Phenology of woody species in a seasonally dry tropical forest: Relationship between phenology parameters, and variation between functional groups and habitats with contrasting abiotic conditions

A thesis

submitted in partial fulfilment of the requirements

of the degree of

Doctor of Philosophy

by

Souparna Chakrabarty

20123179

Indian Institute of Science Education and Research, Pune

2020

Certificate

Certified that the work incorporated in the thesis entitled “Phenology of woody species in a seasonally dry tropical forest: Relationship between the phenology parameters, and variation between functional groups and habitats with contrasting abiotic conditions” submitted by Souparna Chakrabarty was carried out by the candidate, under my supervision. The work presented here or any part of it has not been included in any other thesis submitted previously for the award of any degree or diploma from any other University or institution.

Date: 31-12-2020

Dr. Deepak Barua
Supervisor

Declaration

I declare that this written submission represents my ideas in my own words and where others' ideas have been included, I have adequately cited and referenced the original sources. I also declare that I have adhered to all principles of academic honesty and integrity and have not misrepresented or fabricated or falsified any idea/data/fact/source in my submission. I understand that violation of the above will be cause for disciplinary action by the Institute and can also evoke penal action from the sources which have not been properly cited or from whom proper permission has not been taken when needed.

Date: 31-12-2020 Souparna Chakrabarty

Acknowledgements

At the very onset, I would like to thank Dr Deepak Barua for his continuous support and critical insights into my work. He has invested an enormous time and energy in mentoring me. This work would not have been possible without his contribution.

I am thankful to my research advisory committee members, Dr Hema Somanathan and Dr Ramana Athreya, for their valuable suggestions. They have provided fresh perspectives and have helped expand my viewpoint and understanding of my work.

I am also grateful to the Maharashtra Forest Department for allowing me to conduct my research in the protected areas. I thank IISER Pune for funding me during my PhD. I am particularly grateful to the office staff, including Mrinalini Virkar, Mahesh Rote, Piyush Gadekar, Kalpesh Thakare, Shabnam Patil, and Tushar Kurulkar for their prompt and efficient help. I am also grateful to the Infosys Foundation and the Association for Tropical Biology and Conservation (ATBC) for funding my international travel to attend a scientific conference.

I am greatly indebted to my field assistants, Kalu, Ganpat, and Takku, without whom this work would not have been possible. I would like to thank my lab colleagues, Shatarupa, Sheetal, Ron, Asmi, Neha and Aparna, for their help setting up plots and data collection. I would like to specifically thank Shatarupa and Brihaspati for their contribution to the characterisation of flower and fruit traits of the species in the study site and Aparna for help in some of the analysis. I am also grateful to all other lab colleagues (past and present) for their indirect yet important contribution to this work. Finally, I would like to thank my family members for their unwavering support and patience that have eased me throughout the duration of my PhD. I dedicate this thesis to them.

Table of contents

Synopsis

Title: Understanding the variation in vegetative and reproductive phenology of species, the relationship between the phenology parameters, the variation in functional groups and the community weighted phenology of three habitats with a different microenvironment

Name: Souparna Chakrabarty

Registration number: 20123179

Name of Supervisor: Dr. Deepak Barua

Department: Biology

Date of registration: the 01st of August, 2012

Indian Institute of Science Education and Research, Pune (IISER-Pune)

Chapter 1: Introduction

Phenology is the study of the timing of life cycle events. Timing is a crucial component of growth and reproductive events for both plants and animals that directly influence their fitness. In plants, there are four main phenophases: the vegetative phases include leaf flushing and senescing, while the reproductive phases include flowering and fruiting. Although most phenology studies have concentrated on the timing of phenophases, very few studies have looked at the variation in other phenology parameters like duration, frequency, and synchrony. Phenology in plants is not only constrained by environmental factors like temperature, light and water that limit plant function but are also critically linked to biotic factors like the competition between species, and the availability of pollinators and dispersers. Plants in seasonally dry tropical forest experience a broad range of light and water availability, resulting in a huge diversity in phenology. This diversity has not yet been properly understood. Yet, seasonally dry tropical forests are most vulnerable in a changing environment than temperate and aseasonal forests. We not only do not understand the variation in timing but also the variation in the other phenology parameters and the relationships between them. One way to simplify the diversity in phenology is to look at differences in the groups of species with similar characteristics, called functional groups. For example, species of evergreen category would have similar phenology and starkly different from the deciduous species. But even such differences have rarely been addressed. Finally, very few studies have tried to understand the effect of the local microenvironment in affecting phenology of species.

Such insights are crucial in today's fragmented habitats. Knowing these would help us better understand the plants' productivity and fitness under global climate change and its effect on the primary consumers that depend on them.

Chapter 2: Seasonal variation in vegetative and reproductive phenology of species and relationships between the phenology parameters

Most studies on phenology have concentrated on the timing of phenophase in the context of abiotic cues and biotic interactions. Besides timing, very few studies have attempted to understand the variation in duration, frequency, synchrony, and other phenology parameters. The relationship between timing duration, frequency, and intraspecific synchrony in a phenophase has not been addressed before. Insights into the variation in these parameters, and the relationships between them, are essential to understand plant productivity and fitness under varying environmental conditions. Therefore, in this study, I looked at the general variation in the timing and other parameters for vegetative and reproductive phases and then examined the relationships between them in the context of seasonality in light and water availability in the study site. The most important finding of this study was that the species that are flushing and flowering early in the dry season around the spring equinox had a short, synchronous, high intensity activity with low variation between years than species flushing closer to the rains. The study not only revealed the essential relationships between these parameters but also which of these parameters contributed most to the variation in phenology between species. Finally, it gives insight into how the variation in activity between species cueing to light versus water gives rise to the overall pattern of activity across time.

Chapter 3: Variation in vegetative and reproductive phenology between plant functional groups

Plant species can be grouped into functional groups based on the limitations of light and water availability or biotic interactions like pollinators and dispersers. Plant species within each group are expected to show similarity in phenology and differences from species belonging to other groups. These functional groups might simplify the large diversity of phenology in the tropical dry forests. However, even for the common categories of evergreen and deciduous species, such similarities and differences have seldom been addressed comprehensively. Another important aspect is that there exists a lot of variation, even between species within each group. But such variation has received

even less attention. In this study, I examined variation in phenology between some of these functional groups. I explored the continuous nature of leafing behaviour in evergreen and deciduous species. The broad range of species deciduousness and its effect on producing a wide variety of vegetative and reproductive phenology is one of the important findings of this study. These results provide essential support for the insolation-limitation hypothesis. In examining categories based on sexual systems, dioecious species flowered a month earlier than hermaphrodite species, likely to avoid competition for pollinators with the more copiously flowering hermaphrodite species. Rarer species in the study site had lower flowering frequency but a higher intensity of flowering than the more abundant species. High intensity flowering may result from compensation for rarer species to increase their mating opportunity. I did not find any evidence to suggest that the timing of flowering for species with different pollination syndromes corresponded to the timing of peak abundance of the pollinators, but the timing of fruit dispersal was related to the availability of dispersers.

