Journal of Ecology

BRITISH ECOLOGICAL SOCIETY

*Journal of Ecology* 2017, **105**, 627–633 doi: 10.1111/1365-2745.12701

# A global test for phylogenetic signal in shifts in flowering time under climate change

**Nicole E. Rafferty*[,1,2] and Paul D. Nabity[1]**

[1]*Department of Entomology, Washington State University, Pullman, WA 99164, USA; and* [2]*The Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA*

## Summary

**1.** Shifts in the timing of flowering are a conspicuous biological signal of climate change. These shifts have been documented across the globe for diverse communities. Although many species are flowering earlier, others have exhibited no shifts or delays in flowering.

**2.** How species respond phenologically will shape interactions both with other community members and with the abiotic environment, altering fitness, abundance and ultimately persistence.

**3.** To understand if variability in phenological response is influenced by evolutionary history, we tested for phylogenetic signal in shifts in flowering onset for 13 communities representing 116 families across the Northern Hemisphere. We compared the fit of models of neutral evolution (Brownian Motion) with models that incorporate selection (Ornstein–Uhlenbeck).

**4.** We found significant signal in whether species had shifted and the magnitude of response, with both traits conforming to an Ornstein–Uhlenbeck model of trait evolution.

**5.** *Synthesis*. These results show there is global phylogenetic signal in the direction and magnitude of shifts in flowering onset and indicate selection has shaped flowering time responses of related species under climate change; thus, environmentally determined optima may constrain whether and to what degree species respond phenologically to climate change. Our findings further demonstrate the value of testing for phylogenetic signal across multiple communities and comparing multiple models of trait evolution.

**Key-words:** Blomberg's K, Brownian motion, flowering onset, Ornstein–Uhlenbeck, Pagel's lambda, phenology, plant–climate interactions, plasticity

## Introduction

Flowering plants across the Northern Hemisphere are exhibiting shifts in the timing of life-history events. These phenological shifts are associated with changes in climatic cues, including altered temperatures and precipitation patterns, and thus provide a strong biological signal of global climate change (Fitter & Fitter 2002). The magnitude and direction of phenological shifts are variable, even among species in the same communities. For example, flowering onset has shifted to varying extents among species within urban, semi-arid, woodland, prairie and subalpine communities (Bradley *et al.* 1999; Abu-Asab *et al.* 2001; Crimmins, Crimmins & Bertelsen 2011; Calinger, Queenborough & Curtis 2013; CaraDonna, Iler & Inouye 2014), with some species showing advances and others showing delays or no change. The duration of flowering has changed, as well, with the flowering periods of some species lengthening and others shortening with shifts in the onset of flowering (CaraDonna, Iler & Inouye 2014; Rafferty, Bertelsen & Bronstein 2016).

The timing of flowering has important consequences for both ecological and evolutionary processes. For example, flowering time can shape interactions, dictating resource availability for other community members and trophic levels, such as pollinators and florivores. Flowering time can also have a large influence on the fitness of individuals and demography of populations (Franks 2015). In some cases, climate change-driven shifts in flowering phenology have caused mismatches between interacting species. Interactions between spring-flowering forbs and pollinating bumblebees have been disrupted when warm temperatures have led to advanced flowering, resulting in depressed seed set (Kudo & Ida 2013). Theoretical models suggest such shifts in flowering time and resulting mismatches with pollinators can lead to co-extinction, depending on the densities and phenologies of other community members (Gilman *et al.* 2012). On the other hand, experimental studies indicate mismatches are unlikely in some communities (Rafferty & Ives 2011), and data from historical specimens show some plants and pollinating insects are

*Correspondence author. E-mail: nicole.rafferty@wsu.edu

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.
This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

maintaining synchrony under climate change (Bartomeus *et al.* 2011). Regardless of whether phenological shifts lead to complete mismatches, they will almost certainly alter interaction strengths, their costs and benefits, and thus selection.

What factors shape the flowering times of individuals, populations and species? The genes underlying flowering time have been well-characterized (e.g., Putterill, Laurie & Macknight 2004; Jung & Müller 2009), and abiotic variables such as temperature and photoperiod are known to be important triggers of flowering (reviewed by Wilczek *et al.* 2010). Scaling up, genetic variation in flowering time, as well as seasonal patterns and interannual variation in climatic variables, shape flowering at the population level, along with mutualistic, facilitative and antagonistic interactions. At the species level, flowering time can be shaped by evolutionary constraint, adaptive plasticity or environmental differences that shape responses independently of evolutionary history (reviewed by Elzinga *et al.* 2007).

