

A phylogenetic analysis of trait convergence in the spring flora¹

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Abstract: In temperate deciduous forests, spring flowering plants exhibit remarkable similarity in a number of characteristics, including reproductive, vegetative, and ecological traits. The apparent convergence of floral traits, especially corolla colour, among spring flowering species has been well documented, but remains poorly understood. Here we review adaptive hypotheses and predictions that have been proposed to explain the apparent correlation between spring flowering and a suite of traits. We investigated the correlation between flowering phenology (i.e., spring or nonspring) and several key traits using phylogenetic comparative methods. Through this analysis we were able to confirm the existence of a correlation for five of the six traits examined. Specifically, spring flowering is shown to have evolved in a correlated fashion with reproductive schedule (perennial vs. annual), light corolla colour, fruit type, growth form, and forest strata layer. In general, our survey determined that spring flowering species are perennial, have light coloured corollas, a herbaceous growth form, and tend to occupy the understory of the forest. These results are discussed in light of the reviewed adaptive hypotheses and the spring pollination environment.

Key words: correlated evolution, spring, phenology, pollinator-mediated interactions, pollination, BayesTraits.

Résumé : Dans les forêts décidues tempérées, les plantes à fleurs printanières montrent une remarquable similarité chez un nombre de caractéristiques, incluant des traits reproductifs, végétatifs, et écologiques. Il existe une bonne documentation sur l'apparente convergence des traits floraux, surtout la couleur de la corolle, parmi les espèces de plantes fleurissant au printemps, mais notre compréhension demeure limitée. Les auteurs passent en revue les hypothèses adaptatives et les prédictions proposées pour expliquer l'apparente corrélation entre la floraison printanière et une séquence de traits. Ils ont examiné la corrélation entre la phénologie florale (c.-à-d., printemps ou non) et plusieurs traits clés, en utilisant des méthodes phylogénétiques comparatives. Ces observations leur ont permis de confirmer l'existence d'une corrélation avec cinq des six traits examinés. Spécifiquement, on montre que la floraison printanière a évolué de façon corrélative avec la cédule de reproduction (pérenne vs. annuelle), la couleur claire de la corolle, le type de fruit, la forme de croissance et l'étage de la strate forestière. En général, les observations déterminent que les espèces à floraison printanière sont pérennes, ont des corolles de couleur claire, possèdent une forme de croissance herbacée, et ont tendance à occuper les sous-bois de la forêt. On discute ces résultats à la lumière des hypothèses adaptatives révisées et l'environnement pollinique printanier.

Mots-clés : évolution corrélée, printemps, phénologie, interactions via les pollinisateurs, pollinisation, BayesTraits.

[Traduit par la Rédaction]

Introduction

The timing of reproduction is a key component of an organism's life history. Indeed, phenotypic variation in the timing of reproduction has been found to influence fitness for a variety of animal and plant species (Frick et al. 2010; Visser et al. 1998; Walther et al. 2002). In animal-pollinated plants, mating success can vary with the timing of reproduction because of temporal variation in mate availability, pollinator availability, and the suitability of the environment for breeding (Brody 1997; Ehrlen and Munzbergova 2009; Houle 2002; Inouye 2008; Sargent and Roitberg 2000; Thomson 2010). Selection on the timing of reproduction likely explains some fascinating patterns in nature, such as synchronous

mast flowering in the aseasonal forests of Southeast Asia, where over 80% of the canopy members, from distinct families such as Burseraceae, Dipterocarpaceae, Fabaceae, Myristicaceae, and Polygalaceae, flower simultaneously over a period of a few weeks to a few months (Ashton et al. 1988).

In temperate deciduous forests, flowering in spring blooming species is thought to be initiated by patterns of snowmelt and the accumulation of suitable climatic conditions (Kudo et al. 2008). Spring in temperate deciduous forests is marked by the sudden onset of multiple understory species flowering simultaneously, which results in synchronous, community-level flowering (Kudo et al. 2008; Macior 1978a; Motten 1986; Schemske et al. 1978). For these species, mating is constrained to the period of suitably warm conditions prior to

Received 15 September 2011. Accepted 5 February 2012. Published at www.nrcresearchpress.com/cjb on 25 June 2012.

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¹This article is part of a Special Issue entitled "Pollination biology research in Canada: Perspectives on a mutualism at different scales".

