

Convergence, Consilience, and the Evolution of Temperate Deciduous Forests*

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ABSTRACT: The deciduous habit of northern temperate trees and shrubs provides one of the most obvious examples of convergent evolution, but how did it evolve? Hypotheses based on the fossil record posit that deciduousness evolved first in response to drought or darkness and preadapted certain lineages as cold climates spread. An alternative is that evergreens first established in freezing environments and later evolved the deciduous habit. We monitored phenological patterns of 20 species of *Viburnum* spanning tropical, lucidophyllous (subtropical montane and warm temperate), and cool temperate Asian forests. In lucidophyllous forests, all viburnums were evergreen plants that exhibited coordinated leaf flushes with the onset of the rainy season but varied greatly in the timing of leaf senescence. In contrast, deciduous species exhibited tight coordination of both flushing and senescence, and we found a perfect correlation between the deciduous habit and prolonged annual freezing. In contrast to previous stepwise hypotheses, a consilience of independent lines of evidence supports a lockstep model in which deciduousness evolved in situ, in parallel, and concurrent with a gradual cooling climate. A pervasive selective force combined with the elevated evolutionary accessibility of a particular response may explain the massive convergence of adaptive strategies that characterizes the world's biomes.

Keywords: *Viburnum*, biome assembly, freezing tolerance, leaf habit, climate change, phylogeny.

Introduction

Biologists have long been attracted to convergent evolution, and for good reason, as it provides powerful evidence of natural selection on organismal performance. Many convergent traits reflect organismal interactions, both mutualistic and antagonistic (Fenster et al. 2004; Agrawal and Fishbein 2006; Wilson et al. 2007), but past climate change has undoubtedly also driven convergence on a global scale. For example, the latter half of the Cenozoic witnessed the formation and spread of deserts and grasslands, resulting in the repeated evolution of succulent life-forms and C_4 photosynthesis (Edwards et al. 2010; Arakaki et al. 2011).

Convergence also provides insights into the relative evolutionary accessibility of certain phenotypes and how structural features of organisms may influence their evolutionary response (Sanderson and Hufford 1996; Donoghue and Ree 2000; Christin et al. 2013). The degree to which a particular character repeatedly emerges must be a function of both the pervasiveness of the selection pressure(s) and the relative ease of its evolution. As climate change is experienced by virtually all organisms in a region concurrently, it makes sense that it would be one of the most powerful agents of massive convergent evolution. However, whether such massive convergence is the outcome depends on whether a given adaptive response is also the most evolutionarily accessible (e.g., Weinreich 2006; Meyer et al. 2012; Agrawal 2017) in multiple lineages. The combination of a ubiquitous selective force with the evolutionary accessibility of a particular adaptation virtually guarantees rampant convergence.

On the surface of it, massive convergence would appear to lend itself perfectly to comparative phylogenetic analyses. It is only through a phylogenetic lens that convergence can be identified, after all, and a multitude of comparative methods have been developed to measure convergence and

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the factors that are correlated with it, perhaps causally. In characters with moderate levels of convergence, phylogenetic approaches can work well, but for extremely labile traits, uncertainties in phylogenetic inference can become limiting (Schultz et al. 1996; Schluter et al. 1997). This situation is complicated further by the observation that convergence itself is often distinctly concentrated in particular regions of the tree of life (Edwards and Donoghue 2013). For example, C_4 photosynthesis has evolved over 60 times in plants, but fully two-thirds of these origins occur in just two flowering plant lineages, the grasses and the Caryophyllales (Sage et al. 2011), and even within grasses, C_4 origins are clustered yet again in a clade that includes roughly half of all grass species (Christin et al. 2013). Furthermore, if evolutionary responses are rapid enough, it becomes impossible to identify the evolutionary sequences and transitional conditions that might provide us with clues about cause and effect, especially about evolutionary events that happened long ago. Faced with these difficulties, convincing answers may not be achieved using phylogenies alone (Christin et al. 2010; Hancock and Edwards 2014). Progress, then, depends on the integration of phylogenetic studies with other lines of evidence (Weber and Agrawal 2012; Olson and Arroyo-Santos 2015) and, as we highlight, perhaps by further deconstruction of the traits and potential selective factors of interest.

Here we focus on the evolution of the deciduous leaf habit, one of the most obvious and highly convergent adaptations of woody plants to temperate environments that experience an annual period of prolonged freezing temperatures. Deciduous plants shed their leaves with the onset of the cold period and remain leafless until they flush a new set of leaves in the spring. This habit dominates northern hardwood forests and has evolved independently many times in distantly related plant groups (e.g., maples and oaks). It is important to note that deciduousness has also evolved many times in settings that we will not consider here, particularly in dry tropical forests where there is also a season unfavorable for growth—in this case, determined by drought, not cold (Murphy and Lugo 1986). We do not know of any attempts to infer the number of independent origins of the deciduous leaf habit in angiosperms, but considering the extremely broad phylogenetic distribution of deciduous plants and its demonstrated lability within smaller lineages (e.g., Schmerler et al. 2012), we guess that it has evolved more frequently than other well-known convergent plant traits (e.g., >62 origins of C_4 photosynthesis [Sage et al. 2011]; >130 origins of bilaterally symmetrical flowers [Reyes et al. 2016]).

As a case study, we analyze the evolution of deciduousness in the woody plant clade *Viburnum*, combining standard phylogenetic analyses with a phenological field study along a latitudinal transect in eastern Asia. Independent of the traditional evergreen versus deciduous leaf habit cat-

egories, our fieldwork revealed a natural decomposition of phenological behavior into two distinct and potentially independently evolving elements: the flushing of new leaves and the senescing of old ones. It also exposed the inadequacy of the standard binary breakdown of biome or habitat type into tropical versus temperate forests. Specifically, we found it important to also recognize the existence of subtropical montane and warm temperate lucidophyllous forests (Tang 2010; Tang et al. 2013). These Asian forests are characterized by the dominance of broad-leaved angiosperm trees (typically Lauraceae and Fagaceae) in a climate that is distinctly monsoonal in comparison to tropical rainforests but where freezing is infrequent and winter temperatures are mild compared to cold temperate forests. The *Viburnum* species that we studied in these forests show patterns of leaf flushing and senescence that provide important clues to the transition between the archetypal evergreen and deciduous conditions.

Considered in isolation, our phylogenetic and field studies each provide insight into the evolution of deciduousness but not overwhelming support for a particular evolutionary pathway. Considered together, however, the consilience of evidence leads us to propose a model in which the deciduous habit evolves quite rapidly, in lockstep with a gradual in situ transition to a routinely freezing climate. We hypothesize that the novel behavior that emerged with the deciduous habit was the tight coordination of leaf senescence, perhaps as a means of ensuring the resorption of nutrients prior to leaf death by freezing (Feild et al. 2001; Niinemets and Tamm 2005). To our surprise, this lockstep model appears to be novel, as prior theories have envisioned a distinctly stepwise process. As we review below, these entail either the evolution of the deciduous habit, first in response to a period of drought or darkness (with establishment in freezing climates emerging only later), or the establishment of evergreen plants in freezing climates, followed later by the evolution of deciduousness. We suggest that the stepwise perspective that has explicitly or implicitly oriented many phylogenetic studies of adaptation may be inappropriate or even misleading when studying past evolutionary responses to the gradual climate changes that have shaped the assembly of the world's biomes.

Background Information

Evolution of the Deciduous Habit in Temperate Forests

In general, the deciduous leaf habit in woody plants is understood to be a response to long periods of time that are unfavorable for growth, which can result from episodes of freezing or drought (Chabot and Hicks 1982). By definition, annually deciduous plants must have leaf life spans of less than 12 months, with many cold temperate woody plants averaging no more than 6 or 7 months (Reich et al. 1992;

van Ommen Kloeke et al. 2012). Deciduous plants also tend to fall on the fast or resource-acquisitive end of the leaf economic spectrum (Wright et al. 2004), and their leaves are typically thinner, with higher nitrogen contents and higher photosynthetic rates than evergreen species. Soil fertility has thus been identified as an important secondary variable: nutrient-poor, cold sites tend to have a higher representation of broad-leaved evergreens, presumably because leaf nitrogen contents are too low to maintain the higher photosynthetic rates required to balance investment costs in a short-lived leaf. These arguments, revolving around trade-offs in leaf carbon and nutrient economy, are well developed elsewhere (Chabot and Hicks 1982; Kikuzawa 1991; Givnish 2002), and our aim here is not to elaborate on the adaptive significance of the deciduous leaf habit. Instead, we simply assume that deciduousness is adaptive for all of the reasons above and consider a related question that has received far less attention, namely, how the deciduous habit evolved from an evergreen state. In particular, we analyze leaf flushing and leaf senescence as two potentially independent behaviors that became coordinated with the emergence of the deciduous habit.