One way to determine whether evolutionary history or environmental differences shape flowering responses to climate change is to test for phylogenetic signal. We adopt here the definition of phylogenetic signal used by Blomberg, Garland & Ives (2003): the tendency for closely related species to be similar in phenotype. Although few studies have tested for phylogenetic signal in shifts in flowering phenology, findings have been mixed and interpretations have differed. For example, using phenological responsiveness, defined as the effect of temperature on flowering date, Calinger, Queenborough & Curtis (2013) did not find phylogenetic signal in a data set of 161 species assembled from herbarium records in Ohio, USA. Similarly, CaraDonna & Inouye (2015) did not detect signal in phenological sensitivity of first flowering to temperature or snowmelt date in a subalpine community of 60 species in Colorado, USA. Davis *et al.* (2010) found significant signal in the correlation between date of first bloom and seasonal temperature variation (i.e. flowering time tracking) for 167 and 323 species but not in shifts in flowering time for 342 and 323 species for two communities in the USA and UK. However, Willis *et al.* (2008) found both flowering time tracking (for 175 species) and shift in flowering time (for 319 species) from 1850 to 1900 were phylogenetically conserved for a community in Massachusetts, USA.

To date, almost all tests for phylogenetic signal in flowering time shifts have used data from a single community or region (but see Davis *et al.* 2010), from which species relatedness and local environmental conditions (phylogeographic clustering) cannot be easily disentangled. Furthermore, previous studies have been limited to testing for signal according to a Brownian motion (BM) model of trait evolution: a model of neutral evolution which posits that trait evolution is proportional to branch lengths, or time since species shared a common ancestor (e.g., Blomberg, Garland & Ives 2003; Butler & King 2004). However, shifts in flowering time may reflect adaptive processes shaped by selection, which can be better captured by an Ornstein–Uhlenbeck (OU) model of trait evolution. Under an OU model, selection is incorporated in the form of a selective optimum, which differs from BM where only drift is expected (Butler & King 2004).

To understand whether drift or selection has shaped flowering time responses, we assembled a global data set on shifts in flowering onset from 13 locations across the Northern Hemisphere, spanning diverse ecological communities and 116 families. We used these data to test for phylogenetic signal, considering both neutral models of trait evolution and models that incorporate selection. We addressed the questions: (i) Is there phylogenetic signal in whether species have shifted in flowering onset? (ii) Is there phylogenetic signal among species in the magnitude of the response of flowering onset? (iii) What model of trait evolution best describes these flowering onset responses?

## Materials and methods

We surveyed the literature for data sets on flowering onset and compiled a list of studies spanning at least 20 years, with a minimum of four data points through time per species (after compilation, all usable data sets had at least seven data points through time per species). We searched systematically using Web of Science (using the terms 'flowering' and 'phenolog') and also followed references to other studies within papers we located. Several data sets were not included because either they did not meet these criteria, or the requisite data for determining shifts in flowering time were not available. We assembled 15 data sets from across the Northern Hemisphere, ranging in duration from 29 to 172 years from 1837 to 2012 (Table 1). The data come from a diversity of habitats and include forbs, grasses, shrubs and trees. From all 15 data sets, we extracted information on whether species had shifted in flowering onset. When that summary information was not available, we used the raw data to test for shifts using simple linear regressions of year against day of year of first bloom. Species shifts in flowering onset were coded as: 1 for significant delay; 0 for no shift; −1 for significant advance. In a second analysis, we used a continuous measure of shift, the slope of the relationship between first flowering and year, which we could extract or calculate for only eight of the data sets that either reported slopes or provided raw data from which they could be calculated.

Three of the data sets (Bradley *et al.* 1999; Miller-Rushing & Primack 2008; Ellwood *et al.* 2013) have species in common from the same locations but for differing time spans. We therefore combined data from these three studies to yield the longest time series possible for species for which data were available in multiple data sets. For example, the data for *Sisyrinchium campestre* as reported in Bradley *et al.* (1999) indicate there has been no shift in flowering onset for this species; however, updating those data to include more recent phenological observations as reported in Ellwood *et al.* (2013) yielded a significant shift to earlier flowering. We therefore coded *S. campestre* as shifting earlier in our aggregate data set.

For analyses of the pooled data sets, we averaged the data for shift or slope for species for which we had multiple records from different communities because each species is represented only once in the phylogenies and can have only a single value per trait. Mean responses (averaged for 2–7 records per species) were used for 133 (10·7%) of the 1245 species used for phylogenetic analyses with shift as the trait; mean responses (averaged for 2–4 records per species) were used for 70 (11·6%) of the 606 species used for phylogenetic analyses with slope as the trait.