Chapter 4: Seasonal variation in community weighted phenology across three habitats with contrasting abiotic conditions, and the relationship of pollinators abundance to floral resource availability

The effect of local microenvironment on the phenology of species have received very little attention in past studies. This is especially relevant today in a fragmented landscape with increasing human disturbance. However, we still do not have a clear understanding of how microenvironment affects plant phenology. Both plants and their pollinators are influenced by climate change and human disturbance. Studies show that the pollinators are declining worldwide, thereby incurring huge loss to seedling recruitment and agricultural productivity. In this study, I looked at the variation in leafing, flowering and fruiting phenology at the community level, and the relationship of floral abundance to the abundance of pollinators in three habitats with varying abiotic conditions and species composition. The variation in flushing phenology in the open habitats compared to the edge and closed habitats are likely due to the proportion of evergreen and deciduous species in the open which showed different flushing behaviour. Comparison between an unweighted pattern of phenophase intensity, intensity weighted by number and intensity weighted by the total basal area of the species revealed that the role of local microenvironment, light, and water availability, might be putting similar constraints on different species that overwhelms the variation that might arise due to differences size

and composition of species in these three habitats. There was no consistent similarity of temporal pollinator availability or habitat preference of pollinators reported previously to what was observed in the study site. Also, contrary to expectation, pollinators abundance was negatively related to floral resource availability. These suggest that other factors may influence the abundance of pollinators that are independent of flowering.

Chapter 5: Conclusions

This was a comprehensive study attempting to understand the variation in phenology between species, not only in timing but also in the other parameters, trying to understand the relationships between these parameters and the variation in phenology between habitats with a different microenvironment. Additionally, I also looked at the biotic interactions with pollinators to understand if the variation in floral resources affects pollinators' abundance in these habitats. The overall pattern of seasonal variation in flushing phenology revealed that it was likely brought about by a mixture of a gradient of species having lower dependence on water and responding to light availability post rains, to those which are highly dependent on water and flushing closer to the rains. The relationships between the phenology parameters revealed critical aspects species' dependence on light and water availability and limitations of plant resources in affecting species' phenology. The study also highlighted stark differences in phenology between evergreen and deciduous species and showed deciduousness could be measured as a continuous trait which would be more useful in revealing the differences in leaf shedding behaviour between species. This study described the actual community weighted phenology pattern, both within and between years, and contrasted it among three different habitats with varying light and water microenvironment in a tropical dry forest. This finding suggests that the role of local microenvironment, light, and water availability, might be putting similar constraints on different species that overwhelms the variation that might arise due to differences size and composition of species in these three habitats.

Chapter 1: Introduction

Phenology, the study of the timing of life cycle events, became a popular topic of research since Charles Morren coined it in the early 1850s (Demaree & Rutishauser 2011). Early on, phenology was mainly studied in the context of agriculture (Sparks & Menzel 2002; Hudson & Keatley 2009). Phenology of plants and its effect on plant fitness as well as on primary consumers were recognised in the '60s and early '70s (Bassett, Holmes & MacKay 1961; Lieth 2013). The study of phenology really took off in the '90s when people began to realise the value of understanding the changes phenology of species in the context of climate change, and its subsequent impact on the biodiversity, forestry, agriculture, economy and human health (IPCC 2001).

Timing is a crucial component of growth and reproductive events for both plants and animals that directly influence their fitness. Constraints of temperature, light, and water pose limits on when leaves can perform optimal photosynthesis. Thus, the timing of leaf shedding and putting new leaves determines the amount of water, nutrients and photosynthates accumulated by the plant towards growth and future storage. Resource accumulation, in turn, affects the ability of the plant to produce flowers and fruits. The timing of flowering and fruiting is also critically linked to the availability of pollinators, dispersers and abiotically to optimal time of germination, thereby directly contributing to fitness of the plant. Plants provide primary food sources for herbivores, pollinators, and dispersers. Thereby anything that disrupts plant productivity and reproduction affects the primary consumers as well.

In plants, there are four main phases (termed phenophase) of plant growth and reproduction. Vegetative phases include leaf flushing – putting out new leaves and senescing – withdrawing nutrients from old leaves and leaf shedding. Reproductive phases include – flowering and fruiting. As already mentioned, each phase is characterised by the timing of the phase. Additionally, phenology is also described by other parameters, including duration, frequency, synchrony, intensity, skewness, kurtosis, and interannual variation. Duration describes the length of the activity period, frequency describes the number of events in a calendar year, synchrony describes the overlap in timing of events between individuals in a species, intensity describes the amount of

activity, skewness, and kurtosis both describe the nature of the cumulative activity of all individuals of a species across time, and interannual variation describes the variability of the timing of the phase across years.

Phenology can be studied at different levels of organisation, and each level can answer a different aspect of phenology. Starting at the level of the individual, variation between individuals can tell us about the response of individuals to the local microenvironment, forest fragmentation or effect of disturbance (Fuchs, Lobo & Quesada 2003). Variation in phenological characteristics between species helps us to accurately understand the proximate and ultimate causes driving phenology (Borchert 1994). Going up another level, species can be categorised into groups based on common characteristics. Variation in phenology between such groups can help us predict species' behaviour in these groups under limiting abiotic conditions and explain patterns at community (Williams-Linera 1997; Sakai *et al.* 1999b; Ramirez 2002). At the community level, patterns of phenology might depict broad effects of light and water on ecosystem productivity and function, and its consequences for interaction with primary consumers (Aide 1993; Chapman *et al.* 1999; Elzinga *et al.* 2007). Huge variation exists between communities at the level of an ecosystem. Such aggregated effects help us understand the seasonality of various biogeographical cycles. Here, I look at the three levels of organisation, starting from variation between species to variation between functional groups and finally variation in community level phenology between three contrasting habitats.

Vegetative and reproductive phenology of plants is cued to abiotic factors like temperature (Walter & Burnett 1971; Morellato *et al.* 2000), sunlight (Rivera *et al.* 2002; Borchert *et al.* 2005; Elliott, Baker & Borchert 2006) and water (Walter & Burnett 1971; Lieberman 1982; Reich & Borchert 1984; Borchert 1994) and to biotic interactions like herbivores (Aide 1992; van Schaik, Terborgh & Wright 1993; Coley & Barone 1996), pollinators (Elzinga *et al.* 2007) and dispersers (van Schaik, Terborgh & Wright 1993; Batalha & Martins 2004). Increasing of daylength have been shown to induce flushing (Borchert *et al.* 2005) and flowering in the dry season (Rivera *et al.* 2002) thereby acting as proximate cues to phenology. Ultimate causes for phenology involve evolutionary adaptations of species like dropping of leaves in anticipation of upcoming seasonal drought, flowering together and in high intensity to attract pollinators and dispersers, and flushing in the dry season to escape (van Schaik, Terborgh & Wright 1993).

