($F = 758.8$, $P < 0.0001$; Fig. 2, Table 2). Trees were the earliest to flower (mean = day 137, 17 May), followed by shrubs (day 162, 11 June), perennials (day 200, 19 July) and annuals (day 212, 31 July). Woody vines flowered significantly earlier than herbs (including annuals and perennials), but later than trees ($P < 0.001$). There was no significant difference in flowering time between woody vines and shrubs ($P = 0.97$). We obtained similar results using Tukey's honest significant difference (HSD) method when flowering date was treated as circular data (Appendix S1 in Supporting Information).

Deciduousness

Evergreen species flowered significantly earlier (51 days earlier) than deciduous species for all growth forms pooled (Fig. 3a;
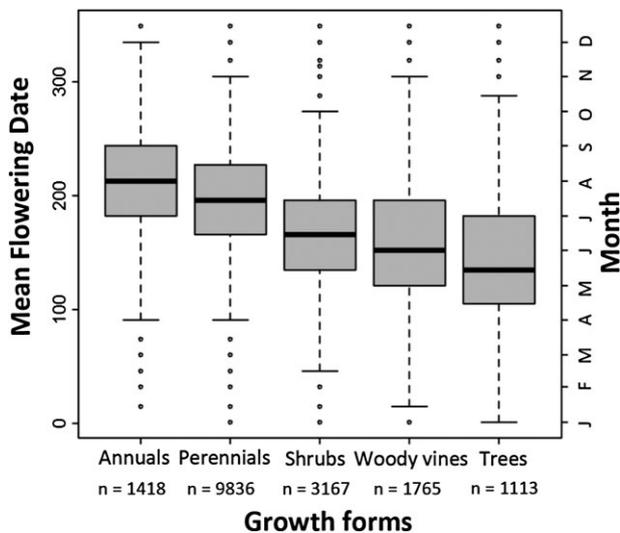
Figure 2 Flowering dates (in Julian days) for five growth forms. The box indicates median (heavy line) and quartiles; whiskers reach to points ≤ 1.5 times the interquartile ranges. The number below the boxplot is number of species of each growth form.

$F = 1113$, $P < 0.0001$). This pattern was repeated for shrubs and woody vines, where evergreen species flowered 21 days (Fig. 3c; $F = 77.3$, $P < 0.0001$) and 34 days (Fig. 3d; $F = 26.3$, $P < 0.0001$) earlier, respectively, but not herbs (Fig. 3b). Conversely, in trees, deciduous plants flowered significantly earlier (9 days) than evergreen plants (Fig. 3e; $F = 6.6$, $P = 0.01$). Direction and significance were maintained in phylogenetic analyses for all growth forms except woody vines. There was evidence of a significant interaction effect between deciduousness and growth form (Fig. 3f; $F = 23.1$, $P < 0.0001$).

Pollination type

Animal-pollinated species flowered significantly earlier (7 days) than wind-pollinated species for all growth forms pooled (Fig. 4a; $F = 4.4$, $P = 0.03$), but there were significant differences between growth forms (Fig. 4f; $F = 8.8$, $P < 0.0001$). Herbs and shrubs followed a similar pattern, with animal-pollinated species flowering significantly earlier (4 days earlier, $F = 8.6$, $P < 0.01$, Fig. 4b; 17 days earlier, $F = 7.3$, $P < 0.01$, Fig. 4c, respectively) than wind-pollinated species . Trees showed the opposite pattern, with wind-pollinated species flowering 8 days earlier, (Fig. 4e; $F = 4.4$, $P < 0.05$). The significant difference in woody vines between animal- and wind-dispersed species was not maintained in phylogenetic analyses, maybe due to the small sample size ($n = 18$).

Fruit type

Fleshy fruited plants flowered significantly earlier (43 days) than non-fleshy-fruited plants for all growth forms pooled (Fig. 5a; $F = 1216.4$, $P < 0.0001$). There was a significant interaction between fruit type and growth form (Fig. 5f; $F = 30.2$,

$P < 0.0001$). For herbs, shrubs and woody vines, fleshy fruited plants flowered significantly earlier than non-fleshy-fruited plants (Fig. 5b–d; $F = 156.6$, 35.3, and 49.4, respectively, all $P < 0.0001$), but for trees there was no significant difference in flowering date between non-fleshy species and fleshy-fruited species ($F = 0.1$, $P = 0.71$). A similar pattern was found when we accounted for phylogenetic relationships.