Climate Change and the Origin of Temperate Deciduous Forests

In spite of its importance as a modern biome, there are relatively few hypotheses about the origin of broad-leaved deciduous forests. Inferences based on fossil leaves indicate that deciduous angiosperm species have existed for a long time, appearing as elements of fossil floras from the Late Cretaceous through the Cenozoic (Wolfe 1987). There is evidence for the dominance of the deciduous habit in the highest northern latitudes (polar deciduous forests) during the Late Cretaceous, when global temperatures were significantly warmer than today. These polar forests persisted through the Paleocene and Eocene periods, with broad-leaved evergreen forests occupying significant areas in midlatitude and tropical regions (Axelrod 1966; Wolfe and Upchurch 1986; Wolfe 1987). Post-Eocene global cooling shifted many of these midlatitude zones toward the tropics, but it was not until the late Miocene that the modern distribution of cool temperate deciduous forests was established (Tiffney and Manchester 2001; Utescher and Mosbrugger 2007; Pound et al. 2011).

Axelrod (1966) proposed that deciduousness first evolved in a warm, subtropical climate zone that experienced mild winter drought. He hypothesized that such forests were widespread throughout the midlatitudes of the Northern Hemisphere in the Late Cretaceous and early Cenozoic but became restricted during the Miocene. As modern analogues, he specifically cited the lucidophyllous forests of Asia (particularly Taiwan) and the cloud forests of southern Mexico,

which experience strong seasonality in both rainfall and temperature but rarely freeze. Axelrod hypothesized that the deciduous leaf habit first appeared in such forests and that this later enabled these plants to expand into the freezing zone.

Wolfe and Upchurch (1986) and Wolfe (1987) explained the origin of deciduous forests in another way. They proposed that deciduousness evolved in situ at high latitudes, when even areas at 80°N did not experience significant freezing. However, winters at such high latitudes were as dark as they are today, and they hypothesized that the deciduous habit evolved there as a response to many months with little or no sunlight. At the Cretaceous-Paleogene (K-Pg) boundary, the brief impact winter was credited with reorganizing plant communities at lower latitudes, and Wolfe and colleagues suggested that it was during this time that polar deciduous lineages migrated south and became established as elements of midlatitude floras. Only during the late Miocene cooling did they outcompete warm-adapted evergreen lineages to establish a new deciduous biome.

It is noteworthy that both the Axelrod and Wolfe hypotheses rest on the idea that deciduousness was a preadaptation to freezing—that is, it evolved first as a response to some other stress but then allowed lineages to tolerate freezing climates when they were eventually exposed to them. Neither author explained why they preferred such an order of events as opposed to the perhaps simpler hypothesis that deciduousness evolved directly in response to freezing. More recently, Zanne et al. (2014), without reference to these older hypotheses, addressed the same question using a megaphylogeny for angiosperms and concluded that most lineages first became established in the freezing zone as evergreen plants and only later evolved the deciduous habit. Elsewhere we reanalyzed the data of Zanne et al. and raised doubts about their conclusions (Edwards et al. 2015), but we highlight this study here because it focused directly on freezing as a driver. Like Axelrod and Wolfe, Zanne et al. envisioned a stepwise evolutionary process but with a reversed order of events. In the terminology of Zanne et al. (2014), Axelrod and Wolfe favored a trait-first hypothesis, whereas they favored a climate-first hypothesis.

The Viburnum Study System

Viburnum (Adoxaceae, Dipsacales, Campanulidae) is an angiosperm clade of ~165 species of shrubs and small trees that is broadly distributed (and widely cultivated) around the Northern Hemisphere. *Viburnum* species all occupy mesic forests, but they have adapted to a range of climatic conditions and forest environments (fig. 1). At one end of the spectrum, multiple (and distantly related) species in tropical forests are never subjected to freezing temperatures. At the other end, upwards of 10 *Viburnum* lineages appear to have

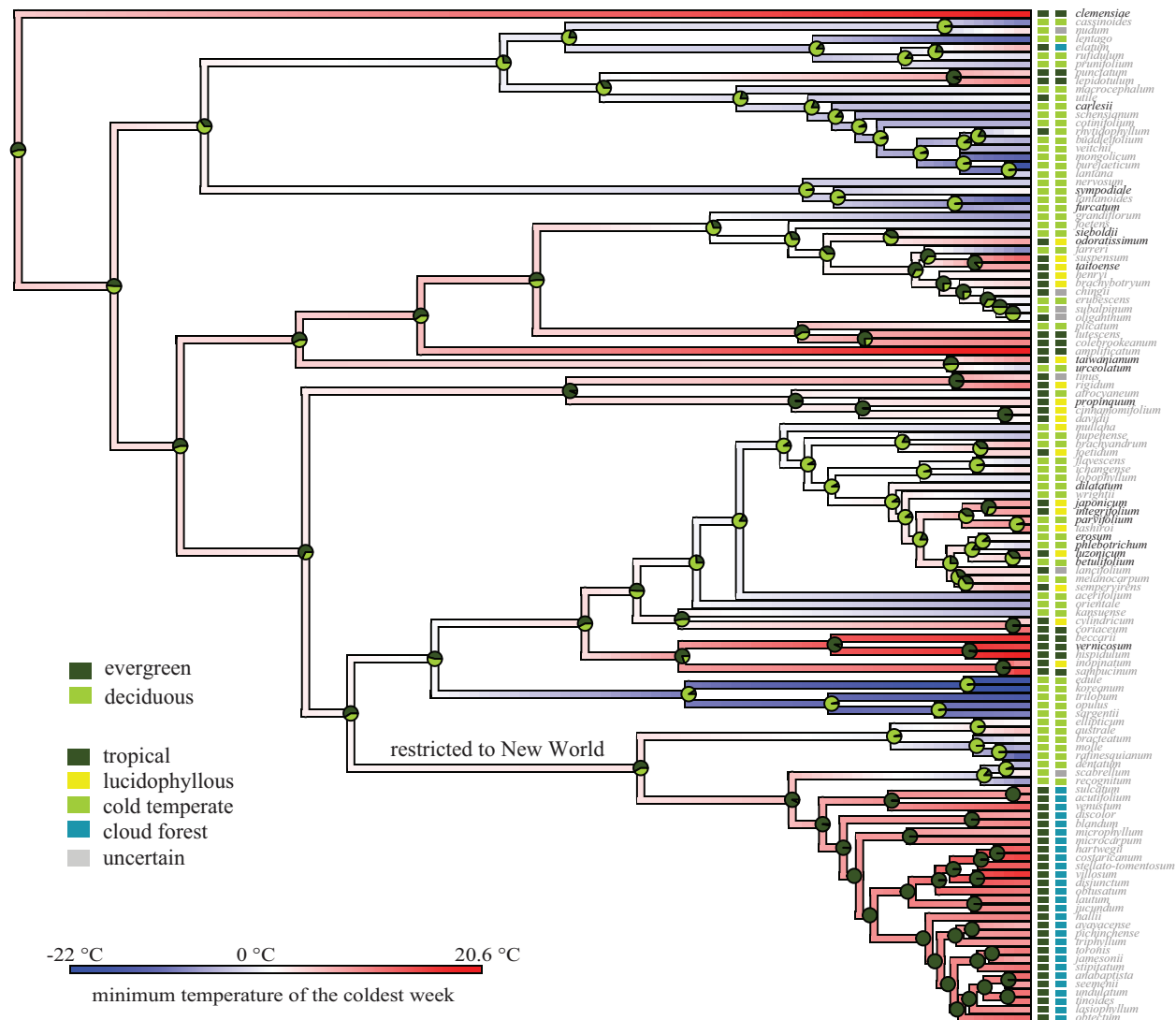


Figure 1: Phylogeny, climatic envelope, forest habitat, and leaf habit of *Viburnum*. A 120-taxon phylogeny, pruned from Spriggs et al. (2015). Branch colors represent inferred ancestral minimum weekly temperatures (BIO6). Pie charts at internal nodes are ancestral state estimates of leaf habit, inferred using the threshold model (Revell 2012). Species at tips are coded by leaf habit in the left column (evergreen vs. deciduous) and habitat in the right column (tropical, lucidophyllous, cold temperate, or cloud forests). Species with names in boldface were included in the phenological monitoring study.

evolved independently into cool temperate forests that experience consecutive months of below freezing temperatures. In Asia, members of several clades occupy lucidophyllous forests, and members of the Neotropical *Oreinotinus* clade occupy montane cloud forests, with reduced temperature seasonality and only rare and intermittent freezing temperatures.

Evolutionary shifts between these different environments have been accompanied by transitions in leafing habit (fig. 1). In tropical, lucidophyllous, and cloud forests, *Viburnum* plants are most often evergreen, while, with very few ex-

ceptions, in cool temperate forests they are seasonally deciduous. Of the 165 species of *Viburnum* that we currently recognize, we consider 84 to be evergreen and 81 to be deciduous. Eight of the well-supported major clades within *Viburnum* include both evergreen and deciduous species, implying a minimum of eight evolutionary shifts. However, we infer no fewer than 20 transitions in leaf habit using any of our recently published phylogenetic trees (Clement et al. 2014; Spriggs et al. 2015; Eaton et al. 2017), including some clear-cut evolutionary shifts in both directions. For example, the deciduous species *Viburnum plicatum* appears to

have been derived from evergreen ancestors within the *Lutescentia* clade. Likewise, the evergreen species *Viburnum rhytidophyllum* and *Viburnum utile* appear to have originated from deciduous ancestors within the *Euviburnum* clade, as did *Viburnum sempervirens* and its several evergreen relatives within *Succotinus*.

