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Regional variation in the reproductive phenology of a tropical rainforest tree species, *Cardwellia sublimis*

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Abstract

Phenology is one of the most reliable tools for understanding the effect of climate change on forests. Although there has been increasing research into the effect of climate on phenological activity, little is known about how phenological patterns for the same species may vary among environments, particularly for tropical species. Here we analyzed the reproductive phenology of an important tropical rainforest tree species in northeastern Australia, *Cardwellia sublimis*, and compared the patterns among five different sites. We also tested and compared the climate drivers of reproductive phenological activity among sites for this species. Degree of seasonality varied across sites with most sites presenting moderate to high seasonality. Flowering and fruiting peaked in different seasons at the different sites and we found flowering and fruiting phenology were often influenced by different climate drivers at the different sites. Where the climate drivers were the same, the magnitude and direction of the effect of the drivers differed among sites. Precipitation was the most common climate driver of flowering, being significant for all sites, while fruiting was predominantly influenced by temperature and solar radiation. Finally, we found evidence that relationships between climate drivers and phenological patterns were dependent on inter-site differences in climate and geography. Our results demonstrate that species may present varied phenological patterns and varied responses to climate drivers depending on environmental conditions and site location. These results have important implications for modelling phenological patterns based on limited field information, as well as for understanding species vulnerability to climate change.

Keywords: flowering, fruiting, climate change, global warming, geographic range, tropical phenology

热带雨林树种北银桦繁殖物候的区域差异及其驱动因素

摘要：植物物候是理解气候变化对森林生态系统影响的重要工具。尽管以往研究报道了气候变化对物候活动的影响，但对于不同环境中相同物种，尤其是热带物种的物候模式差异，仍缺乏深入认识。本研究分析了澳大利亚东北部热带雨林中一种重要树种—北银桦(*Cardwellia sublimis*)繁殖物候在5个地点的差

异及其与气候因子的关联。结果发现，不同地点的季节性程度存在显著差异，大多数地点表现出中高季节性。不同地点北银桦开花和结实高峰出现在不同季节，且开花和结实物候通常受气候因子的影响。开花一般受到降水的驱动，在所有地点的影响均显著，而结实主要受温度和太阳辐射的影响。此外，气候因子与物候模式之间的关系取决于地点间气候和地理条件的差异。上述结果表明，热带雨林树种的物候模式及其对气候因子的响应可能因环境条件和地点的不同而存在差异。这些发现对于植物物候模式建模以及理解物候的气候敏感性具有重要意义。

关键词：开花，结实，气候变化，全球变暖，地理分布范围，热带物候

INTRODUCTION

Plant phenology studies are an important tool in understanding ecological dynamics and the response of plant and animal communities to global change. Changes in reproductive phenological patterns of tree communities, for example, can have significant impacts on the structure and health of forests and the fauna they support. Similarly, species-level variation in phenological patterns shapes long-term patterns of species abundance, and hence have significant implications for plant community composition and structure, as well as resource provision for herbivores (Borchert 1983; Iler *et al.* 2021; Morellato *et al.* 2016; Wright and Calderón 2018). Environmental variables such as precipitation and temperature are key drivers of phenology as these climate variables often cue changes in season, a plant may respond by directing the allocations of photosynthetic products to different outcomes such as leafing, flowering, fruiting, root development, and more. At a community level, a change in the timing or intensity of flower and fruit production for a species, in response to changes in temperature and rainfall, may result in impacts on dependent pollinators and frugivores (Butt *et al.* 2015; Mendoza *et al.* 2018; Morellato *et al.* 2016; Pau *et al.* 2018), as well as a shift in species diversity due to changes in seedling recruitment (Iler *et al.* 2021; Morellato *et al.* 2016; van Schaik *et al.* 1993). Studies such as these demonstrate the importance of understanding the impacts of global change on reproductive phenology, both at the community and species level.

Most studies of phenological response to environmental conditions are conducted in temperate regions, such as in Europe, North America (Menzel *et al.* 2006, Wang *et al.* 2024), and China (Dai *et al.* 2014; Ge *et al* 2015; Zhang *et al.* 2022). Species-level studies of tree species phenological responses to environmental conditions are less common in tropical forests. Additionally, while many tropical tree species have wide geographic and climatic ranges (dry/wet), there has been very little assessment of the phenological patterns of species across multiple locations. Environmental drivers of phenological behaviour can exhibit significant spatial variability, due to variations in the plasticity of populations and communities (Park *et al.* 2021). Park *et al.* (2021) who reviewed the knowledge gaps in landscape phenology point out that more work is needed across different types of ecosystems and communities to understand the broad consequences of scale-dependent phenology. The phenology of many organisms remains understudied at landscape to regional spatial scales. Understanding how organisms interact with landscapes at different spatial and temporal scales is extremely important to predict their response to climate change, which may be varied. Studies of edge effects, for example, have found that species phenological patterns are altered by their position relative to the edge of a forest fragment (Camargo *et al.* 2011; Laurance *et al.* 2003; Müller *et al.* 2021; Vogado *et al.* 2016). If the environmental variation between the edge and interior of a forest causes changes in phenological activity, one would expect that sites in different geographical locations and with different climatic conditions would also vary in terms of phenological behaviour. Somewhat surprisingly, this topic has received little research attention, particularly in the highly biodiverse and climatically complex Asia-Pacific region. We found, however, two studies on the effects of geography on the phenology of a herb species across Asia and Australia (Song *et al.* 2020, 2021). These studies suggest that phenological divergence increased with stronger temperature sensitivity at lower latitudes, and that phenological divergence was found to be larger at lower latitudes in humid regions.

The Wet Tropics of northern Australia, a global hotspot of biodiversity (Williams *et al.* 2011) and plant endemism, has a distinct paucity of phenological studies (but see Boulter *et al.* 2006; Spencer and Flick 1996; Vogado *et al.* 2020, 2022). Despite being a region under the influence of major climatic drivers such as cyclones and ENSO, and being considered highly vulnerable to climate change, the phenology of endemic tree species is poorly documented. The Wet Tropics is a region with upland and lowland areas that vary considerably in rainfall and temperature due to elevation and proximity to the ocean. Knowing how species phenology may vary among these areas could provide important information on how such species might respond to climate change. Understanding the phenological patterns of species from the Wet Tropics is essential to better predict how climate and land use change affect reproduction and seedling recruitment and from this improve management actions, particularly for threatened species.

Although species with biotically dispersed fruits receive more attention for being important resources for frugivores, species with abiotically dispersed fruits also represent important resources providing flowers for pollinators and nectivores, and leaves for herbivores. This study focuses on *Cardwellia sublimis*, an emergent endemic tree species of the Wet Tropics that produces high-intensity flowering, fruit that is eaten by Sulfur Crested Cockatoos (*Cacatua galerita*) and leaves that are eaten by threatened species such as the Lumholtz's tree kangaroo (*Dendrolagus lumholtzi*) and lemuroid ringtail possum (*Hemibelideus lemuroides*) (Tree Kangaroo and Mammal Group 2010). Here we have explored how this species behaves phenologically at five geographically well separated sites, and how the phenologically responds to climate variables. We aimed to answer the following questions: Does the species phenology vary significantly among sites? Do climate drivers of phenology differ between sites? Does the phenology respond to site-level differences in climate? We expected that solar radiation would be an important predictor of flowering activity, as seen in Boulter *et al.* (2006). We expected the species would have the same climate drivers among locations, however, we also expected the less abundant climate variable to have a bigger effect on phenological activity (Wright and van Schaik 1994), which would be also dependent on location.

