

**The importance of ecological versus phylogenetic effects in
determining *Rhododendron* flowering phenology**

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Abstract

Species across the globe are responding to changes in climate, with one of the most evident responses that of changes in species phenology. Phenology is important in determining the abiotic environment and biotic interactions that organisms are exposed to. This study investigates 1) the responses of first, peak, and last flowering dates of 41 species of *Rhododendron* to increases in temperature; and 2) the relative contributions of ecology and phylogeny to these responses. All three flowering phases of Rhododendrons were most influenced by temperatures in a window of 69 days prior to the flowering phase. With a one degree Celsius increase in temperature, these species flower approximately one week earlier. Latitude was the only significant ecological predictor of plasticity, and only for last flowering dates. Species varied in their plasticity for first and peak flowering dates, while there was within-species variation of plasticity for peak and last flowering dates. Phylogenetic relatedness did not explain plasticity at any of the flowering phases. Responses in flowering dates suggest that *Rhododendron* species will be able to track changing temperatures, but the limits to their plasticity and the consequences to their fitness is uncertain. The factors driving phenological plasticity in these species remain unknown, and further investigation should consider biotic factors and finer-scale phylogenetic data.

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Introduction

Across the globe, there is a coherent footprint of climate change, which is a persistent driver affecting the long-term existence of species across the world (Parmesan and Yohe, 2003). These changes are predicted to continue in coming years, even becoming more pronounced and severe (IPCC, 2013). Predictions made decades ago on certain elements of climate have recently proved to be true (Fischer and Knutti, 2016). Research into the impacts that climate change has on biotic communities has increased and indicates that consequences of these changes could include extinctions (Thomas et al., 2004), changes in species' distributions (Parmesan and Yohe, 2003) and changes to ecosystem functioning (e.g. Stige and Kvile, 2017).

A sound understanding of how climate change will influence biodiversity and ecosystem services is crucial to conserving biota and intact systems (Jones et al., 2016), as well as for human wellbeing which is delicately linked to the wellbeing of living organisms. As temperatures warm, species are shifting their ranges poleward and upwards in elevation (Pecl et al., 2017). These range shifts lead to a loss of certain species interactions, and the creation of new interactions which ultimately affect ecosystem functioning (Pecl et al., 2017). The equilibrium and functioning of ecosystems is important not only for the organisms surviving in them, but also for society and human wellbeing (Chiabai et al., 2018).

Ecosystems provide us with many services which would otherwise be very costly to obtain. They range from the provision of raw materials that are used for manufacturing many items and food to protection against natural disasters. Changes in ecosystems can therefore have profound impacts on people's daily lives. Species range shifts that are occurring are not random in direction and will consequently leave some areas at a much bigger disadvantage in terms of food provision and disease occurrence than others (Pecl et al., 2017). These patterns of inequality can cause conflict among people. To date, climate change has already affected the timing of floods, the frequency of fires, and economic losses due to agriculture, crime, and natural disasters (Abatzoglou and Williams, 2016; Blöschl et al., 2017; Hsiang et al., 2017).

Changes have been observed across taxa and geographic regions, with changes in species' distributions and abundances, and shifts in species phenology becoming common occurrences. One of the most evident responses to climate change is that of changes to phenology (Thackeray et al., 2016; Keogan et al., 2018). Phenology describes the science of

seasonally recurring life-history events (Badeck et al., 2004), for example timing of leafing, flowering and fruit development in plants, and egg-laying, and birth of young in animals. Phenology is important in determining the abiotic (e.g. frost, drought) and biotic (e.g. competition for resources, interactions with pollinators) conditions that an organism is exposed to.

Phenological events have been important cultural milestones in the year to many people, and therefore some rare long-term datasets exist. One of these long-term datasets is from the Marsham family, that have collected phenology data on more than 20 animal and plant species for a period of 211 years close to Norfolk. Analysis of these data show that some species have a greater response to warming temperatures than others, however, all four species for which first flowering dates are collected show a reaction to the temperature in the months preceding flowering (Sparks and Carey, 1995).

Other datasets have corroborated these trends and phenological shifts have been demonstrated across a wide range of species, for example a meta-analysis of 677 species of plants, birds, insects, amphibians, and fish over a time period ranging between 16 and 132 years (median 45 years) found that 87% of the shifts were in the direction predicted by climate change (Parmesan and Yohe, 2003), while another meta-analysis of 694 species found that more than 80% of the species were showing changes in the direction expected (Root et al., 2003). Advances in phenologies tend to be more pronounced at lower trophic levels, leading to possible disruptions of species interactions and consequences for ecosystem functioning (Thackeray et al., 2016). Life history traits, such as plant growth form (herbaceous or woody) and life form (annual or perennial) also influence when plants are able to flower, relating to amount of resources that they are able to store over the growing season (Bolmgren and Cowan, 2008). In terms of plants, trees have been shown to respond slower than other plants (Rich et al., 2008). In Britain, there has been a major shift in the flowering time of plants, with an average advancement of the first flowering date by 4.5 days in 1991-2000 compared to 1954-1990 over 385 species (Fitter and Fitter, 2002). Spring-flowering species are the most sensitive to changes in temperature (Fitter and Fitter, 2002), and appear to respond to temperatures one to two months before flowering (Fitter et al., 1995). Changes to the phenology of species may increase chances of hybridization in nature, as temporal barriers for gene flow are broken down. Hybridization will be particularly important for rare species, which may become extinct because of it but could also be the salvation of inbred populations (Todesco et al., 2016).

Given that long-term records are sparse and there is an urgent need to understand phenology, other approaches have been used to infer phenology. These include the use of so termed “legacy datasets” which include information from herbaria, museums and photographs. Recently a creative approach has used historic television footage from cycling races to determine changes to the phenology of plants growing along the route (De Frenne et al., 2018).

For plants, the timing of flowering is an important event which affects their prospects for pollination and the time at which seeds ripen and are dispersed, defining their fitness and having community-level consequences (Fitter et al., 1995; Fitter and Fitter, 2002). Plants are very responsive to changes in climate due to temperature’s dominant role in determining vegetative growth (Polgar and Primack, 2011). Climate is known to be an important driver of plant phenology (Schwartz et al., 2006), with plants advancing their flowering in accordance with warming temperatures (e.g. Wolfe et al., 2005). Changes in plant phenology have impacts on the rest of the ecosystem. The reproductive phenology of a species is closely linked to the phenology of other organisms essential to the success of reproduction (Both et al., 2009). The timing of flowering is very important for plant species, in particular when they rely on an insect pollinator as changes to flowering time could lead to mismatches with the presence of their pollinator (Rafferty and Ives, 2012). In an alpine community it has been illustrated that early in the season there is a low pollinator availability compared to a high pollinator availability later in the season (Kameyama and Kudo, 2015). Therefore, plants that flower very early are at risk of not being pollinated due to a shortage of pollinators, while plants flowering late have to compete with other flowering species for pollinators. The composition of the pollinator community also changes as the season progresses, with different groups of pollinators showing a preference for different taxa (Kameyama and Kudo, 2015). Additionally, pollinators may become more experienced as time progresses and therefore more successful at pollinating plants later in the season (Rafferty and Ives, 2012).

Any changes to the flowering time of an individual which is not also matched by a change in the appearance of its pollinator could have massive impacts on its reproductive success, as well as having implications on competition for pollinators. Changes to plant phenology may have cascading effects across the food chain. At four different levels in the food chain in a temperate forest, shifts in phenologies of different magnitudes over 20 years have created a decrease in synchrony at all of the levels (Both et al., 2009). Changes are also occurring to the structure of pollination networks, with one documented loss showing an

overall loss of 46% of pollinators and only 24% of original interactions remaining (Burkle et al., 2013).

Changes to plant phenology due to changes in temperature can affect the productivity of food crops, and also whether particular crops can be grown in certain regions. Many tree crops, for example, require winter chills in order to produce flower buds. Predicted declines in the number of chilling hours in California will make the area unsuitable for most of the tree crops currently grown there by the end of the century (Luedeling et al., 2009). When phenological changes cause mismatches with pollinators, this can also have massive implications on food production. In the European Union alone, four out of five of all crops and wildflowers rely on insect pollinators, resulting in €15 billion of agricultural output every year (European Commission, 2018).

One of the big and still largely open questions in phenology regards the extent to which species are able to adjust to a changing climate, and whether there are evolutionary constraints. Flowering time is a highly variable trait (Chuine, 2010), and may therefore be expected to be primarily driven by the environment, with little phylogenetic signal (Davies et al., 2013). However, species that occupy similar environments show a large variation in their flowering time, suggesting that phenological traits are at least to some extent governed by intrinsic factors like phylogeny (Davies et al., 2013). If species are constrained by their evolutionary history we would expect to see similar relationships between temperature and phenology (e.g. in first flowering dates) in closely related species. If species are not phylogenetically conserved we would expect that the responses of individual species and/or plants to warming temperatures will be better explained by their ecology or the characteristics of the habitats in which they originate, rather than by phylogenetic relatedness. This has been tested across broad groups of organisms, for example across major plant families (Kochmer and Handel, 1986; Davis et al., 2010), but to my knowledge this has rarely been tested within narrower taxonomic groups such as within a single genus.

Not all species respond to climatic changes equally (Willis et al., 2008). Closely related species often flower at similar times which points to phylogenetic conservatism, either due to physiology which determines sensitivity to climate cues, or due to phylogenetic niche conservatism where related species grow in and are adapted to a similar environment (Davies et al., 2013). Even in geographically isolated temperate floras, plant species from major clades show phylogenetic conservatism in flowering time tracking (Davis et al., 2010).

Similarly, animal-pollinated angiosperms from Japan and the USA (over 2000 species) show consistent flowering times among families, with life forms also clustering to a lesser degree (Kochmer and Handel, 1986). It has been shown that species loss is phylogenetically clustered due to conservatism of flowering-time responses to climate change (Willis et al., 2008).

The relative contributions of phylogeny and ecology may give insight into how species will respond to changing climates in the future. Phenological studies that are restricted to one or a few taxonomic groups are a powerful tool to explore plant cycles in more detail (Carvalho et al., 2015). Few studies have examined the relative contribution of environmental and phylogenetic factors within a specific taxonomic group, and with differing results. The flowering phenology of the Myrteae (Myrtaceae) for example is influenced by both ecology and phylogeny, with ecology playing a more important role (Staggemeier et al., 2010). Conversely, a study focusing on one taxonomic group in a particular environment, the Bromeliaceae, found that abiotic and phylogenetic factors were not the main determinants of flowering phenology, suggesting that biotic factors may play an important role (Suizani et al., 2012).

In this study we use flowering phenology data of 46 species in the genus *Rhododendron* growing in the same location, spanning ten years. Using data from a common garden experiment is beneficial since all of the individuals are experiencing the same environmental conditions and photoperiod, and the dates for phenology correspond to the exact same environmental conditions (e.g. onset of spring occurs on the same day). Focussing on one genus allows us to test for subtle lineage effects which might not be detectable at larger taxonomic scales.

The genus *Rhododendron*, in the family Ericaceae, is found across a large latitudinal gradient from 20 °S to 80 °N. The greatest diversity of the genus is found in the Asian tropics, but on mountains, indicating their preference for cooler climates (Shrestha et al., 2018). The genus has been known for a long time, with the type specimen of the genus (*R. ferrugineum* (L.)) being described by Linnaeus in 1753 (Cullen, 1980). Rhododendrons are small to large shrubs, and rarely large trees which may be evergreen or deciduous. The leaves are arranged in a spiral, and the undersides of leaves are often covered in scales or hairs that are used to identify taxa. Flowers are grouped in inflorescences and have superior ovaries, and stamens bearing agglutinate pollen. There is a very large variation of morphology across

the genus which has made it taxonomically complex. They are used extensively in horticulture and are popular garden plants, evident from the existence of thousands of cultivars. The group is culturally significant and the national flower of Nepal is that of *Rhododendron arboreum*, and several other species are state flowers or state trees in different provinces in India and two US states. An herbal brew is made from the flowers of three species which is called Labrador tea. In Nepal, the flowers *R. arboruem* are pickled, used in fish stews, and used to make a juice. Traditional medicine has used Rhododendrons for a long time to treat inflammation, pain, gastro-intestinal disorders, skin problems, and colds, and modern studies have found support for its effectiveness to treat these symptoms (Popescu and Kopp, 2013). Honey from some species causes intoxication due to the presence of grayanotoxins in the genus that are extracted by bees (Ullah et al., 2018). *Rhododendron ponticum* has become invasive in several countries, including the British Isles (Cross, 1975), taking over woodlands and producing a thick canopy under which native plants cannot survive and is difficult to eradicate.

The aims of this study were to determine (1) species-level phenological responses to temperature; and (2) the relative contribution of phylogenetic versus ecological traits to phenological plasticity.