As we have shown previously (Schmerler et al. 2012), these repeated evolutionary shifts in forest environment and leafing behavior have been accompanied by specific changes in leaf form. Adaptation to cool temperate forests at more northerly latitudes has entailed coordinated shifts to rounder leaf shapes with more marginal teeth or lobes. Marked seasonal heteroblasty in the temperate species (the development of preformed leaves with more derived leaf shapes and neoformed leaves with more tropical shapes) suggested to us that the evolution of temperate leaf forms may relate to the development of leaf primordia within the resting buds of deciduous species (Edwards et al. 2016). In any case, *Viburnum* provides clear evidence, directly in line with global trends (Bailey and Sinnott 1916; Wolfe 1995; Royer and Wilf 2006; Peppe et al. 2011), of repeated evolutionary changes in both leaf habit and leaf form in connection with shifts between tropical and temperate forests.

Material and Methods

Phenology. To monitor *Viburnum* leafing behavior across a wide range of environments, we established a latitudinal transect spanning 27° latitude, from montane tropical forests in Kinabalu National Park, Sabah, Malaysia, at 6°N to temperate forests in the mountains surrounding Fukuoka, Japan, on Kyushu Island at 33°N (fig. 2). Sites were chosen to represent different forest types (tropical rain forest in Borneo, both lucidophyllous and cool temperate forests in Taiwan and Japan) and also to maximize the number of co-occurring *Viburnum* species in each location. From May to June 2013, we selected a total of 19 populations representing 18 species in Taiwan and Japan, and in February 2014 we added two species in Borneo. For logistical reasons, not all populations were monitored for the same length of time. The Borneo populations were monitored for 13 consecutive months, the Japanese populations for 10–19 consecutive months, and most of the Taiwanese populations for 25 consecutive months. We achieved our best sampling in Taiwan, where we were also able to monitor two populations of *Viburnum luzonicum* that spanned its elevational range (120 m, 2,100 m).

In each population of each of our focal species, we tagged three to six individuals (mostly four individuals per species) for monitoring. We marked four branches per individual and made biweekly to monthly census trips to record the persistence of each leaf on these branches, the emergence of new leaves, and all events of leaf senescence using meth-

ods described in Edwards et al. (2014). At the start of the study, each branch usually had only a few apical meristems, but due to the growth architecture of most *Viburnum* species (stems typically terminate in an inflorescence, with growth recommencing from two subtending buds; Donoghue 1981; Edwards et al. 2014), by the end of the study each branch consisted of multiple independent leafy shoots, sometimes bearing over 100 leaves.

Viburnum-wide climate data, leaf habit, and forest type. We downloaded georeferenced locality data for *Viburnum* from the following databases: Global Biodiversity Information Facility (<http://www.gbif.org/>), Chinese Virtual Herbarium (<http://www.cvh.org.cn/>), Interactive Agricultural Ecological Atlas of Russia and Neighboring Countries (<http://www.agroatlas.ru/>), Plant DNA Bank in Korea (<http://pdbk.korea.ac.kr/>), and Virtual Viburnum (<http://viburnum.peabody.yale.edu/>). We also georeferenced occurrence records from Hara's (1983) treatment of the *Viburnum* species of Japan. The raw data were filtered to remove spurious records. Specifically, we matched taxon names with those in Spriggs et al. (2015) and removed records with coordinates at 0°, 0° (and those from botanical gardens and herbaria) and records of the same species with identical coordinates. We also plotted the records for each species using the R package ggmap (Kahle and Wickham 2013) and removed points outside of the known geographic ranges of these species based on floristic treatments and herbarium specimens examined in preparation for our worldwide monograph of *Viburnum*.

We used the CliMond database (Kriticos et al. 2012) at a 10-min resolution (~18 km² at the equator) to extract estimates of climate for each locality in the filtered data set using the R package raster (Hijmans and van Etten 2012). This spatial grain best matches the georeferencing precision of our data set. The species locality data were then spatially rarefied so that there was no more than one occurrence per climate grid cell using SDMtoolbox (Brown 2014), which increased the evenness of coverage across the species' entire range. Species with fewer than three grid cell occurrences were removed from the data set. We calculated the mean minimum temperature of the coldest week (BIO6) and seasonality of precipitation (BIO15) for each species. We note that although CliMond estimates BIO6 as a weekly measure, their variable is interpolated from monthly temperature data and is strongly correlated with the more commonly used BIO6 variable, the mean minimum temperature of the coldest month ($R^2 = 0.995$). In all, our data set consists of 7,718 records for 120 *Viburnum* species. We also used the CliMond database to extract mean monthly temperature and precipitation data for the sites of our monitored populations.

We scored each species in our data set as (1) belonging in the traditional evergreen or deciduous category and

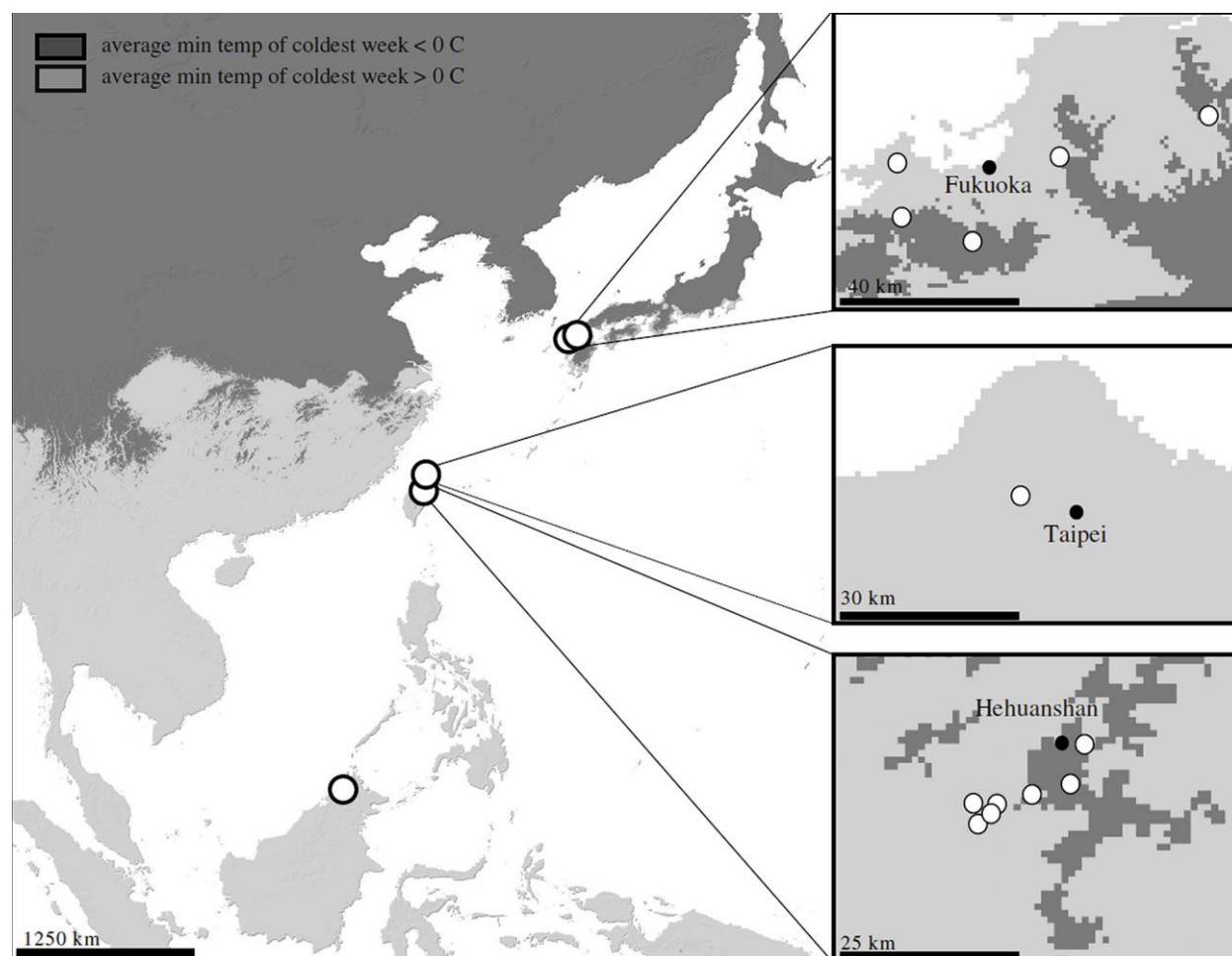


Figure 2: Locations of the phenological monitoring transect in eastern Asia. Insets provide greater resolution of our different population locations. *Top inset*, Sites situated around Fukuoka, Japan, on the island of Kyushu. *Middle inset*, Location of our low-elevation population of *Viburnum luzonicum* in the suburbs of Taipei, Taiwan. *Bottom inset*, The majority of our Taiwan monitoring sites scattered around the Hehuanshan Mountain district of the Central Mountain Range. In both Japan and Taiwan, sites occupied both freezing and nonfreezing climates.