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

**Table 1.** Data set references, locations, time spans (duration in years), habitats represented, number of species included in each data set, and whether data on shifts in flowering onset, slopes of flowering onset or both were used

| Reference | Location | Time span (duration) | Habitat | No. species | Flowering response |
|---|---|---|---|---|---|
| Abu-Asab *et al.* (2001) | Washington DC, USA | 1970–1999 (29) | Metropolitan area | 100 | Shift, Slope |
| Bolmgren, Vanhoenacker & Miller-Rushing (2013) | Sweden | 1934–2006 (72) | Temperate farm | 25 | Shift |
| Bradley *et al.* (1999) | Wisconsin, USA | 1936–1945, 1977–1998, 1999–2007 added for present study (38) | Tallgrass prairie | 33 | Shift, Slope |
| Calinger, Queenborough & Curtis (2013) | Ohio, USA | 1895–2009 (115) | Temperate woodland and grassland | 141 | Shift |
| CaraDonna, Iler & Inouye (2014) | Colorado, USA | 1974–2012 (38) | Subalpine meadows | 60 | Shift, Slope |
| Crimmins, Crimmins & Bertelsen (2010, 2011) | Arizona, USA | 1984–2003 (29); 1984–2009 (35) | Semi-arid montane | 428; 240 | Shift |
| Dunnell & Travers (2011) | North Dakota and Minnesota, USA | 1910–1961, 2007–2010 (54) | Temperate woodland and grassland | 23 | Shift, Slope |
| Ellwood *et al.* (2013) | Massachusetts; Wisconsin, USA | 1852–1858, 1878, 1888–1902, 2004–2006, 2008–2012; 1935–1945, 1977–2012 (66) | Temperate forest, wetland; tallgrass prairie | 32; 23 | Shift, Slope |
| Fitter & Fitter (2002) | Oxfordshire, England | 1954–2000 (56) | Temperate woodland and grassland | 372 | Shift, Slope |
| Menzel, Estrella & Fabian (2001) | Germany | 1951–1996 (45) | Various | 5 | Shift, Slope |
| Miller-Rushing & Primack (2008) | Massachusetts, USA | 1852–1858, 1878, 1888–1902, 2004–2006 (123) | Temperate forest and wetland | 43 | Shift, Slope |
| Molnár *et al.* (2012) | Hungary | 1837–2009, 1980–2011 (172, 31) | Various | 39 | Shift, Slope |
| Ovaskainen *et al.* (2013) | Karelia, Russia | 1960–2010 (50) | Boreal forest | 66 | Shift, Slope |
| Panchen *et al.* (2012) | Pennsylvania, USA | 1840–2010 (150) | Greater metropolitan area | 28 | Shift, Slope |

To test for phylogenetic signal, we used two phylogenetic trees that were constructed to address similar questions by Davies *et al.* (2013). The first of the Davies *et al.* (2013) trees comprises 4494 taxa, was constructed using the Angiosperm Phylogeny Group 3 tree as the backbone in Phylomatic (Webb & Donoghue 2005) and is 25% resolved (hereafter the 'Phylomatic tree'). Following Davies *et al.* (2013), we also used a molecular phylogeny that differs in topology for comparison; this tree was calibrated with penalized likelihood and is fully resolved for 1246 genera (hereafter the 'molecular tree'). Both trees are available in Davies *et al.* (2013). Our aggregate data set for shift covered 1245 (27·7%) of the species in the Phylomatic tree and 582 (46·7%) of the genera in the molecular tree. Our aggregate data set for slope covered 610 (13·6%) of the species in the Phylomatic tree and 328 (26·3%) of the genera in the molecular tree. We added species to the molecular tree as polytomies (Davies *et al.* 2013), resulting in trees with 1172 and 585 species for shift and slope, respectively. A handful of species in our data set were not included in the Phylomatic tree, and some genera were not in the molecular tree; we removed these species/genera ($n$ = 14/55) from our compiled data set.

We tested for phylogenetic signal in (i) whether and in what direction shifts have occurred ('shift') and (ii) the magnitude of shifts ('slope') based on the variance of phylogenetically independent contrasts (PIC) for our empirical data set relative to the variance of PIC for randomly reshuffled species identities across the trait data set (iterated 20 000 times). *P*-values assess the fraction of reshuffled data sets that have lower PIC variance scores than our empirical data set, as implemented in the R library 'picante' (Kembel *et al.* 2010; R Core Team 2016).