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canopy closure (Kudo et al. 2008; Macior 1978a; Motten 1986; Schemske 1977; Schemske et al. 1978). With canopy closure comes a sudden decline in the abundance of understory species in flower that is as remarkable as the onset of the spring bloom. As the spring progresses, the earliest flowering species experience a dramatic drop in the availability of light as canopy closure occurs (Ida and Kudo 2008; Kudo et al. 2008). It has frequently been noted that many species that share a spring flowering phenology also exhibit a shared set of unique life-history traits, including similarities in corolla colour and symmetry, fruit type, reproductive schedule, and seed dispersal mechanisms (Bierzychudek 1982; Jolls 2003; Motten 1986; Schemske et al. 1978; Whigham 2004). While a few authors have put forward adaptive hypotheses for the correlations (i.e., Macior 1978a; Motten 1986; Schemske et al. 1978), rigorous tests are currently lacking.

The pattern of similarity in life-history traits among spring flowering plants may be the result of common evolutionary history, or, alternatively, it may signify adaptation by disparately related taxa to the spring flowering environment. Traits are often shared among species within genera and families as the result of common ancestry, and if a spring flowering phenology evolves more frequently within certain clades, or, within a clade that diversified rapidly subsequent to adopting the strategy, the apparent correlation may be an artefact of a shared evolutionary history. As a result, the use of phylogenetically controlled analyses is critical (Harvey and Pagel 1991). Taking phylogenetic relationships into account, we set out to determine whether there is evidence to support the notion of correlated evolution among flowering phenology and other reproductive, vegetative, and ecological traits. In the following sections we review the suite of traits under examination and discuss the adaptive mechanisms that could potentially explain their apparent correlation with a spring flowering phenology.

Reproductive schedule

Fewer than 10% of forest herbs exhibit an annual reproductive schedule (Jolls 2003; Struik 1965). Instead, most species are iteroparous, i.e., perennials that reproduce many times throughout their life span (Bierzychudek 1982; Jolls 2003; Struik 1965; Whigham 2004). In cool temperate climates, flowers of the earliest blooming entomophilous species may frequently experience pollinator-limited reproductive success as the result of the extreme variation in pollinator abundance inherent to early spring climatic conditions. Indeed, this is the case for flowering species found in both the temperate deciduous forests (Kudo et al. 2004; Schemske et al. 1978) and temperate boreal forests (Barrett and Helenurm 1987). Annual variation in pollination services can be mitigated by flowering over several years (Barrett and Helenurm 1987); iteroparity may therefore be an adaptation to the spring pollination environment.

Corolla colour

It has frequently been noted that during peak spring flowering, many co-flowering species exhibit white, or light-coloured corollas (Motten 1986; Schemske et al. 1978), suggesting that a spring flowering phenology may select for the evolution of white or light corolla colour, or vice versa. Few adaptive hypotheses for this phenomenon have been put forward, although

Schemske and colleagues (1978) suggested that white may be the most conspicuous colour against the brown leaf litter background of the forest floor (but see Endler 1993). High visibility to potential pollinators is likely to be an important trait in the variable pollination environment of the spring.

Fruit type

Biotic interactions influence reproductive success in the spring flora through pollination, seed production, and seed dispersal. For spring flowering species, ant-mediated seed dispersal (myrmecochory) occurs in approximately 30% of species compared with an occurrence rate of less than 5% in all angiosperm species (Lanza et al. 1992; Lengyel et al. 2010). Elaisome-bearing seeds (i.e., those with an ant-specific food reward) are well suited to ant-mediated seed dispersal and are often packaged within fleshy fruits prior to dispersal (Dunn et al. 2007). While many forest plants exhibit adaptations to animal fruit dispersal, ant-mediated seed dispersal may be adaptive in spring blooming species because of the numerical dominance of ants in this environment (Lengyel et al. 2010), as well as seasonal patterns in the foraging behaviour of frugivorous birds (Thompson 1981).