DISCUSSION

We examined the effects of phylogenetic constraints and correlates of biological traits on flowering phenology for nearly 20,000 angiosperm species throughout China – the largest flowering phenological dataset to date. Our results showed that overall flowering date is a conserved trait in angiosperms, verifying previous findings in independent datasets (e.g. Kochmer & Handel, 1986; Wright & Calderon, 1995; Chang-Yang *et al.*, 2013). Further, if phylogenetic constraints are regional or even global properties of taxa, then closely related species should flower at similar times regardless of their geographic location (Kochmer & Handel, 1986). Our results were based on data from the whole of China and suggest that phylogenetic constraints on flowering may therefore be stronger than local selective pressures. Closely related species tend to share similar physiological and morphological traits, such as flower size, shape, scent and nectar production, through common descent; these will determine the attraction and success of pollination (Westoby *et al.*, 1995). Optimization of pollination success may be a key driver of flowering plant phenology over large spatial scales (Boulter *et al.*, 2006).

We evaluated phylogenetic signal in flowering date at two spatial scales – country (China) and province (28 provinces). We detected stronger phylogenetic signals in flowering date at the province scale. This is congruent with one recent study on phylogenetic conservatism in plant phenology (Davies *et al.*, 2013). Aggregating published data on first flowering at 23 sites across the Northern Hemisphere, the authors observed greater phylogenetic conservatism within sites than across sites. Several mechanisms could explain this phenomenon. First, closely related plants could disperse together to a different region and adapt equally to local conditions (Kochmer & Handel, 1986). Second, closely related species tend to have similar distribution ranges (phylogenetic niche conservatism; Losos, 2008), and thus the degree of relatedness within a range (e.g. a province) tends to be higher than across provinces. In this case, all traits, including flowering phenology, will be likely to show a strong phylogenetic signal. Third, flowering phenology is tightly controlled by climatic cues that vary consistently across a latitudinal gradient, such as temperature and photoperiod; thus a weak phylogenetic signal would be observed when we average flowering time across this latitudinal gradient (Lessard-Therrien *et al.*, 2014).

Latitudinal gradient in phylogenetic signal

There is a general consensus that species richness is higher in lower latitudinal regions than in higher latitudinal regions

Table 2 *T*-values of post-hoc tests to compare the mean flowering dates among growth forms which accounts for the potential effect of species' shared evolutionary history.

Group	Annual herb	Perennial herb	Shrub	Tree	Woody vine
Annual herb	0	6.8**	23.6**	28.6**	17.9**
Perennial herb	−6.8**	0.0	26.4**	30.9**	16.1**
Shrub	−23.6**	−26.4**	0.0	9.0**	0.6
Tree	−28.6**	−30.9**	−9.0**	0.0	−6.0**
Woody vine	−17.9**	−16.1**	−0.6	6.0**	0.0

**0.001 < *P* < 0.01.
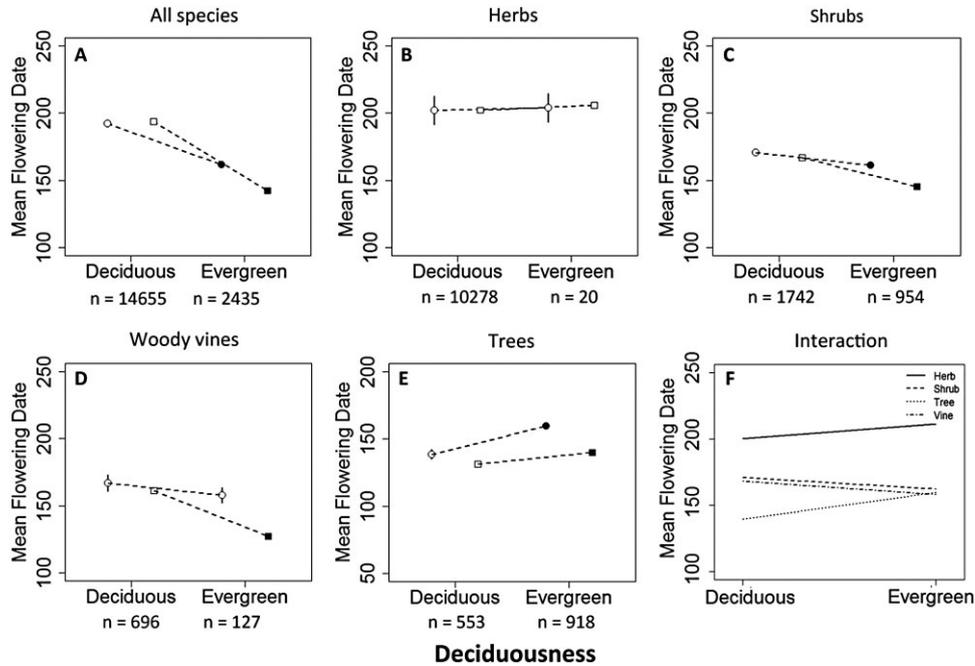
Figure 3 Comparison of mean flowering dates between deciduous and evergreen angiosperm species from throughout China. We show estimates that account for phylogeny (squares) and those that do not (circles). Significant differences between flowering dates are indicated with filled circles (*P* < 0.001), and error bars are standard errors. The interaction between deciduousness and growth form is also shown (f).