Methods

Study area

The Royal Botanic Garden Edinburgh (RBGE) is located in Edinburgh, United Kingdom (55°57' N, 3°12' W). The garden, which covers an area of over 28 hectares and lies at an elevation of approximately 30 m a.s.l., has a temperate, maritime climate. The mean daily minimum and maximum temperatures are 5.91 °C (range -15.5 to 18.9 °C; 1976 - 2017) and 12.71 °C (range -4.5 to 29.9 °C; 1976 - 2017), with annual rainfall averaging 719 mm (1981 - 2010).

RBGE has been focussed on *Rhododendron* collection and taxonomy since the 19th century, and together with its three satellite gardens (Benmore, Dawyck, and Logan) contains the largest collection of *Rhododendron* species in the world. This includes approximately half of all known species (Royal Botanic Garden Edinburgh, 2018).

Study species

Forty-one species of *Rhododendron* are included in these analyses (Table 1). This includes species from Asia (the centre of distribution for the genus), America, and Europe. All of the individual plants considered in this study had been at the RBGE for at least seven years before the start of phenology monitoring, and would thus have adapted to the prevailing climatic conditions.

Table 1 List of *Rhododendron* species included in this study

Species	Series	Number of accessions (with 5+ years data)	Niche breadth
<i>Rhododendron adenogynum</i> Diels	Taliense	3	-1.013
<i>Rhododendron anthosphaerum</i> Diels	Irroratum	3	-1.351
<i>Rhododendron arboruem</i> Sm.	Arboreum	5	-4.686
<i>Rhododendron augustinii</i> Hemsl.	Triflorum	4	-1.689
<i>Rhododendron auriculatum</i> Hemsl.	Auriculatum	1	-2.499
<i>Rhododendron barbatum</i> G.Don	Barbatum	3	-1.418
<i>Rhododendron calendulaceum</i> (Michx.) Torr.	Azalea	3	-1.688
<i>Rhododendron calophytum</i> Franch.	Fortunei	2	-2.094
<i>Rhododendron calostrotum</i> Balf.f. & Kingdon-Ward	Saluenense	3	-0.338
<i>Rhododendron campanulatum</i> D.Don	Campanulatum	3	-0.608
<i>Rhododendron canadense</i> (L.) Torr.	Azalea	3	-0.203
<i>Rhododendron cinnabarinum</i> Hook.f.	Cinnabarinum	4	-0.270
<i>Rhododendron dauricum</i> L.	Dauricum	4	1.553
<i>Rhododendron decorum</i> Franch.	Fortunei	4	-2.026
<i>Rhododendron degronianum</i> Carrière	Ponticum	4	-1.688
<i>Rhododendron ferrugineum</i> L.	Ferrugineum	5	-0.608
<i>Rhododendron groenlandicum</i> (Oeder) Kron & Judd	Ledum	2	1.148
<i>Rhododendron hippophaeoides</i> Balf.f. & W.W.Sm.	Lapponicum	5	-0.473
<i>Rhododendron irroratum</i> Franch.	Irroratum	2	-2.229
<i>Rhododendron lapponicum</i> Wahlenb.	Lapponicum	2	1.958
<i>Rhododendron lepidotum</i> Wall.	Lepidotum	3	-0.878
<i>Rhododendron leptothrium</i> Balf.f. & Forrest	Ovatum	1	-2.363

<i>Rhododendron liliiflorum</i> H.Lév.	Maddenii	1	-3.309
<i>Rhododendron lutescens</i> Franch.	Triflorum	3	-1.959
<i>Rhododendron luteum</i> Sweet	Azalea	3	-0.203
<i>Rhododendron meddianum</i> Forrest	Thomsonii	2	-2.499
<i>Rhododendron mucronulatum</i> Turcz.	Dauricum	4	-1.318
<i>Rhododendron neriiflorum</i> Franch.	Neriiflorum	4	-2.229
<i>Rhododendron ponticum</i> L.	Ponticum	4	-1.891
<i>Rhododendron praeevernum</i> Hutch.	Fortunei	4	-2.769
<i>Rhododendron racemosum</i> Franch.	Scabrifolium	3	-1.418
<i>Rhododendron reticulatum</i> D. Don ex G.Don	Azalea	5	-3.039
<i>Rhododendron russatum</i> Balf.f. & Forrest	Lapponicum	3	-0.878
<i>Rhododendron schlippenbachii</i> Maxim.	Azalea	3	-1.553
<i>Rhododendron semibarbatum</i> Maxim.	Semibarbatum	3	-2.229
<i>Rhododendron siderophyllum</i> Franch.	Triflorum	3	-2.094
<i>Rhododendron strigillosum</i> Franch.	Barbatum	3	-2.026
<i>Rhododendron trichostomum</i> Franch.	Anthopogon	3	-0.608
<i>Rhododendron wadanum</i> Makino	Brachycalyx	3	-2.094
<i>Rhododendron wallichii</i> Hook.f.	Campanulatum	3	-0.473
<i>Rhododendron yunnanense</i> Franch.	Triflorum	3	-1.418

Data collection

The collection of phenological data for *Rhododendrons* at RBGE was started in the summer of 2007 based on dedicated volunteer efforts and is ongoing to date. Every Wednesday, each *Rhododendron* individual was visually assessed and the first flowering date (FFD), peak flowering date (PFD), and last flowering date (LFD) recorded as the week of the year. The FFD was recorded when the first fully open flower, with the stigma and stamens visible, was seen (Figure 1). The PFD was recorded when the majority of the plant was in bloom, when few flowers had fallen off and few buds remained unopened. The LFD was defined as the date at which there were no fresh flowers remaining on the plant.

The permanent weather station at RBGE includes readings of air temperature and precipitation. For these analyses, the weekly average temperatures have been used, calculated with data from 2008 to 2017.

Ecological traits for each species, including plant height, leaf length, and habitat were collected from books (Davidian, 1982; Davidian, 1989; Davidian, 1992; Davidian, 1995).

Data cleaning

The weather station data was imported into R (R Core Team, 2018) and cleaned to provide a uniform dataset. Dates were entered differently before 2003 (e.g. 18-Sep-2001) compared to after the year 2003 (e.g. 18/01/2017). This was standardized to the format used post-2003 across the entire dataset. The dates were then converted to julian days, which range between one and 365 (366 in a leap year). Missing values in the temperature dataset were filled in by using a linear interpolation function in the “zoo” package (Zeileis and Grothendieck, 2005). All data from 2018 were removed, since the full year is not represented yet and would influence yearly averages. All data formatting and cleaning was carried out in R, using the package “tidyr” (Wickham and Henry, 2018).

Phylogeny

Aligned RPB2 sequence data from Goetsch et al. (2005) was downloaded from TreeBASE (Study 1370; Piel et al., 2009). The phylogeny produced by these authors was reconstructed using RAxML BlackBox (Stamatakis et al., 2008) with a maximum likelihood search, to produce a maximum likelihood phylogenetic tree rooted with *Empetrum nigrum*. However, this most recent phylogeny available for the genus *Rhododendron* (Goetsch et al., 2005) only contains 15 of the species included in this study (36.59%). In order to investigate all of our species, the series into which each species is placed (obtained from Davidian, 1982; Davidian, 1989; Davidian, 1992; Davidian, 1995) was used as a proxy, and since series in the genus match previously produced phylogenies (Hart et al., 2016), were assumed to be a good proxy for phylogenetic information. A current project in China, which is working on producing a full molecular phylogeny of the genus, is expected to be published in the near future and when this becomes available we aim to rerun our analyses to incorporate this new and more complete information.

Sliding window analyses

All statistical analyses were conducted in R statistical software (R Core Team, 2018). The mean air temperature for each day was calculated as the average of the minimum and maximum daily temperature values. The mean daily maximum temperature for each year was calculated and plotted with a linear regression line fitted.

To determine the time window before the phenology phase (FFD, PFD or LFD) during which temperature most influences the date of the phenology phase, a sliding window analysis was run across all accessions for each of the three phases. The end of each time window was kept the same as the mean date of the phenological observation for that accession. The start date of the window was changed by subtracting 7 days from the start of the window at each increase, resulting in 13 time windows (ranging from 6 to 69 days prior to the phenology phase). A linear model was run for the flowering phenology against the predictors mean temperature and year to produce a slope, standard error, and model log likelihood for each individual accession. Using the sum of the log likelihood scores across all of the accessions, the window with the overall best performance for FFD, PFD and LFD was identified as window ten, which is the window up to 69 days before the flowering stage. Only individuals with data for at least five years were included in the analyses.



Figure 1 *Rhododendron* flowers a) in bud; and b) fully open with the stamens and stigma visible

Niche breadth

Geographic occurrences for each species were downloaded from the Global Biodiversity Information Facility (GBIF) through the “rgbif” library in R (Chamberlain, 2017). The records were limited to preserved specimens with coordinates, to exclude individuals growing in botanic gardens. For each species, the occurrences were mapped, and any errors in the dataset (e.g. coordinates in the ocean or outside of the species range) were manually removed.

Climatic predictor variables that were thought to be biologically important (mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual precipitation, precipitation of the driest month, precipitation of the wettest month, temperature annual range, temperature diurnal range, and altitude) were chosen and downloaded from WorldClim version 2.0 at a resolution of 30 arc seconds (Fick and Hijmans, 2017). Some of these variables represent extremes (e.g. precipitation of the driest month), while others represent total resource availability (e.g. annual precipitation).

Following the methods presented by Broennimann et al. (2012), the niche breadth for each species was calculated through the “adehabitat” library (Calenge, 2006), using R code written by Broennimann et al. (2012). A principal component analysis (PCA) was performed on the chosen environmental variables and altitude. The environmental space formed by the first two components was gridded (explaining 66.53% of the variance), and the species were then mapped into the gridded space using a kernel density function. The niche position of each species was then identified as the median position of the species within the environmental grid, and the variation from this median position measured as the niche breadth on both axes of the PCA. Six species had insufficient records to produce a value for niche breadth (*R. anwheiense*, *R. collettianum*, *R. lanigerum*, *R. macabeanum*, *R. maculiferum*, *R. tolmachevii*). Additionally, for those with no geographic occurrence records, no altitude and latitude values could be extracted. These species were excluded from further analyses. The niche breadth along the first axis of the PCA captured most of the variation (45.53%), and therefore this was the value used in further analyses. Species with a higher value for niche breadth occupy a broader range of environmental conditions (Table 1).

Mixed effect models

To determine the relative effects of the different traits on the flowering phenology of Rhododendrons, a random effects meta-analytic approach using a mixed effect model, fitted via restricted maximum likelihood estimation, in the “metafor” library was used (Viechtbauer, 2010). Each phenological phase (FFD, PFD, and LFD) was analysed separately. The slope of the phenological shift of each species (i.e. plasticity) was modelled against predictor variables. Niche breadth, maximum altitude, median altitude, maximum latitude, and median latitude were included as fixed effects. Series (proxy for phylogeny), species, and accession number were added to the model as random effects. Adding these variables to the model as random effects allows estimating the variation in plasticity across the different levels of the variable (e.g. species). This is used when you are interested in the overall effect, and not in the effects of the subgroups within the variable. Using random effects also mitigates the issue of imbalance in the data (e.g. some series may be better represented than others) and provide an estimate for the overall effect. To determine the significance of random effects, each random effect was dropped from the model in turn and the log likelihoods of the two models compared using a likelihood ratio test.

Results

The mean daily maximum temperature showed no significant increase from 2008 to 2017 ($R^2 = 0.152$, $p=0.265$; (Figure 2). The mean daily mean temperature also showed no significant increase in the study period ($R^2=0.125$, $p=0.316$).

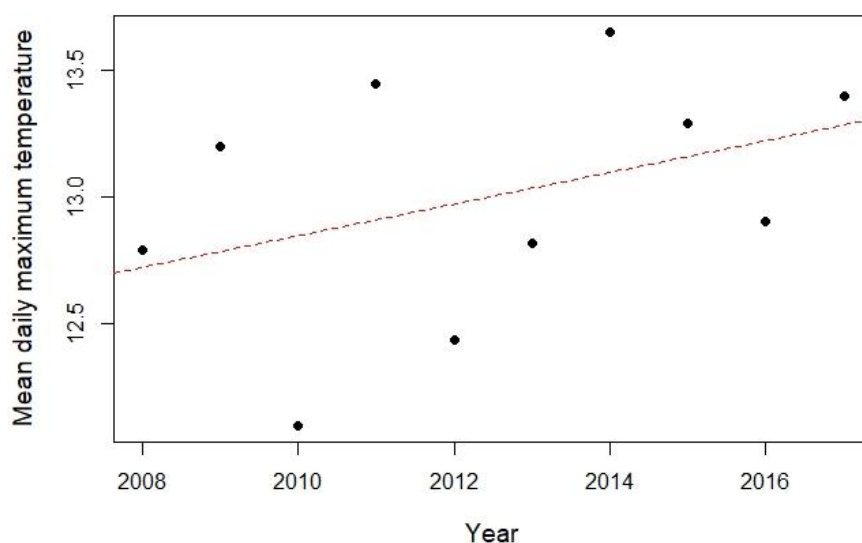


Figure 2 The mean daily maximum temperature per year from 2008 to 2017, with a linear regression line fitted

Sliding window analyses indicated that temperatures between 69 days prior to the first flowering date and the actual date had the biggest influence on the date at which the first flowers emerged (Figure 3A). The best window and the window nearest to it were significantly different from one another (log likelihood 11.59 units higher). The slope of the first flowering date of all of the individuals studied converged around the mean of -7.643 days (see Appendix Table A1 for responses of individual plants), indicating that on average the studied species first flowered 7.643 days earlier per one degree warming (Figure 3D). The same trend was seen for the peak and last flowering dates, which also responded most strongly to temperatures in the 69 days before the date of first flowering (Figure 3B and 3C), with a significant difference between the best window and the next-best window for both peak (log likelihood difference of 7.01) and last flowering dates (log likelihood difference of 7.49). The mean slope for peak flowering date was -7.116 (Figure 3E; responses for individual plants in Appendix Table A2), and -6.419 for the last flowering date (Figure 3F; responses for individual plants in Appendix Table A3).

