Flowering and fruiting patterns of woody species in the tropical montane evergreen forest of southern India

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Reproductive phenology in tropical forests has been potentially influenced by climatic cues, biotic interactions and phylogenetic constraints at the community level. Studies on this relationship in the tropical montane evergreen forest of south India are rather lacking. We made reproductive phonological observations on 497 individuals falling under 66 species, in 52 genera and 31 families, at weekly intervals for a period of three years from January 2002 to December 2004 consecutively. At the community level, most of the woody species had annual rhythm and showed regular seasonal reproductive cycle. Flowering and fruiting patterns were significantly related with climatic variables, seasonal patterns were significantly associated with biotic factors and further found that closely related species of flowering and fruiting showed similar in times at climatic seasonality. Therefore the study suggests that community level reproductive phenology was influenced by climatic variables, biotic interaction and evolutionary perspectives.

Keywords: Biotic interactions, climatic factors, reproductive phenology, tropical forests.

FLOWERING and fruiting patterns ultimately determine the reproductive success in plants[1–3]. These phenological events are strongly controlled by climatic factors and evolutionary processes[1,4–6]. The timing of flowering and fruiting has major influences on biological processes from the organismal to ecosystem scales. For instance, studies have shown that flowering and fruiting seasonality influences species demography, biotic interactions and other ecosystem processes[7–11].

Asia has a variety of forest types, including temperate forests, subtropical forests, montane evergreen rainforests and lowland tropical rainforests with varying degrees of seasonality[12–16]. The reproductive phenology of some of these forests has been extensively studied at the individual, population and community level[6,14,15,17]. However, in the southern parts of Asia, especially India, relatively few phenology studies have been conducted in tropical wet evergreen and dry deciduous rainforests[13,18]. At present and to the best of our knowledge, there is no reliable and long-term information on community-level reproductive phenology of tropical montane evergreen rainforests. Knowledge of how climate change and evolutionary constraints affect flowering and fruiting patterns is critical because it provides useful insight and in-depth understanding for monitoring plant responses to environmental change and for predicting its consequences on ecosystem functioning[19].

In South India, a majority of tropical wet evergreen and dry deciduous rainforest species exhibit annual flowering patterns due to regular reproductive cycles[13,18]. However, studies predict that climate seasonality might shape community-level flowering frequency within this region. On the other hand, in aseasonal lowland rainforests, most species tend to show irregular flowering patterns (occurrence of mast flowering every 3–4 years), and these patterns are predominantly driven by periodic drought[14]. Supra-annual flowering events (mass flowering once every two years) have been recorded in tropical rainforests of Costa Rica[20,21] and subtropical forests of Taiwan[5]. However, previous studies did not find supra-annual flowering patterns in the forests of North East and South India[12,13,18]. Global climate change causes variation in the timing, duration and synchronization of phenological events in tropical forests[22,23]. The major drivers of changes in phenology patterns in tropical rainforests include rainfall, temperature and day length[1,4]. Previous studies of plant communities under seasonal climate reported that phenological events usually correlate with moisture availability[24,25]. Temperature and/or precipitation seasonality may also influence regular flowering, while solar-related factors could influence flower synchrony[4]. In tropical wet and dry deciduous forests, reproductive phenology negatively correlates with monthly rainfall[13,18]. Fruiting patterns in tropical montane rainforests showed significant positive correlations with the number of rainy days but not with temperature[26], whereas leaf initiation showed positive correlation with temperature[27].

Seasonal changes in reproductive phenology resulting from environmental variability are crucial in shaping biotic interactions such as pollination and dispersal syndromes. These changes in environmental determinants interact with other biotic factors leading to selective pressures that influence overall reproductive strategies and ecological processes[5]. Consequently, seasonal activities of pollinators, seed predators or seed dispersers are often associated with plant reproductive patterns[28,29]. For instance, the peak fruiting of fleshy-fruited species coincides with the period when dispersers are most abundant[28,30,31]. Wind-dispersed species generally shed their seeds during the windiest season[32–35]. The timing of community peak flowering during the dry season attracts

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*For correspondence. (e-mail: dmohandass997@yahoo.com) more pollinators[36], because pollinators are more active in the dry season[20]. Therefore, seasonal reproductive patterns are highly associated with biotic interactions resulting from mutual benefits for collective reproductive success and high survival rate.

In order to understand the evolutionary perspectives we examined the relationship of closely related species with climatic variables, seasonal patterns and biotic interactions. The closely related species with similar reproductive phenology and seasonal patterns attract more pollinator assemblage and dispersal modes[36–39]. The high-altitude region is wet, sky is relatively cloudy and the daylight is shorter. The upper Nilgiris being a high-altitude region, temperature and rainfall can better indicate the relationship between climatic variables and reproductive phenology.

The main questions being addressed in this study are: (i) What are the flowering and fruiting patterns available in tropical montane evergreen forests of the Nilgiri Mountains? (ii) How are climatic variables correlated with rainfall and temperature among all the species and between closely related species? (iii) How are flowering and fruiting seasonal patterns related to biotic interactions? (iv) Do closely related species have similar flowering and fruiting time/season?

The study was conducted in the tropical montane evergreen forests of the upper Nilgiri Mountains. The study plot was established in the Korakundah Reserve Forest located 60 km from the southwestern side of the Nilgiri Headquarters (11°13.617′N, 76°35.546′E). Detailed site and topographic information is reported elsewhere[40,41]. There are many discrete patches of montane forests in the upper Nilgiri Mountains. However, most of these forest patches are surrounded by exotic tree plantations (e.g. Australian black wattle and Blue gum), thus preventing natural forest expansion. Furthermore, most of the natural forest areas are under high pressure from anthropogenic activities, especially agricultural expansion and human settlement. These have led to progressive forest fragmentation and isolation[40,41]. The dominant understorey species include *Psychotria nilgiriensis* and *Lasianthus venulosus* (Rubiaceae), and the dominant canopy trees are *Litsea wightiana*, *Symplocos foliosa*, *Mahonia leschenaultiana* and *Neolitsea cassia*. Lauraceae and Rubiaceae are the two dominant plant families with high diversity and stem density for certain species[40].