MATERIALS AND METHODS

Studied species

Cardwellia sublimis F. Muell. (Proteceace; Northern Silky Oak), hereafter *Cardwellia*, is endemic to the rainforests of the Wet Tropics region of northeastern Queensland, Australia, and is found from Mt Spec near Townsville, to Bloomfield just south of Cooktown. The species is often a canopy emergent tree that can reach up to 40 m in height, and more than 2 m in diameter (Boland *et al.* 2006). As such *Cardwellia* has been an important timber species in the region where it has the common name northern silky oak. It has an altitudinal range from sea level to 1200 m a.s.l. (Hyland and Whiffin 1993). Cream-white flowers are arranged in pairs on spike-like racemes, either terminally or from upper axils. Fruits are dehiscent woody follicles each 8–12 cm, held prominently above the canopy in clusters, each containing 8–12 winged seeds. The species is locally abundant in the Daintree and Cairns regions (Tng *et al.* 2016), and it is an important species in restoration plantings across the Wet tropics (Engert *et al.* 2020).

Sites

Phenological data were collected from five different sites: Davies Creek, Mount Lewis, Robson Creek, Daintree Rainforest Observatory (hereafter 'DRO'), and Skyrail Rainforest Cableway (hereafter 'Skyrail'). All sites are located in the Wet Tropics World Heritage area and present varying soils and climates (Fig 1, Supplementary Table S1).

Davies Creek (17.04° S, 145.23° E) is a 1.7-hectare forest dynamics plot located 25 km southwest of Cairns in northeastern Australia. The site occurs on low-fertility soils derived from granitic parent material, at an average elevation of 830 m. The vegetation at the site varies from simple notophyll evergreen vine forest on and near ridges, to complex mesophyll vine forest on lower slopes (see Connell *et al.* 1984; Green *et al.* 2014). The region receives an annual mean rainfall of approximately 3000 mm, with the majority occurring during the wet season from December to April (P. Green unpublished data). Notably, the plot has remained free from significant cyclonic disturbances since the commencement of monitoring in 1963.

Daintree Rainforest Observatory (DRO) (16.06° S, 145.26° E) is a 1-hectare lowland tropical rainforest site located at the James Cook University-administered Daintree Rainforest Observatory,

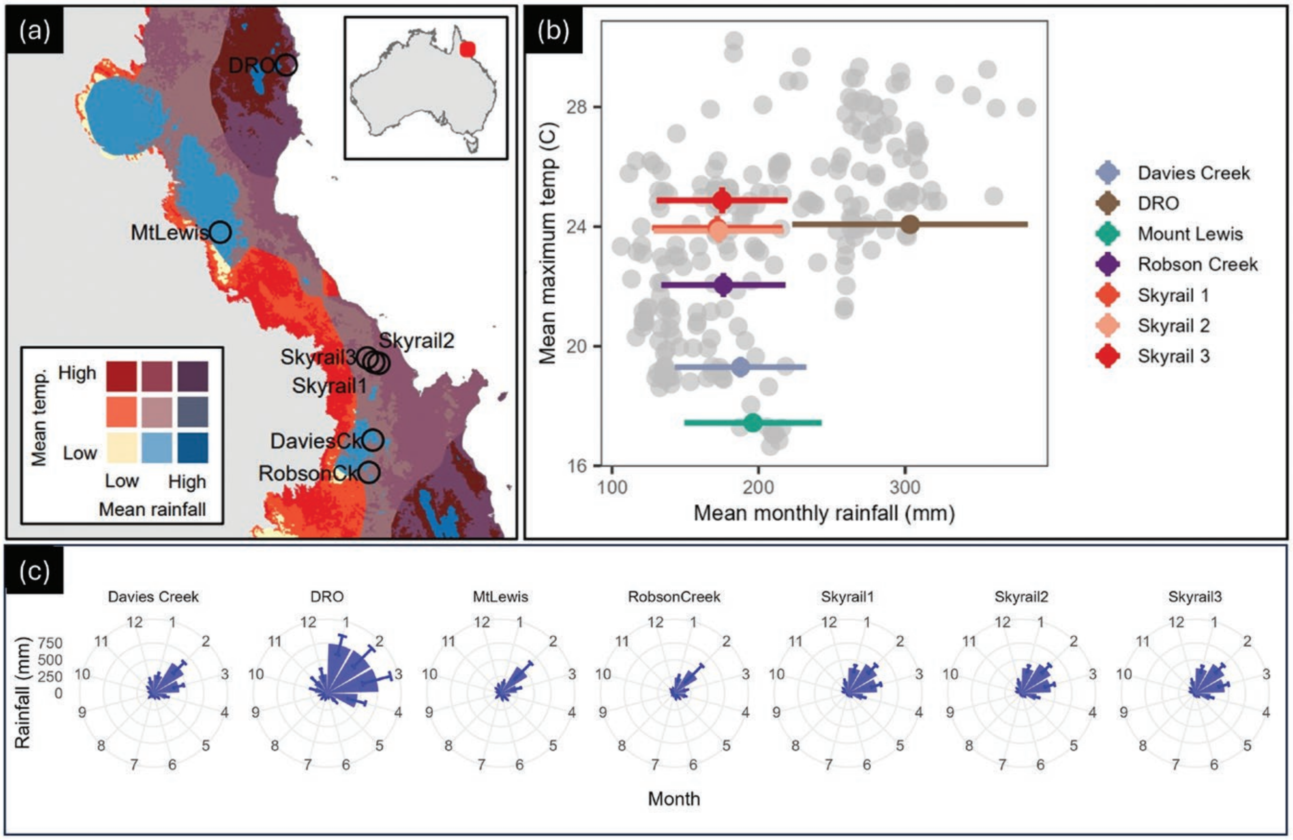

Figure 1: (a) Map showing the study sites and their respective range of mean temperature and mean rainfall, (b) mean annual maximum temperature (maximum temperatures of each month averaged over the year) and rainfall, and (c) rainfall seasonality in each site (average ± SE), in the Wet Tropics of Queensland, Australia. Grey dots indicate the climatic conditions of all location records for *Cardwellia sublimis* contained in the Atlas of Living Australia.

near Cape Tribulation in northeastern Queensland, Australia. The Daintree rainforest, classified as a complex mesophyll vine forest (Tracey 1982), hosts the highest levels of floral endemism in Australia (Metcalfe and Ford 2008). During the wet season, the area is frequently subject to tropical cyclones and as a result, this forest type is colloquially known as 'cyclone scrub' due to the damaging effects of recurrent cyclones on forest structure (Turton 2012).

The Mount Lewis site (16.52° S, 145.28° E) is located in the pristine lower montane rainforest on the Carbine Tablelands in the World Heritage listed Mt Lewis State Forest, at an altitude of 1100 m. It is classified as Simple Microphyll Vine-Fern Forest in the scheme of Tracey (1982), on low fertility soil derived from parent material.

Robson Creek (17.12° S, 145.62° E) is a 25-hectare rainforest census plot situated approximately 30 km northeast of Atherton, in North Queensland, Australia, at an elevation ranging from 680 to 740 meters (Bradford *et al.* 2014). The plot is located within Danbulla National Park and is moderately inclined with a low relief. The plot is traversed by three permanent creeks and is characterized as a complex mesophyll vine forest on granite and meta-sediment alluvium. However, higher elevations on the plot resemble a simple notophyll vine forest on meta-sediment. As altitude increases to the north, the forest type transitions from simple to complex notophyll vine forest on granite. The parent material on the plot is primarily meta-sedimentary, leading to moderately low soil fertility. Observations were conducted in the core plot, which is 1 hectare in area and close to the access road to the site.