Growth form and forest strata layer

Most canopy forming species in the temperate deciduous forests of eastern North America are wind pollinated, while most spring flowering species that occupy the understory of the forest rely on a biotic pollen vector (Ulyshen et al. 2010 and references within). In temperate deciduous forests, insects are the most abundant potential animal pollinators in early spring conditions (Hannan and Prucher 1996; Macior 1978a, 1978b; Motten et al. 1981; Motten 1986; Schemske et al. 1978) and many studies have noted that insect diversity is greatest near the ground level (Hirao et al. 2009; Ulyshen and Hanula 2007). Moreover, the spring flora may experience selection to jointly attract potential pollinators in the variable spring climate (i.e., facilitation). As a result, spring blooming species may be under selection to jointly attract more potential pollinators to spring flowering communities than species flowering in solitude. Selection to increase fitness in the variable spring environment could lead to community-level convergence to both a herbaceous growth form and understory layer occupation.

Here, using a recent molecular phylogeny of the angiosperms (Angiosperm Phylogeny Group 2009) and a database of plant traits for 465 temperate forest flowering plant species, we investigated the evidence for correlated evolution among spring flowering phenology and other reproductive, vegetative, and ecological traits. Specifically, we investigated whether reproductive schedule (iteroparous vs. semelparous), white corolla colour (white vs. nonwhite) or light corolla colour (light, i.e., white, yellow, or green, vs. nonlight), fruit type (fleshy vs. dry dehiscent), growth form (woody vs. herbaceous), and forest strata layer (understory vs. overstory) have evolved in a correlated fashion with a spring flowering phenology.

Materials and methods

Literature survey

A list containing 1947 potential study species was generated from the PLANTS Database of the US Department of

Agriculture (USDA 2011; www.plants.usda.gov/java/); the PLANTS Database was queried for those species with ranges known to be shared between the northern and southern limits of the temperate deciduous forest floristic region, as delineated by Ontario–Quebec and Virginia–Kentucky, respectively. This distribution coincides with the vast majority of temperate broadleaf forests in North America (Olson and Dinerstein 2002) and lies within the geographic region covered in *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* (Gleason 1952). By including only those species that occupy a continuous range within this region, nonforest species (i.e., those species with ranges limited to the great plains, maritime, subarctic, or subtropical regions), are expected to be excluded from the potential study species list. One limitation of this method is that rare or endemic forest species with discontinuous ranges in this region may be unintentionally omitted from the potential study species list. We confirmed that spring flowering species that have been extensively studied and that motivated this study (e.g., Macior 1978a, 1978b; Motten et al. 1981; Motten 1986; Schemske et al. 1978) were present in the potential study species list. We then used the list to generate a list of species and their traits (i.e., growth form, reproductive schedule, corolla colour, and seasonal flowering phenology) where available, as described below.

The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada (Gleason 1952) was searched systematically to confirm the habitat specificity (forest vs. nonforest), flowering phenology (months), reproductive schedule, corolla colour, fruit type, growth form, and forest strata layer for all potential study species. If more than one character state was reported for a trait in the species description, the species was recorded as having the most frequent trait state for that character. Families (or species) with pollination syndromes described as “anemophilous” (wind-pollinated) and (or) “hydrophilous” (water-pollinated) were excluded from the data set. Furthermore, all species described as occurring exclusively in nonforest habitats were excluded (e.g., coastal, alpine). Species that were described as occurring in both nonforest and forest habitats were included in the data set. No subspecies or varieties were included in the study.

Monthly flowering phenology data from Gleason (1952) was transformed into a seasonal classification of spring versus nonspring; spring was defined as beginning and completing flowering between the months of March through June, while nonspring encompassed all other flowering phenology schedules. Species that began and finished flowering in the month of June were considered to be nonspring flowering. This definition of spring flowering is consistent with the seasonal phenology reported from USDA PLANTS Database for the species for which this trait was reported (ca. 20% of the 1947 species).

If a species was not immediately located within Gleason (1952), a synonym was identified using the Integrated Taxonomic Information System Database (www.ITIS.gov). If a synonym was identified, it was queried within Gleason (1952) and traits were recorded where appropriate. If a synonym was not located in Gleason (1952), the species was excluded from the study; in total 54 species were excluded (of

the initial 1947) for this reason. The survey was limited to one source (Gleason 1952) to ensure that data were limited to species occurring in the temperate deciduous forest region. This approach also takes into account the fact that information gathered from different floras may not represent independent data points, as different floras may obtain species description information from the same sources. In total, data was collected for 465 species; a summary of the species and traits included in the analysis have been deposited at Dryad (www.datadryad.org; <http://dx.doi.org/10.5061/dryad.f3b66>).