Climate within the region is mostly influenced by two monsoons; the southwest monsoon runs from May to September and the northeast monsoon from October to November, while the remaining months (December to April) are dry season. The mean annual rainfall (1996–2006) and temperature (2000–2006) were recorded from Korakundah Tea Estate (Figure 1). Seasonal patterns were classified into dry (December–April), first wet (May–August) and second wet (September–November) seasons.

Within the selected forest patch (size = 1.08 ha), 6–10 reproductive individuals of each tree species were located, marked and tagged with sequentially numbered aluminum tags. Voucher specimens of each species were collected and identified using expert opinion and with the help of flora keys. Where possible, specimens were taken to the Herbarium of the Botanical Survey of India, Coimbatore, for taxonomic cross-validation. All phenological observations were conducted on weekly intervals from January 2002 to December 2004. Phenological events monitored included budding, first flowering (bud opening), peak flowering, last flowering (flower fall), fruit initiation, fruit maturation and ripening. In the present study, we only focus on two phenological events – first flowering (henceforth flowering) and fruit ripening (henceforth fruiting).

Flowering patterns were classified based on the frequency of flowering and on previously published literature[5,21,42] and included annual (once a year), sub-annual (twice a year) and supra-annual (once every two years) flowering.

The pollination mode, fruit type and dispersal mode of each target species were carefully recorded through direct field observations. Pollination mode was categorized into insect (bees, beetles, butterflies, small diverse), bird and wind pollination (D.M., pers. obs.). Fruits types recorded were either fleshy (berries, syncarps, drupes and pomes) or dry (including dehiscent fruits such as legumes, follicles and capsules, and indehiscent fruits such as achene, samara, nuts, caryopsis and schizocarp[43,44]. Dispersal mode and syndrome was also recorded as follows: (i) autochory, dispersed via explosive mechanisms triggered by natural factors; (ii) anemochory, dispersed by wind, and (iii) zoochory, dispersed by animals.

We used generalized linear model (GLM) to find the relationship between climatic variables (monthly rainfall and temperature) and flowering and fruiting of species, to test their estimates of standard errors and type I errors are more realistic relationship between climate and phenology pattern. The same test was conducted to find the relationship between climatic variables and flowering and

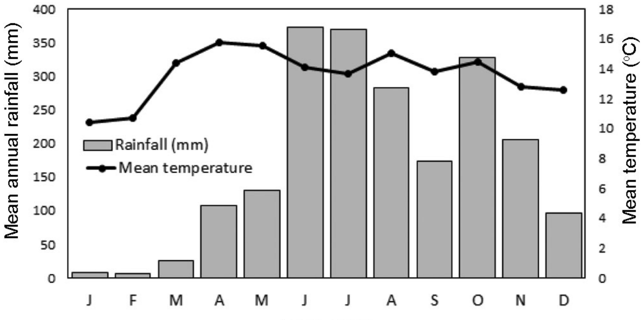

Figure 1. Rainfall and temperature pattern of Korakundah study area in the Nilgiri Mountains, South India.

Table 1. Generalized linear model of multiple regression on effect of climate on flowering and fruiting among overall species. Effect of climate is assessed by the number of species in flowering and fruiting in the tropical montane evergreen rainforests of Nilgiri Mountains, southern India

Independent variables	Coefficient	Standard error	*t*-test	*P*-value
Flowering				
Intercept	–42.4189			
Rainfall	–0.01965	0.01122	–1.751	0.0892
Temperature	3.2161	0.7990	4.025	0.0003
Fruiting				
Intercept	22.7002			
Rainfall	0.02711	0.008091	3.351	0.0020
Temperature	–0.4388	0.5762	–0.762	0.4517

Table 2. Mean flowering and fruiting duration over three consecutive years analysed by Tukey HSD pairwise comparison in the tropical seasonal rainforests of southwestern China

Phenology	2002 (mean ± SE)	2003 (mean ± SE)	2004 (mean ± SE)
Flowering duration	7.91 ± 0.37^{ns}	8.35 ± 0.33^{ns}	8.93 ± 0.22**
Fruiting duration	17.16 ± 0.97	17.23 ± 1.03*	18.9 ± 0.78**

Tukey HSD pairwise comparison, $P < 0.05$, $P < 0.01$.

fruiting of closely related species. The duration of flowering and fruiting was tested by ANOVA. Comparison of flowering and fruiting duration between the years was analysed by Wilcoxon pairwise comparison. The duration of flowering and fruiting of each species was tested by one-sample test. Percentage of flowering and fruiting frequency in relation with seasonal patterns and reproductive traits (pollination mode, fruit types and dispersal mode) was tested by chi-square *G*-test. Statistical analyses were carried out using SPSS statistical software version 17.0.

A total of 497 individuals falling under 66 species, 52 genera and 31 families were observed for their reproducetive phenology. Among them, 51 species were trees (77%), 8 were shrubs (12%) and 7 lianas (11%). Forty-eight (73%) species were annual, 9 (14%) supra-annual and 9 (14%) were sub-annual. Among the sub-annual species, two were seasonal sub-annual (dry and second wet season) and seven were aseasonal sub-annual (flowered during December–March) (Appendix 1).