Skyrail (16.84° S, 145.64° E) is a 7.5 km scenic gondola cableway running above the Barron Gorge National Park. The vegetation community of the park, part of the traditional lands of the Djabugandji people (traditional owners), is composed of a closed-canopy mesophyll/notophyll vine forest (Tracey 1982). The Skyrail transect was divided into three main gradients: Skyrail G1(~2 km), Skyrail G2 (~1.2 km), and Skyrail G3 (~1 km). Skyrail G1 represents elevation from 63 to 526 m, Skyrail G2

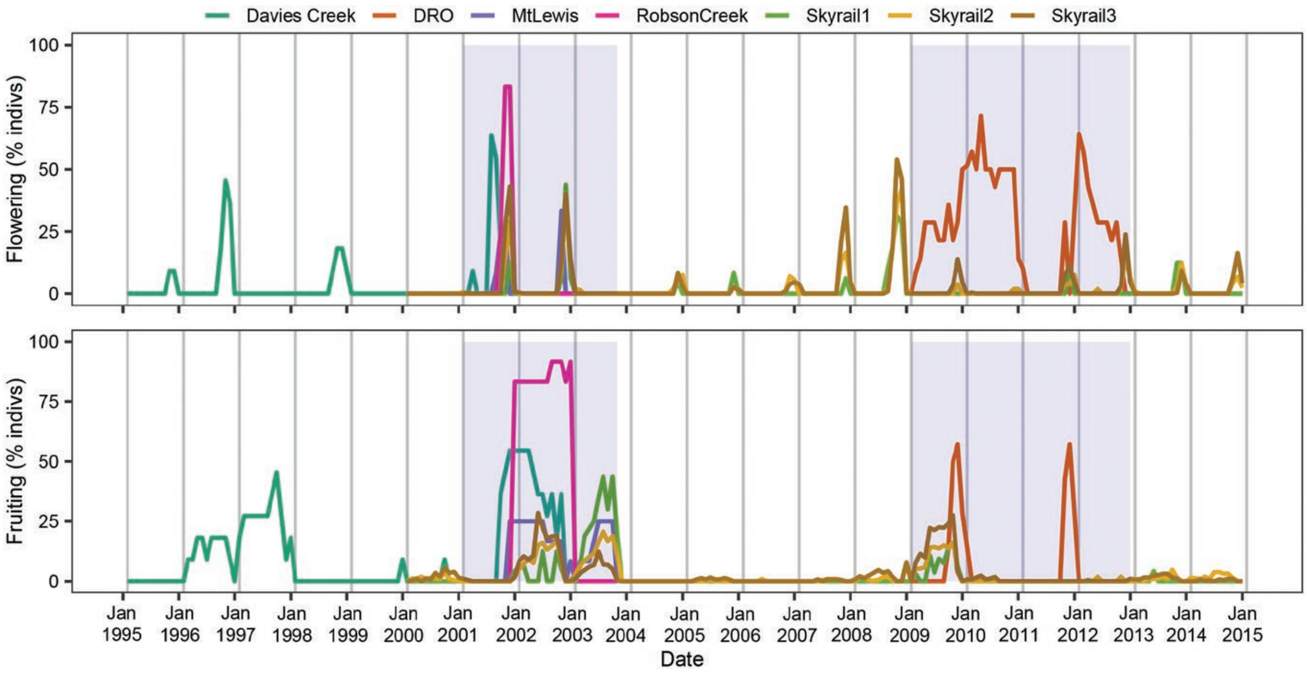

Figure 2: Time series from 1995 to 2015 showing the patterns among sites. All sites, except DRO, were measured between January 2001 and October 2003. DRO was measured from 2009 to 2012, making a comparison possible to Skyrail (observations from 2000 to 2014). Grey bars indicate years.

represents elevation from 542 to 382 m, and Skyrail G3 represents elevation from 365 to 381 m. As the Skyrail transect was substantially larger than the other sites, we divided it into three separate gradients in order to test for intra-site variation in phenological patterns and climate drivers, these will be referred to as Skyrail gradients as a group.

Phenological observations

We compiled datasets from the five different sites across different time-periods (Fig. 2):

Davies Creek (1995–2003), Mount Lewis (2001–2003), Robson Creek (2001–2003), DRO (2009–2012) and Skyrail (2000–2014). For all sites, phenological observations were conducted monthly, considering flowering (flower buds and open flowers) and fruiting (unripe and ripe fruits) activity. Phenological observations in some sites were conducted using the Fournier index, giving a score from 0 to 4 (interval of 25% between scores), which we converted to presence/absence scores (0 for no activity, 1 for activity) for further analysis. We did this as some of the datasets only presented activity, ensuring all sites had the same index allowed us to compare the phenological patterns. While an intensity index such as the Fournier index provides more information it is known that activity and intensity index are very similar to each other (Morellato *et al.* 2010). For the Skyrail site, phenological observations were conducted fortnightly, with these values converted to monthly values by considering the presence at any point in the month as a presence for the whole month. The total number of individual trees observed varied among sites, with 12 at DRO, 12 at Robson Creek, 11 at Davies Creek, 12 on Mount Lewis, 34, 46, and 110 for the three Skyrail gradients G1–G3, respectively.

Climate and soil data

Climate data was obtained using accuCLIM (Storlie *et al.* 2013) gridded temperature data and Bureau of Meteorology gridded data for rainfall and solar radiation (BOM 2009). Bureau of Meteorology rainfall data was interpolated between the registered measurement stations used, while accuCLIM models temperature values based on underlying biophysical conditions and incorporates a greater number of measurement stations. We focussed on including climate variables captured using consistent methodologies so that comparing across the sites could be done with comparability assured in the climate data that was used.

Additionally, we extracted elevation data from SRTM (Jarvis *et al.* 2008) and soil variables for each study site from the SoilGrids (Poggio *et al.* 2021). Soil variables, at ~250m resolution, were available at 5 to

15 and 30 to 60 cm depth and they included: cation exchange capacity (CEC), nitrogen, clay, sand and silt. For the analyses, we used the average of the soil depths. All environmental variables were aggregated at the site level by creating a 1km circle buffer around the site centre point and averaging values within this buffer.

Statistical analyses

For the phenology, we used circular statistics to test if the seasonality and synchrony of individuals differed among the sites for both flowering and fruiting. We determined the onset dates of flowering and mean activity of flowering and fruiting for all individuals of *Cardwellia* in each environment. We focused on flowering for analysis of onset because *Cardwellia* fruit development is slow and extracting onset dates of fruiting activity was not possible. To understand phenological patterns and seasonality, we first extracted, from each year of each time series, the onset month of each individual tree. To maximize the sample size, we used the whole study period for each site for the analysis. We then converted the months into angles (January = 0°, February = 30°, March = 60°, etc) and conducted circular statistical analysis to obtain important phenological parameters, such as mean angle (mean date) and the length of vector *r* which indicated synchrony amongst individuals (Morellato *et al.* 2010; Zar 1999).