Phylogeny reconstruction

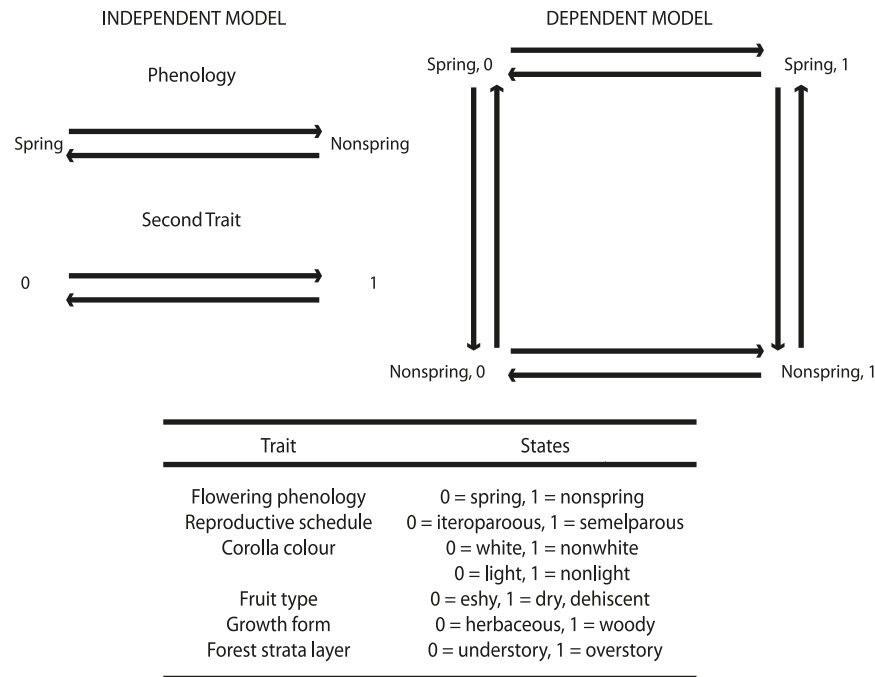
We used the software package Phylomatic (www.phylodiversity.net/phylomatic; Webb et al. 2008), to create a phylogeny based upon the megatree of the Angiosperm Phylogeny Group (APG; Angiosperm Phylogeny Group 2009). Phylomatic places the study species on the backbone of the APG megatree and prunes the remaining taxa from the tree. If branch lengths are missing from the base phylogeny, as is the case in this study, Phylomatic produces an ultrametric tree with branch lengths. These branch lengths were retained in the phylogenies used in the analysis. The analysis was repeated with the branch lengths set to one and the results were not significantly impacted. The megatree is primarily a family-level resolution of angiosperm evolutionary history. As is the case in most comparative studies, a certain amount of phylogenetic uncertainty was present in the tree (i.e., polytomies). We used the APE package (Paradis et al. 2004) in statistical software platform R (R Development Core Team 2011) to randomly resolve the polytomies to account for potential error associated with the resolution of polytomies we performed our analyses on a sample of 100 randomly resolved, dichotomously branching trees.

Testing for correlated evolution

To test for correlated evolution among flowering phenology and the reproductive, vegetative, and ecological traits of the species in the data set, we used the Discrete module within the comparative phylogenetic analysis software package BayesTraits (Pagel and Meade 2006). Discrete (as described in Pagel 1994) investigates correlated evolution between two discrete binary traits by fitting two continuous-time Markov models to the character state data. The first model of evolution allows the traits to evolve independently of one another within the phylogeny. The independent model estimates two transition rates per trait, and calculates a likelihood for both character states of each trait, for every node within the phylogeny. The second (dependent) model of evolution allows the traits to evolve in a correlated fashion, where the transition rates for each character state of a trait depend in part on the character state of the other trait at that node in the phylogeny. The dependent model of evolution estimates eight character state transition rates, and calculates a maximum likelihood for the four possible character state combinations of the dependent model for each node in the phylogeny (see Fig. 1 for a graphical depiction of the character states, transition rates, and possible evolutionary pathways for the two models of evolution).