(2) occurring in tropical, lucidophyllous, cool temperate, or cloud forests. These scores were based on monographic and floristic treatments of *Viburnum* (e.g., Rehder 1908; Killip and Smith 1931; Morton 1933; Kern 1951; Hara 1983; Yang and Malecot 2011). For the majority of these species we have first-hand knowledge based on our own field and herbarium studies, but for Japanese species we also relied on Hara (1983) and for Chinese species we followed Yang and Malecot (2011). We were uncertain about assignment to forest type for seven species and scored these as unknown.

Analysis of phenological data. We recorded leaf gain and loss using hand-drawn sketches of branches, and dates of emergence and disappearance of each leaf were transcribed into a spreadsheet. The total number of leaves gained or lost at each census was summed across branches within an in-

dividual and averaged across individuals within a population. Only a small subset of leaves were observed for their entire life span in the evergreen species in our sample; the majority of leaves were either present when we initiated the study and senesced partway through the monitoring period or emerged during the study and were still present at the end. Population-level patterns in flushing and senescence were visualized using the ribbon function in ggplots2 (Wickham 2016) in R. Most species appeared to exhibit strong seasonality in leaf flushing and sometimes also in senescence. To evaluate the statistical significance of these patterns, for each species we compared our observed data with a null distribution of phenological events. Because the timing of our population visits was not perfectly spaced throughout the year, we could not assume a flat null distri-

bution; just by chance we would expect to see more events in spring and fall seasons, when our visitation rates were slightly higher. For each species, we pooled all visitation dates (as Julian days) and generated 1,000 data sets each of new leaf and senesced leaf observations, sampled with replacement from the pool of Julian day visits, with the total number of events equal to that in the observed data. We then tested whether observed distributions were statistically different from the null distribution using a Mann-Whitney test. All data and scripts for analyses are publicly available in a GitHub repository (https://github.com/ejedwards/amnat_2017/phenology/null_analyses).

Analysis of *Viburnum*-wide climate data, leaf habit, and forest type. We conducted comparative analyses using the maximum-clade credibility phylogeny from Spriggs et al. (2015). We pruned the phylogeny to the 120 species (of the 165 species of *Viburnum*) represented in our data set using the `drop.tip` function in *ape* (Paradis et al. 2004). These species represent all of the named clades in the comprehensive phylogenetic classification of *Viburnum* developed by Clement et al. (2014). We conducted several analyses to test the relationship between leaf habit and climate. First, we estimated the significance of the relationship between these traits using phylogenetic independent contrasts (Felsenstein 1985) as implemented for use with a discrete and continuous character in the function `crunch` in the R package *caper* (Orme 2013), treating leaf habit as the dependent variable and either BIO6 or BIO15 as the independent, continuous variable. Second, we inferred evolutionary shifts in leaf habit using the threshold model first proposed by Wright (1934) and developed as an explicitly phylogenetic method by Felsenstein (2012). The threshold model assumes that discrete character changes are governed by shifts in an underlying, unobserved continuous variable called the liability. As the value of the liability reaches a particular threshold, the binary character changes. This is an appealing approach to examine possible evolutionary relationships between observable continuous and discrete characters by evaluating the relationship between the continuous character and the estimated liability parameter. We estimated the liability values underlying shifts in leaf habit using the function `threshBAYES` in *phytools* (Revell 2012), running Markov chain Monte Carlo for 10^6 generations, sampling every 1,000, and discarding the first 20% of steps as burn-in. We regressed estimated liability values to inferred ancestral estimates of BIO6 and BIO15. Third, we utilized standard methods for assessing the correlated evolution of two binary characters with likelihood ratio tests (Pagel 1994). In this case, we converted BIO6 into a binary character, binning species into whether their mean value of BIO6 was greater or less than 0°C. Because six species with mean values just above or just below 0°C were assigned to categories incongruent with our field knowledge, we created an additional binary variable

where we adjusted these assignments. We ran Pagel tests using both the curated and the uncurated binary variable. All data and scripts for analyses are available in a GitHub repository (https://github.com/ejedwards/amnat_2017/final_analyses/phylogeny). All data used in all analyses are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k505s> (Edwards et al. 2017).

Results

Phenology. The two tropical *Viburnum* species that we followed in Borneo (*Viburnum clemensiae*, *Viburnum vernicosum*) are evergreen and exhibited little leaf turnover during the course of our study (fig. 3). This was especially true for leaf senescence, with some individuals losing no more than a single leaf over the course of 13 months. *Viburnum clemensiae* produced leaves from October to April and no leaves at all during the months of May–September. In contrast, *V. vernicosum* produced leaves throughout the year despite the fact that these two species occupy the same montane tropical forest, with individuals less than 1 km apart. The very low rates of leaf turnover in both species necessitates a much longer period of data collection to make robust observations of seasonality.

In both Taiwan and Japan, we included evergreen and deciduous species in our sample, though the ratios were inverted: in Taiwan we monitored three deciduous species and six evergreen, while in Japan we monitored six deciduous and three evergreen. In each location, one of the evergreen species is perhaps better described as a leaf exchanger; *Viburnum luzonicum* (Taiwan) and *Viburnum erosum* (Japan) plants shed almost all of their leaves as they produced a new flush.

Across all species and all sites in Taiwan and Japan, there was a striking coordination of the timing of new leaf flushes; all species, whether deciduous or evergreen, produced a significant flush of new leaves in the months of March, April, and May (fig. 3; table A1). In sharp contrast, senescence patterns were more variable across species and across the seasons. In deciduous species, as expected, leaf senescence was highly seasonal and varied little between species or locations; all deciduous species demonstrated coordinated leaf shedding as winter approached, typically in November and December. In evergreen species, senescence periods were typically much longer, occurring in the months preceding, during, and after spring leaf flushes (fig. 3; e.g., *Viburnum propinquum*, *Viburnum taitoense*). The tightest coordination of flushing and senescence appeared in *V. luzonicum* and *V. erosum*, but as noted, these do not fit neatly into the strictly evergreen or deciduous category. Indeed, they may have a short leafless period in one year but not the next (e.g., *V. luzonicum* was evergreen