Majority of the species studied at community level had flowering peak in the dry season and fruiting peak in the wet season. The average flowering was 16.1 ± 2.4 and fruiting was 18.5 ± 1.5 throughout the study period. The average flowering in 2002 was 15.4 ± 4.2, in 2003, 15.5 ± 4.1 and in 2004 it was 17.4 ± 4.4; the average fruiting in 2002 was 17.5 ± 2.8, in 2003 was 18.0 ± 2.6 and in 2004 it was 19.9 ± 2.9. This indicates flowering and fruiting frequency differed significantly (flowering: *t*-test = 24.74; d*f* = 2, $P = 0.0016$; fruiting: *t*-test = 25.26, d*f* = 2, $P = 0.0016$) over three consecutive years.

In 2002, 61% of species had peak in flowering, in 2003 it was 62% and in 2004 it was 65%. In all the three years, peak flowering occurred in March. During these years peak fruiting occurred in June; in 2002, 53% of species had peak fruiting, 52% in 2003 and 56% in 2004 (Figure 2).

In the case of a few trees like *Michelia nilagirica* and *Symplocos foliosa*, the onset of flowering occurred during the second wet season. Dominant supra-annual species included *Cinnamomum malabatrum* and *Syzygium calophyllifolium*. *Mahonia napaulensis* and *Photinia integrifolia* were sub-annuals. All species are evergreen, except *Nothopodytes nimmoniana* that withered during the dry season.

In tropical montane evergreen forest of the Nilgiris, the GLM model revealed that flowering did not show any significant relationship with monthly rainfall ($r = –0.33$, $t = –1.75$, $P = 0.089$) and showed significant positive relationship with temperature ($r = 0.589$, $t = 4.025$, $P = 0.0003$). On the contrary, fruiting showed significant positive relationship with monthly rainfall ($r = 0.52$, *t*-test = 3.351, $P = 0.002$) and there was no significant trend with temperature ($r = –0.197$, *t*-test = –0.762, $P = 0.452$; Table 1).

Duration of flowering and fruiting differed significantly ($F_{66,198} = 7.91$; $P = 0.00057$; fruits; $F_{66,198} = 4.521$, $P = 0.012$) for the three years. At the community level, duration of flowering significantly differed in 2004 when compared with that in 2002 and 2003. However, duration of flowering did not differ between 2002 and 2003. Duration of fruiting significantly differed in 2003 and 2004 compared to 2002 (Table 2). This indicates that flowering and fruiting duration is not consistent over three consecutive years at the community level.

At the community level, flowering and fruiting was significantly associated with seasonal patterns (*G*-test = 82.83, d*f* = 5, $P = 0.00001$). It showed 82% of peak

Table 3. Frequency relationship between seasonal patterns and reproductive phenology (flowering and fruiting) in the tropical montane evergreen forests of the Nilgiri Mountains, South India

Phenology	Dry	Dry/first wet	First wet	First/second wet	Second wet	Second wet/dry
Flowering	53 (35)	29 (19)	9 (6)	2 (1)	5 (3)	3 (2)
Fruiting	3 (2)	23 (15)	38 (25)	17 (11)	17 (11)	3 (2)

Percentage values are displayed while frequency is indicated within brackets.

Table 4. Frequency relationship between seasonal patterns and reproductive traits of phenology of the studied species in the tropical montane evergreen forests of the Nilgiri Mountains

Reproductive traits	Dry	Dry/first wet	First wet	First/second wet	Second wet	Second wet/dry
Pollination mode						
Bees	12 (8)	11 (7)	6 (4)	2 (1)	2 (1)	0 (0)
Beetles	2 (1)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Birds	6 (4)	2 (1)	0 (0)	0 (0)	0 (0)	2 (1)
Butterfly	5 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Small diverse insects	24 (16)	14 (9)	3 (2)	0 (0)	3 (2)	2 (1)
Wind	5 (3)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Fruit types						
Dry	0 (0)	6 (4)	0 (0)	0 (0)	0 (0)	0 (0)
Fleshy	3 (2)	17 (11)	38 (25)	17 (11)	17 (11)	3 (2)
Dispersal mode						
Anemochory	0 (0)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Autochory	0 (0)	6 (4)	0 (0)	0 (0)	0 (0)	0 (0)
Zoochory	3 (2)	15 (10)	38 (25)	17 (11)	17 (11)	3 (2)

Percentage values are displayed while frequency is indicated within brackets.

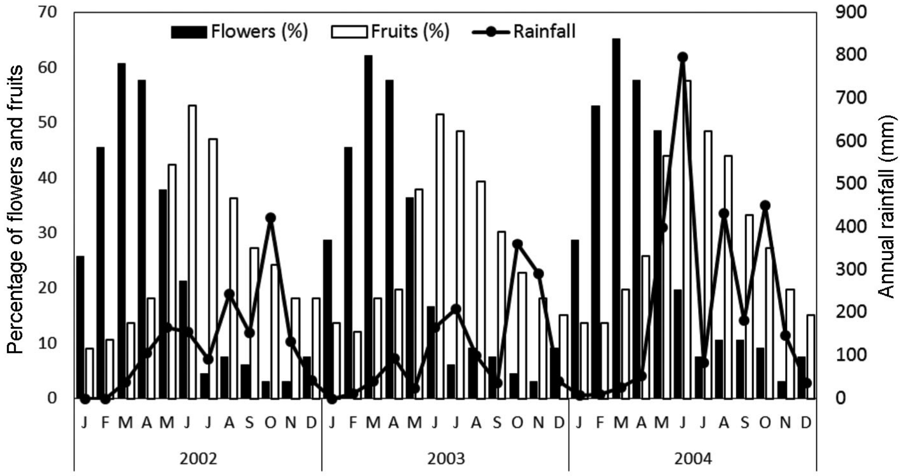

Figure 2. Frequency of flowering and fruiting in relation to rainfall in the tropical montane evergreen forests of the Nilgiri Mountains.

flowering in the dry season (December–April), which extended into the first wet season (May–July; Table 3). However, most of the species had flowering peak in the dry season (February–March; Figure 2). Peak fruiting was recorded at the end of the dry season and first wet season in 61% (May–July) of the species. This extended to the second wet season (August–October) in 17% of the species, but in another 17% of the species fruiting occurred in the second wet season (August–November) only (Table 3).