We also used Blomberg's K (Blomberg, Garland & Ives 2003) and Pagel's λ (Pagel 1999) to measure the strength of signal relative to a BM model of trait evolution. K ranges from almost 0 to greater than 1, whereas λ ranges from 0 to 1; for both measures, values of 1 indicate BM evolution. Values of K less than 1 indicate related species resemble each other less than would be expected under BM, implying selection over drift, whereas values of K greater than 1 indicate related species resemble each other more than would be expected under BM (Blomberg, Garland & Ives 2003), also implying selection. Because K can depend on tree resolution, and the Phylomatic tree was only 25% resolved, we thinned the tree to eliminate terminal polytomies as recommended by Davies *et al.* (2012). After randomly removing species to leave only one per node, we then iteratively estimated K on the thinned trees, performing 30 iterations each for the phylogenies used to test for signal in shift and slope. We followed the same procedure to thin the molecular tree (which is fully resolved to genus level but to which species were added as polytomies). For our analyses using individual data sets, we present K values for unthinned trees because no trees were less than 60% resolved (Davies *et al.* 2012). However, we note that K values for thinned trees were similar. K and λ were calculated using the R library 'phytools' (Revell 2012), which provides P-values for the K statistic itself, gained by reshuffling species identities in the trait data set, calculating K for each iteration, and comparing the observed K to this null K distribution. The 'phytools' library also provides *P*-values for λ by performing a likelihood ratio test against the null hypothesis that $\lambda = 0$. We performed each of these tests for the pooled data sets and each individual data set, using both the Phylomatic and the molecular trees. We excluded two data sets (Menzel, Estrella & Fabian 2001 and

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

Molnár *et al.* 2012) from the individual community analyses because after pruning only 3 and 10 species remained respectively.

We also tested the fit of an OU model of trait evolution to determine if shifts in flowering phenology might be constrained by stabilizing selection. We fit a single-optimum OU model for the pooled data and each data set, using both trees. Tests of OU model fit and significance were performed with the R libraries 'geiger' (Harmon *et al.* 2008), 'phylolm' (Ho & Ane 2014) and 'OUwie' (Beaulieu & O'Meara 2015), using likelihood ratio tests to compare the fit of OU vs. BM models.

## Results

We found significant phylogenetic signal globally in both flowering time response (whether and in what direction species had shifted; $P_{PIC} = 0{\cdot}001$) and magnitude of response (slope of flowering onset regressed against year; $P_{PIC} = 0{\cdot}02$) using the Phylomatic tree (Table 2; Figs 1 and 2). For both traits (shift and slope), an OU model of trait evolution fit better than a BM model (shift: $P_{OU} < 0{\cdot}00001$ and slope: $P_{OU} < 0{\cdot}00001$; Tables 2–4). Using the molecular tree, we detected significant signal in shift ($P_{PIC} = 0{\cdot}03$) but failed to detect signal in slope ($P_{PIC} = 0{\cdot}16$) in our global data set (Figures S3 and S4). An OU model fit significantly better than a BM model for both traits using the pooled data and the molecular tree (Tables S1 and S2, Supporting Information).

At the individual community level using the Phylomatic tree, we detected signal in only 2 of 13 communities: the Oxfordshire, UK (Fitter & Fitter 2002) and Wisconsin, USA (Bradley *et al.* 1999) communities (Tables 2 and 3). For the Oxfordshire community, an OU model fit significantly better than a BM model, whereas this was not the case for the Wisconsin community. The Wisconsin community had the highest (and the only significant) K and λ values for both traits,

**Table 2.** Descriptive statistics and tests for phylogenetic signal in shift in flowering onset using Phylomatic tree for pooled data and individual data sets

| Data set | n | $P_{PIC}$ | K or $K_{thinned}$ | $P_K$ | λ | $P_\lambda$ | $P_{OU}$ |
|---|---|---|---|---|---|---|---|
| Pooled | 1245 | **0·001** | 0·17 ± 0·003 | 0·17 | 0·34 | **<0·00001** | **<0·00001** |
| Abu-Asab *et al.* (2001) | 97 | 0·82 | 0·29 | 0·85 | 0·000072 | 1·00 | **<0·00001** |
| Bolmgren, Vanhoenacker & Miller-Rushing (2013) | 21 | 0·20 | 0·71 | 0·18 | 0·000076 | 1·00 | **0·054** |
| Bradley *et al.* (1999) | 46 | **0·001** | 0·81 | **0·003** | 1·07 | **<0·00001** | 0·097 |
| Calinger, Queenborough & Curtis (2013) | 128 | 0·24 | 0·28 | 0·34 | 0·18 | 0·24 | **<0·00001** |
| CaraDonna, Iler & Inouye (2014) | 57 | 0·40 | 0·36 | 0·53 | 0·000073 | 1·00 | **<0·00001** |
| Crimmins, Crimmins & Bertelsen (2010, 2011) | 535 | 0·94 | 0·12 | 0·94 | 0·052 | 0·11 | **<0·00001** |
| Dunnell & Travers (2011) | 23 | 0·90 | 0·15 | 1·00 | 0·000073 | 1·00 | **<0·00001** |
| Fitter & Fitter (2002) | 376 | **0·019** | 0·17 | 0·25 | 0·000067 | 1·00 | **<0·00001** |
| Ellwood *et al.* (2013) | 47 | 0·40 | 0·32 | 0·42 | 0·000069 | 1·00 | **<0·00001** |
| Ovaskainen *et al.* (2013) | 56 | 0·77 | 0·35 | 0·82 | 0·000072 | 1·00 | **<0·00001** |
| Panchen *et al.* (2012) | 20 | 0·81 | 0·61 | 0·85 | 0·000079 | 1·00 | **0·002** |