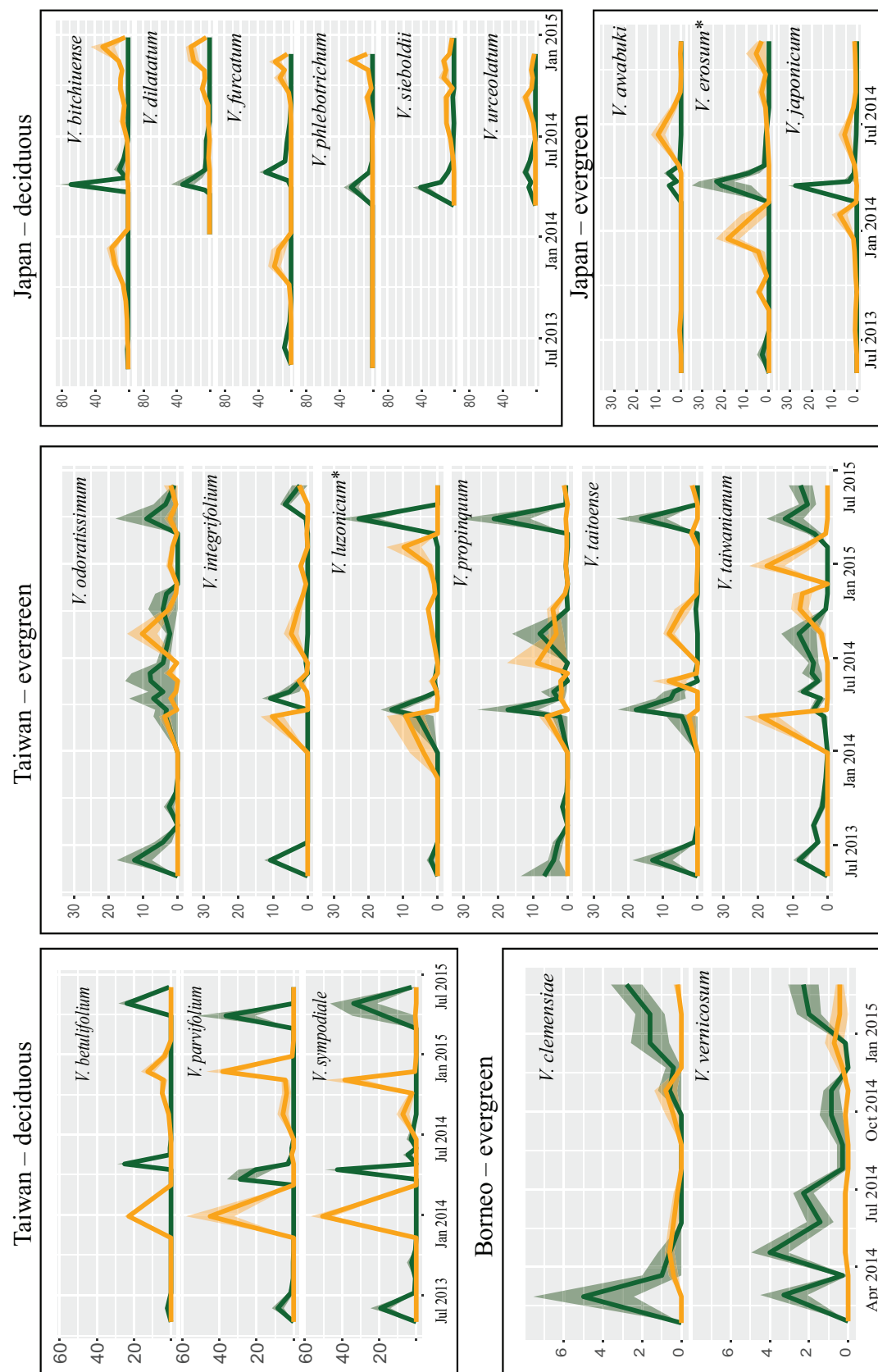


Figure 3: Flushing and senescence patterns of 20 *Viburnum* species living along a tropical-temperate gradient. Lines represent the mean number of leaves gained or lost per observational period across three to six individuals per species; shading represents ± 1 SE. Green lines indicate new leaf flushes, and yellow lines represent leaf senescence. Species are grouped by geographical area (Borneo, Taiwan, Japan) and leaf habit (evergreen, deciduous). Asterisks indicate species that may be better described as leaf exchangers rather than strictly evergreen.

in 2014 but deciduous in 2015; *V. erosum* was deciduous in 2014 but evergreen in 2015).

The significance of these visual patterns was confirmed by comparison to our null distributions of flushing and senescence (table A1). All deciduous species exhibited highly significant clustering of both flushing and senescence. Flushing patterns were all significant in our evergreen species; in contrast, in most cases senescence was indistinguishable from our null distributions (table A1; see additional files and analyses at https://github.com/ejedwards/amnat_2017/final_analyses/phenology/null_analyses). The three exceptions were *Viburnum japonicum* in Japan and *V. propinquum* and *Viburnum integrifolium* in Taiwan. These species all exhibit a similar senescence pattern, with a period of senescence directly preceding and then directly following the spring leaf flush (fig. 3). We note that both *V. japonicum* and *V. integrifolium* belong to the *Succotinus* clade along with *V. erosum* and *V. luzonicum* and likely evolved an evergreen habit from a deciduous ancestral state.

Correlation of phenology with climate. We chose sites in both Taiwan and Japan that spanned freezing and non-freezing climates, reflecting differences in elevation. In both countries, there is a pronounced monsoonal climate, with the heaviest rains falling during the warm summer months. As precipitation is indistinguishable across the freezing/nonfreezing boundary, we were able to compare phenology in contrasting temperature regimes while holding rainfall patterns constant (fig. 4).

As noted above, leaf flushes were coordinated across all sites and species in both freezing and nonfreezing zones. These flushes occurred in the spring as temperatures warmed and monsoonal rains returned. Due to the correlation between temperature and rainfall, it is not possible at this time to discern which climatic factor the flush is primarily responding to. Ancillary evidence that rainfall may be the primary driver is provided by our two populations of *V. luzonicum* (fig. 5). Our high-elevation site showed a strong monsoonal rainfall pattern and, correspondingly, a well-defined spring flush; our low-elevation site experienced pronounced temperature seasonality but with high rainfall year-round, and its leaf flushing patterns were considerably more erratic (fig. 5).

In contrast to flushing, we found evidence for a single environmental driver of coordinated senescence and deciduousness: in both Taiwan and Japan, our deciduous species all lived in areas experiencing routinely freezing temperatures during the coldest months of January and February (fig. 4). In contrast, all of our evergreen species lived in areas where minimum monthly mean temperatures remained above freezing year-round. It is important to note that this does not mean that they never experienced occasional frosts, only that the mean monthly minimum temperatures never fell below 0°C. Fortunately, our sampling allows us to sep-

arate the influence of temperature from the influence of drought, as our evergreen and deciduous species in these areas all experienced similar periods of relative drought from November to February (fig. 4).

The clear association between the deciduous leaf habit and regular exposure to freezing temperatures but not changes in precipitation seasonality was corroborated in our *Viburnum*-wide analyses. Figure 1 maps the mean minimum temperature of the coldest week (BIO6) on a *Viburnum* phylogeny derived from Spriggs et al. (2015), together with ancestral reconstruction of leaf habit inferred from the threshold analyses. This implies that the first viburnums lived in warm climates without significant freezing and that there were multiple independent transitions into colder (and then back again into warmer) environments. Scanning the distribution of the leaf habit and forest type characters gives the impression of a strong correlation: species living in warmer climates tend to be evergreen and to occupy tropical or lucidophyllous forests, while species living in colder climates are generally deciduous and occupy cool temperate forests. This is confirmed by our independent contrast analyses, which showed a significant relationship between leaf habit and BIO6 ($R^2 = 0.607$, $P = .00001$) but not BIO15 ($R^2 = 0.037$, $P = .3785$). Likewise, our threshBAYES analysis yielded a strong positive relationship between leaf habit and BIO6 ($R^2 = 0.868$, $P = 2.2e^{-16}$) but not BIO15 ($R^2 = 1.6e^{-5}$, $P = .9647$). Similarly, our binary tests strongly favored a model of correlated evolution of leaf habit and habitat (uncurated BIO6 binary: $\Delta AIC = 58.56$, $P = 1.22e^{-13}$; curated BIO6 binary: $\Delta AIC = 73.2$, $P = 9.63e^{-17}$).

Discussion

Flushing, senescence, and emergence of the deciduous habit. The deciduous habit so characteristic of Northern Hemisphere temperate forests involves two distinct behaviors: in the spring, there is a rapid and dramatic flush of new leaves, and in the fall, there is an equally dramatic, coordinated, and often colorful display of leaf senescence. By monitoring the flushing and senescing of leaves as independent behaviors in both evergreen and deciduous *Viburnum* species, we can begin to understand how these two aspects of phenology relate to different climatic factors and how their coordination may have evolved along an evergreen-to-deciduous evolutionary trajectory.

The preliminary data on *Viburnum* phenology presented here clearly document several patterns. Unfortunately, the very low leaf turnover in the essentially aseasonal tropical site (Borneo) limits interpretation of that data set for now. We note only that our single year of data collection provides some evidence of seasonality to new leaf production (fig. 3) and that periods of leaf flushing are not uncommon in tropical

