of the Fungi imperfecti group were phytopathogens. Their occurrence may be correlated with the surrounding environment which is full of plants. Efforts are on to study the deteriorating potential of *E. nivea* on museum materials and to suggest effective control measures.

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Phenology of understorey species of tropical moist forest of Western Ghats region of Uttara Kannada district in South India

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Vegetative and reproductive phenology of 107 (52 shrubs, 8 liana, 11 climbers and 36 herb species) understorey species of tropical moist forests of Uttara Kannada district in the Western Ghats of South India was monitored from November 1983 to December 1985, through fortnightly visits to eight one-hectare sites. A prominent peak in leaf flush, flowering and fruiting occurred in the pre-monsoon period in shrubs and lianas, while leaf abscission occurred during the post-monsoon winter period. In the climbers and herbs, flowering and fruiting were concentrated in a single peak during the post-monsoon period. Leaf flush and flowering in deep-rooted shrubs and lianas may have been triggered by changes in day-length and temperature; moisture availability may govern these events in the shallow-rooted climbers and herbs. It is argued that moisture availability, herbivore, pollinator and disperser abundance may have shaped the phenological patterns of the species in these forests.

TROPICAL plant communities with their high levels of species diversity display phenological events staggered in time and space[1,2]. Understanding of such behaviour of the communities is useful in evolving proper management

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strategy and information on phenology which is helpful in predicting the interactions of plants and animals to the changing environment. Studies from different parts of the world have shown climatic factors to be mainly responsible for vegetative and reproductive phenology, at both community and species level. Studies have reported that various phenological events are triggered by rainfall[3–5], water availability[6], temperature[7], photoperiodism[8], duration of dry spell[9,10] and change in day-length and temperature[11].

The understorey of tropical forest, which has a distinctive array of species different from the overstory, is an integral part of the tropical forest community. It supports a different fauna and many understorey plants are major food sources for a variety of biota[12–19]. Little attention has been focused on the phenology of understorey plants, though they are easily accessible[20]. Apart from a few studies on shrubs[21,22], understorey species have been looked at only incidentally, either to compare their phenological behaviour with that of canopy trees[23] or to assess their interactions with dispersers or pollinators[1]. In India, although reports are available on the phenology of tree species from Kumaun Himalayan forests[24], subtropical humid forests[25], seasonally dry tropical forests[26], tropical moist forests[11], tropical deciduous forests[10] and tropical dry evergreen forests[27], studies concerned with the understorey species are very few. While Ralhan *et al.*[28] explained the general pattern of phenology of shrubs of Kumaun forests, and Baruah and Ramakrishnan[29] reported the leaf dynamics of few selected shrub species and phenology of shrubs along successional gradient from north-eastern India, the phenology of understorey species of the Western Ghats is less understood, except for the reports on gregarious flowering in *Strobilanthes* and bamboo species[30,31]. The purpose of this communication is to describe vegetative and reproductive phenology of understorey species of the tropical moist forest of the Western Ghats region of Uttara Kannada district in south India.