Phenology in temperate regions is largely governed by temperature and photoperiod (Tooke & Battey 2010). Low temperature and winter frost restrict and often arrests plant productivity and growth. In contrast, in the aseasonal tropics, plant species, are relatively less limited by resources, are expected to flush, flower and fruit throughout the year. However, even under most aseasonal environment, species rarely exhibit continuous leafing, flowering, and fruiting (Newstrom, Frankie & Baker 1994; Morellato *et al.* 2000). Most species show some form of seasonal rhythm and synchrony between individuals of the population, indicating phenology is as an adaptation to some biotic or abiotic selection (van Schaik, Terborgh & Wright 1993). Tropical forests are characterised by a wide range of annual rainfall and number of dry months. Total annual rainfall ranges from around 800 mm per year to higher than 3000 mm a year. The number of dry months ranges from as low 3 months to as long as 9 months. Not only abiotic factors, but biotic interactions may lead to the staggering of phenology to avoid competition for pollinator or dispersers or may lead to convergence of timing to attract pollinators or avoid herbivores and predators. Whenever biotic factors lead to convergence of phenology, the influence of those factors is often weaker, irregular, or arbitrary as compared to abiotic factors. Therefore, in such cases, biotic processes are thought to determine the sharpness of peak activity while abiotic processes determine the timing of phenophase (van Schaik, Terborgh & Wright 1993). This considerable variation in abiotic factors and biotic interactions bring about a great diversity of vegetative and reproductive phenology in tropical dry forest, the likes of which have not been sufficiently explored and understood. In Chapter 2, I looked at the seasonal variation of vegetative and reproductive phenology of woody tree species in a dry deciduous forest in India to understand this diversity of phenology.

Phenology is characterised not only by the timing of the events but also by other parameters like duration, frequency, synchrony. However, apart from timing, other parameters have received little attention (Bawa, Kang & Grayum 2003). Insight into the relationships between duration, synchrony, intensity, interannual variation etc. are essential to understand plant productivity and fitness under varying environmental conditions, responses to biotic interaction and ultimately, their effect on primary consumers. Therefore, in Chapter 2, I examined variation in the timing, quantified other

parameters for vegetative and reproductive phases, and then examined the relationships between these phenology parameters.

Plant species can be grouped into categories based on similar functional attributes. Such groups are hereby termed plant functional groups. A common example of such functional groups based on leafing behaviour is the evergreen and deciduous categories. Species belonging to such functional groups are expected to share similarities in their phenology as abiotic cues, and biotic interactions are likely to influence them similarly. However, we still do not have a complete understanding of such similarities within groups and differences between groups, even for the well-known functional groups like evergreen and deciduous species (Kushwaha & Singh 2005). Even rarer is an understanding of the variation that exists between species within groups (Williams, Bunyavejchewin & Baker 2008). Therefore, in Chapter 3, I looked at the variation in phenology between some of these functional groups. I then explored the variation between species in each group as a continuous trait for evergreen and deciduous species.

The effect of the local microenvironment in influencing phenology of species have rarely received any attention in past studies (Frankie, Baker & Opler 1974; Murali & Sukumar 1994). However, understanding such effects are crucial to recognise the effect of disturbance, habitat fragmentation and climate change on the phenology of species. Changes in plants' phenology alter their relationship to primary consumers like pollinators and dispersers since the plants provide them with crucial food resources. Pollinators provide critical ecosystem services in both natural forest and agricultural fields. However, very little is known about their seasonality and habitat preferences. Yet, pollinators have been shown to be highly susceptible to changes in temperature and habitat disturbance (Fowler, Rotheray & Goulson 2016). They are declining worldwide, thereby resulting in huge loss to seedling recruitment and agricultural productivity (Aizen *et al.* 2009; Gonzalez-Varo *et al.* 2013; Vanbergen *et al.* 2013). Understanding the seasonality of insects and the influence of food resources on their abundance is of utmost importance in this changing environment. In Chapter 4, I looked at the variation in leafing, flowering and fruiting phenology at the community level and the relationship of floral abundance to the abundance of pollinators in three habitats with varying abiotic conditions, canopy structure and plant species composition.

Climate change involving a rise in temperature and increasing seasonal drought poses significant challenges to plants. A shift in phenology is usually the first response of plants to climate change (Cleland *et al.* 2007). In dry forests, species that are adapted to maintain leaves during the dry season can benefit from increased CO_2 level by increasing water use efficiency, reducing transpiration and thereby delaying leaf shedding (Scheiter *et al.* 2020). In contrast, species which shed leaves during the dry season might be expected to experience greater stress from elevated temperatures, lower precipitation, and reduced leaf lifespan. These may lead to early shedding accompanied by a longer leafless period in hotter and drier climates. Future climates may be disadvantageous for such species in terms of reduced photosynthesis as compared to species adapted to maintain leaf during the dry season (Scheiter *et al.* 2020). This may result in shifts in species composition, thereby affecting the primary consumers that depend on these plants. Thus, understanding this intricate network of causes and consequences is crucial to obtain a complete picture of the underlying processes that shape the overall organisation of the whole community. It may also help predict how interactions will be affected by future climate change, through the study of plant phenology.

Chapter 2: Seasonal variation in vegetative and reproductive phenology of species and relationships between phenology parameters

Introduction

Phenology, the study of the timing of life cycle events, is critical for understanding plant productivity and fitness. In contrast to aseasonal tropical forests, plants in seasonal tropical forests experience wide variation in light and water availability, and thus they display a broad range of vegetative and reproductive phenology (Reich 1995; Kushwaha, Tripathi & Singh 2011). Most studies on phenology have concentrated on the timing of phenophase in the context of abiotic cues and biotic interactions. Very few studies have attempted to understand variation in duration, frequency, and synchrony in seasonal or the aseasonal forests (Bawa, Kang & Grayum 2003). Even less attention has been paid to understanding relationships between duration, frequency, synchrony, and intra-specific variation in a phenophases. Besides timing, insight into variation in these parameters, and the relationships between them, are essential to understand plant productivity and fitness under varying environmental conditions, responses to biotic interaction and ultimately their effect on primary consumers. These phenophase parameters describe different aspects of phenology that may directly affect plant fitness. For example, decreasing water availability may increase the leafless period for some species that may reduce the annual accumulation of photosynthates that may be necessary for flowering and fruiting. Lack of strong environmental cue and thereby a decrease in intensity and synchrony of flowering between conspecifics may impact mating opportunities of individuals which may directly affect plant fitness. The interaction of limitations in light, water availability and nutrient status of the plant, the hierarchy between them, and their effect on phenology are still unclear. In this study, I examined variation vegetative and reproductive phenology of woody tropical species from a seasonally dry forest and examined the relationships between phenology parameters.