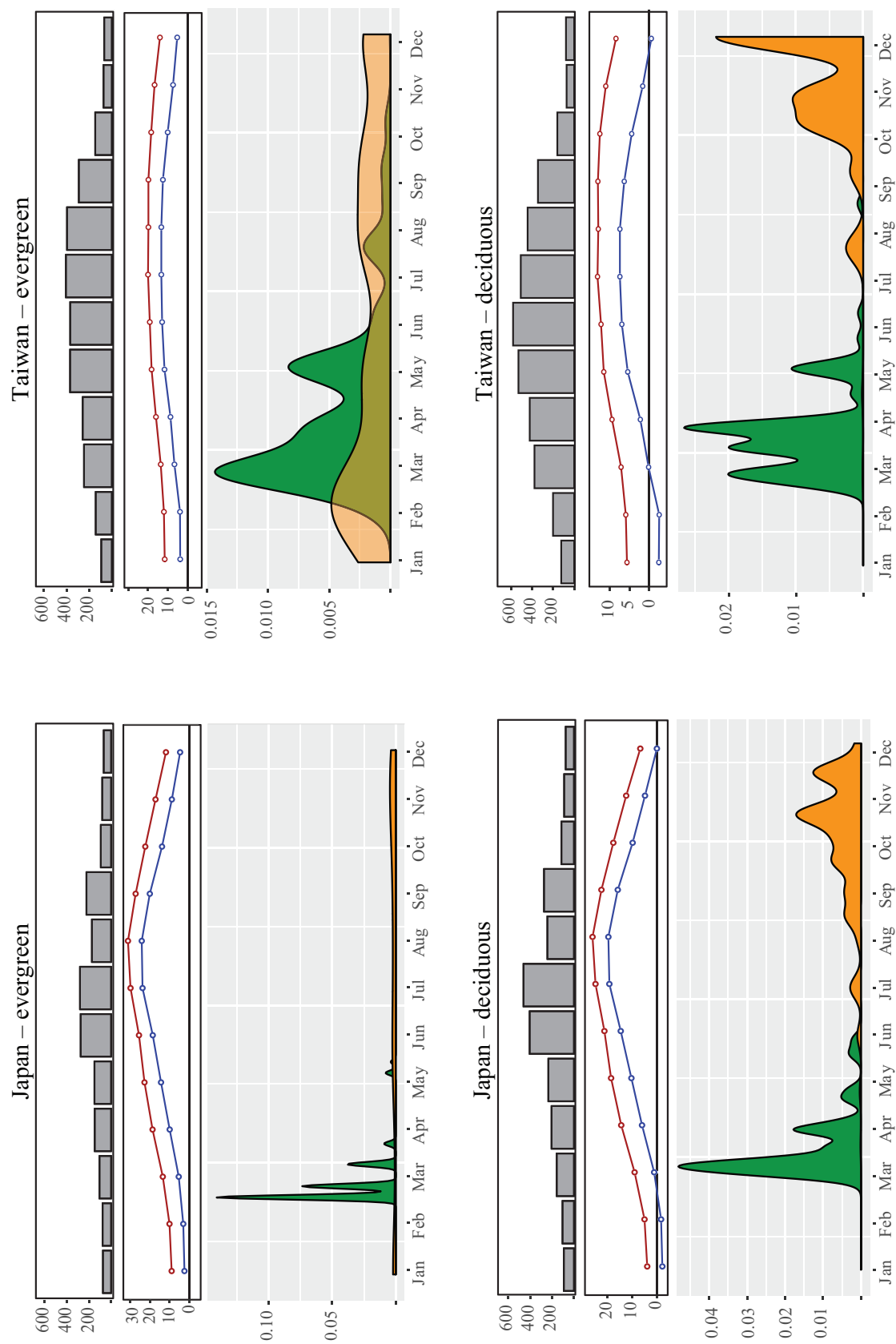


Figure 4: Seasonal drought, freezing, and the coordination of flushing and senescence. Box plots represent mean monthly maximum temperature (red) and minimum temperature (blue) in °C. Density curves below the climate plots were derived from pooling all new (green) and senesced (orange) observation events from all species within that category (e.g., evergreen Japan includes *Viburnum japonicum*, *Viburnum awabuki*, and *Viburnum erosum*). Climate data are from one representative field site per category. In cases where we had multiple locations of evergreen or deciduous populations within a country, their climate diagrams were virtually indistinguishable.

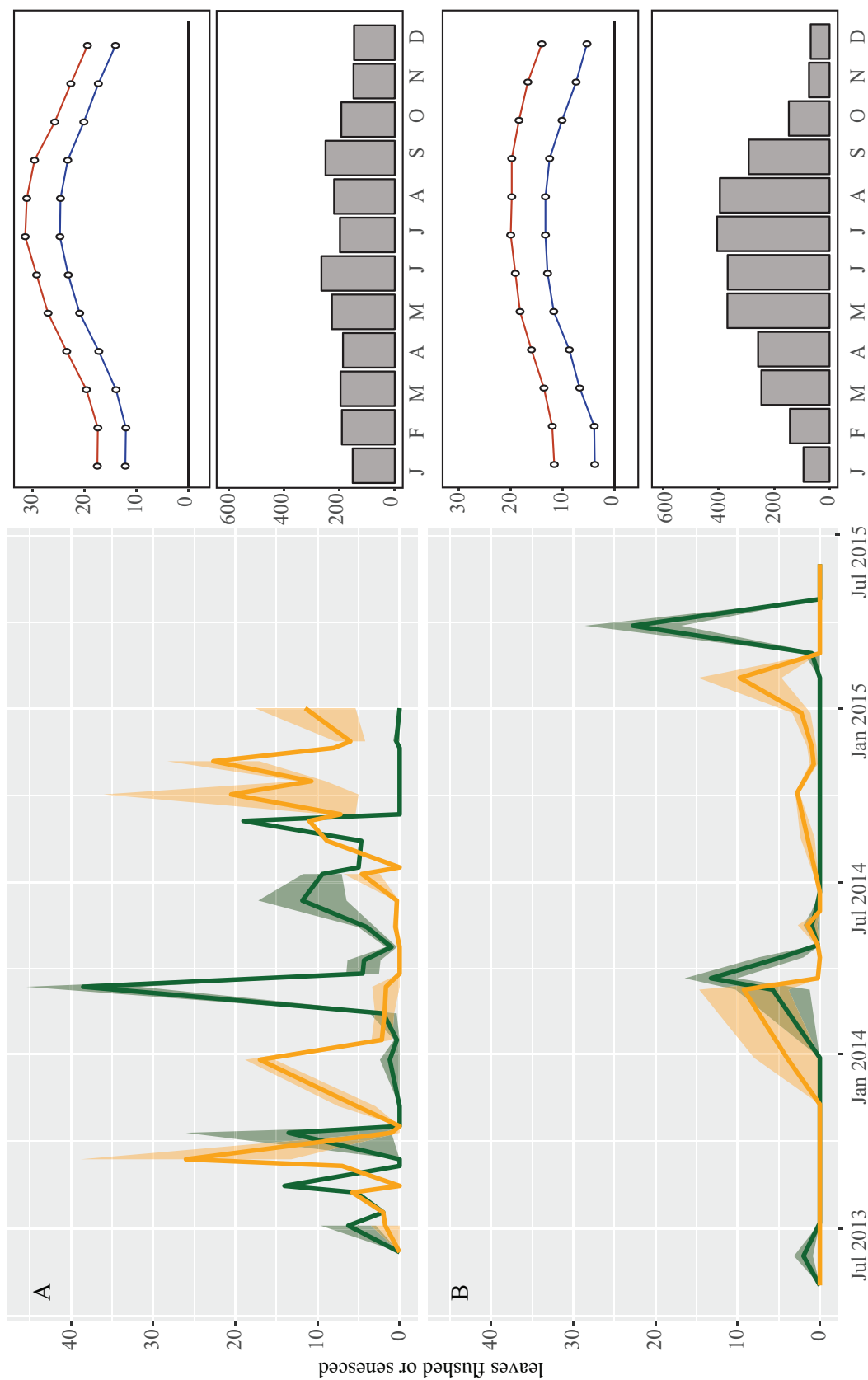


Figure 5: Variation in phenological behavior in *Viburnum luzonicum*. Lines on left-hand graphs represent the mean number of leaves gained or lost per observational period across four to six individuals per species; shading represents ± 1 SE. Green lines represent new leaf flushes, and yellow lines represent leaf senescence. Climate diagrams on the right are similar to figure 4. A, *V. luzonicum* population in the Danfeng region just outside of Taipei, Taiwan, at an elevation of 120 m. B, *V. luzonicum* population in the Hehuanshan area of the Central Mountains of Taiwan at an elevation of 2,124 m.

plants more generally, perhaps in response to herbivore pressure (Coley and Barone 1996). We focus instead on our observations in Taiwan and Japan, where all of our sites are mesic but with strong rainfall seasonality. Here it is clear that a pronounced and coordinated leaf flush is present in all species. Senescence patterns, on the other hand, are quite varied, and leaf drop appears to be less concentrated in time. Although our evergreen species varied considerably, most exhibited patterns that were indistinguishable from a random null distribution (table A1). The senescence period could be quite extended in these species, and the intensity (i.e., the absolute number of leaves gained or lost per event) of senescence was generally reduced compared with leaf flushing. Our results are remarkably similar to an earlier study of phenology in lucidophyllous Japanese forests, where most species produced a single spring flush of leaves but presented at least four different senescence patterns (Nitta and Ohsawa 1997). In marked contrast, our deciduous species all had short and coordinated senescence periods that commonly matched their spring flush in intensity. Senescence also occurred concurrently, in the late fall, in all of these species. Owing to the high level of homoplasy, the directionality of character change in *Viburnum* is still difficult to infer in some areas, but our sample of nine deciduous species likely captures a minimum of five independent origins of the deciduous habit (i.e., within the *Euiviburnum*, *Pseudotinus*, *Urceolata*, *Solenotinus*, and *Succotinus* clades; Clement et al. 2014; Spriggs et al. 2015). Therefore, this provides a clear case of the convergent evolution of coordinated leaf senescence.

Several species stand out as notable exceptions. Two, *Viburnum luzonicum* and *Viburnum erosum*, are what we describe as leaf exchangers, as their senescence events directly preceded or were concurrent with their flushes. The range of *V. luzonicum* extends to warm temperate forests in southern China and south to the Philippines. In contrast, we sampled *V. erosum* in the warmest part of its range in Japan; it extends northward into colder forests, where it is certainly deciduous (Hara 1983). Two other exceptions are *Viburnum integrifolium* and *Viburnum japonicum*, two evergreen species that exhibit senescence patterns that appear to be slightly concentrated in two bouts, one preceding and one following their annual leaf flush. Interestingly, all of these species are nested within the large eastern Asian *Succotinus* clade and have close relatives in cool temperate forests (Clement et al. 2014; Spriggs et al. 2015). We infer that these species have extended their ranges back into warmer climates and have shifted (at least in the southern parts of their geographic ranges) in the direction of an evergreen habit. Without a phylogenetic context, one might consider a leaf exchanging phenology to be an intermediate phenotype in the transition from an evergreen to a deciduous habit. However, in the case of *Viburnum* it seems more likely to be an intermediate phenotype in the transition from a deciduous to an

evergreen habit. This makes sense given that a coordinated senescence period had already evolved in deciduous species; in the absence of freezing, senescence may have become delayed until it effectively co-occurred with new leaf production. A single peak of senescence might have been disrupted in shifting to a more fully evergreen condition, as evidenced by *V. integrifolium* and *V. japonicum*.