Pollination mode was not significantly associated with seasonal patterns (*G*-test = 20.99, d*f* = 25, $P = 0.72$). In the dry season 43% of species was pollinated by diverse insects and 12% by bees only, while in the following wet season it was 14% by diverse insects and 11% by bees (Table 4). This indicates that the percentage frequency of

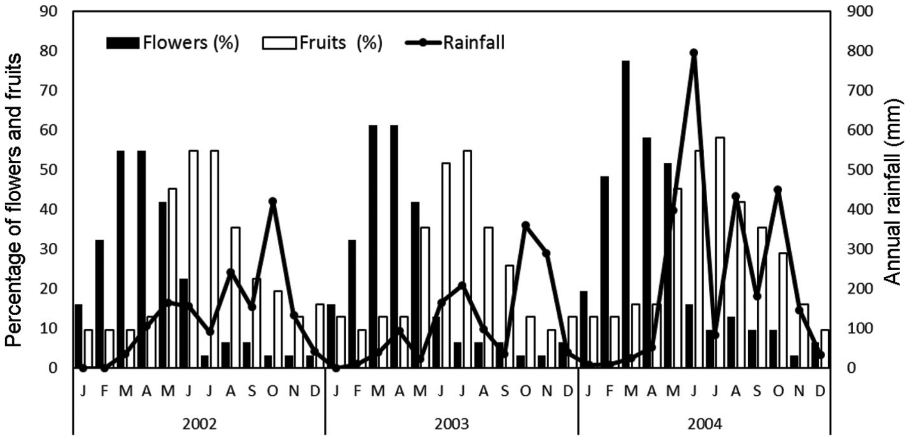

Figure 3. Frequency of flowering and fruiting of closely related species in relation to rainfall in the tropical montane evergreen forest of the Nilgiri Mountains.

Table 5. GLM of multiple regression on the effect of climate on flowering and fruiting among closely related species. Effect of climate is assessed by the number of species in flowering and fruiting in the tropical montane evergreen rainforests of the Nilgiri Mountains

Independent variables	Coefficient	Standard error	*t*-test	*P*-value
Flowering				
Intercept	–23.9313			
Rainfall	–0.00711	0.005255	–1.352	0.1855
Temperature	1.6849	0.3744	4.501	0.0001
Fruiting				
Intercept	10.4068			
Rainfall	0.01260	0.04739	2.658	0.012
Temperature	–0.2232	0.3376	–0.661	0.513

Table 6. Frequency relationship between phylogeny of flowering and fruiting and seasonal patterns in the tropical montane evergreen forests of the Nilgiri Mountains

	Flowering						Fruiting					
Phylogeny	Dry	Dry/ first wet	First wet	First/ second wet	Second wet	Second wet/dry	Dry	Dry/ first wet	First wet	First/ second wet	Second wet	Second wet/dry
Celastraceae	6	3	0	0	0	0	0	0	6	0	3	0
Lauraceae	16	13	3	0	0	0	0	0	19	3	6	3
Myrtaceae	10	0	0	0	3	0	0	10	3	0	0	0
Rosaceae	3	10	0	0	0	3	0	6	3	6	0	0
Rubiaceae	10	3	3	3	0	0	0	3	10	6	0	0
Symplocaceae	3	3	0	0	3	0	3	3	3	0	0	0

Percentage values are displayed while frequency is indicated within brackets.

pollination mode is significantly higher during the dry season and extend into the wet or peak flowering season. Fruit types are significantly associated with different seasonal patterns (*G*-test = 21.8, d*f* = 5, *P* = 0.0006). The percentage of fleshy fruits (38) was higher in the first wet season, followed by dry/first wet season and second wet season. Dispersal mode was significantly associated with seasonal patterns (*G*-test = 25.72, d*f* = 10, *P* = 0.0041). Zoochory dispersal mode (38%) was significantly higher in the first wet season followed by the second wet season. A few species were autochory and anemochory, and they dispersed fruits during the dry/first wet season. The above shows that dispersal mode in majority of the species is significantly higher in the wet season that facilitates seed germination and seedling regeneration.

Flowering in closely related species did not show any significant trends with rainfall (Figure 3), but showed significant positive relation with temperature (*r* = 0.62;

Table 7. Frequency relationship between phylogeny and reproductive traits of studied phenological events in the tropical montane evergreen forests of the Nilgiri Mountains

	Pollination mode				Fruit type		Dispersal mode
Phylogeny	Bees	Beetles	Butterfly	Small diverse insects	Fleshy	Dry	Zoochory
Celastraceae	0 (0)	0 (0)	0 (0)	10 (3)	10 (3)	0 (0)	10 (3)
Lauraceae	0 (0)	3 (1)	0 (0)	30 (9)	32 (10)	0 (0)	32 (10)
Myrtaceae	0 (0)	0 (0)	3 (1)	10 (3)	13 (4)	0 (0)	13 (4)
Rosaceae	10 (3)	0 (0)	0 (0)	6 (2)	16 (5)	0 (0)	16 (5)
Rubiaceae	16 (5)	0 (0)	3 (1)	0 (0)	19 (6)	0 (0)	6 (19)
Symplocaceae	6 (2)	3 (1)	0 (0)	0 (0)	10 (3)	0 (0)	10 (3)

Percentage values are displayed while frequency is indicated within brackets.

$t = 4.50$, $P = 0.0001$). On the contrary, fruiting in closely related species showed significant positive relationship with rainfall ($r = 0.43$; $t = 2.66$, $P = 0.012$), but did not show any significant trend with temperature (Table 5).