This study was conducted in Sirsi and Kumta taluks of Uttara Kannada district (lat. 13°55′ to 15°31′N, long. 74°9′ to 75°10′E) of Karnataka in peninsular India. Geologically this is a transitional zone between the younger rocks of Deccan trap formation and the older crystalline rocks of Archean shield of the Indian peninsula. It is a tract of hilly terrain with gentle slopes and broad valleys, with altitude ranging from the sea coast to a little over 1000 m. The soil on the exposed slopes is shallow, while in valleys it is loamy laterites with pH ranging from 5 to 5.8. The rainfall is largely restricted to the period from June to September. The study sites receive an average annual rainfall of 2500 to 3500 mm in Sirsi and Kumta taluks, respectively (Figure 1). The mean maximum monthly temperature at Sirsi ranges from 25 to 32°C, while that for Kumta ranges from 28 to 33°C. The mean minimum monthly temperature ranges from 13 to 21°C for Sirsi and from 20 to 25°C for Kumta. The climate is monsoonal and it can be divided into summer season extending from February to May, rainy season from June to September and winter season from October to January. Pre-monsoon showers are received during April and May. Post-monsoon showers are received during October and December. The natural vegetation is an evergreen/semi-evergreen type of forest along the western slopes, grading to secondary/moist deciduous types in the lower rainfall tracts to the east[32–35]. In evergreen/semi-evergreen forests, *Hopea wightiana*, *Bischofia javanica*, *Holigarna arnottiana*, *Flacourtia montana*, *Ixora brachiata*, etc. dominate the canopy layer, while undergrowth consists of *Strobilanthes* sp., *Calamus* sp. and *Uvaria*. *Xylia xylocarpa*, *Lagerstroemia lanceolata*, *Terminalia tomentosa*, *T. bellerica* and *T. paniculata* are the emergent tree species in secondary/moist deciduous forests and the undergrowth includes species such as *Psychotria dalzellii*, *Eupatorium divergens*, *Wagatea spicata* and *Zizyphus*. Puri[36] has classified the zone facing the western slope as moist tropical wet evergreen forest and included the eastern zone in the tropical moist deciduous forest type. Champion and Seth[37] classified the forest on the western slope as tropical evergreen type and included the forest of the eastern zone in the category of South Indian moist deciduous type. Bhat *et al.*[38] and Gadagkar *et al.*[39] give further details of the floristics of the study sites. Table 1 summarizes the salient features of the study sites.

Four of the eight one-hectare study plots were in the evergreen/semi-evergreen zone; the other four were in the drier secondary/moist deciduous zone of the district. All the woody plants having a circumference of 10 cm and above at the breast height (132 cm) were enumerated in each study plot. These included tree, shrub, lianas and climber species. Saplings of trees and shrubs with circumference less than 10 cm at the breast height were enumerated in 10 randomly selected sub-quadrats, each of 10 m × 10 m. Herbs were enumerated in 20 randomly chosen sub-quadrats, each of 0.5 m × 0.5 m. The boundaries of the one-hectare plot, and the sub-quadrats were marked permanently. These plots were visited every

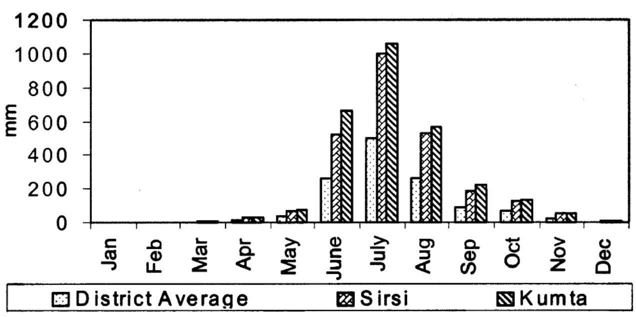

Figure 1. Average rainfall pattern of Uttara Kannada district, Sirsi and Kumta towns.

Table 1. Brief description of study sites in two different vegetation zones of Uttara Kannada district