(Ricklefs, 2004). However, it remains untested whether there is a latitudinal gradient in the strength of phylogenetic conservatism of functional traits, and whether this pattern of functional traits could in part explain the latitudinal gradient in species richness. To our knowledge, our study is the first to observe this latitudinal gradient in phylogenetic signal for functional traits (herein flowering phenology). We found that the phylogenetic signal of flowering phenology tended to be stronger towards the temperate regions. This latitudinal pattern could be explained by the phylogenetic niche conservatism hypothesis that species tend to be more phylogenetically clustered and ages of clades tend to be younger in colder regions compared with those in warmer regions, as tested and supported by Qian *et al.* (2013). Because of this phylogenetic clustering, flowering time is likely to be more similar in closely related species at higher latitudes. In addition, mild climate throughout the growing season at lower latitudes provides more favourable conditions for growth, which might lead to species at lower latitudes having a wider range of flowering dates, spreading the timing of flowering across the longer growing season. Less strict abiotic constraints allow species to diverge in flowering dates over evolutionary time, and therefore a weak phylogenetic signal would be detected at lower latitudes. Whether the phylogenetic signal of other functional traits increases with latitude remains to be tested.

We also found a trend that the strength of phylogenetic conservatism is positively correlated with latitude, rising to a peak around 40° N, and may then decrease at higher latitudes. As discussed above, the phylogenetic signal of flowering is lower in tropical zones, and tends to increase towards higher latitudes. But conditions become much harsher at latitudes greater than 40°. The higher probability of frost or drought because of stronger winds, and rocky environments that do not retain water, may limit species growth (Cavender-Bares *et al.*, 2009). Convergent evolution due to these strong abiotic selection pressures may lead to low phylogenetic conservatism. Here we propose a novel pattern that the strength of phylogenetic conservatism of flowering phenology along latitude may be hump-shaped, with the highest value at mid-latitudes. This pattern
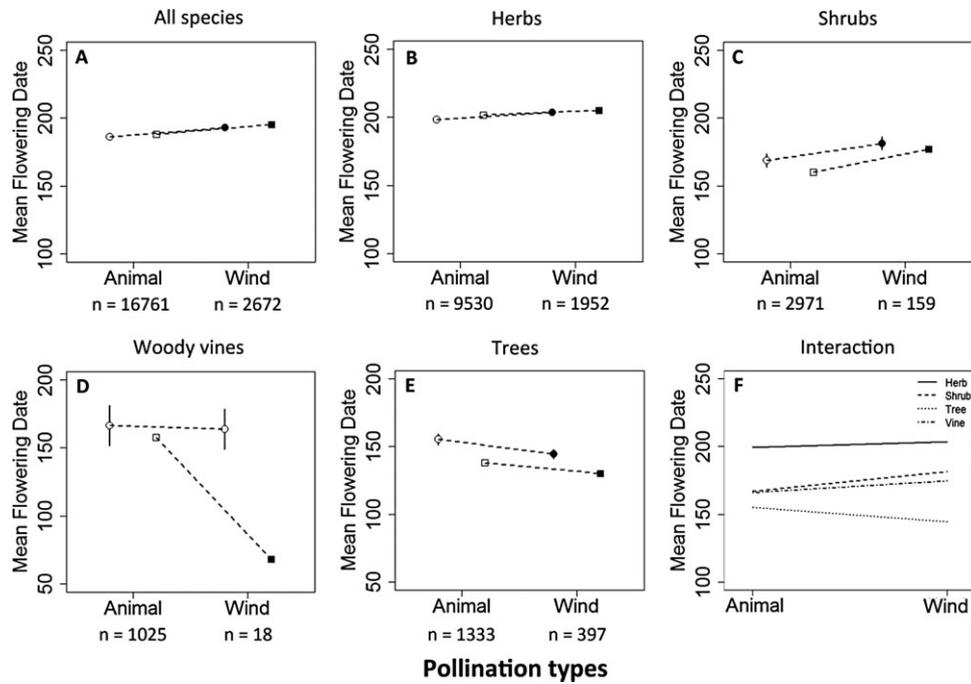
Figure 4 Comparison of mean flowering dates between animal- and wind-pollinated angiosperm species from throughout China. We show estimates that account for phylogeny (squares) and those that do not (circles). Significant differences between flowering dates are indicated with filled circles ($P < 0.001$), and error bars are standard errors. The interaction between deciduousness and growth form is also shown (f).
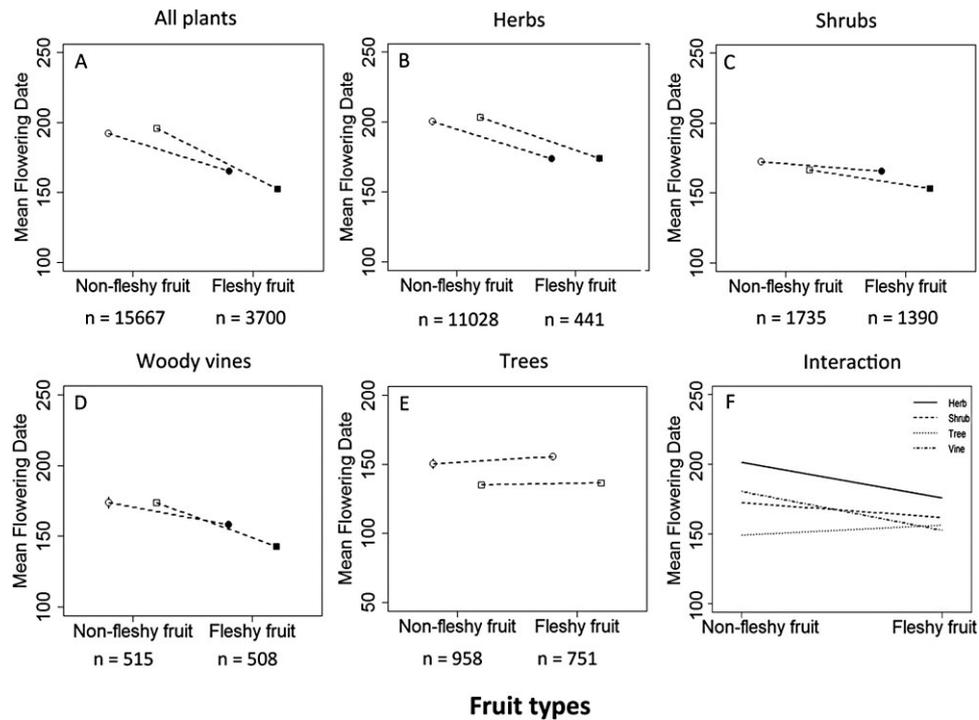