We tested the significance of the mean angle by applying the Rayleigh *Z* test, which indicates the significance of seasonality (Morellato *et al.* 2010; Zar 1999). The vector *r* length indicates the concentration around the mean angle and is used as an index of phenological synchrony among individuals in each environment (Morellato *et al.* 2010; Zar 1999). To test possible differences in the flowering onset and flowering and fruiting mean dates among the environments, we applied the Watson–Williams *F* test. Circular statistics were conducted using the whole time series for onset and only the time period from 2001 to 2005 for analyses of mean activity as this was the period common to all sites.

For the climate data, we first tested for differences in climate variables among sites using ANOVA on mean annual minimum and maximum temperature, mean annual solar radiation, and mean annual precipitation. Mean annual climate variables were calculated averaging the monthly time series into years. To compare how soil characteristics varied among sites, we conducted a k-means cluster analysis using the R package "*cluster*" (Maechler *et al.* 2022).

To assess the climate drivers of phenology for each site, we created generalized linear mixed models (GLMM) with the presence/absence of phenological activity as the response variable and minimum temperature, maximum temperature, precipitation, and solar radiation as the independent variables. Tree identity (or individual subplot in the case of Skyrail) was added as a random effect to the model. GLMMs were conducted using the binomial family (R Core Team 2023). All models were tested for multicollinearity by calculating the variance inflation factor (VIF, accepted models had a VIF below 10) using the "*Performance*" package (Lüdecke *et al.* 2021).

To test the effect of site-level variation in climatic and geographic variables on phenological responses to climate, we compared the beta coefficients of the GLMM models to site environmental variables. We conducted Pearson correlations using the absolute value of model beta coefficients (for each climate variable) as the response variable and ran separate correlations using mean annual rainfall, rainfall seasonality (coefficient of variation), mean maximum temperature (mean monthly temperature averaged by year), mean minimum temperature (mean monthly temperature averaged by year), temperature range, latitude, and elevation as independent variables. Due to the small sample size in Pearson correlations ($n = 7$), these results should be taken as evidence of a potential pattern rather than conclusive proof of a relationship. All analyses were conducted in R using packages "*glmmTMB*" and "*circular*" (R Core Team 2023). Finally, we tested the relationship between flower onset date and all soil variables using circular-linear correlations, and between flowering onset date and mean dates of rainfall, minimum and maximum temperature using circular-circular correlations. Circular correlations were conducted in R using the package "*Directional*" (Tsagris *et al.* 2024), and circular correlation plots were made using the trial version of ORIANA 4.0 (Kovach 2011).

RESULTS

Site climate

The 5 sites are all driven by the annual monsoon pattern which gives the region a characteristic wet-dry climate, with one site, the DRO being particular wet (Fig. 1; Supplementary Table S2). We compared the average climate of each site, from 1995 to 2014, using an analysis of variance (ANOVA; Supplementary Table S2). When comparing the

Table 1: Circular statistics of flowering and fruiting mean activity based on the mean pattern from January 2001 to October 2003 for *Cardwellia sublimis* individuals sampled at Davies Creek, Robson Creek, Mount Mount Lewis, Daintree and the three gradients at Skyrail. The table presents the corresponding mean angles, date as month, vector *r*, concentration, circular variance and SD, and results from Rayleigh test. Superscript letter next to mean dates represent the sites that were grouped together in the cluster analysis (two groups).

Flowering Onset

Site	Davies Creek	Robson Creek	Mount Lewis	DRO	SkyrailG1	SkyrailG2	SkyrailG3
Number of observations	10	16	7	17	91	196	594
Mean agle (μ)	231.118°	256.505°	253.331°	281.8°	282.719°	289.39°	286.875°
Mean date	23rd Aug[a]	17th Sep[a]	14th Sep[a]	13th Oct[b]	14th Oct[b]	21st Oct[b]	18th Oct[b]
Length of mean vector (*r*)	0.983	0.912	0.94	0.901	0.882	0.915	0.934
Concentration	20.979	5.962	5.316	5.364	4.525	6.198	7.8
Circular variance	0.017	0.088	0.06	0.099	0.118	0.085	0.066
Circular standard deviation	10.721°	24.605°	20.147°	26.099°	28.754°	24.083°	21.249°
Rayleigh test (*Z*)	9.656	13.305	6.186	13.815	70.74	164.259	517.667
Rayleigh test (*P*)	<1E-12	6.00E-07	1.68E-04	4.30E-07	<1E-12	<1E-12	<1E-12

Flowering frequency

Site	Davies Creek	Robson Creek	Mount Lewis	SkyrailG1	SkyrailG2	SkyrailG3
Number of observations	56	78	30	33	49	62
Mean angle (μ)	205.868°	283.41°	256.474°	300.886°	300.451°	297.105°
Mean date	28th Jul	15th Oct	18th Sep	2nd Nov	2nd Nov	29th Oct
Length of mean vector (*r*)	0.795	0.951	0.951	0.991	0.96	0.969
Concentration	2.799	10.383	10.512	56.438	12.684	16.41
Circular variance	0.205	0.049	0.049	0.009	0.04	0.031
Circular standard deviation	38.841°	18.245°	18.127°	7.661°	16.426°	14.37°
Rayleigh test (*Z*)	35.367	70.478	27.142	32.415	45.134	58.22
Rayleigh test (*P*)	<1E−12	<1E−12	1.41E−11	<1E−12	<1E−12	<1E−12

Fruiting frequency

Site	Davies Creek	Robson Creek	Mount Lewis	SkyrailG1	SkyrailG2	SkyrailG3
Number of observations	236	419	150	97	80	74
Mean angle (*μ*)	300.481°	318.102°	170.529°	181.866°	169.855°	151.505°
Mean date	1st Nov	19th Nov	22nd Jun	4th Jul	22nd Jun	3rd Jun
Length of mean vector (*r*)	0.255	0.178	0.072	0.426	0.366	0.381
Concentration	0.528	0.362	0.145	0.941	0.786	0.824
Circular variance	0.745	0.822	0.928	0.574	0.634	0.619

Table 1: Continued

	Fruiting frequency					
Site	**Davies Creek**	**Robson Creek**	**Mount Lewis**	**SkyrailG1**	**SkyrailG2**	**SkyrailG3**
Circular standard deviation	94.712°	106.463°	131.276°	74.86°	81.241°	79.606°
Rayleigh test (*Z*)	15.353	13.267	0.787	17.595	10.714	10.737
Rayleigh test (*P*)	2.15E-07	1.73E-06	0.455	2.28E-08	2.22E-05	2.17E-05

mean annual climate variables, we found that DRO was significantly different than the other sites for precipitation (Supplementary Table S2). Sites varied substantially in minimum temperature, with the three Skyrail gradients, being similar. For maximum temperature, DRO was similar to Skyrail. Solar radiation was similar among Davies Creek, DRO, Mount Lewis, Robson Creek and Skyrail.

Sites soil components

Cluster analyses grouped Davies Creek, Robson Creek and Mount Lewis together in one cluster, with the other cluster being composed of the DRO site and the Skyrail gradients (Supplementary Fig. S1). Interestingly, the first cluster group was the group with earlier onset of flowering (Table 1). The circular-linear correlations showed a significant relationship between the flowering onset date and clay ($r = 0.91$, $P = 0.01$), nitrogen ($r = 0.94$, $P < 0.01$), silt ($r = 0.87$, $P = 0.018$), and elevation (dem) ($r = 0.88$, $P = 0.017$). The relationship between sand and flowering onset date was marginally significant ($r = 0.775$, $P = 0.062$). The visual representation of circular–linear relationships can be seen in Supplementary Fig. S2. The circular–circular correlation between flowering onset date and mean dates of rainfall, minimum and maximum temperature showed significant relationships, with rainfall being negatively correlated with flowering onset date ($r = -0.63$, $P < 0.05$), and solar radiation ($r = 0.66$, $P < 0.05$), minimum ($r = 0.77$, $P < 0.05$ and maximum temperature ($r = 0.81$, $P < 0.05$) being positively correlated with flowering onset date.