Table 2 Results from the null models for each flowering phase, including only random effects

Phenology stage	Intercept		Accession		Species		Series	
	Slope	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
FFD	-7.6623	<0.0001	0.0000	1.0000	4.0312	0.0034	0.0000	1.000
PFD	-7.4779	<0.0001	1.8872	0.0005	2.5107	0.0274	0.0000	1.000
LFD	-6.7405	<0.0001	7.8378	<0.0001	0.3931	0.7970	0.0000	1.000

As a null model, including only random effects in the model, the mean plasticity for first flowering date was -7.6623 ($p < 0.0001$). There was significant variation among different species, but not within-species or among series (Table 2). When including fixed effects in the model, the plasticity of first flowering date was not significantly affected by any of the fixed effects and the fixed effects did not explain the variation in plasticity (test for residual heterogeneity, $QM=107121$, $p=0.057$). There was true random variation in random effect sizes ($QE=164.4822$, $p=0.0074$). None of the random effects were significant (Table 3).

Peak flowering date was the only one of the three phenological phases with a significant intercept of -12.9899 (± 4.7336 S.E., $p=0.0061$) when all effects were included in

the model (Table 4). With only random effects, the mean plasticity was -7.4779 (Table 2). The random effects accession number and species were significant in driving plasticity (indicating variation both within-species and between species) in both models, with all other variables being non-significant (Table 4). Fixed effects overall did not explain the variation in plasticity (QM=2.8608, $p=0.7214$), and random effects contained variation (QE=236.0247, $p<0.0001$).

The mean plasticity of last flowering date highly significant in the null model which only included random effects (intercept=-6.7405; Table 2). In the model accounting for all effects (Table 5), maximum latitude (estimate=0.3178, lower confidence interval=0.0798, upper confidence interval=0.5557), median latitude (estimate=-0.4214, lower confidence interval=-0.7257, upper confidence interval=-0.1170) and accession (estimate=8.2545, lower confidence interval=2.6233, upper confidence interval=13.8857) were significant effects driving the plasticity of species' last flowering dates (Table 5). Therefore, species at a lower maximum latitude will have higher plasticity than those at a higher maximum latitude, but plasticity decreases with a species' increase in median latitude. After accounting for fixed effects, accessions differ in their plasticity. The last flowering date was the only phase for which any of the fixed effects has a significant impact on plasticity. Species growing at a higher maximum latitude had higher plasticity in the response of their last flowering date, while species growing at higher median latitudes showed lower plasticity. Despite the significance of maximum latitude and median latitude, fixed effects overall did not significantly explain the variation in plasticity (QM=9.7029, $p=0.0841$). The test for residual heterogeneity indicated that there is variation in the plasticity across the random effects (QE=273.8633, $p<0.001$).

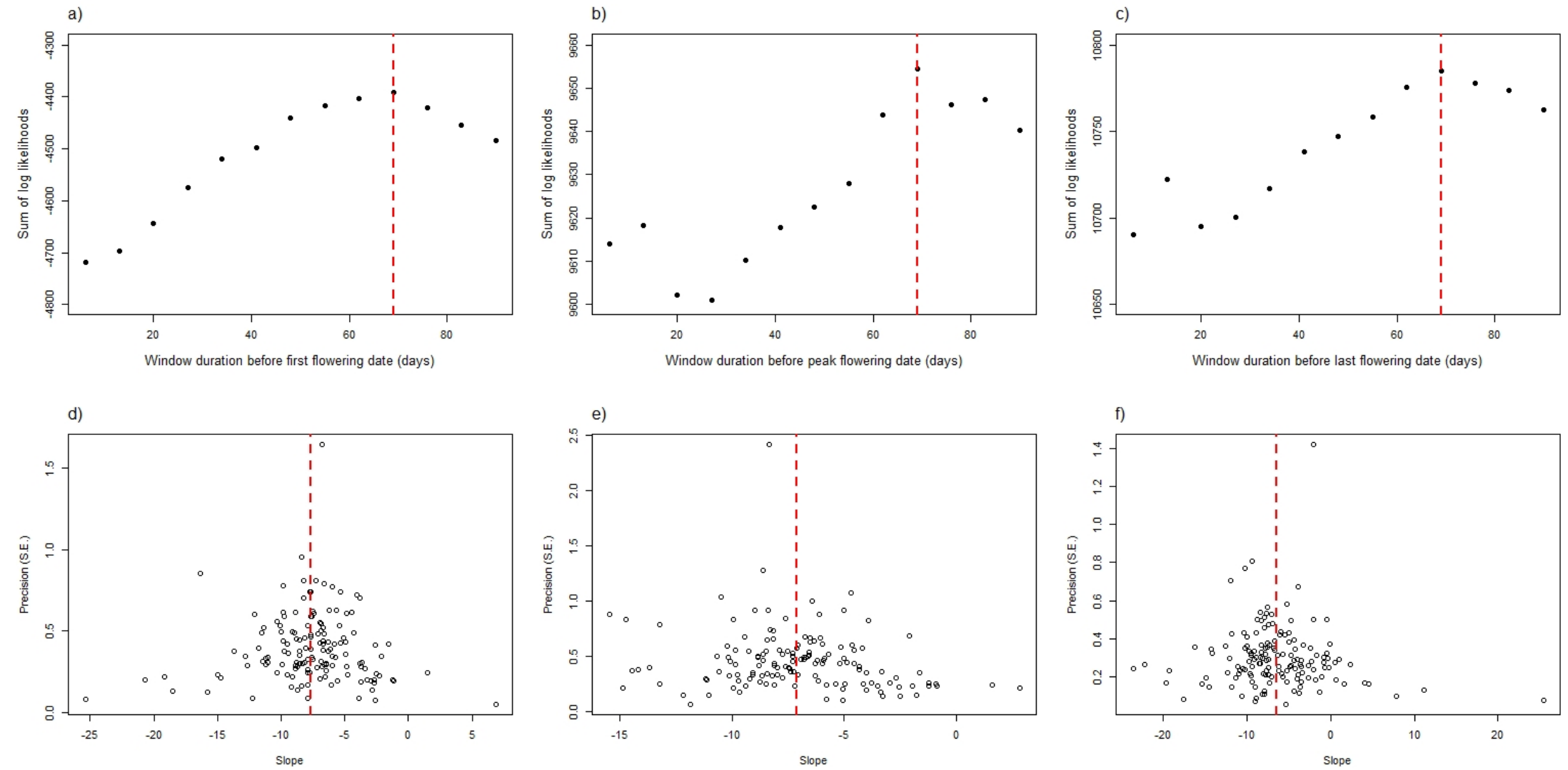


Figure 3 Results from sliding window analyses indicating the temperature window best predicting a) first flowering date, b) peak flowering date, and c) last flowering date; and funnel plots showing convergence of individual slopes around the mean for d) first flowering date, e) peak flowering date, and f) last flowering date

Table 3 Mixed effect model results for plasticity of first flowering date

Variable	Fixed effects			
	Estimate	Standard error	Z value	p-value
Intercept	-2.3055	4.5803	-0.5033	0.6147
Maximum altitude	0.0000	0.0007	0.0721	0.9426
Maximum latitude	-0.1244	0.1158	-1.0741	0.2828
Median altitude	0.0000	0.0010	0.0171	0.9863
Median latitude	-0.0101	0.1568	-0.0645	0.9486
Niche breadth	0.3156	0.5840	0.5404	0.5889
Random effects				
	Estimate	p-value (likelihood ratio test)		
Accession	0.0000	1.0000		
Species	1.9444	0.1352		
Series	2.0839	0.9188		

Table 4 Mixed effect model results for plasticity of peak flowering date

Variable	Fixed effects			
	Estimate	Standard error	Z value	p-value
Intercept	-12.9899	4.7336	-2.7442	0.0061
Maximum altitude	-0.0005	0.0006	-0.8771	0.3804
Maximum latitude	0.0404	0.1092	0.3703	0.7111
Median altitude	0.0014	0.0009	1.6238	0.1044
Median latitude	0.0753	0.1601	0.4703	0.6381
Niche breadth	-0.6753	0.5777	-1.1689	0.2424
Random effects				
	Estimate	p-value (likelihood ratio test)		
Accession	1.7669	0.0008		
Species	3.1462	0.0125		
Series	0.0000	1		

Table 5 Mixed effect model results for plasticity of last flowering date

Variable	Fixed effects			
	Estimate	Standard error	Z value	p-value
Intercept	-4.3502	4.3098	-1.0094	0.3128
Maximum altitude	-0.0005	0.0007	-0.7220	0.4703
Maximum latitude	0.3178	0.1214	2.6172	0.0089
Median altitude	0.0006	0.0009	0.6801	0.4965
Median latitude	-0.4214	0.1553	-2.7138	0.0067
Niche breadth	0.1320	0.5757	0.2294	0.8186
Random effects				
	Estimate	p-value (likelihood ratio test)		
Accession	8.2545	<0.001		
Species	0.0000	1.0000		
Series	0.0000	1.0000		

Discussion

Rhododendron species show large responses in their flowering phenologies to increasing temperatures. All three stages of flowering, first flowering date, peak flowering date and last flowering date, occur earlier under temperature increases. Shifts in the first and last flowering dates are similar in magnitude, although the last flowering date is shifting one day less and therefore prolonging their overall flowering period by approximately one day. Taxonomic-level information on phylogenetic relationships, and information on the species' ecologies did not explain these shifts, and other factors may be at play here. This suggests that *Rhododendrons* are able to adapt to changing climatic conditions, but the limits to their plasticity and biological consequences of these shifts remain unknown.

Previous phenology studies considering *Rhododendrons* have found advances in flowering time, but have not investigated the factors driving these responses. Flowering data from herbarium records and long-term weather data suggest that *Rhododendron arboreum* in the Indian central Himalaya is flowering 88 to 97 days earlier than 100 years ago, corresponding with a significant increase in the annual mean maximum temperature (Gaira et al., 2014). Thirty-six species of *Rhododendron*, represented by 1147 herbarium specimens from Yulong mountain over a period of 125 years, showed that flowering responds positively to annual temperature (2.27 days per 1 °C increase), and negatively to fall temperature (2.54 days per 1 °C) and elevation (1.4 days per 100 m) (Hart et al., 2014). These results show a much more pronounced advancement in first flowering date at more than seven days per one degree Celsius increase in spring temperatures. Shifts of this magnitude have rarely been observed in other angiosperms, for example an average advancement of seven days for an increase of 2.4 °C over 473 species (Willis et al., 2008). However, some extremes of first flowering dates up to 55 days earlier have been recorded (Fitter and Fitter, 2002).

The temperatures most strongly driving these shifts in flowering dates are those roughly two months before the flowering phase. Species flowering in May and June in England have been shown to respond most strongly to temperatures in February (Fitter and Fitter, 2002). For English summer-flowering species, temperatures up to four months before flowering affected the flowering date (Fitter et al., 1995). Mean annual temperatures and autumn temperatures have also been found to predict flowering dates of *Rhododendrons* in the Himalayas (Hart et al., 2014).

The plasticity of flowering dates for *Rhododendrons* was not well explained by the variables investigated. None of the phylogenetic or ecological variables were significant for both first and peak flowering dates. This suggests that other factors are driving these species' responses to increasing temperatures. Suizani et al. (2012) also found that abiotic and phylogenetic predictors did not explain the phenological responses of Brazilian Bromeliaceae, and suggest that biotic factors may play a role shifting flowering dates. Many other studies considering larger taxonomic groups, however, have found significant phylogenetic conservatism in flowering phenology (Willis et al., 2008; Davies et al., 2013). Despite previous evidence that the last flowering date of *Rhododendrons* is phylogenetically clustered due to later flowering species having less time for fruit development and thus smaller fruits (Hart et al., 2016), no such signal is evident here. It is possible that patterns of phylogenetic clustering are not detectable at the species level, but these results need to be supported by a complete molecular phylogeny as the series information might not adequately capture evolutionary relationships.