$P_{PIC}$ values give the significance of tests for phylogenetic signal using phylogenetically independent contrasts; $P_K$ and $P_\lambda$ values give the significance of K or $K_{thinned}$ (mean ± SD) and λ respectively; and $P_{OU}$ values give the significance of a likelihood ratio test comparing the fit of an OU vs. BM model. Significant *P* values are shown in bold.

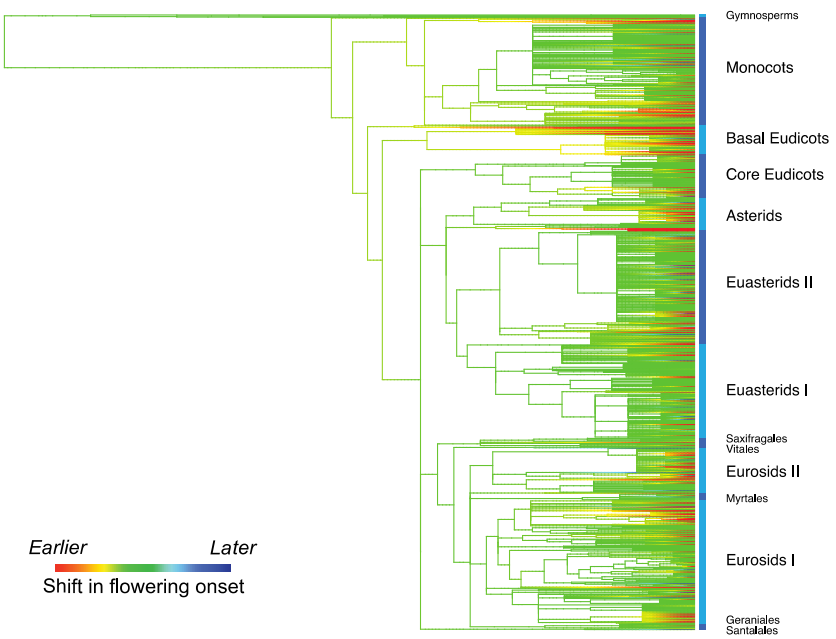


**Fig. 1.** Phylogenetic distribution of shift in flowering onset (ranging from −1 for significantly earlier to 1 for significantly later) on the Phylomatic tree topology for the pooled data set. For a high-resolution image with species names, see Figure S1. [Colour figure can be viewed at wileyonlinelibrary.com]