A close comparison of the climates occupied by our evergreen versus deciduous *Viburnum* species highlights the climatic factor that most likely drove the initial evolution of coordinated senescence. All of our sites in Taiwan and Japan experience an annual dry season beginning in October–November, but in the evergreen species this is not associated with coordinated leaf loss; instead, coordinated senescence appears only when plants are subjected to prolonged freezing. All of our deciduous species and only our deciduous species occur in locations where minimum monthly temperatures routinely dip below freezing in winter (January–February; fig. 4). This perfect correlation in our 20-species data set was corroborated by our *Viburnum*-wide phylogenetic analyses, which strongly supported minimum temperature of the coldest week (BIO6) as a significant correlate of shifts in leaf habit across the clade and strongly rejected any influence of precipitation seasonality (BIO15). Taken together, our data indicate that periods of leaf flushing are universal in *Viburnum*, perhaps even in the tropical forest species (where more data are clearly needed). A more concentrated burst of leaf flushing may have evolved first in lucidophyllous forests that experience monsoonal rainfall patterns with a period of drought in the cool season. Specifically, we suggest that the initiation of flushing might be triggered by the onset of spring rains (generally in April–May), though given the obvious correlation, it is difficult to disentangle the relative effects of rainfall versus temperature or even rainfall versus lengthening photoperiod at that time of year. In the case of leaf senescence, on the other hand, the environmental trigger seems quite clear. Our data suggest that a regular and prolonged period of freezing temperatures was the primary driver of highly coordinated leaf senescence and consequently the emergence of a fully deciduous leaf habit.

How do our results square with expectations from the Wolfe, Axelrod, and Zanne et al. hypotheses outlined above? Although we cannot rule out Wolfe's hypothesis that darkness at high latitudes favored the evolution of deciduousness in the Late Cretaceous in some plant lineages (Wolfe and Upchurch 1986; Wolfe 1987), we doubt that this explanation applies to *Viburnum*. Our phylogenetic analyses, the *Viburnum* fossil record, and the absolute dates that we have inferred (Spriggs et al. 2015) are not consistent with Cretaceous origins of deciduousness in *Viburnum*. Instead, most origins probably occurred in the late Miocene, when temperate vegetation was becoming more common at lower latitudes (Utescher and Mosbrugger 2007; Pound et al. 2011).

Axelrod's hypothesis that deciduousness evolved in warm but monsoonal forests with seasonal drought (Axelrod 1966) does not apply neatly to *Viburnum* either, considering both the phylogenetic and phenological analyses. Breaking deciduousness into two components—leaf flushing and leaf senescence—allows us to consider the possibility that these may have had separate evolutionary causes. Temporally restricted and coordinated leaf flushing might have evolved in response to the strong rainfall seasonality of monsoonal climates, with the onset of leafing possibly controlled by the onset of rains or increasing temperatures in the spring. Restricted and coordinated leaf senescence, on the other hand, might have been driven by exposure to freezing temperatures. Drought is potentially also a factor in senescence, as Axelrod supposed, but as we have shown, our evergreen species also experience similar periods of significant drought in the fall without dropping their leaves. Freezing, not drought, seems to be most directly related to coordinated senescence in our deciduous species.

We concur with a simple physiological explanation for a direct link between freezing and deciduousness: a coordinated period of senescence allows plants to remobilize key nutrients prior to the inevitable death of leaves by predictable freezing (Feild et al. 2001; Keskitalo et al. 2005; Niinemets and Tamm 2005). In all of the varied senescence patterns observed in our evergreen species, it is worth noting that no peaks in senescence coincide with the onset of the dry season; instead, they are scattered throughout the rainy season. It appears that viburnums can weather dry periods by either tolerating lower water potentials or maintaining low stomatal conductance. A modest drought tolerance combined with interannual variation in the strength of drought periods may render drought a weaker selection pressure for coordinated senescence, as many leaves may be able to persist and continue to function during the following rainy season. It is important to note, of course, that there are evergreen woody plants in the northern temperate zone (e.g., *Rhododendron*, *Ilex*) and that these species instead produce freezing-tolerant leaves with longer life spans. With very few exceptions (fig. 1), *Viburnum* has not evolved this alternative strategy, suggesting that deciduousness was the more evolutionarily accessible adaptation in this lineage. Investigating the very few instances of evergreen viburnums that experience freezing (e.g., *Viburnum rhytidophyllum*, which is nested within a cold temperate deciduous clade) might provide insights into the relative advantages of these two distinct ecological strategies to the cold temperate zone.

In proposing that deciduousness evolved directly as an adaptation to predictable and prolonged freezing, we might appear to be more aligned with the hypothesis of Zanne et al. (2014). These authors concluded that many lineages first became established in the freezing zone as evergreen plants and that deciduousness evolved later. Our data, how-

ever, do not support this order of events. One expectation of such a stepwise model is the existence of one or more ancestrally evergreen clades living in freezing climates, with one or more deciduous species nested within it. However, there is no unambiguous pattern of this type in *Viburnum* phylogeny. Furthermore, in the species that we monitored, evergreens never occur in forests that experience predictable freezing. On these grounds we judge the Zanne et al. (2014) explanation to be unlikely in this case, although the hypothesis could be salvaged by imagining the systematic extinction of evergreen species in cold climates.

An alternative model of evolution. As we have emphasized, the previously proposed hypotheses envision a sequence of steps ending in the association of cold climates with a deciduous habit. A slightly different view seems much simpler in the face of the evidence that we have presented for *Viburnum*. We might consider the possibility that the deciduous habit and in particular the coordinated senescence of leaves in the fall evolved in some plant lineages directly in response to freezing. By “directly” we mean that the senescence component of the deciduous habit evolved in situ as populations were subjected to a gradually cooling climate and the establishment of a prolonged and predictable period of freezing during the winter. We envision that this change in climate took place in fits and starts over the course of thousands to millions of years (Zachos 2001; Herbert et al. 2016), and this is a timescale during which the final steps in the evolution of a fully deciduous habit could certainly have evolved. Under this hypothesis the deciduous habit is not a preadaptation that first originated as the solution to some other problem, nor did it evolve in lineages that got there first and adapted later. Instead, we are suggesting that climate change and evolutionary adaptation occurred together, effectively in lockstep with one another. This scenario is especially realistic for an adaptation related to leafing phenology, which we have shown to be quite sensitive to climate even within a single species across its range (fig. 5).

The distinction we are making between stepwise and lockstep may seem like a subtle one, but we think it is crucially important in considering biome assembly and the causes of concerted convergence. At the very least it warrants greater care in our use of phrases like “moved into” or “shifted into” in relation to biome transitions. Likewise, the Zanne et al. (2014) terms “climate first” and “trait first” quite explicitly describe a stepwise process—in other words, that one thing happened first and the other thing happened later. In the case of the emergence of the temperate deciduous biome, it appears that a widespread and floristically rich warm evergreen forest (the boreotropical flora sensu Wolfe 1975; Tiffney 1985a, 1985b) was subjected to late Miocene cooling, eventually resulting in a climate with annual periods of freezing temperatures. The many existing lineages of woody plants in these forests would have experienced this in situ di-

rectional trend. Some of them probably fared poorly, either going extinct or shifting their ranges accordingly, but many others simply kept up with the changing times and stayed put.

What factors determine the winners and losers as large geographical regions gradually become reconfigured and new biomes emerge? In our case, the deciduous habit might have been more accessible to species that already produced resting buds and that flushed their leaves annually in response to variation in precipitation or temperature. The key step in such lineages would be the consolidation of leaf senescence, and it is this, we argue, that likely was a direct response to freezing, not drought. Indeed, such predispositions likely explain the repeated evolution of the deciduous habit within particular lineages and in general the clustering of the origin of certain traits in particular regions of the tree of life (Edwards and Donoghue 2013; Donoghue and Edwards 2014). *Viburnum* provides an excellent example, with possibly as many as 10 separate origins of deciduousness, but we suspect that other familiar temperate lineages that were present in boreotropical forests (e.g., *Acer*, *Carya*, *Nyssa*, *Hamamelis*, *Sassafras*, *Cornus*; Tiffney 1985a), when analyzed carefully, will show similar patterns of in situ convergence.

It is certainly the case that biome assembly also reflects other processes, including preadaptation, habitat filtering (cf. Ackerly 2004), and even occasional long-distance dispersal events (Pennington and Dick 2004; Crisp et al. 2009). We also do not doubt that all of these pathways have contributed to the assembly of temperate deciduous forests. However, we believe that these other phenomena may have had a relatively minor influence as compared to the in situ adaptation of multiple lineages to gradual climate change. We suggest that such concurrent responses may largely underpin the assembly of new biomes and that this process may be responsible for the extremely high number of origins of certain traits.