Plant phenology is influenced by abiotic factors like temperature (Walter & Burnett 1971; Morellato *et al.* 2000), sunlight (Rivera *et al.* 2002; Borchert *et al.* 2005; Elliott, Baker & Borchert 2006), and water (Walter & Burnett 1971; Lieberman 1982; Reich & Borchert 1984; Borchert 1994) and by biotic interactions like herbivores (Aide 1992; van Schaik, Terborgh & Wright 1993; Coley & Barone 1996), pollinators (Elzinga *et al.* 2007) and

dispersers (van Schaik, Terborgh & Wright 1993; Batalha & Martins 2004). The insolation-limitation hypothesis (van Schaik, Terborgh & Wright 1993; Sun *et al.* 1996) states that unless limited by water availability, community-wide leafing and flowering peaks in tropical forests should coincide with the period of maximal insolation. Wet season flushing has been reported several studies in Neotropics (Boinski & Fowler 1989; Machado, Barros & Sampaio 1997; Funch, Funch & Barroso 2002; Marques, Roper & Salvalaggio 2004), Africa (Lieberman 1982), Australia (Bach 2002) and flowering in Neotropics (Ramirez 2002; Borchert *et al.* 2004; Marques, Roper & Salvalaggio 2004; McLaren & McDonald 2005), Africa (Lieberman 1982), Asia (Singh & Kushwaha 2006), and Australia (Bach 2002). However, dry season flushing and flowering are also well documented in Neotropics (Frankie, Baker & Opler 1974; Bullock & Solismagallanes 1990; Justiniano & Fredericksen 2000; Rivera *et al.* 2002), Africa (Kinnaird 1992; de Bie *et al.* 1998), Asia (Murali & Sukumar 1994; Kushwaha & Singh 2005; Sundarapandian, Chandrasekaran & Swamy 2005; Elliott, Baker & Borchert 2006; Selwyn & Parthasarathy 2006; Williams, Bunyavejchewin & Baker 2008), and Australia (Williams *et al.* 1997; Williams *et al.* 1999). Studies in the tropical dry forests worldwide indicate that sites with as low as 500 mm of annual rainfall with as long as 7-8 dry months are restricted to wet season peaks in flushing and flowering (Griz & Machado 2001; de Vasconcelos, de Araujo & Lopes 2010). In contrast, both dry and wet season peaks in leaf flushing and flowering occur in equal frequency in relatively wetter sites with as much as 2000 mm of annual rainfall and 6-7 months of dry period (Shukla & Ramakrishnan 1982; Batalha & Martins 2004; Anderson *et al.* 2005). In wetter sites receiving more than 3000 mm of annual rainfall, and with shorter, 4 months or less dry period, exclusively dry season peak in flushing and flowering have been reported (Bentos, Mesquita & Williamson 2008; Bajpai, Pandey & Chaudhary 2017). Based on these studies and patters, I predicted that my study site with an annual rainfall of 2266 mm and 7 months of dry period would have predominant peaks of flushing, flowering in the dry season.

The timing of phenology events, the onset dates of events and the peak dates of activity are most commonly studied. Other aspects depicted by the shape of phenological activity over time are captured by parameters like duration, frequency, synchrony, mean and maximum intensity, interannual variation, and skewness. For each phenophase, duration describes the length of the activity period, frequency describes the number of events in a calendar year, synchrony describes the overlap in timing of events between individuals in

a species, intensity describes the amount of phenophase activity, interannual variation describes the variability of the timing of the phase across years, and skewness describe the nature of the cumulative activity of all individuals of a species across an annual cycle. While such parameters are recognised as important attributes of phenological schedules, such traits are understudied, and the causes and consequences of variation in these parameters are not well understood (Rathcke & Lacey 1985; Elzinga *et al.* 2007). These parameters, hereafter referred to as supplementary phenology parameters can directly influence plant fitness and have important ecological consequences. Longer duration, higher frequency, and intensity of flushing for example increase plant photosynthetic output. Similarly, longer duration and higher frequency, synchrony and intensity increase plant mating opportunities and thereby reproductive success of species. Species that flush, flower, and fruit for long duration or multiple times a year may provide sustained food resources for primary consumers. Changes in phenology between years are usually the first response of plants to climate change (Pau *et al.* 2011). Understanding the relationship of other phenology parameters to the timing of a phenophases can give us a better picture of the overall productivity of plants. Our knowledge of how these parameters vary over the years is still in its infancy but is of utmost importance to predict how plants will respond to climate change.

Species growing in drier sites typically show shorter phenophase duration than those from the wetter sites (Aronson *et al.* 1992; de Vasconcelos, de Araujo & Lopes 2010). In tropical wet evergreen forests, flowering duration has been reported to be around 2.5 months (Morellato *et al.* 2000). In contrast, studies in the tropical dry forest have shown most species to have a shorter flowering duration of a month while very few species have a duration of as much as five months (Bullock & Solismagallanes 1990; Luna-Nieves *et al.* 2017). Fruiting duration in dry forests is usually longer in the range of 4 to 6 months (Luna-Nieves *et al.* 2017). In terms of frequency, studies have tried to classify phenology of species into continual, sub-annual, annual, and supra-annual (Newstrom, Frankie & Baker 1994). They have shown a wide variation in flowering frequency in tropical forests ranging from more than half of the species being sub-annual and flowering more than once a year to about one-tenth of species being supra-annual and flowering once in more than a year. Very few species flowered continually throughout the year. Annual reproductive phenology was more synchronised for thorn scrub than for thorn woodland (de Lampe *et al.* 1992). Studies have also shown interannual variation in timing and

intensity of leaf fall and flush (Haugaasen & Peres 2005) of about seven days between years (Williams *et al.* 1997) and the duration of leafless period to as much as 1.5 months between years (Williams, Bunyavejchewin & Baker 2008).

With the limited exploration of phenology parameters like duration, frequency, and synchrony, they have been looked at in isolation from one another. Although there are hypotheses to expect these parameters may be related and be influenced by each other, such relationships have rarely been explored. When compared across species at the same site, species that flush in the early dry season have been shown to flower early (Lacerda *et al.* 2018) and have longer flowering duration than species flowering in the late dry season (Bhat 1992; Crimmins, Crimmins & Bertelsen 2013; Borges, Henrique & Prado 2014). However, it is also shown that at other sites species that flower in the cool dry season, flower and fruit (Kushwaha, Tripathi & Singh 2011) for the shortest duration while species that flower in the hot dry season have a longer duration (Murali & Sukumar 1994; Singh & Kushwaha 2006) of flowering. Although a few studies have explored the relationship between timing and other phenology parameters, only one has explicitly examined the relationship between flowering duration and frequency (Bawa, Kang & Grayum 2003). They expected and reported flowering duration to be negatively related to the flowering frequency. There has been no study looking at a similar relationship in vegetative phases or looking at the relationship between synchrony, intensity, skewness, interannual variation, duration, and frequency. Flushing and flowering are expected to be related in time and influenced by similar environmental cues (van Schaik, Terborgh & Wright 1993). Additionally, fruiting follows flowering, and hence their phenology parameters are expected to be related to each other.