Majority (81%) of closely related species flowered in the dry/first wet season. A few species had flowering scattered in different seasons (Table 6). Sixty-eight per cent of closely related species fruited in the dry/first wet season and 16% in the second wet season. This shows that majority of flowering and fruiting are synchronized among closely related species (Figure 3).

Majority of closely related species was pollinated by small diverse insects (55%) and bees (32%). A few species were pollinated by beetles and butterflies, especially in members of Lauraceae and Symplocaceae (Table 7). Most of the closely related species were fleshy fruits (100%), and thus favoured by zoochory (100%) dispersers. None of the closely related species produced dry fruits. This indicates that closely related species favour similar pollinators and dispersal pattern.

A large number of species in the tropical montane evergreen forests of the upper Nilgiris displayed a seasonal reproductive cycle. Majority of the woody species showed regular and annual flowering pattern. There were several species with irregular flowering and were considered as supra-annual. A few species were sub-annual that flowered during the dry and second wet season. A few species (such as *M. nilagirica* and *S. foliosa*) flowered during the second wet season only; this might be influenced by rainfall and temperature. In the study area, flowering was influenced by temperature and fruiting by rainfall; thus climatic variables played a major role in shaping community reproductive patterns. Pollination and seed dispersal were influenced by the season when the plant flowered and fruited as these were controlled by biotic factors like pollinators and dispersal agents. For example, pollinators were more in numbers when peak flowering took place during the dry season. Dispersers were high in number when fleshy fruits were in peak in the first and second wet season. Flowering and fruiting of closely related species were significantly influenced by climatic variables. Moreover, closely related species had similar flowering and fruiting time, which showed that reproductive phenology is also linked to evolution of the species.

In the tropical forest of the Nilgiris, peak flowering took place at the end of the dry season (March–April) and in the early wet season (May). This is similar to previous reports from other tropical rainforests of Southeast Asia and wet evergreen of the Western Ghats[5,13,14]. Nevertheless, in the tropical montane forests of the Nilgiris, peak flowering in a large number of species occurred during the dry season, a phenomenon similar to that of tropical dry deciduous forests[45]. Previous studies showed that flowering peaked within one month of the onset of the rainiest season[46], a pattern displayed by plants with seasonal reproductive cycle. In the tropical dry forests, high temperature, low humidity and low soil moisture make flowering peak during the dry season. In the present study, temperature showed significant positive responses to flowering, similar to the observations made in the Atlantic rainforest[47]. Rainfall did not show any significant trends with flowering, a finding similar to that of a previous study from tropical wet forests of the Western Ghats[13]. As majority of the species flowered during drier months, the factors controlling flowering may be related to daylight (stronger sunrise in high altitude, more sunlight and thus higher temperature), which helped in bud break and flower opening, as was previously reported from the tropical dry and deciduous forests[4,45]. In the present study, climatic variables were highly correlated with reproductive phenology, with a little annual variation among several species. This indicates that photoperiod, which has no significant inter-annual variation, triggers flowering in plants in the study area and can be considered as the most reliable environmental variable for reproductive phenological study[48]. In aseasonal rainforests, photoperiod is generally regarded as the most reliable flowering trigger for many woody tree species[4,34,47,49–51]. Thus, photoperiod or sun-related factors could be the primary signal for flowering in most upper Nilgiri woody species.

Majority of fruiting was observed in the first wet season during May–July and extended into the second wet season due to variation at the population level, where some individuals showed seasonal fruiting cycle. Flowering in some species during the second wet season coincided with the species showing sub-annual flowering. This indicates that fruiting phenology at the community level followed the optimal time for seed germination, which is during prolonged wet season, as supported by the germination hypothesis[46]. In the seasonal dry forest of Barro Colorado Island and dry forest of Jamaica, germination showed a community-wide peak at the onset of rainfall[52,53]. During the first wet season that is during May–August, the study area receives its 60% of its annual rainfall through the SW monsoon. During this time seed germination takes place in majority of the species, as was reported in previous studies[5,46,47].

Duration of flowering and fruiting was measured by the number of weekly episodes of flowering and fruiting. Flowering and fruiting duration varied significantly over the three year study period in 92% and 91% of the species respectively. Change in environmental parameters associated with the season might have influenced the duration and timing of flowering and fruiting[20]. The change in timing of first flowering decides the timing and duration of fruiting phenophase[23]. In the upper Nilgiris, duration of flowering was shorter (8.4 ± 0.3) and fruiting was longer (17.76 ± 0.57) at the community level and extended into two distinctive seasons, i.e. first and second wet season. However, some species that flowered in the early dry season had short duration fruiting and mature fruits were available at end of the dry season itself, just in a span of two months. Further studies are needed to understand the relationship between duration of reproductive phenology and climatic variables.

Flowering in majority of plants took place during the dry season; and this may increase the visits of shared pollen vectors, which is in agreement with the facilitation hypothesis[51]. This flowering pattern attracts many pollinators to the flowers, thereby increasing the possibility of better fertilization and co-existence of diverse pollinators. During peak flowering, majority of the species were pollinated by insects; this indicates flowering seasonality attracts diverse pollinators and thus pollination is influenced by pollinators[18,36]. Bees, birds, diverse insect pollination guild were active during the dry season. In the early dry season (February and March), when flowering started, *Apis cerana*, *Nomia ellioti*, carpenter bees, flies and other diverse insects were the major pollinators. *Apis dorsata* was a delayed pollinator and visited only during late-dry season (April and May).