Seasonality

Flowering onset was significantly seasonal and highly synchronic in all sites, peaking in August for Davies Creek, September for Robson Creek and Mount Lewis, and October for DRO and the Skyrail gradients (Fig. 3). The mean date of onset varied significantly among all site combinations except between Mount Lewis and Robson Creek (Supplementary Table S3).

Flowering activity was significantly seasonal and synchronic among sites, peaking in July in Davies Creek, September in Mount Lewis, October in Robson Creek and November at the Skyrail gradients (Fig. 4). Flowering synchrony was high in all sites, but slightly lower in Davies Creek (Table 1). Fruiting activity was significantly seasonal in all sites except Mount Lewis, peaking in June-July at the Skyrail gradients, November in Davies Creek and Robson Creek (Fig. 4). Fruiting activity had a low to moderate synchrony in all sites except Mount Lewis where it was not existent, the peak in asynchronous fruiting activity for Mount Lewis was in June. Flowering and fruiting activity mean dates varied significantly between all sites (Table 1).

Climate driver

The GLMMs indicated different climate drivers among the sites. Flowering in Davies Creek was significantly influenced by precipitation and maximum temperature, while fruiting was significantly influenced by minimum temperature and solar radiation (Supplementary Tables S4 and S5; Fig. 5). In the Daintree, flowering was mostly influenced by precipitation and minimum temperature, while fruiting was mainly influenced by precipitation and both maximum and minimum temperature (Supplementary Tables S4 and S5; Fig. 5). Flowering in Mount Lewis was mostly influenced by precipitation and minimum temperature (Supplementary Table S4), while fruiting did not correlate with any climate variable (Supplementary Table S4). Flowering in Robson Creek responded mostly to precipitation, maximum temperature and solar radiation, while fruiting responded mostly to solar radiation (Supplementary Tables S4 and S5; Fig 5).

Flowering in Skyrail G1 responded mostly to precipitation, minimum temperature and solar radiation while fruiting responded to precipitation, maximum temperature and solar radiation (Supplementary Tables S4 and S5; Fig. 5). Flowering and fruiting of Skyrail G2 and Skyrail G3 responded to precipitation, maximum temperature and solar

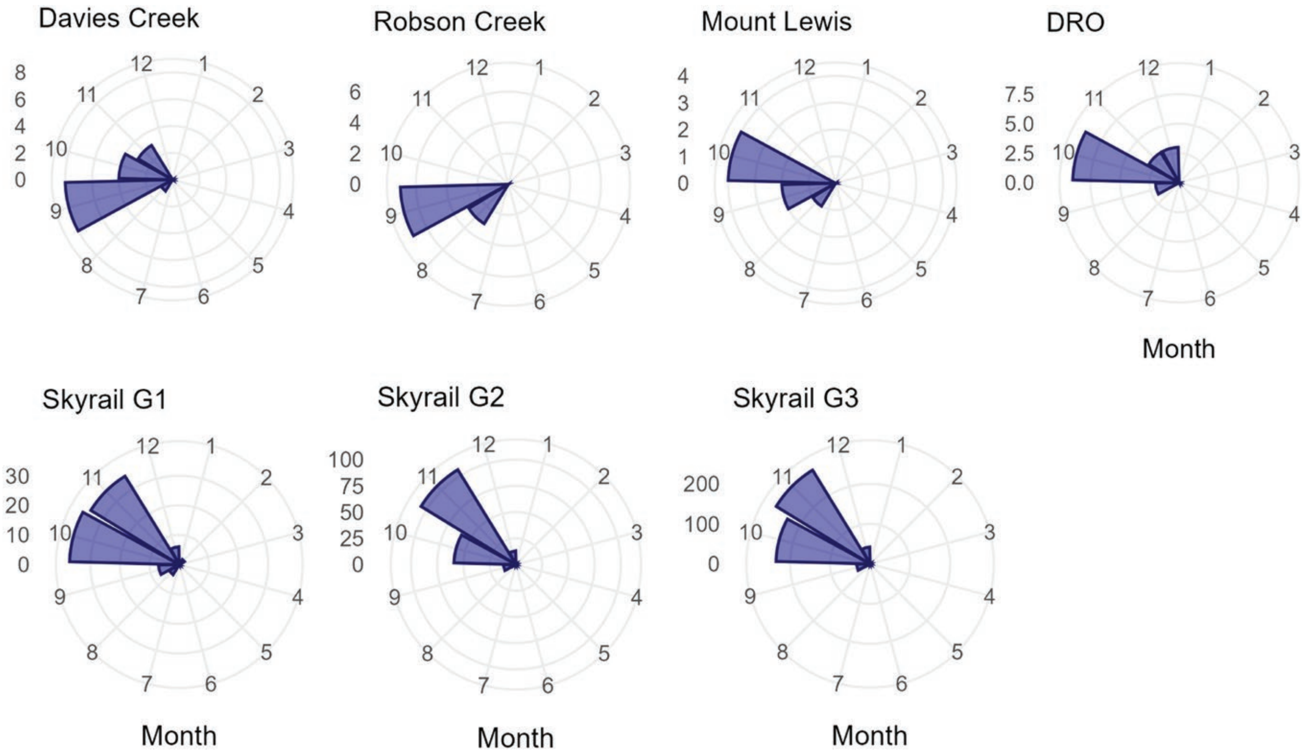

Figure 3: Circular distribution of onset of flowering for *Cardwellia sublimis* individuals sampled in Davies Creek (1995–2003), Skyrail (2000–2014), Robson Creek (2001–2003), DRO (2009–2012), and Mount Lewis (2001–2003), in the Wet Tropics of Queensland, Australia. Y-axis shows the sum of the number of individual observations of flowering onset across all years (activity).

radiation (Supplementary Tables S4 and S5). These results indicate the presence of intra-site variation in climate drivers of phenology, however, this variation was less than the inter-site variation.

Relationships between climate drivers and phenology patterns were quite variable among sites. For example, the relationship between flowering phenology and mean rainfall and solar radiation was substantially stronger in Robson Ck than in any of the other sites (Fig. 5). The relationship between fruiting activity and rainfall, solar radiation, and maximum temperature was strongest in Skyrail in the Skyrail gradients. Additionally, the relationship between fruiting and minimum temperature at the DRO site, and between fruiting and solar radiation in Davies Creek, had the opposite sign compared to the Skyrail gradients (Fig. 5).

Site climate and climate drivers

When assessing the effect of site-level differences in climate, we found that elevation and minimum temperature had a significant influence on the effect of precipitation on flowering (Fig. 6a; Supplementary Fig. S3). The effect of minimum temperature on flowering was found to be positively influenced by mean rainfall, negatively influenced by temperature range and positively influenced by latitude (Fig. 6a; Supplementary Fig. S3).