To test for correlated evolution we conducted six pair-wise tests of association among flowering phenology and the traits described above. To assess statistical significance, a Likeli-

Fig. 1. Character states, estimated model transition rates, and possible evolutionary pathways in the independent and dependent models of evolution. Adapted from Friedman and Barrett (2008).



hood Ratio Test was used to compare the likelihood estimates of the independent and dependent models of evolution. The likelihood ratio for these tests approximates the χ^2 distribution with the degrees of freedom being equal to the difference between the number of parameters estimated for the dependent and independent model of evolution (Pagel 1994). Support for a model of correlated evolution is indicated if the likelihood ratio statistic exceeds the χ^2 critical value, indicating a significantly better fit of the dependent model of evolution. Standard errors of the test statistics are based on the analysis of the 100-tree sample.

We note some caveats of this approach for this data set. Ancestral state reconstruction may be compromised when the traits in question are correlated with faster or slower diversification (Schluter 2000). In particular, traits associated with low diversification tend to be located on the terminal points of long branches, which frequently results in traits associated with low diversification rates appearing to evolve prior to traits associated with faster diversification. Previously, woody growth forms have been associated with a reduced diversification rate (Dodd et al. 1999), consequently results involving this trait must be interpreted with caution. Furthermore, ancestral state reconstruction can be sensitive to the number of observations of each character state observed. The most common state is more likely to be reconstructed as the ancestral state when parsimony methods are used, however, Discrete should minimize this because it considers all possible ancestral states (Vamosi et al. 2003). Regardless, our analyses may be sensitive to this potential bias because spring was the rarer character state in all of our analyses.

Results

We first considered whether the reproductive, vegetative, and ecological traits examined were correlated with flowering

phenology irrespective of phylogenetic relationships (Table 1). These analyses confirmed that in the absence of a phylogenetic approach, all the reproductive, vegetative, and ecological traits we examined were associated with flowering phenology (Table 1).

When the analyses were conducted using the phylogenetic comparative method as described above, likelihood ratio tests indicated that the correlated model of evolution fit the character state data significantly better than an uncorrelated model for three of the four reproductive traits, as well as the two vegetative and ecological traits that were examined. Specifically, reproductive schedule, light corolla colour, fruit type, growth form and forest strata layer were shown to have evolved in a correlated manner with flowering phenology. Cumulatively, these results suggest that a spring flowering phenology has indeed evolved in association with a distinct suite of traits (Tables 1 and 2).

Reproductive schedule

Our results indicate that flowering phenology (i.e., spring vs. other) and reproductive schedule (i.e., perennial vs. annual life history) have evolved in a correlated fashion (Table 2). This finding was well-supported by the 100-tree sampling method (Table 2), however, the broader range of likelihood ratio statistics suggests that the analysis is sensitive to the phylogenetic hypothesis being used. Although the majority of spring and nonspring flowering species were perennials, fewer spring flowering species were annuals (ca. 10%) compared with nonspring flowering species (ca. 27%; Table 1).

Corolla colour

We found only weak support for the hypothesis that a white corolla colour had evolved in a correlated fashion with a spring flowering phenology (Table 2). However, when we tested whether a light corolla colour (i.e., white, green, or

Table 1. Distribution of species among the flowering phenologies and trait states.

Trait and state	Flowering phenology		Total	χ^2 ^a	P
	Spring	Nonspring			
Reproductive schedule					
Iteroparous	148	204	446	18.27	<0.001
Semelparous	17	77			
Total	165	281			
Corolla colour					
White	84	89	376	8.21	0.004
Nonwhite	69	134			
Total	153	223			
Corolla colour					
Light (green, yellow, and white)	122	142	376	11.19	<0.001
Nonlight	31	81			
Total	153	223			
Fruit type					
Fleshy	78	30			
Dry dehiscent	87	207	402	59.32	<0.001
Total	165	237			
Growth form					
Herbaceous	108	198	408	13.46	<0.001
Woody	57	45			
Total	165	243			
Forest strata layer					
Understory	119	234			
Overstorey	46	9	417	33.0	<0.001
Total	165	243			

Note: Species that had more than one state for a trait were categorized according to the most frequent state of the trait according to Gleason (1952) or the first state of the trait mentioned if the primary state was not explicitly mentioned.

^aThe χ^2 is compared with the χ^2 distribution with 1 degrees of freedom to determine whether the distribution of species among the states for each trait is associated with flowering phenology.

Table 2. Phylogenetic tests for correlated evolution between flowering phenology and reproductive, vegetative, and ecological traits in a 100-tree sample of 465 species using the Discrete module of BayesTraits.