Environmental factors were expected to have a large impact on flowering phenology. Elevation did not prove to be important in determining plasticity, despite previous results of *Rhododendron* flowering phenologies responding to elevation (Hart et al., 2014). The last flowering date, however, did respond to latitude parameters. Species growing at higher latitudes are predicted to be most sensitive to climate change and have the most conserved phenologies (Pau et al., 2011). Here we find the opposite of these predictions, with species growing at higher maximum latitudes exhibiting higher plasticity. Growing at higher latitudes may have implications of shorter growing seasons (Schwartz, 2003), making it imperative for species growing far north to flower soon after snowmelt (Bliss, 1971). Having a higher plasticity may help these species survive changing climatic conditions in these areas where adaptation has already been important for their reproductive success in the past.

Rhododendron species show large advancements in early, peak, and last flowering dates in response to warming temperatures in the two months prior to the flowering stage. This means that they are capable of tracking climates as temperatures warm across the globe, and this does not appear to be constrained by their evolutionary history. It may, however, put them at risk for temporal mismatch with their pollinators (Rafferty and Ives, 2012). A better understanding of *Rhododendron* phylogenetic relationships is needed to determine whether the absence of phylogenetic signal seen here is a true reflection of their phenological responses. Biotic factors may be important, where some species for instance only advance

flowering when they are not constrained by pollinators (Rafferty and Ives, 2011). Future studies should focus on disentangling the drivers behind species plasticity, as these remain uncertain.

References

- Abatzoglou, J. T. & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* **113**: 11770-11775.
- Badeck, F.-W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J. & Sitch, S. (2004). Responses of spring phenology to climate change. *New Phytologist* **162**: 295-309.
- Bliss, L. C. (1971). Arctic and alpine plant life cycles. *Annual review of ecology and systematics* **2**: 405-438.
- Blöschl, G., Hall, J., Parajka, J., Perdigão, R. a. P., Merz, B., Arheimer, B., Aronica, G. T., Bilibashi, A., Bonacci, O., Borga, M., Čanjevac, I., Castellarin, A., Chirico, G. B., Claps, P., Fiala, K., Frolova, N., Gorbachova, L., Gül, A., Hannaford, J., Harrigan, S., Kireeva, M., Kiss, A., Kjeldsen, T. R., Kohnová, S., Koskela, J. J., Ledvinka, O., Macdonald, N., Mavrova-Guirguinova, M., Mediero, L., Merz, R., Molnar, P., Montanari, A., Murphy, C., Osuch, M., Ovcharuk, V., Radevski, I., Rogger, M., Salinas, J. L., Sauquet, E., Šraj, M., Szolgay, J., Viglione, A., Volpi, E., Wilson, D., Zaimi, K. & Živković, N. (2017). Changing climate shifts timing of European floods. *Science* **357**: 588-590.
- Bolmgren, K. & Cowan, P. D. (2008). Time-size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**: 424-429.
- Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B. & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* **78**: 73-83.
- Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H. & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21**: 481-497.

- Burkle, L. A., Marlin, J. C. & Knight, T. M. (2013). Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. *Science* **339**: 1611-1615.
- Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**: 516-519.
- Carvalho, A. L. G. D., Somner, G. V. & Allen, J. (2015). Is the phenology of all restinga species the same? A taxonomically-focused study of Sapindaceae in a highly threatened coastal environment. *Flora - Morphology, Distribution, Functional Ecology of Plants* **215**: 92-101.
- Chamberlain, S. 2017. *rgbif: Interface to the Global 'Biodiversity' Information Facility API* [Online]. R package version 0.9.9. Available: <https://CRAN.R-project.org/package=rgbif>.
- Chiabai, A., Quiroga, S., Martinez-Juarez, P., Higgins, S. & Taylor, T. (2018). The nexus between climate change, ecosystem services and human health: Towards a conceptual framework. *Science of The Total Environment* **635**: 1191-1204.
- Chaine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B* **365**: 3149-3160.
- Cross, J. R. (1975). *Rhododendron Ponticum* L. *Journal of Ecology* **63**: 345-364.
- Cullen, J. (1980). Revision of *Rhododendron*. I. subgenus *Rhododendron* sections *Rhododendron* and *Pogonanthum*. *Notes from the Royal Botanic Garden Edinburgh* **39**: 1-207.
- Davidian, H. H. 1982. *The Rhododendron Species: Lepidotodes*, B.T Batsford Ltd., London.
- Davidian, H. H. 1989. *The Rhododendron Species: Elipidote species, series Arboreum - Lacteum*, B.T. Batsford Ltd., London.
- Davidian, H. H. 1992. *The Rhododendron Species: Elepidotes, series Neriiflorum - Thomsonii*, B.T Batsford Ltd., London.
- Davidian, H. H. 1995. *The Rhododendron Species: Azaleas*, Timber Press, Portland, Oregon.
- Davies, T. J., Wolkovich, E. M., Kraft, N. J. B., Salamin, N., Allen, J. M., Ault, T. R., Betancourt, J. L., Bolmgren, K., Cleland, E. E., Cook, B. I., Crimmins, T. M., Mazer, S. J., McCabe, G. J., Pau, S., Regetz, J., Schwartz, M. D. & Travers, S. E. (2013). Phylogenetic conservatism in plant phenology. *Journal of Ecology* **101**: 1520-1530.
- Davis, C. C., Willis, C. G., Primack, R. B. & Miller-Rushing, A. J. (2010). The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B* **365**: 3201-3213.

- De Frenne, P., Van Langenhove, L., Van Driessche, A., Bertrand, C., Verheyen, K. & Vangansbeke, P. (2018). Using archived television video footage to quantify phenology responses to climate change. *Methods in Ecology and Evolution* **9**: 1874-1882.
- European Commission 2018. Pollinating insects: Commission proposes actions to stop their decline. Brussels.
- Fick, S. E. & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302-4315.
- Fischer, E. M. & Knutti, R. (2016). Observed heavy precipitation increase confirms theory and early models. *Nature Climate Change* **6**: 986.
- Fitter, A. H. & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants. *Science* **296**: 1689-1691.
- Fitter, A. H., Fitter, R. S. R., Harris, I. T. B. & Williamson, M. H. (1995). Relationships Between First Flowering Date and Temperature in the Flora of a Locality in Central England. *Functional Ecology* **9**: 55-60.
- Gaira, K. S., Rawal, R. S., Rawat, B. & Bhatt, I. D. (2014). Impact of climate change on the flowering of *Rhododendron arboreum* in central Himalaya, India. *Current Science* **106**: 1735-1738.
- Goetsch, L., Eckert, A. J. & Hall, B. D. (2005). The Molecular Systematics of *Rhododendron* (Ericaceae): A Phylogeny Based upon RPB2 Gene Sequences. *Systematic Botany* **30**: 616-626.
- Hart, R., Georgian, E. M. & Salick, J. (2016). Fast and Cheap in the Fall: Phylogenetic determinants of late flowering phenologies in Himalayan *Rhododendron*. *American Journal of Botany* **103**: 198-206.
- Hart, R., Salick, J., Ranjitkar, S. & Xu, J. (2014). Herbarium specimens show contrasting phenological responses to Himalayan climate. *PNAS* **111**: 10615-10619.
- Hsiang, S., Kopp, R., Jina, A., Rising, J., Delgado, M., Mohan, S., Rasmussen, D. J., Muir-Wood, R., Wilson, P., Oppenheimer, M., Larsen, K. & Houser, T. (2017). Estimating economic damage from climate change in the United States. *Science* **356**: 1362-1369.
- Ippc 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

- Jones, K. R., Watson, J. E. M., Possingham, H. P. & Klein, C. J. (2016). Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation* **194**: 121-130.
- Kameyama, Y. & Kudo, G. (2015). Intrinsic and extrinsic factors acting on the reproductive process in alpine-snowbed plants: roles of phenology, biological interaction, and breeding system. *Plant Species Biology* **30**: 3-15.
- Keogan, K., Daunt, F., Wanless, S., Phillips, R. A., Walling, C. A., Agnew, P., Ainley, D. G., Anker-Nilssen, T., Ballard, G., Barrett, R. T., Barton, K. J., Bech, C., Becker, P., Berglund, P.-A., Bollache, L., Bond, A. L., Bouwhuis, S., Bradley, R. W., Burr, Z. M., Camphuysen, K., Catry, P., Chiaradia, A., Christensen-Dalsgaard, S., Cuthbert, R., Dehnhard, N., Descamps, S., Diamond, T., Divoky, G., Drummond, H., Dugger, K. M., Dunn, M. J., Emmerson, L., Erikstad, K. E., Fort, J., Fraser, W., Genovart, M., Gilg, O., González-Solís, J., Granadeiro, J. P., Grémillet, D., Hansen, J., Hanssen, S. A., Harris, M., Hedd, A., Hinke, J., Igual, J. M., Jahncke, J., Jones, I., Kappes, P. J., Lang, J., Langset, M., Lescroël, A., Lorentsen, S.-H., Lyver, P. O. B., Mallory, M., Moe, B., Montevecchi, W. A., Monticelli, D., Mostello, C., Newell, M., Nicholson, L., Nisbet, I., Olsson, O., Oro, D., Pattison, V., Poisbleau, M., Pyk, T., Quintana, F., Ramos, J. A., Ramos, R., Reiertsen, T. K., Rodríguez, C., Ryan, P., Sanz-Aguilar, A., Schmidt, N. M., Shannon, P., Sittler, B., Southwell, C., Surman, C., Svagelj, W. S., Trivelpiece, W., Warzybok, P., Watanuki, Y., Weimerskirch, H., Wilson, P. R., Wood, A. G., Phillimore, A. B. & Lewis, S. (2018). Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change* **8**: 313-318.
- Kochmer, J. P. & Handel, S. N. (1986). Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* **56**: 303-325.
- Luedeling, E., Zhang, M. & Girvetz, E. H. (2009). Climatic Changes Lead to Declining Winter Chill for Fruit and Nut Trees in California during 1950–2009. *PLoS ONE* **4**: e6166.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37-42.
- Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., Betancourt, J. L. & Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* **17**: 3633-3643.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S.,

- Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., Lenoir, J., Linnetved, H. I., Martin, V. Y., McCormack, P. C., McDonald, J., Mitchell, N. J., Mustonen, T., Pandolfi, J. M., Pettorelli, N., Popova, E., Robinson, S. A., Scheffers, B. R., Shaw, J. D., Sorte, C. J. B., Strugnell, J. M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**.
- Piel, W. H., Chan, L., Dominus, M. J., Ruan, J., Vos, R. A. & Tannen, V. (2009). TreeBASE v. 2: A Database of Phylogenetic Knowledge. *e-BioSphere* 2009.
- Polgar, C. A. & Primack, R. B. (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* **191**: 926-941.
- Popescu, R. & Kopp, B. (2013). The genus *Rhododendron*: An ethnopharmacological and toxicological review. *Journal of Ethnopharmacology* **147**: 42-62.
- R Core Team 2018. *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria.
- Rafferty, N. E. & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on plant–pollinator interactions. *Ecology Letters* **14**: 69-74.
- Rafferty, N. E. & Ives, A. R. (2012). Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology* **93**: 803-814.
- Rich, P. M., Breshears, D. D. & White, A. B. (2008). Phenology of mixed woody–herbaceous ecosystems following extreme events: Net and differential responses. *Ecology* **89**: 342-352.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57-60.
- Royal Botanic Garden Edinburgh. 2018. *Rhododendrons at the four gardens* [Online]. Royal Botanic Garden Edinburgh. Available: <http://www.rbge.org.uk/the-gardens/rhododendrons> [Accessed 12 June 2018].
- Schwartz, M. D., Ahas, R. & Aasa, A. (2006). Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* **12**: 343-351.
- Schwartz, M. D. E. 2003. *Phenology: An integrative environmental science*, Kluwer Academic Publishers, Dordrecht.
- Shrestha, N., Su, X., Xu, X. & Wang, Z. (2018). The drivers of high *Rhododendron* diversity in south-west China: Does seasonality matter? *Journal of Biogeography* **45**: 438-447.