Figure 5 Comparison of mean flowering dates between non-fleshy fruited and fleshy fruited angiosperm species from throughout China. We show estimates that account for phylogeny (squares) and those that do not (circles). Significant differences between flowering dates are indicated with filled symbols ($P < 0.001$), and error bars are standard errors. The interaction between deciduousness and growth form is also shown (f).

needs to be tested in the future with a wider range of data covering both tropical and higher-latitude regions.

Our results have implications for our understanding of the role of phylogenetic conservatism in species richness patterns and for evaluating the potential for species to adapt to global change. Closely related species having more similar flowering times would lead to more intense interspecific competition for pollination, and the resultant stronger competitive exclusion at higher latitudes would be unfavourable for species coexistence, suggesting that conservatism in temporal niche could drive species richness along a latitudinal gradient. The phylogenetic distribution of phenology can also provide a means to predict the potential impact of climate change on species for which we have no direct phenological observations. Here we term the phylogenetic niche conservatism of flowering phenology 'phylogenetic temporal niche conservatism' (PTNC; Pau *et al.*, 2011). According to the framework of Cooper *et al.* (2011), if high temporal niche conservatism means that species will find it harder to evolve in the future, PTNC may have consequences for conservation as global change proceeds. We might expect that species with highly conserved niches may struggle to adapt in the face of environmental change and could consequently face a heightened risk of extinction. On the other hand, those species with more labile traits and niches may cope more easily with changes to local climate and colonize or invade new areas, decreasing their risk of extinction (Broennimann *et al.*, 2007). In the system we have studied, this prediction would mean that species at higher latitudes would be likely to face a heightened risk of extinction as a consequence of global warming.