Latitude and mean rainfall had a significant influence on the effect of maximum temperature on fruiting (Fig. 6b). That is, in sites with higher mean rainfall at higher latitudes, maximum temperature had a greater influence on fruiting phenology (Fig. 6b; Supplementary Table S3). Site-level rainfall seasonality had a statistically significant influence on the relationship between minimum temperature and fruiting (Fig. 6b). No other correlations were significant (Fig. 6a and b). However, this analysis was likely significantly constrained by the low sample size (no. of sites = 5).

DISCUSSION

We studied the phenology of *Cardwellia sublimis*, commonly called northern silky oak, in five different sites across the Wet Tropics bioregion of northern Australia with varying topography, local climate, and soil composition. The duration of sampling overlapped between sites and all sites had at least 3 years of data. We found that phenology for this species was variable

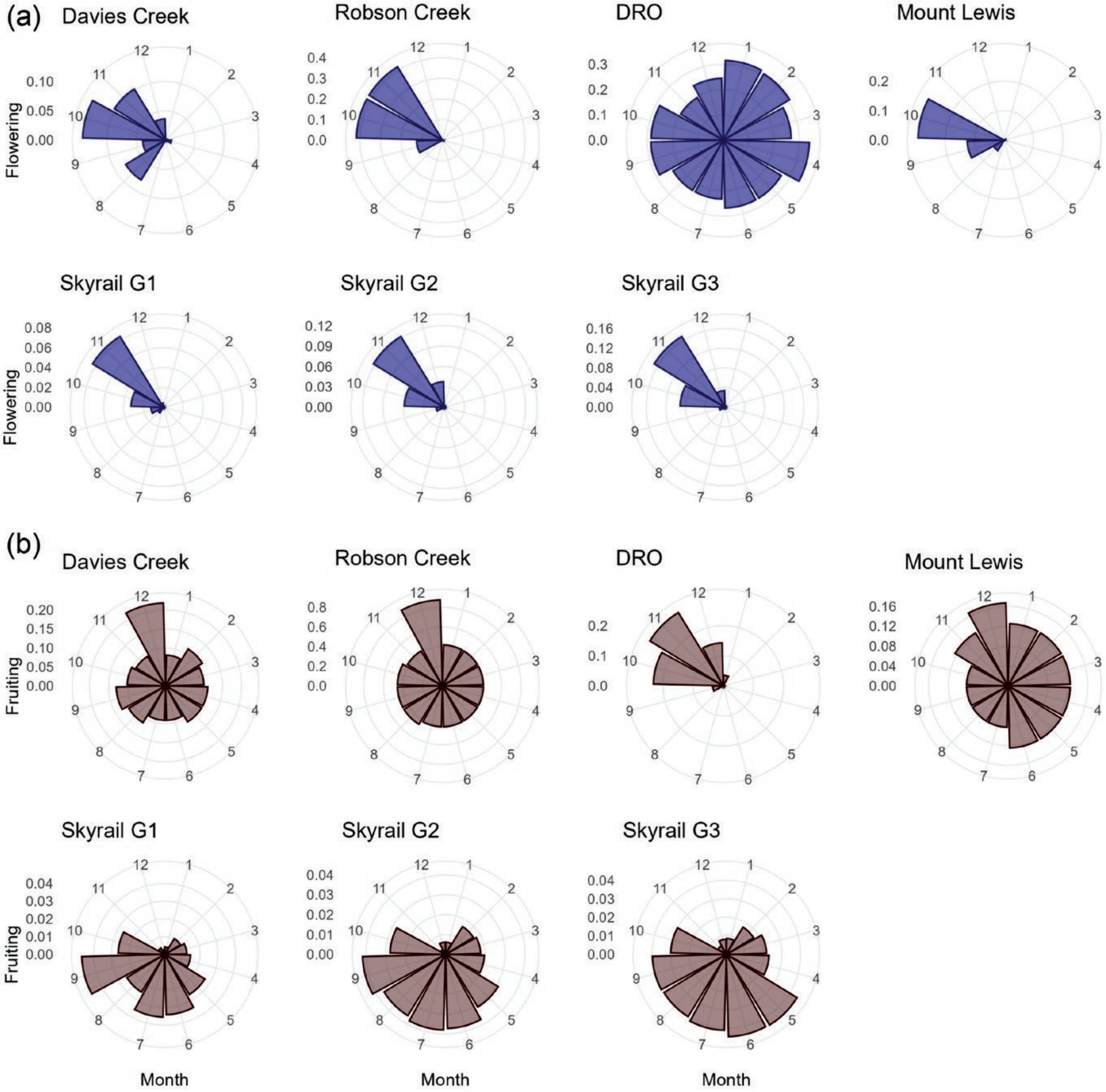

Figure 4: Circular distribution of mean flowering (blue) and fruiting (brown) proportion of activity based on the mean pattern from for *Cardwellia sublimis* individuals sampled in each site for the period 2001–2003, in the Wet Tropics of Queensland, Australia.

in timing and level of activity and influenced by different climate drivers at the different sites.

Variation in timing and seasonality

Differences in timing of phenological activity can be driven by small changes in local climate and microclimate among sites, as well as soil characteristics, and is generally influenced by the limiting resource (Wright and van Schaik 1994). For example, in our study region flowering in the southern area started earlier in the upland sites in the Lamb Range (Davies Ck, Robson Ck) which were generally cooler than the lowland site (Skyrail). In the northern area flowering in Mt Lewis (upland) and DRO (lowland) commenced in September indicating altitude/temperature effects are latitude-dependent. The importance of understanding environmental drivers is supported by negative linear relationships between the onset date of flowering and elevation and the onset date of flowering and