Comparison	Mean likelihood ^a ratio statistic (\pm SE, P)	Likelihood ratio range for a 100-tree sample (P range ^b)
Phenology, reproductive schedule	24.100 (\pm 0.097, <0.001)	21.759–25.372 (<0.001 ^c)
Phenology, corolla colour (white or not)	9.090 (\pm 1.0 \times 10 ⁻⁴ , 0.058)	9.077–9.090 (0.058 – 0.059)
Phenology, corolla colour (light or not)	17.056 (\pm 1.0 \times 10 ⁻⁵ , 0.002)	17.056 (0.002)
Phenology, fruit type	51.254 (\pm 5.0 \times 10 ⁻⁴ , <0.001)	51.211–51.258 (<0.001 ^c)
Phenology, growth form	35.906 (\pm 1.0 \times 10 ⁻⁴ , <0.001)	35.905–35.907 (<0.001 ^c)
Phenology, forest strata layer	82.931 (\pm 0.028, <0.001)	81.445–83.241 (<0.001 ^c)

^aFor each pair of traits two models were compared to calculate the likelihood ratio statistic: a model where the traits evolve independently of one another (independent model) and a dependent model where transitions among character states in one trait depends on the character state of the other trait. The likelihood ratio statistic is compared with the χ^2 distribution with 4 degrees of freedom.

^bThe range of P values associated with the range of likelihood ratio statistics for the 100-tree sample.

^cThe calculated likelihood ratio statistics were significant at $P < 0.001$ over the entire 100-tree sample.

yellow) had evolved in a correlated fashion with flowering phenology, we found that the dependent model fit the data significantly better than the independent model of evolution (Table 2). Among the spring flowering species in our data set, white and nonwhite occur in nearly equal proportions, however, light corollas were far more frequent than nonlight (ca. 80% light vs. 20% nonlight; Table 1).

Fruit type

We found strong support for the hypothesis that fruit type

evolved in a correlated fashion with a spring flowering phenology (Table 2). A remarkable difference was observed in the distribution of fruit types among the spring and nonspring flowering species. While spring flowering species were almost equally likely to have either fleshy or dry dehiscent fruits, only a small proportion of nonspring flowering species had fleshy fruits (ca. 12%; Table 1).

Growth form

In addition, we found strong support for the hypothesis

that a spring flowering phenology tends to evolve in a correlated manner with a woody growth habit (Table 2). While the majority of spring and nonspring flowering species were herbaceous, a greater proportion of spring flowering species were woody (ca. 35%) compared with nonspring flowering species (19%; Table 1). This notable difference in the distribution of herbaceous and woody species between the phenological groups was statistically significant (Table 1). Indeed our phylogenetic analysis indicated that flowering phenology and growth form evolved in a correlated fashion (Table 2).

Forest strata layer

Finally, we found strong support for the hypothesis that spring flowering tends to evolve in a correlated manner with a species' tendency to inhabit the forest overstory layer (Table 2). Similar to growth form, the majority of spring and nonspring flowering species occupy the forest understory, however, a significantly greater proportion of overstory species (ca. 28%) exhibited a spring flowering phenology relative to nonspring flowering species (ca. 7%; Table 1). Flowering phenology and forest strata layer were confirmed to evolve in a correlated fashion (Table 2).

Discussion

Here we show that, for a sample of 465 temperate forest plant species from eastern North America, a spring flowering phenology has evolved in a correlated fashion with particular forms of reproductive schedule, corolla colour, fruit type, growth form, and forest strata layer. We did not find statistically significant support for the commonly held idea that a spring flowering phenology and a white corolla colour have evolved dependently, multiple times across the spring flora, although, we did find support for a similar hypothesis, that light corolla colour (i.e., yellow, green, or white) evolved in a correlated fashion with spring flowering. Our findings highlight the importance of considering phylogenetic relationships when performing comparative studies. We conclude that the nonindependence of species as data points, because of shared evolutionary history, contributed to the contrasting results between the nonphylogenetic and phylogenetic analyses for certain traits (see Tables 1 and 2). To our knowledge, this is the first time the hypothesized association among flowering phenology and a suite of traits has been tested using a phylogenetic comparative method.