Vegetation zone	Evergreen/semi-evergreen zone				Secondary/moist deciduous zone			
Study locality	Chandavar	Mirzan	Nagur	Santgal	Bhairumbe	Bengle-Sugari	Bidralli	Sonda
Forest locality	Minor forest	Minor forest	Reserve forest	Reserve forest	Minor forest	Minor forest	Reserve forest	Reserve forest
Elevation (m)	20	25	105	350	475	565	525	475
Level of biotic disturbance	High	Very high	Moderate	Little	High	High	High	Moderate
Soil character	Exposed laterite	Exposed hard pan laterite	Exposed laterite	Exposed laterite	Loam	Clay-loam	Clay-loam	Clay-loam
Species richness* (no. of spp/ha)								
Tree layer	32	33	51	63	40	44	32	51
Population density*								
Tree layer (no. of spp/ha)	485	280	1536	888	338	388	279	585
Shrub layer (no. of shrub/1000 m^3)	2418	582	953	90	654	2093	3399	2439
Estimated tree biomass† (including that of root) t/ha	147.28	66.15	314.35	259.67	142.16	160.58	185.18	210.10
Dominant species								
Trees	*Aporosa lindleyana* *Flacourtia montana* *Holigama arnottiana* *Hopea wightiana* *Ixora brachiata*	*Alseodaphne semicarpifolia* *Ervatamia leyneana* *Randia dumetorum* *Spondias accuminata* *Wrightia tomentosa* *Zizyphus xylopyra*	*Aporosa lindleyana* *Holigarna arnottiana* *Hopea wightiana* *Myristica attenuata* *Olea dioica* *Stereospermum* sp.	*Bischofia javanica* *Dysoxylum binecteriferum* *Nephelium longana* *Nothopegia colebrookiana* *Mappia foetida* *Pterospermum* sp.	*Buchanania lanzan* *Randia dumetorum* *Strychnos nuxvomica* *Terminalia bellerica* *T. Paniculata* *Xylia xylocarpa* *Zizyphus xylopyra*	*Adina cordifolia* *Cassia fistula* *Ervatamia heyneana* *Lagerstroemia lanceolata* *Phyllanthus emblica* *Terminalia bellerica* *T. paniculata* *T. tomentosa*	*Adina cordifolia* *Lagerstroemia lanceolata* *Schlechiera oleosa* *Terminalia bellerica* *T. Paniculata* *T. tomentosa* *Xylia xylocarpa*	*Aporosa lindleyana* *Ervattiana heyneana* *Flacourtia montana* *Terminalia paniculata* *Xantolis tomentosa* *Xylia xylocarpa*
Shrubs	*Grewia microcos* *Psychotria flavida* *Strobilanthes* sp. *Uvaria* sp.	*Carissa carandas* *Croton* sp. *Hippocratea* sp. *Holarrhena antidysenterica* *Zizyphus oenoplia* *Z. rugosa*	*Dracaena terniflora* *Glycosmis pentaphylla* *Psychotria flavida* *Uvaria* sp.	*Eugenia macrosephala* *Gymnosporia rothiana* *Ixora* sp. *Leea* sp. *Tarenna zeylanica*	*Acacia caesia* *Alangium lamarkii* *Breynia patens* *Eupatorium divergens* *Zizyphus oenoplia* *Z. rugosa*	*Acacia caesia* *Allophylus cobbe* *Clerodendrum infortunatum* *Murraya koenigii* *Pavetta* sp. *Wageatea spicata*	*Allophylus cobbe* *Breynia patens* *Clerodendrum infortunatum* *Eupatorium divergens* *Murraya koenigii*	*Allophylus cobbe* *Grewia microcos* *Psychotria dalzellii*
Liana and climbers	*Gnetum* sp. *Pothos scandens* *Smilax macrophyll*	*Argyreia* sp. *Aristalochia indica* *Calycopteris floribunda* *Hemidesmus indicus*	*Calycopteris floribunda* *Connarus* sp. *Derris scandens* *Gnetum* sp. *Piper* sp.	*Ancestrocladus heyneanus* *Artabotyrs zeylanicus* *Calamus* sp. *Piper* sp. *Sarcostigma clenii*	*Argeria* sp. *Calycopteris floribunda* *Hemidesmus indicus* *Vitis* sp.	*Calycopteris floribunda* *Hemidesmus indicus* *Naravelia zeylanica* *Smilax macrophylla*	*Calycopteris floribunda* *Clematis* sp. *Dioscorea* sp.	*Modecca palmata* *Smilax macrophylla*
Dominant herbs and weeds	*Piper* sp. *Naregamia alata* *Impatiens chinesis*	*Naregamia alata* *Lepidagathis cristata* *Justicia micrantha* *Exacum* sp. *Canscora difusa* *Oldenlandia corymbosa* *Eragrostis* sp. *Themeda* sp.	*Ecbolium linneanum* *Dicliptera* sp. *Asystasia lawiana*	*Ecbolium linneanum* *Ophiorrhiza harrissiana*	*Mimosa pudica* *Sida* sp. *Indigofera* sp. *Elephantopus scaber* *Themeda* sp.	*Sida* sp. *Hibiscus solandra* *Dicliptira* sp. *Justicia micrantha* *Themeda* sp.	*Triumfetta rhomboides* *Elephantopus scaber* *Centrantherum phyllolaenum* *Curculigo orchioides* *Themeda* sp.	*Dicliptera* sp. *Impatiens chinensis* *Elephantopus scaber*