Flowering synchrony was quantified as the variance of flowering date in earlier studies (Rathcke & Lacey 1985), but this did not capture overlap among individuals. Primack (1980) and Augspurger (1983; henceforth referred here as Augspurger's index) developed a method for quantifying overlap from the perspective of both an individual and the population. This index includes the entire flowering time and considers the temporal overlap between each set of two individuals. However, this index did not consider the differences in the intensity of the phenophase between individuals. Later, Marquis (1988) developed an index of synchrony to include the proportion of individuals in flower. However, while it considered the overlap with other individuals, it also did not account

for the intensity. Freitas and Bolmgren (2008) later combined the above to develop a more complete synchrony index, including the actual overlap of intensity between individuals (henceforth referred here as the Freitas index). The Freitas index, however, is insensitive to the duration. For example, consider two species with complete overlap between individuals. Species 1 has a flowering duration of 1 day, and species 2 have a duration of 30 days. The mating opportunity of species 1 should be 100 percent as opposed to an individual of species 2 since its being diluted over the entire flowering duration. That is not the case with the Freitas index as both get equal weightage. To overcome this, I used a modified index where, given the number of flowers produced by all individuals across all days, I quantified the overlap between individuals in proportion to the maximum possible overlap that can be achieved with those flowers from those individuals.

There has been a recent trend in trying to understand the variation in phenology in a multivariate space. Studies have used principal component analysis (PCA) of phenology parameters, along with other leaf and stem functional traits (Ongole *et al.* 2021) or with environmental parameters like temperature, solar insolation, water availability etc. (Lopez *et al.* 2008). While some of these studies have used PCA as a tool for dimension reduction (Lopez *et al.* 2008; Yu *et al.* 2020) and grouping species with similar phenological strategies (de Oliveira *et al.* 2015), others have used it to understand the variation in phenological strategies and assess the shape and structure of the phenotypic space (Morris 2008; Torres & Galetto 2011; Segrestin, Navas & Garnier 2019). However only one study has exclusively tried to understand the variation in timing and other phenology parameters in a multivariate space (Torres & Galetto 2011). They have shown that flowering duration and life forms load on PC1 while dispersal syndrome and taxonomic membership load on PC2. This resulted in 3 different strategies with varying flowering duration, floral display, dispersal syndrome and life form. Thus, understanding these synergies and the coordinated assessment between the phenology parameters is important to identify unique phenological strategies and their correlates. It might in turn help us predict changes in plant phenology under varying environmental conditions. For example, understanding the coordination between flowering duration, intensity and synchrony might help us predict how intensity and synchrony would change if environmental constraints like water limitation reduce flowering duration and thus in turn understand how this coordinated effect ultimately impact plant fitness.

Given that we still do not understand much about the variation of phenology parameters and the relationships between them, I studied the variation in timing and other phenology parameters of woody species in a seasonally dry forest. Here I examined the seasonality in vegetative and reproductive phenophases to understand the variation in phenology between co-existing species as an ensemble in response to seasonal light and water availability. I compared different synchrony measures and looked at their relationship with other phenology parameters to choose an appropriate index of synchrony. I examined variation in phenology parameters at the species level and looked at the relationship between those parameters within and between phenophases. I looked at the relationship between start and stop dates to understand if species stop dates are dependent on start dates. I predicted that given a fixed amount of resources and environmental cues constrain duration of activity, this fixed duration would result in start dates to be related to stop dates. For example, an individual with fixed resource allocated for flowering, if environmental cues result in earlier start of flowering; with during of flowering being constant and the number of flowers produced per day also remaining unchanged, it would correspondingly have earlier stop of flowering.

I looked at the relationship between the timing and the supplementary parameters to understand if phenology is driven by invariance of sunlight hours or limitation of water. I expected that duration should be negatively related, while other parameters would be positively related to timing as explained below. I examined the relationship between the supplementary parameters to understand if and how these parameters influence each other. In the context of the relationship between duration and synchrony, I expected that species with shorter duration would have higher synchrony. I also expected that longer durations and higher frequency of a phenophase would contribute to more significant variation between years. Limited resources are likely to impose a trade-off between flowering duration and intensity. If strong cues drive phenology, species with higher flushing and flowering synchrony should have lower interannual variation. I expected species with higher flowering frequency to have higher mating opportunities and greater resource limitation and thus have a shorter duration and lower intensity and synchrony per flowering episode. Owing to resource accumulation limitations, I also expected species with higher flowering and fruiting intensity to have higher interannual variation. Skewness of phenology activity have been barely reported in literature. Although we

would assume that the shape of the intensity curve for a phenophase would follow a normal distribution, few studies have, for example showed a positively skewed flowering pattern (Thomson 1980). Thus, to understand how variation in species activity and how it influences other phenology parameters, I looked at the relationship between activity skewness and frequency, duration, intensity, synchrony, and interannual variation.

I examined variation in phenology between species in a multivariate space with the objective of understanding if different parameters influence variation similarly and what parameters contribute most to such variation. I examined the relationship between the timing of different phenophases to ask if the timing of these phases is related to each other due to constraints in resource acquisition, storage, and utilisation. To understand if species use last year's resources thus flower before flushing or use resources from newly flushed leaves thus flowering post flushing, I looked at the relationship between the timing of flushing and flowering. Lastly, I examined the relationship between corresponding parameters across phenophases to understand if environmental cues and resource constraints on one phase affect other phases similarly.

Materials and Methods

The study site was around the village Nigdale near Bhimashankar Wildlife Sanctuary. It is located in the Northern limits of the Western Ghats mountain range in peninsular India (19.0837° N, 73.5549° E) at an elevation of over 900 m above mean sea level (850-1050 m) (Fig. 1a). It was formed from basaltic rocks origination from lava flows during the breakup of Gondwana land in the Jurassic period (Ghadage, Theurkar & Patil 2014). The soil depths vary from very shallow (<8 cm) to shallow (8-30 cm), moderately deep (30-60 cm) and very deep (>100 cm) correspondingly from crest to valley that forms part of the Bhima River basin (Ghadage, Theurkar & Patil 2014). The Western Ghats are now recognized as biodiversity hotspot and world heritage site. The Bhimashankar Wildlife Sanctuary is known for *Ratufa indica elphistoii*, a sub species of the Indian Giant squirrel which is endemic to this region.

The study site is a seasonally dry forest. It experiences a mean annual precipitation of 2266 mm (New *et al.* 2002), most of which falls between June and October. The site remains mostly fog bound during this period. Peak rainfall occurs in July when the site

experiences an average rainfall of around 880 mm of rainfall. The rest of the months from November to May are dry with less than 100mm of rainfall per month (Fig. 1b). The temperature starts falling post rains in November with a minimum in January and then rises till May, which marks the hottest and driest month of the year. The percentage of sunshine hours is significantly reduced in the wet season with a minimum in August and then rises and peaks in the middle of the dry season in February.