Trait correlates

Overall, flowering dates were correlated with biological traits. The first key factor was that mean flowering date differed significantly for different growth forms, with trees flowering earliest, followed by woody vines, shrubs and perennial herbs, and then annual herbs. This result is consistent with other studies in the Carolina flora in the United States (Kochmer & Handel, 1986) and for 100 plant species in England (Grainger, 1939). Early flowering may be particularly advantageous for wind-pollinated woody plants, allowing pollination by wind before leaf-out and enabled by the stored resources that may allow for faster development from winter dormancy to flowering in trees than in herbs (Bolmgren & Lönnberg, 2005). The increased light and soil moisture available to trees could explain the pattern that trees flower earlier than shrubs (Opler *et al.*, 1980). In our study, perennial herbs flowered earlier than annual herbs, which is in agreement with previous expectation that perennials, which often have storage of resources available early in the growing season, will flower earlier than annuals (Grainger, 1939).

A second trait related to flowering phenology is deciduousness. Evergreen species flowered earlier than deciduous species when we conducted comparisons for all plants pooled, for shrubs and for woody vines. Evergreen species may flower earlier because they are already photosynthesizing and are therefore able to allocate resources to flowering earlier than deciduous species that need to produce leaves in order to start photosynthesis. In addition, deciduous species (usually winter, cold deciduous species in China) are generally from more northern latitudes and evergreen species (angiosperms) are mainly from subtropical and tropical regions at lower latitudes in China, and then latitude could explain the delayed flowering for the deciduous species. For herbs, no significant difference was detected between evergreen and deciduous species. This might simply reflect the small sample size in the data (only 20 species) which could mask any explicit pattern. Trees had the opposite pattern, with deciduous species flowering earlier than evergreen species. This pattern is likely to reflect a correlation with pollination syndrome, whereby wind-pollinated deciduous species flower early in the spring before leaf-out.

The third key factor is that mean flowering dates differed significantly for different pollination syndromes. Animal-pollinated species flowered earlier than wind-pollinated species when we combined all plants together, but correlations between flowering time and pollination syndrome differed among growth forms. For trees and woody vines, wind-pollinated species flowered earlier than animal-pollinated species. This is consistent with our results above, as well as many other studies (Faegri & van der Pijl, 1979; Proctor *et al.*, 1996), again this is probably the result of selection for spreading pollen before the canopy closes, avoiding physical obstacles for pollen dispersal created by the surrounding vegetation (Whitehead, 1969). The tendency of wind-pollinated trees to flower in the early spring may also be partially explained by the tendency of these species to have large fruits that require more time to mature (Primack, 1987). However, the patterns of shrubs and herbs is different from that of trees and woody vines, with animal-pollinated species flowering earlier than wind-pollinated species. This result suggests that the advantages of wind pollination attuned to the leafless or early leafless condition may be only suitable for taller plants such as trees and woody vines. For smaller-statured plants such as herbs, Kochmer & Handel (1986) provided an alternative strategy, suggesting that early flowering plants attempt to overtop surrounding plants, or at least grow high enough to accomplish adequate pollen dispersal. Thus, due to lineage-specific differences in growth rate and pollen dispersal efficacy, different herbaceous wind-pollinated species would then reach the necessary height at different times of the season, and thus do not need to concentrate their flowering times in spring (Bolmgren *et al.*, 2003).

Another important characteristic affecting flowering time is fruit type, also noted in previous studies (e.g. Eriksson & Ehrlén, 1991; Bolmgren & Lönnberg, 2005). Fleshy fruited plants flowered significantly earlier than non-fleshy fruited plants for all growth forms except trees. Bolmgren & Lönnberg (2005) found that fleshy fruited plants flowered earlier than their non-fleshy fruited sister plants using herbarium phenology data for 77 species in Sweden. In general, more resource-demanding fruits (i.e. fleshy fruits) appear to be larger and heavier than less resource-demanding fruits (i.e. capsules, follicles, achenes), and

these resource-intensive species are forced to flower early in the spring in order to have sufficient time for fruit maturation (Primack, 1987).

CONCLUSIONS

Based on the largest flowering phenology dataset to date, we provided independent confirmation that the flowering phenology of angiosperms is constrained by phylogeny and often correlated with biological traits. Furthermore, the strength of phylogenetic conservatism is weaker at larger scales than at smaller scales and is greater in temperate regions than tropical regions. It is therefore possible to make reasonable predictions of flowering time for many more undocumented species, based on flowering time of their sister or other related taxa, as well as their growth form, pollination syndrome and fruit type, and thereby establish estimates of flowering phenology for a huge range of taxa. Combining this knowledge with data on how changes in flowering cues will affect phenology, it should be possible to predict how entire plant communities will alter their phenology in the future as a function of various climate change scenarios and their latitude.

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SUPPORTING INFORMATION

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Appendix S1 The phenological differences between pairs using Tukey's 'Honest Significant Difference' method when flowering date was treated as circular data, the 95% confidence intervals and the *p*-value of the pairwise comparisons.

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