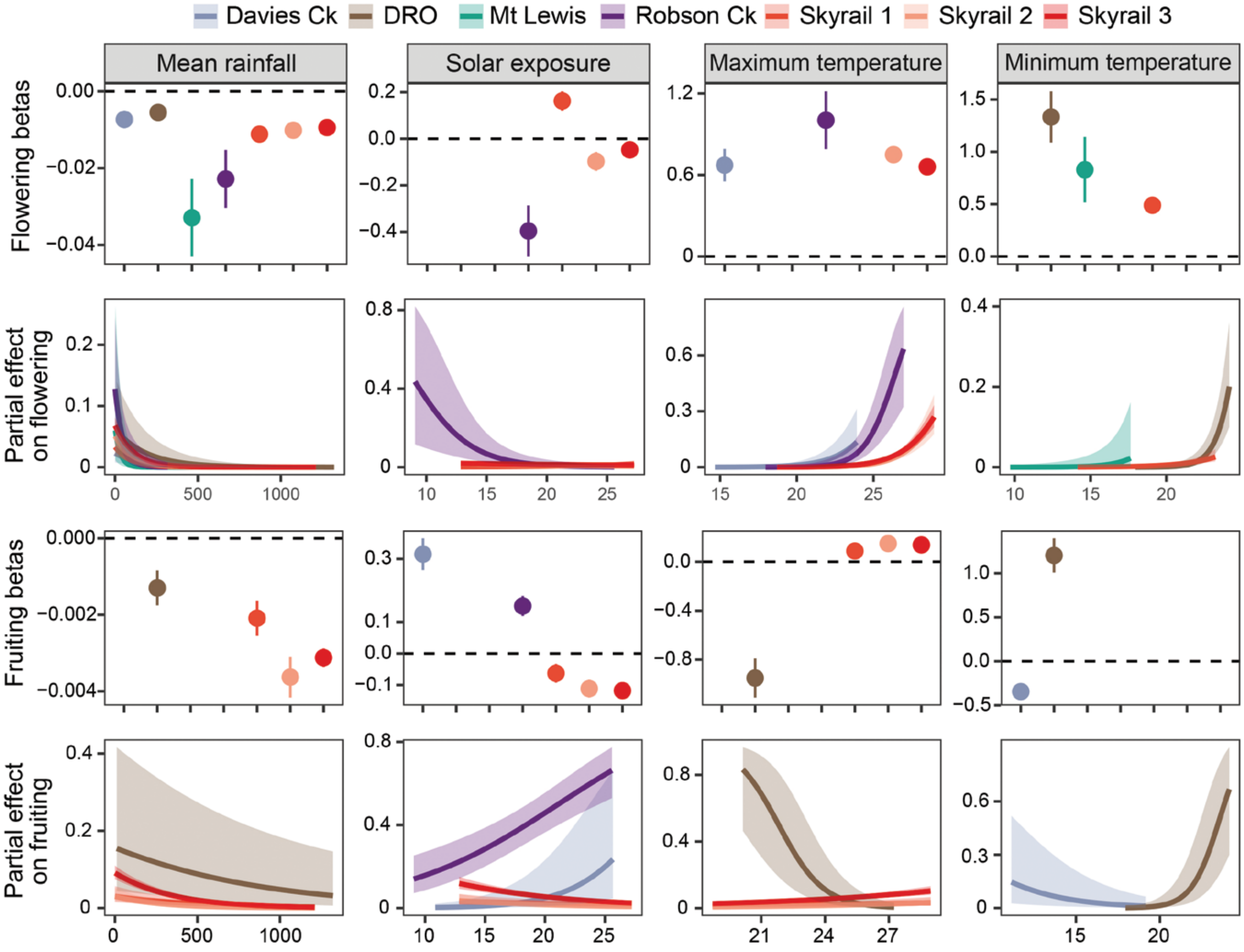

Figure 5: Partial effects of precipitation, minimum temperature (tmin), maximum temperature (tmax), and solar radiation (SolRad) for flowering (above) and fruiting (below) according to GLMM models for each of the seven sites in the Wet Tropics of Queensland, Australia. betas = beta coefficient of GLMM.

soil cation exchange capacity across all the sites (Supplementary Fig. S2). The peaks of flowering were similar (October–November) across all sites except the DRO, the latter had activity all year around. The DRO site is substantially wetter than the other sites but has a similar temperature range to Skyrail, suggesting that rainfall was more important for timing of flowering activity. Fruiting was different from flowering with peak activity at Davies Creek, Robson Creek, Mt Lewis and DRO occurring later in the year during the build-up (November-December) while Skyrail presented peak activity in the dry season (Fig. 4). The upland sites had different soil characteristics to the lowland sites (Supplementary Table S1), and soil properties have been shown to influence phenological timing in previous studies (Cardoso *et al*. 2012; Valdez-Hernández *et al*. 2010). While there are insufficient data points to generate statistically robust conclusions it seems clear that in the timing of phenology in the Wet Tropics there is an interplay among altitude, climate and soils that influences flowering and fruiting differently. This interplay in the factors that are driving the onset and intensity of activity is presumably due to the different cues for flowering versus fruiting that are associated with resource limitations and competition. Sub-regional variation in phenological timing may impact frugivore and pollinator activity. For example, *Cardwellia* produces massive flowering, which is well known to improve pollinator success (Seifan *et al*. 2014), but because *Cardwellia* presents sub-regional variation in flowering seasonality, pollination success might not be the same for each area in a given year.

Effects of soil properties in tree phenology are understudied. We found a significant correlation between the onset date of flowering and various soil characteristics. Earlier flowering onset was

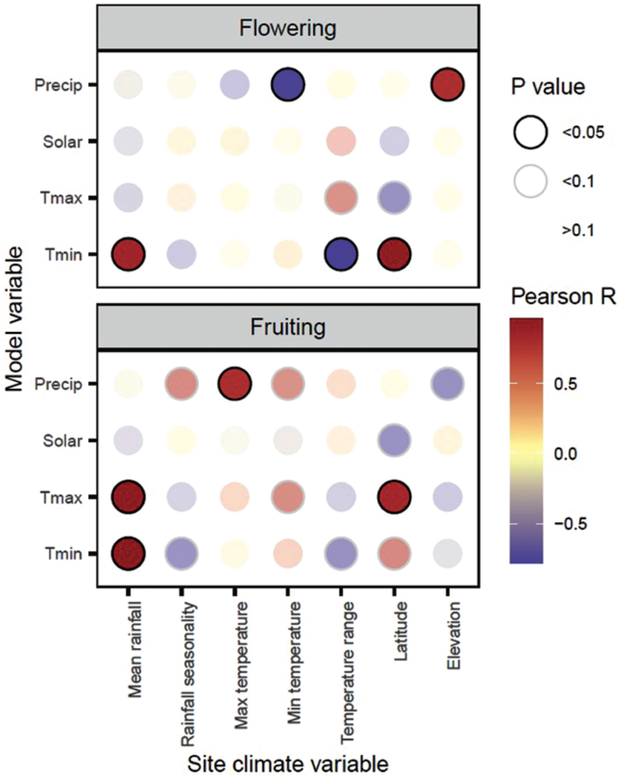

Figure 6: Pearson correlation between the different climate parameters in the GLMM model (absolute value of GLMM beta coefficients) and the site climate variables for a) flowering and b) fruiting across the seven locations in the Wet Tropics of Queensland, Australia. Significant relationships are presented with black outside borders.

correlated with higher clay and nitrogen in the soil, while increased presence of sand was correlated with later flowering onset. Sand is not able to retain high amounts of water (Bordolo *et al.* 2019), while clay in soils make the opposite, leading to higher water retention (Hall *et al.* 1977). Nitrogen effect on flowering time has been previously suggested to be species-specific. In some tree species, the application of N was found to promote flowering and increase flowering intensity (Zhang *et al.* 2022). Our results show that nitrogen in the soil positively affects flowering time in *Cardwellia sublimis*.

The effect of elevation, however, is interesting, as contrasting results, where flowering occurs later in higher areas, have been found in many temperate systems (Du *et al.* 2020). The response to altitude may be species-specific and vary with the type of forest and climate system. For example, studying temperate species in a common garden, Vitasse *et al.* (2009) found that along the same climatic gradient, species can show opposite patterns for leaf flushing. Although they did not study flowering in tropical species, it is interesting to note that relationships between phenological timing and elevation are not consistent across species.

The biggest influence on the timing of flowering onset was minimum and maximum temperature, both total and mean date. Temperature was correlated with flowering in multiple sites, as seen by the models' results. In tropical rainforests, temperature is not as expected to influence flowering as solar radiation. However, our results show that temperature is indeed important for the phenology of *Cardwellia*. Wetter sites had an earlier onset of flowering, while hotter sites had a later flowering onset. Since *Cardwellia* has the flowering onset at the end of the dry season, it is expected that changes to the onset of rainfall would have effects on flowering time. Davies Creek and Robson Creek had the earliest onset of flowering which could mean earlier onset of fruit development, influencing the resources available for seed germination. In agreement with this mean fruiting was advanced at these two sites when compared to Mt Lewis and Skyrail (DRO is a special case as mean flowering activity is evenly spread throughout the year). *Cardwellia* seeds are large and wind dispersed. Wind-dispersed seeds usually have no special adaptations against water loss or herbivory, being protected by a thin papery layer only once the fruit opens to release the seeds. To avoid death due to desiccation, in cases where seeds are released too early before the first rains of the wet season, the seeds would benefit from immediate germination. It is possible then that the timing of the sequence flower initiation-anthesis-fruit maturation-seed release has been evolutionary adapted to have the seeds hitting the ground at the start of the wet season, just when conditions are right to germinate and with a good chance of continued wet weather as the seedlings become established, as proposed by the 'optimal time of germination' hypothesis explored by van Schaik *et al.* (1993). Our results suggest that the ideal timing for seed germination might change with location due to local climate variability, there are very significant differences in rainfall across the sites, which would agree with the ideal time for fruiting and hence seed germination being dependent on local resource availability.