Fruiting was highly concentrated in the first wet season (38%), which showed seasonal fruiting. Most of the fruits were fleshy and thus the seed germination was influenced by soil moisture availability and dispersal influenced by animal dispersal agents. Anemochory and autochory mechanisms of seed dispersal were noticed in a limited number of species only. Species where fruiting occurred in the dry/first wet season (23%) and second wet season (17%), indicated fruiting also followed seasonal pattern. During this period, the common dispersers were recorded as Nilgiri langur, birds, bear and dhole (D.M., pers. obs.). Most zoochorous species in the Nilgiris exhibited a first fruiting peak during the SW monsoon period and second fruiting peak in autumn. Fruiting peak during SW monsoon attracts Nilgiri langur, bear and birds, which act as excellent seed dispersers. During peak fruiting in autumn, birds were seen as the seed dispersers and seasonal migratory birds were the ones most attracted[54]. For zoochorous species in higher latitude and altitude with peak fruiting in autumn, the species richness of local birds might increase the chance of seed dispersal[55].

Climatic variables played a significant role in reproductive phenology of closely related species. Rainfall had a negative effect on flowering but positive effect on fruiting, whereas temperature showed positive effect on flowering and negative effect on fruiting. Thus climatic factors in association with phylogeny influence reproductive phenology of plants in the Nilgiris, but this may not be true at the community level[5,25,51].

Majority of closely related species flowered in the dry season (February and March), which continued to the first wet season (Figure 3). However, there was a single staggered flowering, restricted to single season, as in the case of *S. foliosa* that flowered during the second wet season. This indicates that tropical montane evergreen forests of the Nilgiris show contrasting phenological trends when compared to rainforests of Barro Colorado Island[36]. However, similar duration of flowering in majority of closely related species confirms that flowering phenologies tend to be similar among congeners. Among closely related species, flowering midpoints also differed between the transition season 65% in the dry season and 45% in the wet season. Peak fruiting in closely related species was not restricted to any particular season; however, fruiting phenology of fleshy fruits was synchronized in the first wet season when rainfall was at a peak. Thus fruiting duration was shorter for the plants with peak fruiting in the first wet season and longer for those with peak fruiting in the second wet season. This suggests that fruiting phenology is similar among closely related species.

The present study shows that closely related species have synchronized flowering and fruiting that also increases pollinator activity, as reported in previous studies[56,57]. Likewise, closely related families prefer diverse pollinators. For instance, members of Rosaceae, Rubiaceae and Symplocaceae are pollinated by bees (32%), whereas those of Celastraceae, Lauraceae and Myrtaceae are pollinated by small diverse insects (50%). Least number of species tends to be pollinated by butterflies and beetles. However, we did not find pollination by birds among closely related species, thus indicating the role of

Appendix 1. Species, family, habit, flowering frequency, flowering months (FL), flowering season, fruiting months (FR), fruiting season, pollination mode, fruit type, dispesal mode characteristics of flowering and fruiting woody species in the tropical montane evergreen of the Nilgiri Mountains, South India

Species	Family	Habit	Flowering frequency	FL months	FL season	FR months	FR season	Pollination mode	Fruit types	Dispersal mode
Berberis tinctoria Lesch.	Berberidaceae	Shrub	Annual	February–April	Dry	May–July	First wet	Bees	Fleshy	Zoochory
Casearia thwaitesii Briq.	Flacourtiaceae	Tree	Sub-annual	February April	Dry	October–February	Second wet	Small diverse insects	Fleshy	Zoochory
Celtis timorensis Span.	Cannabaceae	Tree	Annual	April–June	Dry/first wet	September–December	Second wet	Wind	Fleshy	Zoochory
Cinnamomum macrocarpum Hook. f.	Lauraceae	Tree	Supra annual	January March	Dry	August–November	Second wet	Small diverse insects	Fleshy	Zoochory
Cinnamomum malabatrum (Burm.f.) J.Presl	Lauraceae	Tree	Supra annual	January–March	Dry	August–November	Second wet	Small diverse insects	Fleshy	Zoochory
Cinnamomum sulphuratum. Nees	Lauraceae	Tree	Supra annual	April–May	Dry/first wet	July–September	First/second	Small diverse insects	Fleshy	Zoochory
Cinnamomum wightii Meisner.	Lauraceae	Tree	Annual	April–May	Dry/first wet	June–August	First wet	Beetles	Fleshy	Zoochory
Cissampelopsis walkeri C. Jeffrey & Y.L. Chen	Compositae	Liana	Annual	February–April	Dry	April–July	Dry/first wet	Small diverse insects	Dry	Anemochory
Cryptocarya lawsonii Gamble	Lauraceae	Tree	Annual	April–June	Dry/first wet	November–February	Second/dry	Small diverse insects	Fleshy	Zoochory
Daphniphyllum neilgherrense (Wight) K. Rosenthal	Daphniphyllaceae	Tree	Sub-annual	January April	Dry	June–August	First wet	Wind	Fleshy	Zoochory
Elaeagnus kologa Schlecht.	Elaeagnaceae	Liana	Annual	December–February	Dry	May–June	First wet	Birds	Fleshy	Zoochory
Elaeocarpus hygrophilus Kurz	Elaeocarpaceae	Tree	Annual	February–April	Dry	April–June	Dry/first	Bees	Fleshy	Zoochory
Elaeocarpus recurvatus Corner	Elaeocarpaceae	Tree	Annual	May–July	First wet	November–March	Second/dry	Bees	Fleshy	Zoochory
Euonymus crenulatus Wall. ex Wight & Arn.	Celastraceae	Tree	Annual	April–June	Dry/first	August–September	Second wet	Small diverse insects	Fleshy	Zoochory
Eurya nitida Korth.	Pentaphylacaceae	Tree	Annual	May–June	First wet	August–September	Second wet	Small diverse insects	Fleshy	Zoochory
Gardneria ovata Wall.	Loganiaceae	Liana	Annual	May–July	First wet	October–December	Second wet	Bees	Fleshy	Zoochory
Gaultheria fragrantissima Wall.	Ericaceae	Tree	Annual	January–March	Dry	May–June	First wet	Bees	Fleshy	Zoochory
Glochidion candolleanum (Wight & Arn.) Chakrab. & M. Gangop.	Phyllanthaceae	Tree	Annual	March–April	Dry	September–November	Second wet	Small diverse insects	Fleshy	Zoochory
Gomphandra coriacea Wight.	Stemonuraceae	Tree	Annual	February–April	Dry	June–August	First wet	Small diverse insects	Fleshy	Zoochory
Hedyotis swertioides Hook.f.	Rubiaceae	Shrub	Annual	February–March	Dry	June–October	First/second	Butterfly	Fleshy	Zoochory