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

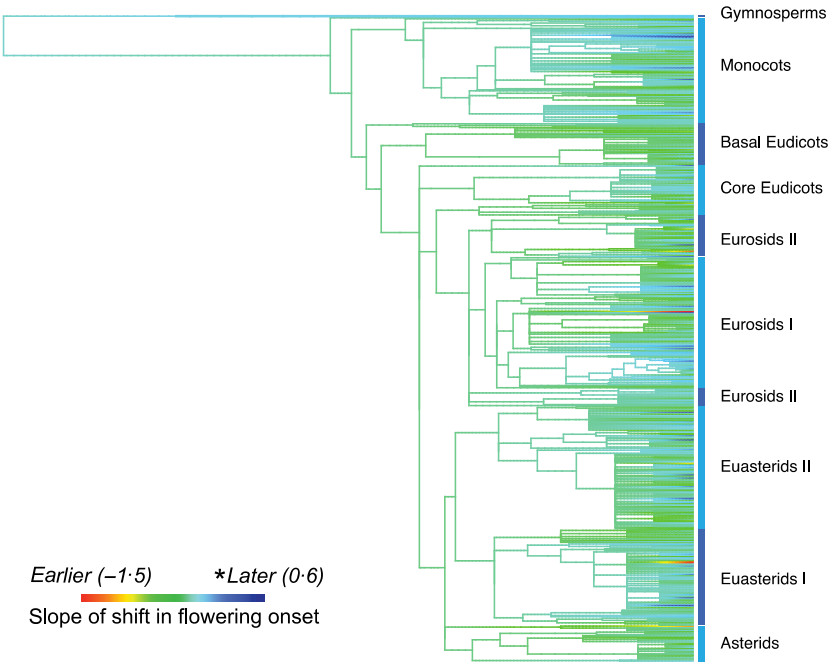


**Fig. 2.** Phylogenetic distribution of slope of shift (ranging from −1·5 to 0·6) in flowering onset on the Phylomatic tree topology for the pooled data set. The asterisk on the scale indicates the colour that corresponds to slope near 0. For a high-resolution image with species names, see Figure S2. [Colour figure can be viewed at wileyonlinelibrary.com]

**Table 3.** Descriptive statistics and tests for phylogenetic signal in slope (flowering onset regressed against year) using Phylomatic tree for pooled data and individual data sets

| Data set | n | $P_{PIC}$ | K or $K_{thinned}$ | $P_K$ | λ | $P_\lambda$ | $P_{OU}$ |
|---|---|---|---|---|---|---|---|
| Pooled | 610 | **0·02** | 0·24 ± 0·005 | 0·07 | 0·000067 | 1·00 | **<0·00001** |
| Abu-Asab *et al.* (2001) | 97 | 0·96 | 0·26 | 0·97 | 0·000072 | 1·00 | **<0·00001** |
| Bradley *et al.* (1999) | 33 | **0·01** | 0·61 | **0·03** | 1·01 | 0·16 | 0·12 |
| CaraDonna, Iler & Inouye (2014) | 55 | 0·45 | 0·37 | 0·50 | 0·000073 | 1·00 | **<0·00001** |
| Dunnell & Travers (2011) | 23 | 0·60 | 0·41 | 0·54 | 0·22 | 0·45 | **0·0002** |
| Ellwood *et al.* (2013) | 31 | 0·28 | 0·46 | 0·28 | 0·35 | 0·20 | **0·0003** |
| Fitter & Fitter (2002) | 376 | **0·02** | 0·18 | 0·11 | 0·000067 | 1·00 | **<0·00001** |
| Ovaskainen *et al.* (2013) | 56 | 0·88 | 0·34 | 0·82 | 0·000072 | 1·00 | **<0·00001** |
| Panchen *et al.* (2012) | 20 | 0·89 | 0·58 | 0·87 | 0·000079 | 1·00 | **0·001** |

$P_{PIC}$ values give the significance of tests for phylogenetic signal using phylogenetically independent contrasts; $P_K$ and $P_\lambda$ values give the significance of K or $K_{thinned}$ (mean ± SD) and λ respectively; and $P_{OU}$ values give the significance of a likelihood ratio test comparing the fit of an OU vs. BM model. Significant *P* values are shown in bold.

**Table 4.** Log-likelihood values (LogLik) and sample sizes for different models of trait evolution for shift and slope of flowering onset

| | Shift | | Slope | |
|---|---|---|---|---|
| Model | LogLik | n | LogLik | n |
| BM | −956·5 | 1245 | −64·5 | 610 |
| OU | −787·0**** | | 14·76**** | |

BM = Brownian motion; OU = Ornstein–Uhlenbeck. Asterisks indicate significance of likelihood ratio tests comparing model fits (****$P < 0·00001$).

approaching 1, suggesting trait evolution is shaped more by drift than selection for species in that community. Using the molecular tree, we detected signal in only the Wisconsin community. An OU model fit significantly better than a BM model for each data set using the molecular tree (Tables S1 and S2).

## Discussion

Shifts in flowering time, when analysed globally, show phylogenetic signal and are best explained by evolutionary models that incorporate selection. Considering either the direction or the magnitude of response, shifts in flowering onset conform to an OU model of trait evolution. To our knowledge, this is the first large-scale, multi-community phylogenetic analysis of response of flowering onset to recent climate change. By testing the fit of multiple models of trait evolution, we gained information about how flowering plants have been shaped by selection to adjust phenologically when climatic cues change. Although previous work has focused solely on applying a BM model of trait evolution to tests of phylogenetic signal in flowering time (e.g., Davies *et al.* 2013; CaraDonna & Inouye 2015), we show that models that incorporate natural selection may be more appropriate, particularly when multiple communities are analysed.