- Sparks, T. H. & Carey, P. D. (1995). The Responses of Species to Climate Over Two Centuries: An Analysis of the Marsham Phenological Record, 1736-1947. *Journal of Ecology* **83**: 321-329.
- Staggemeier, V. G., Diniz-Filho, J. a. F. & Morellato, L. P. C. (2010). The shared influence of phylogeny and ecology on the reproductive patterns of Myrteae (Myrtaceae). *Journal of Ecology* **98**: 1409-1421.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008). A Rapid Bootstrap Algorithm for the RAxML Web-Servers. *Systematic Botany* **75**: 758-771.
- Stige, L. C. & Kvile, K. Ø. (2017). Climate warming drives large-scale changes in ecosystem function. *Proceedings of the National Academy of Sciences* **114**: 12100-12102.
- Suizani, C. V., De Lima, H. A., Rodarte, A. T. A. & Benevides, C. (2012). Flowering phenology of a Bromeliaceae community of an environment protection area (EPA) in the restinga of Maricá (RJ, Brazil) as compared to other habitats of the southeastern Brazilian Atlantic Rain Forest. *Brazilian Journal of Ecology* **1**: 88-95.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., Elliott, J. M., Hall, S. J. G., Harrington, R., Pearce-Higgins, J. W., Høye, T. T., Kruuk, L. E. B., Pemberton, J. M., Sparks, T. H., Thompson, P. M., White, I., Winfield, I. J. & Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**: 241.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L. & Williams, S. E. (2004). Extinction risk from climate change. *Nature* **427**: 145.
- Todesco, M., Pascual, M. A., Owens, G. L., Ostevik, K. L., Moyers, B. T., Hübner, S., Heredia, S. M., Hahn, M. A., Caseys, C., Bock, D. G. & Rieseberg, L. H. (2016). Hybridization and extinction. *Evolutionary Applications* **9**: 892-908.
- Ullah, S., Khan, S. U., Saleh, T. A. & Fahad, S. (2018). Mad honey: uses, intoxicating/poisoning effects, diagnosis, and treatment. *Royal Society of Chemistry Advances* **8**: 18635–18646.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**: 1-48.

- Wickham, H. & Henry, L. 2018. *tidyr: Easily Tidy Data with 'spread()' and 'gather()' Functions* [Online]. R package version 0.8.1. Available: <https://CRAN.R-project.org/package=tidyr>.
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. & Davis, C. C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *PNAS* **105**: 17029-17033.
- Wolfe, D. W., Schwartz, M. D., Lakso, A. N., Otsuki, Y., Pool, R. M. & Shaulis, N. J. (2005). Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International Journal of Biometeorology* **49**: 303-309.
- Zeileis, A. & Grothendieck, G. (2005). zoo: S3 Infrastructure for Regular and Irregular Time Series. *Journal of Statistical Software* **14**: 1-27.

Appendix

Table A1 Responses of first flowering dates of individual plants to a mean daily temperature increase of 1 °C

Species	Accession number	Slope	Standard error	p-value	Log likelihood	R ²
<i>Rhododendron adenogynum</i>	1933.1020A	-3.626	3.252	0.308	-31.834	0.529
<i>Rhododendron adenogynum</i>	1948.0012A	-4.304	2.045	0.073	-32.812	0.542
<i>Rhododendron adenogynum</i>	1987.1535A	-3.371	3.772	0.406	-34.82	0.206
<i>Rhododendron anthosphaerum</i>	1923.0098 D	-20.695	5.019	0.026	-21.057	0.892
<i>Rhododendron anthosphaerum</i>	1949.1012A	-2.277	4.456	0.628	-35.277	0.172
<i>Rhododendron anthosphaerum</i>	1979.0989A	-3.689	5.452	0.536	-25.074	0.444
<i>Rhododendron anwheiense</i>	1971.0038A	-5.821	2.396	0.045	-33.894	0.534
<i>Rhododendron anwheiense</i>	1980.2048A	-6.972	4.826	0.285	-17.397	0.52
<i>Rhododendron anwheiense</i>	1980.2048D	-8.145	3.283	0.068	-20.84	0.609
<i>Rhododendron arboreum</i>	1974.0834B	-8.407	1.049	0.001	-15.492	0.951
<i>Rhododendron arboreum</i>	1976.0141C	-1.544	2.385	0.546	-26.336	0.572
<i>Rhododendron arboreum</i>	1981.1230G	-8.529	2.854	0.02	-35.154	0.562
<i>Rhododendron arboreum</i>	1990.2647A	-8.787	3.305	0.038	-32.137	0.542
<i>Rhododendron arboreum</i>	1996.0562A	-7.694	2.176	0.012	-28.884	0.758
<i>Rhododendron augustinii</i>	1975.4173A	-7.473	3.067	0.051	-30.368	0.514
<i>Rhododendron augustinii</i>	1977.2695 G	-6.635	2.066	0.085	-12.989	0.914
<i>Rhododendron augustinii</i>	1980.5048A	-7.706	1.349	0.001	-28.777	0.823
<i>Rhododendron augustinii</i>	1999.1844A	-8.687	7.404	0.362	-18.336	0.435
<i>Rhododendron auriculatum</i>	1916.0027A	-11.747	2.528	0.002	-33.097	0.743
<i>Rhododendron barbatum</i>	1972.0856*R	-6.902	3.201	0.068	-35.94	0.4
<i>Rhododendron barbatum</i>	1972.0856A	-7.894	6.053	0.24	-35.159	0.229
<i>Rhododendron barbatum</i>	1976.0083 C	-2.628	13.875	0.862	-23.858	0.071
<i>Rhododendron calendulaceum</i>	1977.1140A	-6.619	1.264	0.001	-28.067	0.778
<i>Rhododendron calendulaceum</i>	1979.1536AN	-7.495	1.605	0.002	-30.193	0.748
<i>Rhododendron calendulaceum</i>	1979.1536AS	-6.736	2.293	0.026	-27.552	0.606
<i>Rhododendron calophytum</i>	1969.8430A	-5.614	5.259	0.335	-31.073	0.413
<i>Rhododendron calophytum</i>	1972.4038A	-4.855	3.535	0.212	-35.749	0.264
<i>Rhododendron calostrotum</i>	1971.2351A	-11.513	2.055	0.001	-30.22	0.85
<i>Rhododendron calostrotum</i>	1971.2523A	-6.983	2.337	0.02	-32.807	0.616
<i>Rhododendron calostrotum</i>	1971.2524B	-9.426	2.753	0.014	-29.723	0.664
<i>Rhododendron campanulatum</i>	1955.1016A	-6.675	1.917	0.01	-31.901	0.641
<i>Rhododendron campanulatum</i>	1962.0908A	-6.286	2.31	0.03	-31.628	0.516

<i>Rhododendron campanulatum</i>	1969.8445A	-6.046	5.905	0.414	-17.243	0.365
<i>Rhododendron canadense</i>	1976.0690A	-7.625	2.95	0.032	-40.393	0.486
<i>Rhododendron canadense</i>	1976.0690B	-8.567	2.265	0.007	-33.83	0.709
<i>Rhododendron canadense</i>	1990.0430B	-8.767	2.225	0.008	-29.467	0.723
<i>Rhododendron cinnabarinum</i>	1938.1155G	-7.669	1.693	0.004	-27.246	0.807
<i>Rhododendron cinnabarinum</i>	1957.7184P	-3.776	1.427	0.033	-29.221	0.675
<i>Rhododendron cinnabarinum</i>	1969.8930K	-2.908	5.275	0.596	-44.092	0.206
<i>Rhododendron cinnabarinum</i>	1978.4120A	-6.479	3.349	0.089	-39.094	0.32
<i>Rhododendron collettianum</i>	1970.2019A	-8.765	2.224	0.006	-32.661	0.713
<i>Rhododendron dauricum</i>	1976.1068C	-12.839	2.898	0.003	-34.03	0.852
<i>Rhododendron dauricum</i>	1978.0139 A	-2.661	5.605	0.655	-31.073	0.754
<i>Rhododendron dauricum</i>	1991.1220A	-7.914	11.486	0.517	-44.042	0.137
<i>Rhododendron dauricum</i>	1976.1068 A	-12.247	11.648	0.37	-24.784	0.411
<i>Rhododendron decorum</i>	1969.8512B	-7.098	2.082	0.011	-30.645	0.726
<i>Rhododendron decorum</i>	1969.8512D	-8.253	1.24	0	-27.931	0.864
<i>Rhododendron decorum</i>	1973.4073B	-8.869	3.513	0.065	-23.54	0.62
<i>Rhododendron decorum</i>	1976.1403F	-6.227	1.605	0.006	-30.149	0.683
<i>Rhododendron degronianum</i>	1960.3367A	-6.718	2.402	0.023	-35.762	0.536
<i>Rhododendron degronianum</i>	1961.4659A	-5.122	2.19	0.047	-35.364	0.485
<i>Rhododendron degronianum</i>	1977.3254A	-6.865	1.836	0.006	-33.376	0.642
<i>Rhododendron degronianum</i>	1983.2540A	-6.68	2.629	0.035	-36.846	0.488
<i>Rhododendron ferrugineum</i>	1976.0519 H	-5.432	1.881	0.02	-33.248	0.555
<i>Rhododendron ferrugineum</i>	1976.0519B	-5.348	2.355	0.053	-35.722	0.556
<i>Rhododendron ferrugineum</i>	1976.0519 F	-5.664	1.598	0.012	-25.224	0.839
<i>Rhododendron ferrugineum</i>	1976.0519 G	-4.86	1.649	0.026	-25.033	0.816
<i>Rhododendron ferrugineum</i>	1976.1857 D	-1.143	5.183	0.846	-16.065	0.523
<i>Rhododendron hippophaeoides</i>	1971.2400A	-9.119	4.649	0.091	-38.742	0.582
<i>Rhododendron hippophaeoides</i>	1971.2576A	-9.752	1.698	0.001	-30.992	0.825
<i>Rhododendron hippophaeoides</i>	1971.2594G	-6.828	2.001	0.011	-32.58	0.628
<i>Rhododendron hippophaeoides</i>	1973.4078B	-9.512	4.305	0.063	-37.712	0.43
<i>Rhododendron hippophaeoides</i>	1991.0304C	-9.09	2.017	0.003	-31.681	0.745
<i>Rhododendron irroratum</i>	1991.1093A	-14.998	4.392	0.019	-29.973	0.7
<i>Rhododendron irroratum</i>	1996.0617 G	-6.819	0.608	0.008	-6.875	0.984
<i>Rhododendron lanigerum</i>	1929.1008B	-6.492	3.953	0.145	-37.924	0.296
<i>Rhododendron lanigerum</i>	1929.1008E	-7.883	4.11	0.104	-32.181	0.539
<i>Rhododendron lanigerum</i>	1929.1008H	-10.346	4.08	0.044	-33.255	0.552
<i>Rhododendron lapponicum</i>	1903.0018 A	-15.77	7.934	0.118	-30.371	0.699
<i>Rhododendron lapponicum</i>	1979.3270 A	-18.484	7.835	0.065	-31.492	0.777
<i>Rhododendron lepidotum</i>	1983.0962A	-6.437	3.427	0.097	-39.252	0.347

<i>Rhododendron lepidotum</i>	1983.0963C	-1.209	5.044	0.817	-39.725	0.018
<i>Rhododendron lepidotum</i>	1975.1302 A	-7.657	2.603	0.026	-28.723	0.626
<i>Rhododendron leptothrium</i>	1989.2109A	-19.15	4.585	0.009	-26.34	0.778
<i>Rhododendron liliiflorum</i>	1991.1969B	-7.677	2.102	0.022	-18.929	0.792
<i>Rhododendron lutescens</i>	1996.0608D	-8.532	3.338	0.038	-35.388	0.542
<i>Rhododendron lutescens</i>	1996.0608E	-6.802	3.602	0.101	-37.152	0.391
<i>Rhododendron lutescens</i>	1996.0608F	-8.702	3.548	0.044	-37.031	0.527
<i>Rhododendron luteum</i>	1977.3072E	-11.174	3.017	0.006	-38.358	0.638
<i>Rhododendron luteum</i>	1983.0848A1	-7.719	1.348	0.001	-27.778	0.824
<i>Rhododendron luteum</i>	1983.0848B1	-7.272	1.239	0.001	-26.768	0.831
<i>Rhododendron macabeum</i>	1969.8707A	-7.91	3.833	0.078	-36.556	0.379
<i>Rhododendron macabeum</i>	1928.1023B	-7.734	4.094	0.132	-25.077	0.485
<i>Rhododendron meddianum</i>	1975.4074A	-6.618	3.443	0.096	-35.657	0.536
<i>Rhododendron meddianum</i>	1998.0009 A	1.531	4.101	0.728	-23.447	0.511
<i>Rhododendron mucronulatum</i>	1977.0993A	-13.714	2.691	0.001	-33.008	0.789
<i>Rhododendron mucronulatum</i>	1977.0993C	-10.037	2.019	0.002	-31.595	0.804
<i>Rhododendron mucronulatum</i>	1995.1171B	-9.829	2.293	0.008	-22.388	0.793
<i>Rhododendron mucronulatum</i>	1995.1171G	-12.056	1.667	0	-22.267	0.897
<i>Rhododendron neriflorum</i>	1975.4064B	-9.183	6.463	0.198	-41.771	0.225
<i>Rhododendron neriflorum</i>	1994.3905 C	-4.482	1.63	0.071	-16.611	0.717
<i>Rhododendron neriflorum</i>	1994.3905A	-3.241	5.026	0.537	-46.253	0.147
<i>Rhododendron neriflorum</i>	1919.0100A	-2.816	7.409	0.74	-17.645	0.37
<i>Rhododendron ponticum</i>	1971.5872A	-9.8	1.285	0	-24.3	0.908
<i>Rhododendron ponticum</i>	1971.5872B	-8.921	2.06	0.003	-32.995	0.73
<i>Rhododendron ponticum</i>	1972.4007A	-5.348	1.347	0.004	-28.992	0.758
<i>Rhododendron ponticum</i>	1974.4139A	-5.993	2.895	0.084	-32.156	0.429
<i>Rhododendron praecox</i>	1969.8794Beast	-7.87	3.081	0.038	-35.433	0.593
<i>Rhododendron praecox</i>	1969.8794Bmid	-12.635	3.518	0.009	-35.879	0.694
<i>Rhododendron praecox</i>	1969.8794Bwest	-11.082	3.286	0.012	-35.428	0.689
<i>Rhododendron praevernum</i>	1924.0357A	-6.325	2.652	0.054	-29.909	0.488
<i>Rhododendron praevernum</i>	1924.0357D	-6.1	2.572	0.049	-33.625	0.446
<i>Rhododendron praevernum</i>	1924.0357E	-4.903	2.328	0.073	-32.939	0.393
<i>Rhododendron praevernum</i>	1969.8798A	-5.964	3.498	0.139	-32.394	0.332
<i>Rhododendron racemosum</i>	1973.4084B	-11.181	3.39	0.013	-35.98	0.648
<i>Rhododendron racemosum</i>	1932.1028	-7.547	1.699	0.003	-30.809	0.739
<i>Rhododendron racemosum</i>	1991.0867A	-8.839	3.741	0.05	-36.313	0.462
<i>Rhododendron reticulatum</i>	1975.2245BNE	-7.875	1.874	0.006	-27.091	0.772
<i>Rhododendron reticulatum</i>	1975.2245BSE	-25.396	12.868	0.089	-48.846	0.379
<i>Rhododendron reticulatum</i>	1975.2245BW	-11.072	2.98	0.007	-33.937	0.673