*Bhat *et al.*[38]; †Prasad and Hegde[10]. Nomenclature follows Cooke[40].

fortnight, from November 1983 to December 1985, to record the phenological events, which included emergence, maturation and abscission of leaves, initiation of floral buds, anthesis and withering of flowers and ripening of fruits. The tagged individuals belonging to these life forms were visited and the phenological event was recorded. In case of herbs, the plots were visited and observed for the phenological events and recorded. The proportion of the population of each species at different phenological stages was assessed qualitatively. Observations of other individuals of the species occurring elsewhere in the forest were used as supplemental information whenever the species was very rare in the plot itself. Grasses and members of Cyperaceae observed have been clubbed as a single taxon because of the difficulty in identification. All other species were identified at least to the genus level, in most cases to the species level as well. Unless specified, the nomenclature follows Cooke[40]. All the herbs, shrubs, lianas and climbers are collectively referred to as understorey species in the present communication.

The species other than herbs were classified into insect-, wind- and water-pollinated, based on their pollination modes and animal-, explosive-, passive- and wind-dispersed, based on the dispersal modes, according to Murali and Sukumar[41] and Dayanandan *et al.*[42]. Pattern of fruiting and flowering based on their dispersal and pollination modes was studied, to know the specificity of season for species with different pollination and dispersal modes. To know the influence of rain on the pattern of leaf flushing, fruiting and flowering, correlation coefficient using the frequency of species in flower or fruit in that month and the rainfall of that month was computed. Correlation using a 2–3 month period lag was also undertaken, to understand whether any moisture-related patterns emerge for the phenology of vegetative and reproductive events.

Of the 107 understorey species observed for different phenological events, 52 (48.6%) were shrubs, 8 (7.5%) were lianas, 11 (10.3%) were climbers and 36 (33.6%) were herbs. Thirty-eight species were common to the forest plots of both the zones, 30 species were present only in the plots of secondary/moist deciduous tract and 39 species were restricted to the localities of the evergreen/semi-evergreen forest tract. *Acacia caesia* exhibited two annual episodes of production of young leaves, senescence and flowering. Flowering was continuous in 4 shrubs (*Glycosmis pentaphylla*, *Ixora coccinea*, *Leea* sp. and *Mussaenda frondosa*) and in one herb species (*Mimosa pudica*). In the remaining species, there was a defined season for vegetative and reproductive phenological events. In deciduous shrubs, leaf flush occurred during the pre-monsoon dry period with a peak in February–March, followed by the maturation of leaves (Figure 2). Abscission of leaves occurred throughout the post-monsoon winter period; and the majority (77%) of shrub species were devoid of leaves in December–January. Rainfall and leaf initiation showed strong negative correlation ($r_s = -0.82$, $P < 0.01$) among species studied indicating the absence of moisture availability as a strong force to initiate leaves. Leaves are initiated before the onset of monsoon. One or two months of lag in rainfall did not show any strong correlation with leaf flushing, indicating that time lag probably is too long to capture the pattern observed. On the other hand, abscissing leaves have strong tendency to have one or two month lag correlation with moisture. The one or two months lag correlation was high ($r_s = 0.8$, $P < 0.01$), indicating that the leaves are shed one or two months after the rainy season.