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

When testing for phylogenetic signal within individual plant communities, however, we failed to detect phylogenetic signal in all but two communities. Similarly, using the molecular tree, we failed to detect phylogenetic signal in the magnitude of shifts in flowering time (i.e. slope). Together, these two results indicate that tree size and topology are influential, suggesting numerous species are required for understanding patterns of flowering time response across taxa and results should be compared among trees that differ in resolution. Overall, our results suggest it is important to test multiple models of trait evolution when assessing phylogenetic signal in phenological response traits and to look across communities to increase species representation.

Given that the onset of flowering represents an extreme time point in the distribution of flowering times at the population level, it is reasonable to expect selection to act on shifts in onset. Thus, variance in shifts in flowering time should be constrained, rather than increasing over time in an unbounded way as would be predicted by a BM model (Butler & King 2004). Instead, each lineage evolves towards some optimal plasticity in flowering onset. Such constrained responses in flowering phenology are common, with many species requiring vernalization and other climatic cues to initiate bloom, thereby preventing plants from responding to short-term anomalous cues that could trigger flowering at maladaptive times (reviewed by Wilczek *et al.* 2010). Constraints on flowering time may be further shaped by pollination mutualisms where the partner may be similarly negatively affected by unfavourable abiotic conditions encountered by early emergence, for example.

Flowering time response to climate may oscillate around an optimum within an adaptive zone (sensu Simpson 1953), resulting in plastic responses to abiotic cues. Akin to the finding that behavioural traits tend to show less signal than expected under BM, indicating they are evolutionarily labile (Blomberg, Garland & Ives 2003), flowering onset may be evolutionarily labile to facilitate climate tracking by sedentary organisms at the whim of their environment. Nonetheless, the existence of an optimum means that when individuals fall outside the adaptive zone, selection acts to return the population towards the optimum. When climate variance increases, as occurs with anthropogenic warming, stabilizing selection may be displaced by directional selection if the adaptive zone boundaries shift, thereby pushing the optimum towards or beyond the edge of the old zone into a new zone.

Altogether, the results we report indicate that there is phylogenetic signal in the direction and magnitude of global shifts in flowering onset in response to current climate change. Furthermore, the phenological response of flowering plants to climate change has been shaped by selection. Future investigation of the abiotic and biotic factors that might contribute to those optima would yield additional insight into the constraints influencing plant responses to changing climatic cues. In compiling data from phylogenetically diverse communities from across the Northern Hemisphere and by comparing the fit of multiple models of trait evolution, we have demonstrated the value of looking beyond single communities and neutral models of trait evolution. Such global analyses, which could be expanded by acquisition of data on the flowering phenologies of plants in the tropics and Southern Hemisphere, are valuable for understanding how ongoing climate change will affect ecosystems over time.

## Authors' contributions

N.R. and P.N. conceived the idea, compiled and analysed the data and wrote the manuscript. Both authors contributed equally and critically to the drafts and gave final approval for publication.

## Acknowledgements

We thank A.R. Ives and D.L. Mahler for helpful input on this work. We gratefully acknowledge many researchers who collected the phenological data used in our analyses.

## Data accessibility

Compiled data on shift and slope of shift in flowering onset are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.cm049 (Rafferty & Nabity 2016).

## References

Abu-Asab, M.S., Peterson, P.M., Shetler, S.G. & Orli, S.S. (2001) Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity and Conservation*, **10**, 597–612.

Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. & Winfree, R. (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the USA*, **108**, 20645–20649.

Beaulieu, J.M. & O'Meara, B. (2015) OUwie: analysis of evolutionary rates in an OU framework. R package version 1.45. https://CRAN.R-project.org/package=OUwie.

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.

Bolmgren, K., Vanhoenacker, D. & Miller-Rushing, A.J. (2013) One man, 73 years, and 25 species. Evaluating phenological responses using a lifelong study of first flowering dates. *International Journal of Biometeorology*, **57**, 367–375.

Bradley, N.L., Leopold, A.C., Ross, J. & Huffaker, W. (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the USA*, **96**, 9701–9704.

Butler, M.A. & King, A.A. (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *American Naturalist*, **164**, 683–695.

Calinger, K.M., Queenborough, S. & Curtis, P.S. (2013) Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters*, **16**, 1037–1044.

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 USA*, **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.

Crimmins, T.M., Crimmins, M.A. & Bertelsen, C.D. (2010) Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. *Journal of Ecology*, **98**, 1042–1051.

Crimmins, T.M., Crimmins, M.A. & Bertelsen, C.D. (2011) Onset of summer flowering in a "Sky Island" is driven by monsoon moisture. *New Phytologist*, **191**, 468–479.

Davies, T.J., Kraft, N.J.B., Salamin, N. & Wolkovich, E.M. (2012) Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology*, **93**, 242–247.