<i>Rhododendron reticulatum</i>	1975.2245 (SW)	-9.738	2.681	0.011	-30.193	0.745
<i>Rhododendron reticulatum</i>	1975.2245 N (N)	-9.869	1.635	0.001	-25.715	0.875
<i>Rhododendron russatum</i>	1971.2586B	-2.68	4.958	0.606	-39.029	0.048
<i>Rhododendron russatum</i>	1971.2586D	-2.554	4.276	0.569	-37.651	0.118
<i>Rhododendron russatum</i>	1971.2586G	-6.537	4.657	0.203	-38.877	0.306
<i>Rhododendron schlippenbachii</i>	1975.0765 B (E)	-8.189	2.198	0.007	-32.807	0.67
<i>Rhododendron schlippenbachii</i>	1975.0765B (W)	-11.388	1.932	0.001	-30.794	0.833
<i>Rhododendron schlippenbachii</i>	1977.1391B	-7.445	1.654	0.003	-30.681	0.757
<i>Rhododendron semibarbatum</i>	1976.1907ASW	-2.577	2.434	0.331	-27.94	0.163
<i>Rhododendron semibarbatum</i>	1976.1907ASE	-2.122	2.902	0.492	-28.129	0.082
<i>Rhododendron semibarbatum</i>	1976.1907B	-3.809	3.338	0.287	-38.766	0.141
<i>Rhododendron siderophyllum</i>	1980.0345C	-11.473	3.2	0.009	-37.297	0.658
<i>Rhododendron siderophyllum</i>	1996.0554B	-14.713	4.777	0.022	-34.242	0.659
<i>Rhododendron siderophyllum</i>	1980.0345B	-10.085	1.87	0.012	-16.959	0.911
<i>Rhododendron strigillosum</i>	1975.4050I	-4.759	4.394	0.328	-30.664	0.324
<i>Rhododendron strigillosum</i>	1996.0603A	-3.852	11.313	0.751	-33.827	0.233
<i>Rhododendron strigillosum</i>	1996.0599D	6.874	20.247	0.767	-19.807	0.07
<i>Rhododendron strigillosum x praeevernum</i>	1969.8865A	-3.735	3.534	0.326	-37.193	0.181
<i>Rhododendron tolmachevii</i>	1940.0183A	-5.953	1.296	0.003	-28.259	0.764
<i>Rhododendron tomentosum</i>	1969.5002A	-9.897	3.437	0.028	-30.62	0.599
<i>Rhododendron tomentosum</i>	1978.0135A	-16.365	1.175	0.001	-11.888	0.987
<i>Rhododendron trichostomum</i>	1969.9607C	-9.493	2.389	0.005	-31.36	0.721
<i>Rhododendron trichostomum</i>	1963.3848 A	-10.307	1.804	0.002	-22.952	0.87
<i>Rhododendron trichostomum</i>	1969.9607 B	-8.549	2.66	0.024	-25.594	0.694
<i>Rhododendron wadanum</i>	1976.1072B	-8.85	1.622	0.001	-30.258	0.811
<i>Rhododendron wadanum</i>	1976.1909B+A	-8.081	2.528	0.015	-33.04	0.61
<i>Rhododendron wadanum</i>	1976.1072D	-8.196	1.424	0.001	-25.948	0.853
<i>Rhododendron wallichii</i>	1962.0915B	-5.718	2.942	0.093	-36.599	0.361
<i>Rhododendron wallichii</i>	1981.3602D	-6.941	1.818	0.007	-31.543	0.737
<i>Rhododendron wallichii</i>	1983.0965B	-8.343	3.353	0.042	-36.317	0.641
<i>Rhododendron yunnanense</i>	1996.0662 A	-4.061	1.39	0.1	-10.007	0.811
<i>Rhododendron yunnanense</i>	1996.0662D	-7.224	3.667	0.089	-32.679	0.419
<i>Rhododendron yunnanense</i>	1981.2672C	-8.401	6.243	0.271	-20.346	0.396

Table A2 Responses of peak flowering dates of individual plants to a mean daily temperature increase of 1 °C

Species	Accession	Slope	Standard error	p-value	Log likelihood	R ²
<i>Rhododendron adenogynum</i>	1933.1020A	-6.565	1.879	0.013	-28.234	0.8
<i>Rhododendron adenogynum</i>	1948.0012A	-6.621	2.021	0.022	-23.636	0.762
<i>Rhododendron adenogynum</i>	1987.1535A	1.567	4.196	0.728	-23.85	0.638
<i>Rhododendron anthosphaerum</i>	1923.0098 D	-8.362	0.413	0	-8.309	0.993
<i>Rhododendron anthosphaerum</i>	1949.1012A	-8.736	3.733	0.066	-29.136	0.527
<i>Rhododendron anthosphaerum</i>	1979.0989A	-5.006	1.095	0.02	-12.147	0.934
<i>Rhododendron anwheiense</i>	1971.0038A	-4.348	2.446	0.113	-36.659	0.355
<i>Rhododendron anwheiense</i>	1980.2048A	-12.15	6.892	0.22	-17.292	0.61
<i>Rhododendron anwheiense</i>	1980.2048D	-6.283	3.092	0.112	-20.56	0.517
<i>Rhododendron arboreum</i>	1974.0834B	-7.977	2.517	0.034	-21.921	0.768
<i>Rhododendron arboreum</i>	1976.0141C	-4.014	5.191	0.483	-26.119	0.296
<i>Rhododendron arboreum</i>	1981.1230G	-7.492	2.536	0.021	-33.623	0.611
<i>Rhododendron arboreum</i>	1990.2647A	-7.375	2.804	0.039	-29.931	0.634
<i>Rhododendron arboreum</i>	1996.0562A	-5.696	1.949	0.027	-28.079	0.733
<i>Rhododendron augustinii</i>	1975.4173A	-9.931	4.77	0.082	-31.676	0.439
<i>Rhododendron augustinii</i>	1980.5048A	-8.818	2.398	0.008	-31.539	0.704
<i>Rhododendron augustinii</i>	1999.1844A	-9.829	1.811	0.032	-10.215	0.954
<i>Rhododendron auriculatum</i>	1916.0027A	-14.458	2.724	0.001	-33.262	0.792
<i>Rhododendron barbatum</i>	1972.0856*R	-3.781	3.937	0.369	-37.294	0.175
<i>Rhododendron barbatum</i>	1972.0856A	-4.966	4.03	0.264	-32.625	0.305
<i>Rhododendron barbatum</i>	1976.0083 C	-1.951	4.426	0.689	-20.55	0.424
<i>Rhododendron calendulaceum</i>	1977.1140A	-6.203	2.191	0.025	-29.906	0.568
<i>Rhododendron calendulaceum</i>	1979.1536AN	-7.994	3.07	0.04	-28.004	0.557
<i>Rhododendron calendulaceum</i>	1979.1536AS	-0.943	4.069	0.838	-14.235	0.27
<i>Rhododendron calophytum</i>	1969.8430A	-13.216	3.985	0.08	-11.763	0.98
<i>Rhododendron calophytum</i>	1972.4038A	-4.343	2.645	0.145	-34.992	0.397
<i>Rhododendron calostrotum</i>	1971.2351A	-8.625	1.948	0.003	-32.177	0.761
<i>Rhododendron calostrotum</i>	1971.2523A	-6.786	2.117	0.018	-27.903	0.711
<i>Rhododendron calostrotum</i>	1971.2524B	-9.707	3.704	0.12	-15.865	0.804
<i>Rhododendron campanulatum</i>	1955.1016A	-5.888	2.095	0.023	-35.515	0.498
<i>Rhododendron campanulatum</i>	1962.0908A	-8.486	1.823	0.002	-31.653	0.757
<i>Rhododendron campanulatum</i>	1969.8445A	-10.645	1.992	0.033	-11.629	0.942
<i>Rhododendron canadense</i>	1976.0690A	-8.442	2.912	0.02	-39.137	0.534

<i>Rhododendron canadense</i>	1976.0690B	-9.257	1.84	0.002	-30.416	0.786
<i>Rhododendron canadense</i>	1990.0430B	-10.215	1.705	0.002	-20.679	0.878
<i>Rhododendron cinnabarinum</i>	1938.1155G	-11.13	3.515	0.034	-21.047	0.791
<i>Rhododendron cinnabarinum</i>	1957.7184P	-4.863	2.272	0.07	-31.088	0.652
<i>Rhododendron cinnabarinum</i>	1969.8930K	-10.577	2.808	0.007	-31.326	0.722
<i>Rhododendron cinnabarinum</i>	1978.4120A	-6.101	1.137	0.001	-26.9	0.802
<i>Rhododendron collettianum</i>	1970.2019A	-8.997	1.093	0	-23.43	0.919
<i>Rhododendron dauricum</i>	1976.1068C	-10.134	3.143	0.023	-27.052	0.709
<i>Rhododendron dauricum</i>	1978.0139 A	-5.372	4.094	0.247	-28.226	0.733
<i>Rhododendron dauricum</i>	1991.1220A	-11.045	6.919	0.154	-43.856	0.336
<i>Rhododendron dauricum</i>	1976.1068 A	-3.287	7.604	0.695	-23.689	0.28
<i>Rhododendron decorum</i>	1969.8512B	-8.846	2.024	0.005	-26.033	0.79
<i>Rhododendron decorum</i>	1969.8512D	-7.29	1.999	0.007	-33.667	0.661
<i>Rhododendron decorum</i>	1973.4073B	-7.085	3.015	0.1	-17.718	0.743
<i>Rhododendron decorum</i>	1976.1403F	-7.047	1.659	0.003	-32.393	0.703
<i>Rhododendron degronianum</i>	1960.3367A	-8.216	3.157	0.035	-33.41	0.562
<i>Rhododendron degronianum</i>	1961.4659A	-3.922	1.216	0.012	-27.662	0.661
<i>Rhododendron degronianum</i>	1977.3254A	-6.057	1.505	0.004	-29.865	0.716
<i>Rhododendron degronianum</i>	1983.2540A	-6.427	1	0.001	-19.943	0.934
<i>Rhododendron ferrugineum</i>	1976.0519 H	-4.038	2.884	0.199	-36.68	0.261
<i>Rhododendron ferrugineum</i>	1976.0519B	-5.974	1.651	0.007	-30.47	0.716
<i>Rhododendron ferrugineum</i>	1976.0519 F	-7.295	1.909	0.009	-25.233	0.842
<i>Rhododendron ferrugineum</i>	1976.0519 G	-5.021	2.095	0.062	-21.072	0.871
<i>Rhododendron hippophaeoides</i>	1971.2400A	-9.442	1.488	0	-29.54	0.86
<i>Rhododendron hippophaeoides</i>	1971.2576A	-6.929	2.127	0.014	-30.596	0.648
<i>Rhododendron hippophaeoides</i>	1971.2594G	-7.623	2.494	0.018	-31.932	0.609
<i>Rhododendron hippophaeoides</i>	1973.4078B	-9.068	2.902	0.017	-36.463	0.583
<i>Rhododendron hippophaeoides</i>	1991.0304C	-8.604	2.159	0.005	-32.324	0.694
<i>Rhododendron irroratum</i>	1991.1093A	-15.467	1.142	0	-16.994	0.979
<i>Rhododendron lanigerum</i>	1929.1008B	-1.798	7.036	0.808	-29.944	0.168
<i>Rhododendron lanigerum</i>	1929.1008E	-2.545	4.649	0.604	-34.175	0.239
<i>Rhododendron lanigerum</i>	1929.1008H	-2.505	7.651	0.76	-25.988	0.329
<i>Rhododendron lapponicum</i>	1979.3270 A	-5.081	9.801	0.631	-28.672	0.613
<i>Rhododendron lepidotum</i>	1983.0962A	-3.341	2.815	0.274	-32.411	0.187
<i>Rhododendron lepidotum</i>	1983.0963C	-7.289	2.2	0.013	-30.079	0.668
<i>Rhododendron lepidotum</i>	1975.1302 A	-6.294	2.323	0.035	-27.677	0.658
<i>Rhododendron leptothrium</i>	1989.2109A	-9.385	4.43	0.088	-27.79	0.498
<i>Rhododendron liliiflorum</i>	1991.1969B	-8.475	4.012	0.125	-18.461	0.697
<i>Rhododendron lutescens</i>	1996.0608D	-10.059	2.214	0.004	-28.78	0.782