In spite of differences in the total annual rainfall, altitude, mean monthly maximum and minimum temperatures, there is no time separation in the occurrence of major phenological events in these zones. The season of flowering and fruiting varied in different life forms. In herb and climber species, a single peak was observed for flowering and fruiting during the post-monsoon period (Figure 3). But in lianas and shrubs, there were two peaks for flowering and fruiting in different seasons. The major peak was during the pre-monsoon and minor one was during the post-monsoon period. The flowering and fruiting activity for annuals, seasonals (with perennating parts) and non-woody species was restricted to post-monsoon period immediately following the rainy season, when the soil moisture is abundant and the weather is hot and humid. The peak fruiting was observed in these life

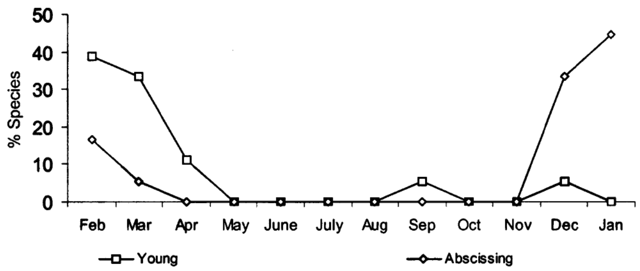

Figure 2. Leaf flushing and abscission pattern of different life forms in Uttara Kannada.

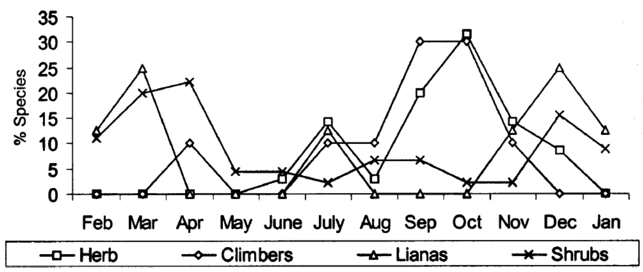

Figure 3. Flowering phenology of different life forms in Uttara Kannada.

forms during post-monsoon dry, cold period (Figure 4). But in the other groups, namely perennials without perennating parts and deciduous as well as evergreen woody species, the major peak for flowering and fruiting was during the pre-monsoon dry period, with high temperatures.

Herbs, lianas and climber species showed a strong negative correlation with rainfall and flowering phenology ($r_s = -0.73$ for herbs, $r_s = -0.62$ for climber and lianas, $P < 0.006$), indicating that flowering occurs mostly after rainy season. However, the correlation of flowering phenology with one month lag period was even stronger ($r_s = -0.93$ for herb, $P < 0.0001$ and $r_s = -0.83$ for climber, $P < 0.04$), indicating that flowering occurs after the rains recede or prior to the onset of rains. Shrubs have positive strong correlation with two month lag correlation with the rainfall ($r_s = 0.72$, $P < 0.0038$). Shrubs have their flowering phenology peak prior to the onset of monsoon and herbs and climbers have their flowering phenology at the end of the rainy season, i.e. during October and November. But no such strong preference was found for phenology of fruiting in different life forms, except in shrubs, which showed strong negative relation with a two-month lag in rainfall ($r_s = -0.65$, $P < 0.023$). It is observed that strong seasonal preferences were shown for flowering, leaf flushing and leaf abscission but not for fruiting for many species observed here.