(*Contd*)

Appendix 1. (*Contd*)

Species	Family	Habit	Flowering frequency	FL months	FL season	FR months	FR season	Pollination mode	Fruit types	Dispersal mode
Ilex denticulata Wall. ex Wight	Aquifoliaceae	Tree	Annual	January–March	Dry	July–October	First/second	Birds	Fleshy	Zoochory
Ilex wightiana Wall. ex Wight	Aquifoliaceae	Tree	Annual	March–April	Dry	August–October	Second wet	bees	Fleshy	Zoochory
Isonandra perrottetiana DC.	Sapotaceae	Tree	Annual	March–April	Dry	October–December	Second wet	Bees	Fleshy	Zoochory
Lasianthus venulosus (Wight & Arn.) Wight	Rubiaceae	Shrub	Sub-annual	April–May; August–September	First/ second wet	June–July; October–November	First/second	Bees	Fleshy	Zoochory
Leucas lanceifolia Desf.	Lamiaceae	Shrub	Annual	January–May	Dry/first wet	February–June	Dry/first	Bees	Dry	Autochory
Ligustrum perrotetii	Oleaceae	Tree	Annual	May–June	First wet	September–October	Second	Bees	Fleshy	Zoochory
Litsea floribunda Gamble	Lauraceae	Tree	Annual	April–May	Dry/first wet	June–August	First wet	Small diverse insects	Fleshy	Zoochory
Litsea oleoides Hook. f.	Lauraceae	Tree	Annual	March–April	Dry	May–July	First wet	Small diverse insects	Fleshy	Zoochory
Litsea wightiana (Nees) Hook.f.	Lauraceae	Tree	Annual	May–July	First wet	Jun–August	First wet	Small diverse insects	Fleshy	Zoochory
Lonicera ligustrina Wall.	Caprifoliaceae	Shrub	Annual	April–May	Dry/first wet	July	First	Birds	Fleshy	Zoochory
Magnolia nilagirica (Zenker) Figlar	Magnoliaceae	tree	Annual	August–October	Second wet	March–May	Dry/first	Small diverse insects	Fleshy	Autochory
Mahonia napaulensis DC.	Berberidaceae	Tree	Sub-annual	February–March; August–September	Dry/ Second wet	April–May; October–November	First/second	Birds	Fleshy	Zoochory
Meliosma simplicifolia (Roxb.) Walp.	Sabiaceae	Tree	Annual	April–June	Dry/first wet	August–November	First/second	Small diverse insects	Fleshy	Zoochory
Microtropis ovalifolia Wight.	Celastraceae	Tree	Annual	March–April	Dry	June–August	First wet	Small diverse insects	Fleshy	Zoochory
Microtropis ramiflora Wight.	Celastraceae	Tree	Supra annual	February–April	Dry	May–July	First wet	Small diverse insects	Fleshy	Zoochory
Neolitsea cassia (L.) Kosterm.	Lauraceae	Tree	Annual	January–April	Dry	May–July	First wet	Small diverse insects	Fleshy	Zoochory
Nothapodytes nimmoniana (J. Graham) Mabb.	Icacinaceae	Tree	Annual	March–May	Dry/first wet	June–August	First wet	Small diverse insects	Fleshy	Zoochory
Olea paniculata R. Br.	Oleaceae	Tree	Supra annual	March–May	Dry/first wet	June–August	First wet	Small diverse insects	Fleshy	Zoochory
Osbeckia leschenaultiana DC	Melastomaceae	Shrub	Annual	February–March	Dry	March-May	Dry/first	Butterfly	Dry	Autochory
Pavetta breviflora DC.	Rubiaceae	Tree	Annual	February–April	Dry	May–June	First wet	Bees	Fleshy	Zoochory
Phoebe wightii Meisn.	Lauraceae	Tree	Annual	December–February	Dry	June–July	First wet	Small diverse insects	Fleshy	Zoochory

(*Contd*)

Appendix 1. (*Contd*)