<i>Rhododendron lutescens</i>	1996.0608E	-9.834	2.367	0.006	-25.929	0.772
<i>Rhododendron lutescens</i>	1996.0608F	-13.671	2.521	0.001	-32.504	0.808
<i>Rhododendron luteum</i>	1977.3072E	-9.077	3.021	0.017	-37.776	0.552
<i>Rhododendron luteum</i>	1983.0848A1	-6.791	2.057	0.011	-34.676	0.594
<i>Rhododendron luteum</i>	1983.0848B1	-5.98	2.295	0.035	-31.52	0.511
<i>Rhododendron macabeaenum</i>	1969.8707A	-8.139	4.139	0.106	-30.996	0.452
<i>Rhododendron macabeaenum</i>	1928.1023B	-9.227	3.414	0.074	-21.348	0.716
<i>Rhododendron meddianum</i>	1975.4074A	-4.574	1.818	0.04	-29.342	0.494
<i>Rhododendron meddianum</i>	1998.0009 A	-5.785	9.232	0.575	-21.45	0.313
<i>Rhododendron mucronulatum</i>	1977.0993A	-7.535	1.854	0.005	-31.609	0.723
<i>Rhododendron mucronulatum</i>	1977.0993C	-13.206	1.273	0	-26.63	0.939
<i>Rhododendron mucronulatum</i>	1995.1171B	-6.145	3.583	0.137	-30.112	0.359
<i>Rhododendron mucronulatum</i>	1995.1171G	-9.749	3.017	0.018	-27.869	0.646
<i>Rhododendron neriiflorum</i>	1975.4064B	-4.545	2.326	0.108	-26.378	0.684
<i>Rhododendron neriiflorum</i>	1994.3905 C	-2.699	3.315	0.501	-14.248	0.288
<i>Rhododendron neriiflorum</i>	1994.3905A	-5.068	4.898	0.335	-40.207	0.136
<i>Rhododendron neriiflorum</i>	1919.0100A	-3.404	5.678	0.61	-17.431	0.444
<i>Rhododendron ponticum</i>	1971.5872A	-7.424	2.563	0.023	-30.188	0.589
<i>Rhododendron ponticum</i>	1971.5872B	-6.762	1.492	0.002	-30.812	0.797
<i>Rhododendron ponticum</i>	1972.4007A	-4.677	1.673	0.023	-31.053	0.7
<i>Rhododendron ponticum</i>	1974.4139A	-8.32	1.346	0	-24.083	0.888
<i>Rhododendron praecox</i>	1969.8794Beast	-5.801	4.136	0.203	-37.311	0.264
<i>Rhododendron praecox</i>	1969.8794Bmid	-8.658	3.123	0.028	-34.98	0.524
<i>Rhododendron praecox</i>	1969.8794Bwest	-7.735	3.269	0.05	-35.337	0.489
<i>Rhododendron praevernum</i>	1924.0357A	-1.234	4.438	0.789	-38.143	0.092
<i>Rhododendron praevernum</i>	1924.0357D	-1.234	3.876	0.759	-36.734	0.051
<i>Rhododendron praevernum</i>	1924.0357E	-3.499	4.387	0.455	-33.445	0.1
<i>Rhododendron praevernum</i>	1969.8798A	-0.859	4.395	0.851	-38.041	0.102
<i>Rhododendron racemosum</i>	1973.4084B	-14.721	1.201	0	-26.046	0.956
<i>Rhododendron racemosum</i>	1932.1028	-6.506	1.588	0.006	-25.76	0.747
<i>Rhododendron racemosum</i>	1991.0867A	-8.125	2.29	0.009	-33.678	0.646
<i>Rhododendron reticulatum</i>	1975.2245BNE	-10.464	0.963	0	-25.393	0.944
<i>Rhododendron reticulatum</i>	1975.2245BSE	-8.406	1.093	0	-26.28	0.902
<i>Rhododendron reticulatum</i>	1975.2245BW	-8.457	1.55	0.001	-29.815	0.81
<i>Rhododendron reticulatum</i>	1975.2245 (SW)	-10.184	2.055	0.004	-22.95	0.832
<i>Rhododendron reticulatum</i>	1975.2245 N (N)	-9.926	1.201	0	-24.44	0.92
<i>Rhododendron russatum</i>	1971.2586B	-8.178	1.532	0.001	-30.049	0.804
<i>Rhododendron russatum</i>	1971.2586D	-6.545	1.497	0.003	-29.5	0.745

<i>Rhododendron russatum</i>	1971.2586G	-7.121	1.743	0.005	-30.953	0.711
<i>Rhododendron schlippenbachii</i>	1975.0765 B (E)	-8.183	1.378	0.001	-28.832	0.842
<i>Rhododendron schlippenbachii</i>	1975.0765B (W)	-7.609	1.183	0	-27.448	0.858
<i>Rhododendron schlippenbachii</i>	1977.1391B	-4.194	1.739	0.047	-30.164	0.499
<i>Rhododendron semibarbatum</i>	1976.1907ASW	-5.183	2.324	0.076	-23.86	0.562
<i>Rhododendron semibarbatum</i>	1976.1907ASE	-1.643	2.877	0.589	-28.031	0.091
<i>Rhododendron semibarbatum</i>	1976.1907B	-2.975	3.97	0.482	-28.879	0.151
<i>Rhododendron siderophyllum</i>	1980.0345C	-6.588	1.975	0.01	-33.897	0.594
<i>Rhododendron siderophyllum</i>	1996.0554B	-14.168	2.674	0.001	-34.048	0.805
<i>Rhododendron siderophyllum</i>	1980.0345B	-9.668	5.832	0.239	-15.521	0.579
<i>Rhododendron strigillosum</i>	1975.4050I	-11.858	15.792	0.494	-32.881	0.256
<i>Rhododendron strigillosum</i>	1996.0603A	-5.923	2.173	0.112	-13.369	0.846
<i>Rhododendron strigillosum x praeevernum</i>	1969.8865A	2.8	4.753	0.577	-33.167	0.267
<i>Rhododendron tolmachevii</i>	1940.0183A	-8.099	2.407	0.015	-28.533	0.655
<i>Rhododendron tomentosum</i>	1969.5002A	-5.15	1.734	0.018	-32.428	0.616
<i>Rhododendron tomentosum</i>	1978.0135A	-14.848	4.717	0.035	-22.778	0.713
<i>Rhododendron trichostomum</i>	1969.9607C	-7.9	1.801	0.002	-32.015	0.779
<i>Rhododendron trichostomum</i>	1963.3848 A	-7.742	1.943	0.01	-22.524	0.772
<i>Rhododendron trichostomum</i>	1969.9607 B	-8.827	2.047	0.013	-19.624	0.847
<i>Rhododendron wadanum</i>	1976.1072B	-6.358	1.576	0.004	-31.748	0.708
<i>Rhododendron wadanum</i>	1976.1909B+A	-8.605	0.781	0	-22.948	0.946
<i>Rhododendron wadanum</i>	1976.1072D	-6.724	2.049	0.017	-27.136	0.705
<i>Rhododendron wallichii</i>	1962.0915B	-7.206	4.431	0.148	-37.537	0.283
<i>Rhododendron wallichii</i>	1981.3602D	-7.23	2.794	0.036	-33.817	0.554
<i>Rhododendron wallichii</i>	1983.0965B	-4.723	0.935	0.004	-19.142	0.858
<i>Rhododendron yunnanense</i>	1996.0662 A	-2.126	1.459	0.241	-11.806	0.491
<i>Rhododendron yunnanense</i>	1996.0662D	-6.582	1.864	0.008	-32.971	0.682
<i>Rhododendron yunnanense</i>	1981.2672C	-11.153	3.371	0.045	-17.733	0.789

Table A3 Responses of peak flowering dates of individual plants to a mean daily temperature increase of 1 °C

Species	Accession	Slope	Standard error	p-value	Log likelihood	R ²
<i>Rhododendron adenogynum</i>	1933.1020A	-2.026	1.995	0.349	-28.763	0.615

<i>Rhododendron adenogynum</i>	1948.0012A	-6.791	2.828	0.047	-33.469	0.502
<i>Rhododendron adenogynum</i>	1987.1535A	-5.147	5.64	0.397	-36.078	0.127
<i>Rhododendron anthosphaerum</i>	1923.0098 D	-9.443	4.862	0.147	-20.776	0.634
<i>Rhododendron anthosphaerum</i>	1949.1012A	4.035	5.825	0.514	-36.36	0.514
<i>Rhododendron anthosphaerum</i>	1979.0989A	-10.02	2.42	0.009	-21.232	0.782
<i>Rhododendron anwheiense</i>	1971.0038A	-6.204	4.292	0.186	-41.566	0.388
<i>Rhododendron anwheiense</i>	1980.2048A	-8.179	8.871	0.454	-19.187	0.346
<i>Rhododendron anwheiense</i>	1980.2048D	-9.383	5.729	0.177	-23.946	0.42
<i>Rhododendron arboreum</i>	1974.0834B	-3.449	5.633	0.567	-30.958	0.072
<i>Rhododendron arboreum</i>	1976.0141C	-19.648	5.868	0.015	-36.103	0.653
<i>Rhododendron arboreum</i>	1981.1230G	-8.698	1.986	0.002	-33.13	0.763
<i>Rhododendron arboreum</i>	1990.2647A	25.419	12.55	0.089	-43.41	0.423
<i>Rhododendron arboreum</i>	1996.0562A	-4.658	3.183	0.187	-34.948	0.348
<i>Rhododendron augustinii</i>	1975.4173A	-4.819	3.907	0.264	-30.364	0.204
<i>Rhododendron augustinii</i>	1977.2695 G	-8.86	11.23	0.513	-19.468	0.279
<i>Rhododendron augustinii</i>	1980.5048A	-7.445	4.698	0.152	-42.592	0.335
<i>Rhododendron augustinii</i>	1999.1844A	-7.234	2.705	0.116	-12.771	0.957
<i>Rhododendron auriculatum</i>	1916.0027A	-17.524	11.924	0.185	-42.922	0.259
<i>Rhododendron barbatum</i>	1972.0856*R	0.515	3.621	0.89	-40.268	0.171
<i>Rhododendron barbatum</i>	1972.0856A	-1.236	8.243	0.886	-41.058	0.375
<i>Rhododendron barbatum</i>	1976.0083 C	-2.375	2.854	0.466	-19.498	0.336
<i>Rhododendron calendulaceum</i>	1977.1140A	-2.264	3.558	0.542	-39.365	0.105
<i>Rhododendron calendulaceum</i>	1979.1536AN	-12.022	3.321	0.007	-35.468	0.676
<i>Rhododendron calendulaceum</i>	1979.1536AS	-7.804	4.692	0.147	-33.133	0.546
<i>Rhododendron calophytum</i>	1969.8430A	-3.333	4.489	0.491	-31.214	0.334
<i>Rhododendron calophytum</i>	1972.4038A	-2.084	4.142	0.628	-44.109	0.184
<i>Rhododendron calostrotum</i>	1971.2351A	-9.999	2.766	0.009	-35.945	0.665
<i>Rhododendron calostrotum</i>	1971.2523A	-8.864	2.3	0.006	-31.518	0.714
<i>Rhododendron calostrotum</i>	1971.2524B	-7.498	2.815	0.037	-31.237	0.595
<i>Rhododendron campanulatum</i>	1955.1016A	-0.707	3.965	0.863	-41.895	0.057
<i>Rhododendron campanulatum</i>	1962.0908A	-10.424	4.041	0.036	-36.562	0.497
<i>Rhododendron campanulatum</i>	1969.8445A	-0.403	3.08	0.904	-16.202	0.073
<i>Rhododendron canadense</i>	1976.0690A	-9.75	3.561	0.026	-39.76	0.532
<i>Rhododendron canadense</i>	1976.0690B	-9.666	2.963	0.011	-38.354	0.581
<i>Rhododendron canadense</i>	1990.0430B	-6.699	2.555	0.034	-31.974	0.497
<i>Rhododendron cinnabarinum</i>	1938.1155G	-2.593	3.791	0.516	-36.323	0.19
<i>Rhododendron cinnabarinum</i>	1957.7184P	-4.985	2.307	0.063	-35.057	0.372
<i>Rhododendron cinnabarinum</i>	1969.8930K	-0.843	3.295	0.805	-38.478	0.055
<i>Rhododendron cinnabarinum</i>	1978.4120A	-2.587	5.072	0.624	-42.024	0.043