Variation in response to climate

The relative importance of climate drivers on phenological activity—as well as the strength of their influence—differed substantially among sites. For example, solar radiation had strong effects on flowering activity at Robson Creek and Skyrail sites, but negligible or no influence at DRO and Davies Creek.

When assessing fruiting, we found that rainfall was influential only at DRO and Skyrail sites 1 and 2, but not at the other sites. At Robson Creek solar radiation was the only influential variable and at Mt Lewis no climate variable had a notable effect. For Davies Creek and DRO, fruiting peaked at low minimum temperature and high maximum temperature, respectively, showing opposite influence—hence when the temperature range was highest. Conversely, at the DRO site, maximum temperature had a negative effect on fruiting, but a positive effect at the three Skyrail sites. The opposite direction of temperature effects on fruiting at DRO shows that fruiting occurs when the temperature range increases. Higher temperature ranges are indicative of transition seasons with increased solar radiation, which has been suggested to promote fruiting in other tropical moist forests (Chapman *et al.* 1999, 2018) and the peak fruiting activity for these sites agrees with this. For Davies Creek for Davies Creek the peak was in the dry-wet transition while for Skyrail the peak was in the wet-dry transition. These results suggest that the factors limiting phenological activity were quite variable across the studied sites and were site specific.

We found evidence of a relationship between the importance of different climate drivers and site-level climate. Solar radiation, for example, was less important for determining fruiting patterns in the northern sites which are somewhat closer to the equator where it varies less throughout the year. Maximum temperature was more important in hotter sites, but the effects differed with a positive effect of higher maximum temperature at Skyrail and a negative effect in the DRO. This pattern—of limiting climate variables influencing phenological patterns in contrasting ways—has been observed in other systems, including leaf flushing in the Amazon (Jones *et al.* 2014) and fruiting patterns at the community level in Uganda (Chapman *et al.* 2005). Conversely, Ramos and Santos (2005) analysed the phenology of *Psychotria tenuinervis* in Atlantic rainforest and found that the phenological patterns of flowering and fruiting were similar among the studied fragments, even though the fragments presented different climate patterns. They argued that these results suggest the influence of evolutionary factors, such as the pressure of animal dispersal vectors on biotically dispersed fruit species.

The hotter and somewhat drier Skyrail site can provide insights into how the species would respond to global warming in the other sites. It is possible that flowering and fruiting, for example, will be delayed at Mt Lewis, Davies Creek and Robson Creek, becoming more similar to the patterns found in Skyrail. How the population in Skyrail will respond to climate change, however, is not possible to predict. It is also possible to imagine that in these sites, the climate drivers of phenological activity may potentially alter as vapour pressure deficit as well as temperature is likely to alter as global change occurs and changes of both in concert will have a significant effect on plant performance (Grossiord *et al.* 2020).

Implications for phenology research

As phenological studies are often focused on a plant community at a single location or a single population of a species, our results have important implications for understanding phenological patterns. For example, single-site studies may not capture the full response of a species or community to environmental drivers, and hence incorrectly assess the potential responses to climate change. Further, our comparison of the intra-site variation in the Skyrail transect reveals that modelled relationships between climate drivers and phenological activity may differ even within a single site, though to a lesser degree than between distant sites. Based on our results it is clear that future phenological studies would benefit from assessing patterns for species over multiple sites which will allow local limiting factors to be properly assessed.

Implications for conservation and restoration

Different phenological responses to climate may have important implications for climate change responses and species conservation if they represent genuine adaptation. For example, different populations of the same species in different locations may respond differently to climate change and hence local populations may go extinct while others experience increased local abundance (Benito Garzón *et al.* 2011). Similarly, ecological restoration programs that rely on mixing provenances of a species may result in plant populations that are not able to interbreed if individuals are reproductive in different periods due to different responses to climate cues. Additionally, understanding the phenological patterns of restoration species is useful to ensure that restored sites can provide resources for fauna species year-round (Buisson *et al.* 2017). Differences in phenological patterns of individuals from different provenances, in particular provenances that have not been studied, may impact this understanding. However, if different phenological responses are due to phenotypic plasticity and changing physiological responses to water availability or temperature patterns rather than adaptation, these issues may not occur. Therefore, long-term pot trials and provenance trials that assess phenological patterns under controlled environmental conditions are needed to delineate the causes of the varied responses to climate (Alberto *et al*. 2013).

Caveats

Studies included in this multi-site assessment varied in their methods, length, and population size. Phenological observations were conducted by different observers and using different methods, including on-the-ground, cable-car gondolas and canopy cranes. We also presented phenological observations that were carried out during different time periods and for different lengths of time. To account for these effects, we made comparisons among sites using comparable indices, and over the same time periods where possible. The datasets also presented different sample sizes, and although the statistical methods chosen were able to cope with this it may nevertheless slightly impact our understanding of populations.

CONCLUSIONS

Phenological studies are an important tool for assessing the ecological responses of species and communities to environmental change, such as climate change and land-use change. However, studies are often carried out at a single site which limits our understanding of how responses to the local environment impact our understanding of the relationship between climate and phenology. By studying the response of a single species, *Cardwellia*, at five geographically well-separated sites, we have shown that the relationship between climate and phenological patterns varies between sites and it may be influenced by local climate, soils, topography and latitude. We also show that the timing and seasonality of phenological activity are specific to local conditions. Current modelling frameworks used to predict the potential impacts of climate change on plant phenology do not take into account the interaction of environmental drivers at the site level and how this may influence phenological timing. These results have important implications then for the study and modelling of phenological phenomena, ecological restoration and for the conservation of species with limited environmental ranges.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Information for each studied site.

Table S2: Analysis of variance of mean annual climate variables among sites.

Table S3: Results of Watson-Williams analysis comparing the circular distribution between sites.

Table S4: GLMMs results for flowering.

Table S5: GLMMs results for fruiting.

Figure S1: Results of cluster analysis grouping the studied sites based on their soil characteristics (CEC, N, clay, silt, sand).

Figure S2: Significant circular-linear relationships between the onset date of flowering soil variables.

Figure S3: Pearson correlation between beta coefficients from GLMMs with flowering as the response variable, and annual climate variables and soil characteristics as independent variables, summarised in Fig. 6.

Figure S4: Pearson correlation between beta coefficients from GLMMs with fruiting as the response variable, and annual climate variables and soil characteristics as independent variables, summarised in Fig. 6.

Authors' Contributions

Nara Vogado (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft), Jayden Engert (Conceptualization, Formal analysis, Methodology, Writing—review & editing), Peter Green (Data curation, Investigation, Writing—review & editing), and Michael Liddell (Methodology, Supervision, Writing—review & editing)

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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