It is a highly fragmented habitat consisting of crest and valley forests. Although the area contains agricultural patches in and around the village (Somanathan & Borges 2000), my specific study areas are a mosaic of natural forest fragments interspersed with open grassy patches and rocky outcrops (Somanathan, Borges & Chakravarthy 2004). Crest vegetation consists of a mixed deciduous and evergreen species type, with most trees 5m high while some are reaching 12-15 m in the hill slopes. The crest vegetation is in open habitats with less than 30 percent of vegetation cover. The valley vegetation consists of closed canopy evergreen forest with most trees around 10 m high and maximum reaching greater than 20 m. The crest forest is dominated by *Memecylon umbellatum* and *Gnidia glauca*, the edge forests by *Memecylon umbellatum*, *Syzygium cumini* and *Xantolis tomentosa* and the closed by *Dimorphocalyx glabellus* var. *lawianus*, *Mangifera indica* and *Memecylon umbellatum*.

The study was conducted from January, 2014 to December, 2017. Fortnightly sampling was done between January to May around 15th and 30th of each month (during the period of intense phenology activity) and monthly between June to December, around 15th of each month. For each census, the observation was completed within a maximum of 4 days. The trees were sampled along forest trails. All available woody species (tree, shrubs, and lianas) for which a minimum of 5 mature individuals was found along the trails were tagged and observed. Wherever possible, 15 individuals of each species were selected for hermaphrodite and monoecious species and 30 individuals for dioecious and polygamous species. Phenology observations were initiated a year before the final study duration. This time was used to calibrate and standardize intensity estimates of all phenophases for each species. All phenology observations were conducted by me to avoid observer bias. Initially, 1659 individuals were selected from 77 species. 14 individuals died or were cut, burnt, or otherwise discontinued within the first year of sampling. Thus,

the final sample consisting of 1645 individuals from 77 species were finally chosen for long term monitoring after the initial year of survey.

Direct visual observation of the canopies was done with the help of binoculars. The phenophases observed were total canopy: composed of flushing, senescing and mature leaf; total flowering: composed of flower buds and open flowers and lastly, fruits. The ripe and unripe fruits were not distinguished. The total canopy fullness of each phenophase of each individual was measured in a semi-quantitative scoring of phenology, as a percentage of maximum total canopy going from 0 to 100 percent in increments of 5 percent (Ouédraogo *et al.* 2018). Here 0 represents complete absence of a phenophase while 100 represents the maximum possible total canopy fullness of the corresponding phenophases. For leafing, the subphases flushing, mature and senescing leaves, distinguished by size, colour and texture of leaves, together comprised the percentage of the current total canopy; similarly, buds and open flowers comprised current total flowering.

I discarded individuals with less than 3 years of continuous observation, or reproductively immature individuals with girth below the minimum size of reproduction. A final number of 1303 individuals from 75 species were used in further analysis. An activity period was essential to be calculated for each phenophase of each species to enable comparison across species for the corresponding calendar year. It was calculated as the earliest and latest month across all years of observation when at least 20% of individuals have started and stopped the activity, respectively. All fortnightly data were later converted to a monthly resolution taking observations from the 15^{th} of the month as the representative for the month unless the 30^{th} had the highest activity for the phenophase for that year (so as not to miss out on peak intensity). With the monthly data, I checked for and filled missing observations with either of the flanking values or their average of the flanking values, whichever was closest to the mean of other individuals on that date. A qualitative sequence anomaly was defined as no activity recorded where activity was expected. As a simple example, a fruiting sequence of three months where no fruiting was reported in the middle month (a sequence of YNY) likely represents an observational error. For such cases, all 1 month of leafing data, up to 2 months of flowering data and up to a maximum of 5 months of missing fruiting data was filled. The duration of consecutive no reports of activity that were filled depended upon the chance of missing the event and the

confidence that filling the data would constitute a single stretch of the event. Fruiting events tended to be longer and continuous than the rest of the phases. To fill the data, the flanking average was used, or the average for all other individuals of the species on that date was used in some synchronous species. In cases where there were no open flowers observed, but there were buds and fruits, the relationship of flowering timing with the timing of buds and information on the flowering duration was used to estimate flowering timing. The mean intensity for that individual in other years was used to assign intensity of flowering. For any activity outside the species activity period and not repeated across years, were marked as an anomaly, and excluded for further analysis. The total number of corrections done to the data, including filling up missing data, correcting qualitative sequence anomalies for all phases, correcting no reports in flowering, and removing anomalous activity outside the activity period amounted to less than 1 percent of the total data. Finally, all the parent phases, i.e., total canopy, total flowering, and fruiting, were normalised to the maximum for the individual across all years. All the sub-phases are also normalised to the maximum of the respective parent phase.

Overall, species ensemble phenology was described as the percentage of species in a phenophase in each month, Rayleigh's test for uniformity was used to test if activity in a phenophase is uniform throughout the year or not. If different from a uniform distribution, a mean angle representing peak activity was calculated using circular statistics. Since the timing of phenophases repeated across years and December of one year is closest to January of next year, a zero point on such a scale is arbitrary. Hence, any calculation involving timing needed to be done through a branch of mathematics called circular statistics. All phenology parameters were calculated for an individual for a year, averaged across years for an individual mean, and then averaged across individuals to get a species level mean. These were characterised as follows: 1) Within the activity period defined for error checking, the start date was defined as the date with activity of any intensity following a date without any activity. Similarly, stop date was defined as the date of no activity following a date with activity. In case of multiple starts and stops (henceforth referred to as bout) within the species activity period, the event corresponding to maximum intensity for the species was defined as the primary phase. The start and stop dates for the primary phase was used as the start and stop dates for the individual. 2) The duration of activity was calculated as the number of days between the start and stop dates. 3) The frequency of each phenophase was calculated as the mean number of events per

individual per year. 4) Synchrony was calculated as the overlap in duration and intensity between pairs of individuals. For details of the calculation, refer to Equation 3 below. 5) Intensity was calculated as the average measure of activity score (in percentage of canopy) of a phase across the duration of activity in a year. Maximum intensity for a species was defined as the mean of the maximum amount of activity (in percentage of canopy) for a phenophase observed, per individual per year. 6) Skewness and kurtosis of intensity distribution across the activity period within a year for an individual were calculated. 7) Interannual variation was calculated as the circular standard deviation of angular concentration across years and expressed in days.