<i>Rhododendron collettianum</i>	1970.2019A	-7.401	2.093	0.01	-31.705	0.654
<i>Rhododendron dauricum</i>	1976.1068C	0.649	5.317	0.906	-40.473	0.003
<i>Rhododendron dauricum</i>	1978.0139 A	-9.412	1.24	0.001	-21.143	0.925
<i>Rhododendron dauricum</i>	1991.1220A	-7.927	7.785	0.342	-44.858	0.185
<i>Rhododendron dauricum</i>	1976.1068 A	1.611	5.973	0.805	-23.167	0.316
<i>Rhododendron decorum</i>	1969.8512B	2.318	3.744	0.555	-35.808	0.5
<i>Rhododendron decorum</i>	1969.8512D	-7.877	1.948	0.004	-32.876	0.764
<i>Rhododendron decorum</i>	1973.4073B	-5.249	4.244	0.304	-19.043	0.351
<i>Rhododendron decorum</i>	1976.1403F	-7.649	3.477	0.059	-39.27	0.584
<i>Rhododendron degronianum</i>	1960.3367A	-3.683	8.501	0.676	-47.706	0.026
<i>Rhododendron degronianum</i>	1961.4659A	-4.298	3.495	0.254	-38.752	0.236
<i>Rhododendron degronianum</i>	1977.3254A	-4.268	2.89	0.178	-36.628	0.335
<i>Rhododendron degronianum</i>	1983.2540A	-2.257	3.539	0.541	-39.21	0.203
<i>Rhododendron ferrugineum</i>	1976.0519 H	-10.855	4.221	0.037	-35.063	0.591
<i>Rhododendron ferrugineum</i>	1976.0519B	-7.741	2.846	0.026	-36.49	0.571
<i>Rhododendron ferrugineum</i>	1976.0519 F	-8.373	1.857	0.004	-25.661	0.887
<i>Rhododendron ferrugineum</i>	1976.0519 G	-7.725	3.127	0.048	-29.753	0.721
<i>Rhododendron ferrugineum</i>	1976.1857 D	-23.574	4.056	0.028	-13.025	0.944
<i>Rhododendron hippophaeoides</i>	1971.2400A	-11.944	1.418	0	-30.584	0.929
<i>Rhododendron hippophaeoides</i>	1971.2576A	-0.844	3.616	0.821	-39.69	0.232
<i>Rhododendron hippophaeoides</i>	1971.2594G	-5.842	4.55	0.235	-41.753	0.282
<i>Rhododendron hippophaeoides</i>	1973.4078B	-7.477	2.642	0.022	-36.812	0.686
<i>Rhododendron hippophaeoides</i>	1991.0304C	-3.245	2.718	0.267	-36.541	0.307
<i>Rhododendron irroratum</i>	1991.1093A	-10.929	4.595	0.055	-34.746	0.523
<i>Rhododendron irroratum</i>	1996.0617 G	-11.799	6.82	0.226	-17.165	0.738
<i>Rhododendron lanigerum</i>	1929.1008B	-1.048	4.885	0.835	-45.172	0.014
<i>Rhododendron lanigerum</i>	1929.1008E	-5.672	4.914	0.286	-41.668	0.227
<i>Rhododendron lanigerum</i>	1929.1008H	4.08	5.912	0.512	-41.604	0.076
<i>Rhododendron lapponicum</i>	1903.0018 A	-11.357	5.008	0.086	-26.281	0.715
<i>Rhododendron lapponicum</i>	1979.3270 A	-10.233	4.201	0.059	-30.678	0.589
<i>Rhododendron lapponicum</i>	1903.0018 A	-10.243	1.299	0.016	-8.945	0.974
<i>Rhododendron lepidotum</i>	1983.0962A	-4.368	2.516	0.121	-35.545	0.288
<i>Rhododendron lepidotum</i>	1983.0963C	-8.378	3.305	0.035	-38.236	0.456
<i>Rhododendron lepidotum</i>	1975.1302 A	-8.078	3.339	0.052	-29.074	0.574
<i>Rhododendron leptothrium</i>	1989.2109A	-6.949	2.088	0.021	-19.716	0.813
<i>Rhododendron liliiflorum</i>	1991.1969B	-7.624	4.273	0.134	-28.135	0.545
<i>Rhododendron lutescens</i>	1996.0608D	-8.444	3.694	0.052	-40.55	0.438
<i>Rhododendron lutescens</i>	1996.0608E	-3.48	3.444	0.342	-39.306	0.212
<i>Rhododendron lutescens</i>	1996.0608F	-1.786	5.343	0.747	-44.285	0.025

<i>Rhododendron luteum</i>	1977.3072E	-6.319	3.171	0.081	-37.967	0.361
<i>Rhododendron luteum</i>	1983.0848A1	-0.412	1.98	0.84	-32.466	0.352
<i>Rhododendron luteum</i>	1983.0848B1	-6.033	2.365	0.034	-34.975	0.49
<i>Rhododendron macabeaenum</i>	1969.8707A	-8.386	3.257	0.033	-39.167	0.603
<i>Rhododendron macabeaenum</i>	1928.1023B	-4.367	7.836	0.601	-33.975	0.132
<i>Rhododendron meddianum</i>	1975.4074A	11.193	7.4	0.174	-45.664	0.393
<i>Rhododendron meddianum</i>	1998.0009 A	7.87	10.12	0.48	-31.693	0.131
<i>Rhododendron mucronulatum</i>	1977.0993A	-6.184	3.913	0.153	-40.625	0.466
<i>Rhododendron mucronulatum</i>	1977.0993C	-11.821	2.343	0.001	-35.58	0.813
<i>Rhododendron mucronulatum</i>	1995.1171B	-8.429	3.68	0.062	-29.639	0.492
<i>Rhododendron mucronulatum</i>	1995.1171G	-0.05	2.693	0.986	-23.018	0.001
<i>Rhododendron neriiflorum</i>	1975.4064B	-3.445	3.907	0.404	-40.351	0.276
<i>Rhododendron neriiflorum</i>	1994.3905 C	-0.278	3.327	0.939	-19.102	0.454
<i>Rhododendron neriiflorum</i>	1994.3905A	4.591	5.987	0.465	-45.236	0.552
<i>Rhododendron neriiflorum</i>	1919.0100A	-22.229	3.776	0.028	-13.125	0.985
<i>Rhododendron ponticum</i>	1971.5872A	-3.67	6.705	0.601	-38.63	0.162
<i>Rhododendron ponticum</i>	1971.5872B	-4.004	3.42	0.275	-39.101	0.203
<i>Rhododendron ponticum</i>	1972.4007A	-3.845	4.658	0.436	-34.749	0.247
<i>Rhododendron ponticum</i>	1974.4139A	-10.535	9.734	0.315	-42.947	0.147
<i>Rhododendron praecox</i>	1969.8794Beast	-7.008	1.895	0.008	-31.903	0.664
<i>Rhododendron praecox</i>	1969.8794Bmid	-8.229	2.719	0.019	-34.669	0.571
<i>Rhododendron praecox</i>	1969.8794Bwest	-6.667	2.917	0.056	-34.918	0.43
<i>Rhododendron praevernum</i>	1924.0357A	-5.699	3.105	0.104	-41.536	0.351
<i>Rhododendron praevernum</i>	1924.0357D	-5.957	2.277	0.031	-38.124	0.555
<i>Rhododendron praevernum</i>	1924.0357E	-7.868	2.186	0.009	-33.332	0.671
<i>Rhododendron praevernum</i>	1969.8798A	-4.737	2.013	0.046	-36.515	0.506
<i>Rhododendron racemosum</i>	1973.4084B	-9.399	3.893	0.042	-41.067	0.471
<i>Rhododendron racemosum</i>	1932.1028	-9.092	2.957	0.018	-34.616	0.598
<i>Rhododendron racemosum</i>	1991.0867A	-7.471	1.768	0.003	-32.678	0.757
<i>Rhododendron reticulatum</i>	1975.2245BNE	-14.793	5.106	0.02	-43.638	0.542
<i>Rhododendron reticulatum</i>	1975.2245BSE	-14.292	2.873	0.001	-38.351	0.792
<i>Rhododendron reticulatum</i>	1975.2245BW	-7.022	4.907	0.196	-38.558	0.289
<i>Rhododendron reticulatum</i>	1975.2245 (SW)	-4.213	4.106	0.344	-33.707	0.151
<i>Rhododendron reticulatum</i>	1975.2245 N (N)	-9.528	3.084	0.021	-31.785	0.622
<i>Rhododendron russatum</i>	1971.2586B	-4.998	2.605	0.091	-36.653	0.38
<i>Rhododendron russatum</i>	1971.2586D	-16.238	2.777	0.001	-33.737	0.833
<i>Rhododendron russatum</i>	1971.2586G	-8.864	3.307	0.028	-38.861	0.504
<i>Rhododendron schlippenbachii</i>	1975.0765 B (E)	-8.223	2.02	0.004	-34.476	0.731

<i>Rhododendron schlippenbachii</i>	1975.0765B (W)	-7.704	1.862	0.003	-32.539	0.685
<i>Rhododendron schlippenbachii</i>	1977.1391B	-1.61	3.194	0.628	-38.986	0.065
<i>Rhododendron semibarbatum</i>	1976.1907ASW	-7.383	3.412	0.062	-37.927	0.498
<i>Rhododendron semibarbatum</i>	1976.1907ASE	-15.383	6.136	0.046	-34.086	0.53
<i>Rhododendron semibarbatum</i>	1976.1907B	-11.094	3.912	0.022	-38.932	0.553
<i>Rhododendron siderophyllum</i>	1980.0345C	-19.288	4.292	0.002	-40.976	0.716
<i>Rhododendron siderophyllum</i>	1996.0554B	-14.525	6.833	0.066	-46.991	0.371
<i>Rhododendron siderophyllum</i>	1980.0345B	-9.571	4.541	0.126	-19.381	0.607
<i>Rhododendron strigillosum</i>	1975.4050I	-9.029	13.684	0.534	-44.102	0.146
<i>Rhododendron strigillosum</i>	1996.0603A	-12.527	2.745	0.01	-23.03	0.861
<i>Rhododendron strigillosum</i>	1975.4050A	-5.297	16.868	0.783	-21.423	0.365
<i>Rhododendron strigillosum</i>	1996.0599D	-10.191	2.832	0.069	-13.653	0.879
<i>Rhododendron strigillosum x praeevernum</i>	1969.8865A	-8.276	3.017	0.029	-36.535	0.556
<i>Rhododendron tolmachevii</i>	1940.0183A	-7.974	4.541	0.117	-41.631	0.29
<i>Rhododendron tomentosum</i>	1969.5002A	-5.209	1.711	0.016	-31.451	0.722
<i>Rhododendron tomentosum</i>	1978.0135A	-9.062	3.381	0.055	-20.607	0.656
<i>Rhododendron trichostomum</i>	1969.9607C	1.073	3.408	0.761	-37.704	0.434
<i>Rhododendron trichostomum</i>	1963.3848 A	-4.728	3.811	0.27	-27.703	0.428
<i>Rhododendron trichostomum</i>	1969.9607 B	-3.993	5.194	0.485	-25.313	0.23
<i>Rhododendron wadanum</i>	1976.1072B	-7.356	4.03	0.105	-41.278	0.297
<i>Rhododendron wadanum</i>	1976.1909B+A	-9.447	3.179	0.018	-38.52	0.532
<i>Rhododendron wadanum</i>	1976.1072D	-3.878	1.483	0.04	-23.756	0.751
<i>Rhododendron wadanum</i>	1976.1909ASW	-7.925	9.033	0.473	-18.209	0.286
<i>Rhododendron wadanum</i>	1976.1909AW	-8.972	6.7	0.312	-16.715	0.516
<i>Rhododendron wallichii</i>	1962.0915B	-12.315	4.51	0.029	-38.251	0.517
<i>Rhododendron wallichii</i>	1981.3602D	-7.225	5.937	0.258	-45.77	0.161
<i>Rhododendron wallichii</i>	1983.0965B	-5.502	2.364	0.048	-36.034	0.475
<i>Rhododendron yunnanense</i>	1994.3155B	-0.178	4.003	0.968	-13.382	0.731
<i>Rhododendron yunnanense</i>	1996.0662 A	-2.075	0.705	0.06	-8.251	0.789
<i>Rhododendron yunnanense</i>	1996.0662D	-10.315	2.306	0.002	-34.767	0.76
<i>Rhododendron yunnanense</i>	1981.2672C	-14.103	3.081	0.02	-16.841	0.882