Considering the dispersal and pollination modes of the species and their fruiting and flowering patterns, the following patterns emerge. In the forests of Uttara Kannada, as indicated in Table 2, there are more species that are dispersed by animals (52) and pollinated by insects (68). Of the 71 species that are analysed, 73% is animal-dispersed and nearly 76% is insect-pollinated. Figure 5 indicates that most species that are insect-pollinated have a peak in March and April and another small peak in September. The other species dispersed by wind and water are found to fruit during June and July. Figure 6 indicates that species that are animal-dispersed, peak during April with another small peak during September. However, the species that are passively-dispersed and wind-dispersed have a peak in December. Thus the species dependent on dominant dispersal agents (such as animal) and pollinating agents (insects) have a major peak of fruiting or flowering during the pre-monsoon season and a small peak at the end of the rainy season.

The vegetative phenology is distinctly seasonal. Leaves emerge and mature in a period with minimal rainfall, high temperature and increasing day-length. Abscission of leaves occurs when the temperature begins to decrease and the day-length is short. Interestingly, among the shrubs leaf flush occurs prior to pre-monsoon showers, when soil moisture is at a minimum. Such synchronized leaf flush and maturation at high temperature and longer days are favourable for photosynthesis[43,44]. It is also possible that such synchronized leaf flushing during the pre-monsoon period reduces herbivory, as insect populations peak later[41,45,46]. This process of refoliation demands plants to invest in food reserves and stored

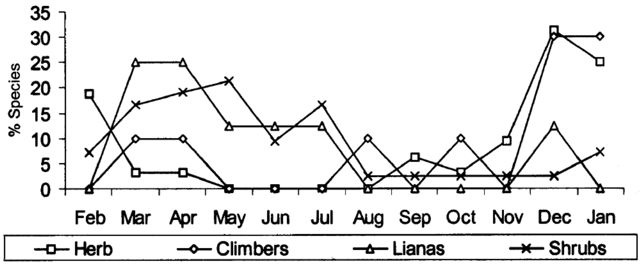

Figure 4. Fruiting phenology of different life forms in Uttara Kannada.

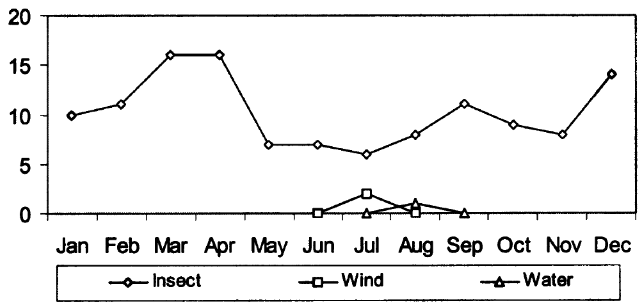

Figure 5. Flowering phenology of species with different modes of pollination.

Table 2. Species having different dispersal and pollination modes among those under study (herbs are not included)

Pollination mode	Dispersal mode				Total
	Animal	Explosive	Passive	Wind	
Insect	49	1	13	5	68
Wind	2				2
Water	1				1
Total	52	1	13	5	71

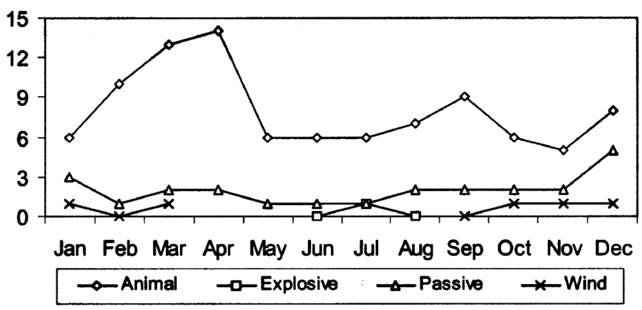

Figure 6. Fruiting phenology of species with different modes of dispersal.