Synchrony was initially calculated using several indices, including the index of synchrony newly developed by me. These were compared, and the newly developed index of synchrony was used for further analysis. The following indices of synchrony were evaluated: the index of synchrony developed by Augspurger (1983), the index of synchrony developed by Freitas and Bolmgren (2008), the newly developed synchrony index, vector length (r) from circular statistics describing a measure of angular concentration (Liuth, Talora & Amorim 2013) and circular standard deviation of mean angles of individuals as a measure of synchrony (Wang, Tang & Chen 2016).

Freitas index for an individual d_i was defined as,

$$d_i = \frac{\sum_{j=1t}^{N} \sum_{t=1}^{T} \sqrt{f_{i,t} * f_{j,t}}}{T_i * (N-1)}, i \neq j \quad \text{..... Equation 1}$$

where f is the intensity of i and j at time t; T is the duration of flowering, and N is the total number of individuals in the population. In other words, the index is defined as the square root of multiplication of intensity of flowering of one individual (i) with that of another individual (j), for a particular census date (t), then summed over the entire duration of the flowering of i and again summed over all pairs of individuals in a population. This is divided by the total duration of flowering of the entire population and the total number of individuals in the population. Now, mean synchrony of all individuals in the population is defined as,

$$S = \frac{\sum d_i}{N}$$ ……..……..……... Equation 2

The newly developed synchrony index was defined as,

$$d_i = \frac{\sum_{j=1t}^{N} \sum_{t=1}^{T} f_{i,t} * f_{j,t}}{\sum_{j=1t}^{N} (\sum_{t=1}^{T} f_{i,t} * \sum_{t=1}^{T} f_{j,t})}, i \neq j$$ …….. Equation 3

This modified index is now defined as the multiplication of intensity of flowering of one individual (i) with that of another individual (j), for a particular census date (t), then summed over the entire duration of flowering of i and again summed over all pairs of individuals in a population. This is divided by the cumulative flowering of individual i multiplied by the cumulative flowering of individual j over the entire activity period for the species and then summed across all pairs of individuals in the population. Quantification for species level synchrony remained identical to what is described for the Freitas index.

All these species parameters were checked for normality using the Kolmogorov-Smirnov test with Lilliefors correction, and appropriate transformation of variables was done. Relationship between dates was calculated using circular correlation from "Directional" package in R. Relationship between dates and other linear phenology parameters like duration, frequency, synchrony, intensity, skewness, interannual variation was calculated using circular linear correlation from "Directional" package in R. Pearson correlation was used to examine the relationship between the linear phenology parameters within and across phenophases. Principle component analysis of phenology parameters was done using R.

Results

Seasonal variation in species activity was calculated as the percentage of species in activity across the year (Fig. 2). Flushing activity did not pass the Rayleigh's test ($z = 0.51$, $p = 0.61$) indicating that flushing activity was not different from uniform throughout the year. The proportion of species in flushing remained similar from the beginning of the wet season, throughout the end of the cool dry season and decreased towards the end of the dry season. Senescing ($z = 3.21$, $p=0.04$), flowering ($z = 12.65$, $p<0.01$), and fruiting

($z = 2.98$, $p=0.05$) had an activity different from uniform. All the three phases peaked in the dry season with senescing peaking on 4th of February, flowering at 25th of February and fruiting at 18th of April.

I compared the Freitas index to the synchrony index developed here using simulated data with varying duration and number of flowers from the same sized tree and with the same overlap between individuals. It revealed that with the same number of flowers in both trees, the Freitas index reached full synchrony (synchrony of 1) in both long (5 months) and short duration (1 day) of flowering. In contrast, the current index showed full synchrony for a short duration, while low synchrony for a long flowering duration. The same was the result for the current index with a different number of flowers in both the trees. Here, the Freitas index showed the same low value of synchrony irrespective of the duration of flowering. This indicated that the Freitas index is insensitive to the duration and sensitive to differences in intensity compared to the current index.

I then compared the synchrony between individuals using the index developed here, with all other synchrony measures. The other measures include the Augspurger index (Augspurger 1983), the Freitas index (Freitas & Bolmgren 2008), vector length (r) and circular standard deviation. For all four phases, all synchrony parameters were generally significantly related to each other, and in the same direction (Table 1a-d). The exceptions where I did observe significant relationships were for: i) Senescing - Augspurger index and vector length and standard deviation; and ii) Flowering Freitas index and circular standard deviation.

The newly developed index had the strongest relationship to all other synchrony indices. Additionally, this index was negatively related to interannual variation across all phases. It showed more significant relationships to other phenology parameters than Augspurger index, Freitas index, vector length or standard deviation across all phases (Supplementary: Fig. S1-4). This indicated that the Freitas index, the Augspurger index, vector length and standard deviation, were redundant parameters conveying similar information. For all further analysis, I used the newly developed index as a measure of synchrony.

There was a wide variation in different phenology parameters, including duration, frequency, synchrony, intensity, skewness, kurtosis, and interannual variation, and across the four phases (Table 2). Species flushed for more than 2.5 months and senesced for more than 3.5 months on average. The flowering duration was shorter, about 1.5 months but fruiting durations were longer, about 4 months on average. Most species had an annual flushing and senescing cycle. Although species had a supra-annual flowering and fruiting on average, this was mainly caused by variation in individual level activity rather than population level behaviour. Synchrony, intensity, and interannual variation of flowering were highest among the four phases while they were lowest for senescence. Interannual variation was around 21-35 days for flushing and senescing, and about 10-20 days for flowering and fruiting. Similarly, flowering phenology was most positively skewed and had the sharpest peak while senescence had the lowest skewness and the flattest peak.

All four phases showed a significant angular-angular correlation between the start and stop dates. Again, flowering showed the highest correlation ($r_{aa} = 0.95$, $p < 0.001$) while senescence showed the lowest correlation ($r_{aa} = 0.27$, $p < 0.05$). Flushing ($r_{aa} = 0.74$, $p < 0.001$) and fruiting ($r_{aa} = 0.44$, $p < 0.001$) showed an intermediate correlation between the start and stop dates.

All the supplementary phenology parameters were related to the timing of flushing (Table 3). Only frequency and interannual variation were related to the timing of senescing. Duration, synchrony, and intensity were related to the timing of flowering. Synchrony and interannual variation were related to the timing of fruiting. Fig. 3 indicated that the species flushing during spring equinox had the shortest duration, highest synchrony and intensity and lowest interannual variation than species flushing at any other time of the year. Species senescing during the spring equinox had the lowest interannual variation while highest for the species senescing during the rains (Fig. 4). Finally, species flowering in the late dry season had shorter durations and lower synchrony and intensity than species flowering in the early dry season (Fig. 5).