Although exceptions exist, spring flowering was generally associated with the expected trait state as described in the literature on this topic. For most traits the expected trait state was the most common state for spring flowering species. However, this pattern was not held for the distribution of fleshy versus dry, dehiscent fruits; spring flowering species were almost equally likely to have either fleshy or dry dehiscent fruits. Generally, spring flowering species tend to be iteroparous, have white or light corolla colour, an herbaceous growth form, and occupy the forest understory. However, contrary to expectation, a greater proportion of spring flowering species (relative to nonspring flowering species) in our data set exhibited woody growth forms and occupy the forest overstory, as opposed to herbaceous growth and understory. It is possible that our method somehow oversampled woody species, in which case these results should be interpreted

with caution. Our decision to limit our analyses to species with wide distributional ranges across the flora may have inadvertently biased our sample towards long-lived woody species found in the overstory, such as the shrubs and small trees in this category.

Reproductive traits

Variation in pollination services can lead to pollinator-limited reproduction (Knight et al. 2005), which can be exacerbated by variance in early spring climatic conditions in temperate regions (Kudo et al. 2004; Schemske et al. 1978), especially under conditions where climate restricts pollinator activity (Motten 1986). The vast majority of spring flowering species in our study exhibited an iteroparous reproductive schedule, which may help to alleviate the effect of annual variance in pollination services on life-time reproductive success (Barrett and Helgen 1987); iteroparity may therefore be an adaptation to the spring environment (or vice versa).

In contrast to our expectation, white corolla colour was not as strongly associated with a spring flowering phenology as the other traits we inspected (Table 2). However, we did find a well-supported correlation between the evolution of a spring phenology and the possession of a light (i.e., yellow, green, or white) corolla colour. The strength of the correlation between flowering phenology and light corolla colour was greater than white for both nonphylogenetic (Table 1) and phylogenetic (Table 2) comparisons, suggesting that the spring flora displays a variety of similar lightly coloured forms instead of converging on a single colour. It may also indicate higher power for the light analysis.

There are several potential explanations for a correlation between light corolla colour and a spring flowering phenology. These include convergent evolution on a particular pollination syndrome (Schemske 1981), selection for a generalist pollination syndrome, and limited resources to invest in potentially expensive floral pigments (e.g., Snell et al. 2009). However, distinguishing among these hypotheses is beyond the scope of this study. It is also important to note that corolla colour as perceived by human observers is likely to be quite different than that perceived by pollinators (Kevan et al. 1996), and thus it is important not to overstate the pattern. Indeed, what appears striking to the human eye may be meaningless to a pollinator.

Spring flowering species were almost equally likely to have either fleshy or dry dehiscent fruits (Table 1); however, the fleshy fruited spring flowering species were far more common than fleshy fruited nonspring flowering species. Spring flowering species also have a comparatively high incidence of myrmecochory (ant-mediated seed dispersal) relative to the rest of the angiosperms (Lanza et al. 1992; Lengyel et al. 2010), which could help to explain the association between spring flowering and fleshy fruits, as myrmecochorous species likely have fleshy fruits. The relative rarity of fleshy fruited nonspring flowering species in our study (Table 1) may suggest that seed dispersal options could play an important role in the evolution of fruit type.

Vegetative and ecological traits

Most spring flowering species were herbaceous and occupied the forest understory. However, we detected a significant

trend of correlated evolution between a spring phenology and woody growth form and inhabiting the overstory. The overstory species in our study tend to be intermediately sized shrubs and small trees; indeed, of the spring flowering species that are woody and that occupy the overstory, approximately half were originally coded by Gleason (1952) as shrubs. It is possible that these woody, overstory, spring flowering species gain pollination service by co-flowering with the herbaceous spring wildflower community, offering a potential explanation for their spring phenology. Alternatively, as described above, this finding may be a result of an inadvertently nonrepresentational sampling of the flora.

In conclusion, we find support for the long-held idea that the spring flora of the deciduous northeast forest floristic region is unique in its suite of reproductive and vegetative traits. Our phylogenetically corrected analyses suggest that adaptation to the distinctive conditions encountered by spring flowering species, largely driven by unpredictable reproductive opportunities, may have played a key role in the evolution of this suite of traits. Future studies should focus on elucidating and testing proposed hypotheses for the patterns described here.

Acknowledgements

We wish to thank B. Hensel and J. Lachapelle for assistance with data collection. In addition, the manuscript benefited greatly from the useful comments provided by two anonymous reviewers, and *Botany* associate editor C. Lacroix. Funding for this project was supplied by a Natural Sciences and Engineering Research Council Discovery grant to R.D.S.

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