water[6], but ensures that the plants are ready with fully-developed foliage to take advantage of favourable wet and warm conditions for growth, by the onset of the monsoon. In spite of abundant moisture in soil, leaf shedding starts in the post-monsoon period. This may save the cost of maintaining aged foliage, since the rate of photosynthesis is closely associated with leaf age, day-length and temperature. It has often been argued that leaf flushing and leaf drop in understorey species are mainly in response to the behaviour of canopy trees, wherein light plays a major role. In addition, moisture in the upper layers of the soil and shallow rootedness of understorey plants also play a role in leafing behaviour of these plants[5,47–49]. Wright and Cornejo[50] concluded that in Barro Colorado Islands for most species, moisture availability was not the proximal cue for leaf fall. In tree species of the Western Ghats, leaf flush and leaf drop have been reported occurring in response to changes in rainfall, temperature and day-length[11,35,51]. The present study shows that shrubs are similar to deep-rooted tree species in their vegetative phenology and mainly respond to changes in temperature and day-length.

Studies have reported more than one peak of flowering and fruiting in wet forests[23,49] and only one major peak in the early wet season in seasonal dry forests[4,23]. Variations in rainfall, photoperiod and temperature have been implicated in governing the timing of flowering[3–10]. In the tropical moist forests of Uttara Kannada, the timing of flowering and fruiting episodes varied in different life forms. In shrubs and lianas, the major peak of flowering is in the pre-monsoon dry period, while for herbs and climbers it falls in the post-monsoon period. Such shifts in the peak phenological events in different life forms in a community[3,52,53] may serve to maintain a population of pollinator and dispersal agents[54–56]. Competition for pollinators and avoidance of inter-specific pollen transfer have been proposed as selective factors influencing staggering of flowering times and floral specialization[57]. Reproductive phenology of liana species has been reported as closely associated with the mode of dispersal[58,59]. But as observed in the present study, shrubs and lianas produced flowers in two peaks along with the tree species of this locality[11]. The post-monsoon peak may be favoured by the ability to draw on stored nutrients and water from moist soil. On the other hand, flowering in pre-monsoon dry-hot period may have the advantage of enhanced visibility of flowers to pollinators, as many species are devoid of leaves. Both reproductive process and vegetative growth require an input of energy and nutrients. Therefore, resource abundance and the plant's ability to assimilate and allocate the resources may influence the phenological patterns[2]. In the life forms such as herbs, annuals, seasonals, non-woody species and climbers, the most favourable time for using the available resources like light, moisture, nutrients and temperature is the post-monsoon period. So, concentration of flowering and fruiting during the post-monsoon period in herbs, annuals, seasonals, non-woody species and climbers may be related to their shallow roots and their inability to sustain growth in the subsequent long and dry period extending over six months.

Seasonality in phenological events has been reported to influence the migration, abundance, feeding, breeding and diversity of fauna[9,60–64]. Major flowering peak of shrubs and lianas along with trees during pre-monsoon dry period in Uttara Kannada may explain the migration and greater colonial activity of bees in this locality (personal observation). This explains further the peaking of flowering frequency of insect-pollinating species during the pre-monsoon period. Although many species of Bamboo and *Strobilanthes* are known to exhibit gregarious flowering at the end of several years[30,31] in our study sites, none of these happened to flower during the study period.

Fruiting time is another important phenological event for which species need to adapt. Though shrubs and lianas show two peaks of flowering, the ripening of fruits has a single peak immediately before the monsoon rainfall. This suggests that survival of seeds and seedlings is critically, dependent on moisture availability. The animal-dispersed species peak their fruiting time during the pre-monsoon period, contrary to the expectations of rainy-season fruiting[3,65]. Animal-dispersed species are expected to bear fleshy fruits and also bear fruits during rainy season, to maintain the moisture in the fruit. Uttara Kannada forests being moist, may not face constraint of moisture for plants to bear fleshy fruits during summer months. Pre-monsoon dry season fruiting may be beneficial as Uttara Kannada forests are rich in bird fauna[32]. The staggered but small peaks of fruiting exhibited by climbers and herbs indicate that such pattern may help to maintain the population of dispersers through fruiting over long periods. The phenological events in Uttara Kannada demonstrate the adaptive ability of species to differing environmental situations.

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