Although we have concentrated here on direct shifts between mesic tropical and temperate forests, we fully appreciate that there have likely been other biome pathways and in particular that some members of cool temperate forests may have been derived within lineages that occupied seasonally dry tropical forests (e.g., possibly *Celtis*). Such a pathway would be far more consistent with a stepwise model, where deciduousness evolved first in response to one variable (drought) and served later as a preadaptation for another (cold). Nevertheless, in both pathways (i.e., with ancestors in either mesic forests or dry forests) the final steps in the process may have been similar. In both cases, senescence may have been relatively uncoordinated at first, as in the case of dry forests, where leaves tend to senesce at different times depending largely on individual plant water status (e.g., Reich and Borchert 1984). However, freezing events are

experienced by all individuals simultaneously, and routine exposure to prolonged cold could have tightly coordinated the senescence period to a more condensed time period across the community.

Consilience and integration in phylogenetic biology. How do we justify our lockstep model? If we approached this with only our phylogenetic tools, we would not be entirely satisfied. The high lability of both the deciduous habit and climate makes it difficult to infer with any confidence many of the deeper and potentially most relevant transitions (fig. 1). We do know that deciduousness and freezing climate are very tightly correlated across our tree, so much so that changes in both of them very often co-occur along the same branches, making it difficult to establish cause and effect (Baum and Donoghue 2001). If there had in fact been a repeated order of events, history has largely erased its signal. We might also be frustrated by our inability to analyze both characters as continuous variables, which would have provided a more direct test of a simultaneous, lockstep evolutionary model. Transforming habitat into a continuous climate variable was possible by using the CliMond database, but assigning continuous values to species along an evergreen-deciduous continuum is logistically and conceptually more difficult and would require detailed phenological studies of every species, not just the 20 that we have presented here.

But what if we consider these conclusions together with the results from the phenological study? Here we also see evidence of a very tight association between freezing in particular and the deciduous habit (fig. 4) and of the extreme lability of phenological patterns, even among populations within a single species (fig. 5). These observations are completely consistent with the strong correlation across the *Viburnum* phylogeny, and together these lines of evidence suggest to us that the “simultaneous” changes that we see in phylogenetic analyses may often be real simultaneous changes rather than artifacts of extinction. If individual species can be evergreen in one part of their range and deciduous in another (as in *V. erosum* and *V. luzonicum*), gradual and concurrent emergence of the deciduous habit as a freezing climate becomes established begins to seem highly likely.

The study of phylogenetic comparative methods appears to be shifting into a more introspective phase, with renewed scrutiny of the limitations of our inferences (Edwards et al. 2015; Maddison and FitzJohn 2015; Pennell et al. 2015; Wright et al. 2015). Critiques typically end with a call for better models, and we agree completely that there is much room for improvement. However, at the end of the day, we need to remind ourselves of the extreme difficulty of convincingly inferring evolutionary events in the distant past with data usually only from extant organisms, especially when convergence is rampant and densely clustered in particular

clades. Under these circumstances, phylogenetic insights will be most powerful when interpreted alongside other, quite independent lines of evidence until (hopefully) consilience emerges (Weber and Agrawal 2012; Olson and Arroyo-Santos 2015).

From this perspective, we believe that research conducted at the scale of *Viburnum* will continue to be highly productive, precisely because the results of multiple independent analyses can most effectively be brought into alignment in such model lineages. For example, the data presented here are relevant to questions about the deciduous leaf habit, but they are also directly connected to our studies of leaf form and function (Chatelet et al. 2013; Scoffoni et al. 2016), growth architecture and leaf life span (Edwards et al. 2014), and even flowering phenology (L. Garrison, M. Donoghue, and E. Edwards, unpublished manuscript) and wood anatomy (D. Chatelet, M. Donoghue, and E. Edwards, unpublished manuscript). Consequently, we have the potential to establish connections between what might at first appear to be unrelated phenomena. It is this form of synthesis that we find most inspiring and most likely to provide new conceptual breakthroughs as we face the formidable chal-

lenge of inferring evolutionary history. Immersion in the messy details of particular lineages, far from being a distraction, may be the most fertile ground for achieving consilience—the moment when multiple, sometimes weakly supported findings all point to the same conclusion.

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APPENDIX

Supplementary Table

Table A1: Significance of leaf flushing and senescence patterns in 20 species of *Viburnum* along a latitudinal gradient in Asia

Species	Location	Leaf habit	Event	Total leaves	Mean Julian day (observed)	Mean Julian day (null)	P
<i>V. awabuki</i>	Japan	Evergreen	Leaf flush	41	89	194	2.60E-12
<i>V. awabuki</i>	Japan	Evergreen	Leaf drop	48	176	195	.239
<i>V. betulifolium</i>	Taiwan	Deciduous	Leaf flush	211	118	187	3.20E-25
<i>V. betulifolium</i>	Taiwan	Deciduous	Leaf drop	195	336	187	1.90E-88
<i>V. bitchiense</i>	Japan	Deciduous	Leaf flush	353	102	207	4.00E-102
<i>V. bitchiense</i>	Japan	Deciduous	Leaf drop	523	305	207	2.60E-115
<i>V. clemensiae</i>	Borneo	Evergreen	Leaf flush	68	110	169	4.20E-06
<i>V. clemensiae</i>	Borneo	Evergreen	Leaf drop	15	183	170	4.80E-01
<i>V. dilatatum</i>	Japan	Deciduous	Leaf flush	353	106	189	6.57E-39
<i>V. dilatatum</i>	Japan	Deciduous	Leaf drop	352	311	189	1.39E-96
<i>V. erosum</i>	Japan	Leaf exchanger	Leaf flush	240	91	195	3.54E-65
<i>V. erosum</i>	Japan	Leaf exchanger	Leaf drop	205	276	195	2.67E-34
<i>V. furcatum</i>	Japan	Deciduous	Leaf flush	229	134	205	1.41E-32
<i>V. furcatum</i>	Japan	Deciduous	Leaf drop	341	311	205	6.47E-106
<i>V. integrifolium</i>	Taiwan	Evergreen	Leaf flush	154	126	187	4.65E-12
<i>V. integrifolium*</i>	Taiwan	Evergreen	Leaf drop	109	170	188	2.00E-02
<i>V. japonicum</i>	Japan	Evergreen	Leaf flush	134	81	195	3.01E-47
<i>V. japonicum*</i>	Japan	Evergreen	Leaf drop	95	156	195	3.28E-04
<i>V. luzonicum</i>	Taiwan	Leaf exchanger	Leaf flush	205	89	187	4.31E-56
<i>V. luzonicum</i>	Taiwan	Leaf exchanger	Leaf drop	133	154	187	3.37E-07
<i>V. odoratissimum</i>	Taiwan	Evergreen	Leaf flush	220	151	187	1.35E-08
<i>V. odoratissimum</i>	Taiwan	Evergreen	Leaf drop	91	180	186	4.26E-01

Table A1 (Continued)

Species	Location	Leaf habit	Event	Total leaves	Mean Julian day (observed)	Mean Julian day (null)	P
<i>V. parvifolium</i>	Taiwan	Deciduous	Leaf flush	405	99	187	2.37E-86
<i>V. parvifolium</i>	Taiwan	Deciduous	Leaf drop	396	332	187	1.95E-174
<i>V. phlebotrimum</i>	Japan	Deciduous	Leaf flush	198	97	202	4.50E-62
<i>V. phlebotrimum</i>	Japan	Deciduous	Leaf drop	196	306	202	1.14E-57
<i>V. propinquum</i>	Taiwan	Evergreen	Leaf flush	295	122	187	8.12E-33
<i>V. propinquum</i> *	Taiwan	Evergreen	Leaf drop	125	165	187	4.10E-02
<i>V. sieboldii</i>	Japan	Deciduous	Leaf flush	333	100	215	3.70E-105
<i>V. sieboldii</i>	Japan	Deciduous	Leaf drop	332	277	215	5.33E-27
<i>V. sympodiale</i>	Taiwan	Deciduous	Leaf flush	508	121	187	3.73E-53
<i>V. sympodiale</i>	Taiwan	Deciduous	Leaf drop	399	328	187	1.31E-156
<i>V. taitoense</i>	Taiwan	Evergreen	Leaf flush	273	105	187	9.60E-47
<i>V. taitoense</i>	Taiwan	Evergreen	Leaf drop	109	180	187	7.10E-01
<i>V. taiwanianum</i>	Taiwan	Evergreen	Leaf flush	326	145	187	1.77E-11
<i>V. taiwanianum</i>	Taiwan	Evergreen	Leaf drop	245	208	187	4.00E-01
<i>V. urceolatum</i>	Japan	Deciduous	Leaf flush	96	111	203	1.62E-19
<i>V. urceolatum</i>	Japan	Deciduous	Leaf drop	96	271	204	1.95E-09
<i>V. vernicosum</i>	Borneo	Evergreen	Leaf flush	126	117	169	3.25E-07
<i>V. vernicosum</i>	Borneo	Evergreen	Leaf drop	17	199	170	3.60E-01

Note: Species in boldface exhibited leaf senescence patterns statistically indistinguishable from our generated null distributions. Evergreen species marked with an asterisk exhibited senescence patterns significantly different from the null at $P < .05$. All species exhibited highly significant leaf flushes, occurring earlier in the year than the null expectation.

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