Species	Family	Habit	Flowering frequency	FL months	FL season	FR months	FR season	Pollination mode	Fruit types	Dispersal mode
Photinia integrifolia Lindl.	Rosaceae	Tree	Sub-annual	March–May; September–October	Dry/ Second wet	July–August; November–December	First/second	Small diverse insects	Fleshy	Zoochory
Pittosporum dasycaulon Miq.	Pittosporaceae	Tree	Annual	February–April	Dry	June–August	First	Small diverse insects	Fleshy	Zoochory
Pittosporum tetraspermum Wight & Arn.	Pittosporaceae	Tree	Annual	April–May	Dry/first wet	July–August	First	Small diverse insects	Fleshy	Zoochory
Prunus ceylanica Miq.	Rosaceae	Tree	Annual	February–March	Dry	April–June	Dry/first	Small diverse insects	Fleshy	Zoochory
Psychotria nilgiriensis Deb & M.G. Gangop.	Rubiaceae	Shrub	Annual	December–April	Dry	May–July	First wet	Bees	Fleshy	Zoochory
Rapanea wightiana (Wall. ex A. DC.) Mez	Primulaceae	Tree	Annual	February–April	Dry	May–June	First wet	Wind	Fleshy	Zoochory
Rhododendron nilagiricum Zenker.	Ericaceae	Tree	Annual	January–March	Dry	March–May	Dry/first	Birds	Dry	Autochory
Rhodomyrtus tomentosa (Aiton) Hassk.	Myrtaceae	Tree	Annual	January–April	Dry	May–July	First wet	Butterfly	Fleshy	Zoochory
Rosa leschenaultiana Red. & Thory	Rosaceae	Liana	Annual	March–May	Dry/first wet	July–September	First/second	Bees	Fleshy	Zoochory
Rubus ellipticus Smith.	Rosaceae	Liana	Annual	February–May	Dry/first wet	May–July	First wet	Bees	Fleshy	Zoochory
Rubus rugosus Smith var. *thwaitesii*	Rosaceae	Liana	Annual	March–May	Dry/first wet	April–June	Dry/first wet	Bees	Fleshy	Zoochory
Saprosma fragrans (Bedd.) Bedd	Rubiaceae	Tree	Annual	May–July	First wet	July–September	First wet	Bees	Fleshy	Zoochory
Sarcococca saligna Mull. Arg	Buxaceae	Shrub	Annual	December–March	Dry	March–April	Dry	Wind	Fleshy	Zoochory
Symplocos cochinchinensis (Lour.) S. Moore	Symplocaceae	Tree	Annual	March–July	Dry/first	April–July	Dry/first wet	Bees	Fleshy	Zoochory
Symplocos foliosa Wight.	Symplocaceae	Tree	Annual	October–December	Second wet	January–February	Dry	Bees	Fleshy	Zoochory
Symplocos obtusa Wall.	Symplocaceae	Tree	Annual	February–April	Dry	May–July	First wet	Beetles	Fleshy	Zoochory
Syzygium calophyllifolium (Wight) Walp.	Myrtaceae	Tree	Supra annual	August–October	Second wet	February–May	Dry/first wet	Small diverse insects	Fleshy	Zoochory
Syzygium densiflorum Wall. ex Wight & Arn.	Myrtaceae	Tree	Annual	January–March	Dry	April–June	Dry/first wet	Small diverse insects	Fleshy	Zoochory
Syzygium grande (Wight) Walp.	Myrtaceae	Tree	Annual	March–April	Dry	March–June	Dry/first wet	Small diverse insects	Fleshy	Zoochory
Tarenna asiatica (L.) Kuntze ex K. Schum	Rubiaceae	Tree	Annual	April–May	Dry/first wet	April–June	Dry/first wet	Bees	Fleshy	Zoochory

(*Contd*)

Appendix 1. (*Contd*)

Species	Family	Habit	Flowering frequency	FL months	FL season	FR months	FR season	Pollination mode	Fruit types	Dispersal mode
Ternstroemia gymnanthera var. *wightii* (Choisy) Hand.-Mazz.	Pentaphylacaceae	Tree	Annual	March–May	Dry/first wet	December–May; following year	Dry/first wet	Bees	Fleshy	Zoochory
Toddalia asiatica Lam	Rutaceae	Liana	Annual	January–March	Dry	March-June	Dry/first wet	Small diverse insects	Fleshy	Zoochory
Turpinia cochinchinensis (Lour.) Merr.	Staphyleaceae	Tree	Annual	March–May	Dry/first wet	July–September	First/second	Small diverse insects	Fleshy	Zoochory
Vaccinium leschenaultiana Wall.	Vacciniaceae	Tree	Annual	January–March	Dry	April–June	First/second	Birds	Fleshy	Zoochory
Viburnum hebanthum Wight & Arn.	Caprifoliaceae	Tree	Annual	January–April	Dry	May–September	First/second	Bees	Fleshy	Zoochory

phylogeny in pollination. Closely related species may experience the same selection force that constrains the alterations in morphological, physiological and ecological traits[5]. We also found that phylogenetic structure alone does not explain the variation in reproductive phonological patterns at the community level. The reproductive phenology of tropical montane evergreen forest communities is also influenced by its ecology and climatic factors of the area, thereby ensuring a successful reproduction of plants at community level. This pattern also suggests that reproductive phenology is under the combined control of ecology and phylogeny, making possible the co-existence of species.

The present study shows that majority of woody species of the upper Nilgiri Mountains have a regular seasonal reproductive cycle. Reproductive phenology at the community level is associated with the seasonality; timing of flowering in dry season is influenced by sun-related factors and fruiting season is associated with water-related factors that influence seed germination and forest regeneration during the wet season. Seasonal patterns of flowering and fruiting increase pollinator and dispersal activity that facilitate community reproductive success. Closely related species show similar duration of flowering and fruiting, thereby demonstrating the role of phylogeny in reproductive phenology of plants in tropical rainforests. Our study suggests that the reproductive phenology in plants of tropical rainforest are related to abiotic, biotic and evolutionary factors. However, long-term and in-depth phenological observations are required to fully support our results.

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Record of Gondwana plant mega- and microfossils in Nimugudem area, Telangana, India: palynodating and palaeoenvironmental interpretation

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The present study is a record of Permian (Lower Gondwana) and late Jurassic–early Cretaceous (Upper Gondwana) palynomorphs in megafossil-bearing beds in Nimugudem area, Godavari sub-basin, Telangana, India. Detailed palynological studies were carried out on outcrop samples from the exposure in a nala of Nimugudem area where leaf impressions of plant megafossils were also observed. Leaf impressions of *Ptilophyllum* and *Pterophyllum* recorded in this section indicate Upper Gondwana affinity for these sediments. Presence of different species of palynomorphs of Upper Gondwana affinity in sandstone beds indicates late Jurassic–early Cretaceous (Tithonian–Berriasian) age for these sediments. It is equivalent to Kota/Gangapur Formation of Godavari Graben. Reworked Permian palynomorphs were recorded in these sediments. The coal exposure yielding late Permian palynomorphs belongs to Raniganj Formation.

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