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B. *et al.* (2013) Phylogenetic conservatism in plant phenology. *Journal of Ecology*, **101**, 1520–1530.

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

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*, **365**, 3201–3213.
Dunnell, K.L. & Travers, S.E. (2011) Shifts in the flowering phenology of the northern Great Plains: patterns over 100 years. *American Journal of Botany*, **98**, 935–945.
Ellwood, E.R., Temple, S.A., Primack, R.B., Bradley, N.L. & Davis, C.C. (2013) Record-breaking early flowering in the eastern United States. *PLoS ONE*, **8**, e53788.
Elzinga, J.A., Atlan, A., Biere, A., Gigord, L.D.B., Weis, A.E. & Bernasconi, G. (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology and Evolution*, **22**, 432–439.
Fitter, A.H. & Fitter, R. (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.
Franks, S.J. (2015) The unique and multifaceted importance of the timing of flowering. *American Journal of Botany*, **102**, 1401–1402.
Gilman, R.T., Fabina, N.S., Abbott, K.C. & Rafferty, N.E. (2012) Evolution of plant-pollinator mutualisms in response to climate change. *Evolutionary Applications*, **5**, 2–16.
Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.
Ho, L.S.T. & Ane, C. (2014) Intrinsic inference difficulties for trait evolution with Ornstein Uhlenbeck models. *Methods in Ecology and Evolution*, **5**, 1133–1146.
Jung, C. & Müller, A.E. (2009) Flowering time control and applications in plant breeding. *Trends in Plant Science*, **14**, 563–573.
Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
Kudo, G. & Ida, T.Y. (2013) Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, **94**, 2311–2320.
Menzel, A., Estrella, N. & Fabian, P. (2001) Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. *Global Change Biology*, **7**, 657–666.
Miller-Rushing, A.J. & Primack, R.B. (2008) Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology*, **89**, 332–341.
Molnár, V.A., Tökölyi, J., Végvári, Z., Sramkó, G., Sulyok, J. & Barta, Z. (2012) Pollination mode predicts phenological response to climate change in terrestrial orchids: a case study from central Europe. *Journal of Ecology*, **100**, 1141–1152.
Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences of the USA*, **110**, 13434–13439.
Pagel, M.D. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.
Panchen, Z.A., Primack, R.B., Aniśko, T. & Lyons, R.E. (2012) Herbarium specimens, photographs, and field observations show Philadelphia area plants are responding to climate change. *American Journal of Botany*, **99**, 751–756.
Putterill, J., Laurie, R. & Macknight, R. (2004) It's time to flower: the genetic control of flowering time. *BioEssays*, **26**, 363–373.
R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rafferty, N.E., Bertelsen, C.D. & Bronstein, J.L. (2016) Later flowering is associated with a compressed flowering season and reduced reproductive output in an early season floral resource. *Oikos*, **125**, 821–828.
Rafferty, N.E. & Ives, A.R. (2011) Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology Letters*, **14**, 69–74.
Rafferty, N.E. & Nabity, P.D. (2016) Data from: A global test for phylogenetic signal in shifts in flowering time under climate change. *Dryad Digital Repository,* http://dx.doi.org/10.5061/dryad.cm049.
Revell, L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
Simpson, G.G. (1953) *The Major Features of Evolution*. Columbia University Press, New York, NY, USA.
Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecological Resources*, **5**, 181–183.
Wilczek, A.M., Burghardt, L.T., Cobb, A.R., Cooper, M.D., Welch, S.M. & Schmitt, J. (2010) Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical Transactions of the Royal Society B*, **365**, 3129–3147.
Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the USA*, **105**, 17029–17033.

*Received 27 May 2016; accepted 26 October 2016*
*Handling Editor: Akiko Satake*

## Supporting Information

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

**Figure S1.** High-resolution version of phylogenetic distribution of shift in flowering onset on the Phylomatic tree topology for the pooled data set with species names.

**Figure S2.** High-resolution version of phylogenetic distribution of slope of shift in flowering onset on the Phylomatic tree topology for the pooled data set with species names.

**Figure S3.** High-resolution version of phylogenetic distribution of shift in flowering onset on the molecular tree topology for the pooled data set with species names.

**Figure S4.** High-resolution version of phylogenetic distribution of slope of shift in flowering onset on the molecular tree topology for the pooled data set with species names.

**Table S1.** Descriptive statistics and tests for phylogenetic signal in shift in flowering onset using molecular tree for pooled data and individual data sets.

**Table S2.** Descriptive statistics and tests for phylogenetic signal in slope of shift in flowering onset (flowering onset regressed against year) using molecular tree for pooled data and individual data sets.

© 2016 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,