Most of the phenology parameters showed significant relationships between them (Fig. 6-9). The intensity was positively related to synchrony except in fruiting in the relationship between duration, intensity, and synchrony. The intensity was also negatively related to

duration except in senescing. While flushing duration was negatively related to synchrony, senescing duration showed a positive relationship to synchrony contrary to expectations. There was no relationship of duration to synchrony for flowering and fruiting. Regarding frequency, except in fruiting, duration was positively related to frequency, again contrary to expectations. Similarly, except in flushing, synchrony was also positively related to frequency. While the intensity of the leafing phases was positively related to frequency, the intensity of the reproductive phase was negatively related to frequency as expected. In the relationship with interannual variation, flushing and flowering duration was positively related to interannual variation as expected, but the senescing duration was negatively related to interannual variation. Flushing and flowering frequency were positively related to interannual variation as expected. Synchrony and intensity were also negatively related to interannual variation as expected. With regards to skewness, duration and frequency were negatively related to skewness while the intensity was positively related to skewness. Except in flowering, synchrony was positively related to skewness while, except in senescing, interannual variation was negatively related to skewness.

A principal components analysis was conducted with the six important linear phenology parameters across phases to understand the variation in phenology between species in multivariate space. The parameters included duration, mean intensity (referred to as intensity), synchrony index developed by me (referred to as synchrony), Augspurger index of synchrony (referred to as Augspurger), interannual variation, and skewness. In flushing (Fig. 10a-c), PC1 explained 50 percent of variation with skewness, synchrony, intensity, and duration having the highest loading on PC1. Augspurger formed PC2 (31%) while interannual variation comprises PC3 (13%). In senescing (Fig. 11a-c), Augspurger, synchrony, and intensity formed PC1 (47%), skewness formed PC2 (34%) and interannual variation formed PC3 (14%). In flowering (Fig. 12a-c), duration and skewness formed PC1 (42%), synchrony and Augspurger formed PC2 (30%), and interannual variation formed PC3 (15%). Finally, in fruiting (Fig. 13a-c), duration, intensity, and skewness formed PC1 (43%), synchrony and Augspurger formed PC2 (33%), and duration formed PC3 (13%). Thus, in the PCA, the phenology parameters can be condensed into three broad axes: the synchrony/intensity axis, the duration/skewness axis, and the interannual variation axis. Each phenophase has different loadings of these three axes.

Several phenology parameters were related across phenophases (Table 4). With regards to the timing of the phenophase, species that flushed in the early dry season senesced in the latter part of the dry season, but flowered, and fruited in the early dry season with flushing. Conversely, species that flush in the late dry season senesce in the early dry season and flower and fruit in the late dry season. Most species (63 out of 73 species) flowered after flushing, using current resources from newly flushed leaves rather than last year's resources. Flushing duration was positively related to flowering duration ($r = 0.41$, $p < 0.05$). Flushing synchrony was positively related to senescing ($r = 0.43$, $p < 0.05$) and flowering synchrony ($r = 0.39$, $p < 0.05$). Flushing intensity was positively related to senescing intensity ($r = 0.51$, $p < 0.05$). Flushing skewness was positively related to senescing ($r = 0.32$, $p < 0.05$) and flowering skewness ($r = 0.30$, $p < 0.05$). Senescing duration was related to flowering duration ($r = 0.26$, $p < 0.05$) and skewness ($r = 0.38$, $p < 0.05$). Flowering frequency ($r = 0.57$, $p < 0.05$), synchrony ($r = 0.35$, $p < 0.05$) and interannual variation ($r = 0.33$, $p < 0.05$) was related to fruiting.

Discussion

This study provides a unique opportunity to understand the variation in phenology parameters between species and their correlates in a tropical dry forest. The study site had an almost equal proportion of species responding to sunlight, and species dependent on water availability for their activity. The most important finding of this study is the relationship between the timing of phenophases, which is an indicator of the possible cue for activity, and parameters like duration, frequency, synchrony, intensity, and interannual variation. The results reveal the essential relationships between other parameters like duration, frequency, and synchrony which have rarely received any attention in past studies. Additionally, the results indicate which of these parameters contribute most to the variation in phenology between species. Finally, these results give insight into how variation in activity between species cueing to light versus water gives rise to the overall activity pattern across time. Here I first discuss the variation in vegetative and reproductive phenophase between species across time in the context of light and water availability. Then the variation in different phenology parameters and the relationships be them and finally discuss which of these parameters are most important in explaining the variance in phenology between species.

Several measures had been used to represent seasonal variation in the timing of any phenophase, but the most prominent of them is the percentage of species in a phenophase (Williams *et al.* 1999; Anderson *et al.* 2005). Other measures include the percentage of individuals irrespective of species (Bullock & Solismagallanes 1990; Haugaasen & Peres 2005), mean intensity of species (Lacerda *et al.* 2018), the intensity of species weighted by relative density and relative dominance (Newton 1988) to name a few. Each has its strengths and caveats and may not yield a similar conclusion and are hence may not be directly comparable. Here I used percentage species as it is the most widely used measure and simple to interpret but may not be representative of the seasonality of variation in abundance of resources as it gives equal weightage to all species. To overcome this issue variation in phenology at the community level that incorporates the abundance and dominance of species was examined in Chapter 4.

Given the seasonality, in light and water availability, I expected a flushing peak in the dry season. Several studies in the seasonally dry tropical forests with similar annual rainfall and dry months indeed report dry season peak flushing (Williams *et al.* 1997; Anderson *et al.* 2005). However, contrary to this expectation, the percent species in flushing does not have a significant angular concentration. An equal proportion of species had flushed from the beginning of the wet season to the middle of the dry season. The proportion gradually decreased towards the end of the dry season. This constant flushing of species in this community can be brought about by a gradient of species having lower dependence on water and responding to light availability post rains to those highly dependent on water and flushing closer to the rains or after the onset of the rains.

As expected, leaf senescence increased post rains and peaked in the middle of the dry season at the beginning of February. Peak senescence preceded the spring equinox when species that cue to light availability are expected to flush. A gradient similar to flushing can also be expected for senescing. Species that are more sensitive to low water availability are expected to senesce early in the dry season. In contrast, those that are less sensitive to water are expected to senesce later, before they flush leaves during the spring equinox. Such dry season peak in senescing is prevalent in seasonally dry forests and

reported in several studies (Reich & Borchert 1984; Williams *et al.* 1997; Nanda, Suresh & Krishnamurthy 2014). This interplay of light and water in driving variation in flushing and senescing behaviour among species will be further explored in Chapter 3.

Like senescing, flowering, and fruiting also exhibited a peak in the dry season as expected. Flowering peaked around spring equinox at the end of February, while the fruiting peaked middle of April. Similar dry season peak in flowering and fruiting has been reported from Brazil (Bentos, Mesquita & Williamson 2008), Africa (Chapman *et al.* 1999), India (Sundarapandian, Chandrasekaran & Swamy 2005; Bajpai, Pandey & Chaudhary 2017) and Australia (Bach 2002). Flowering near the spring equinox might indicate solar insolation as a cue for flowering in the study site, as shown in previous studies (Calle *et al.* 2010; Wright & Calderon 2018). Fruit peaking at the end of the dry season and dispersing by the start of the rains ensure optimal germination when water is available while avoiding the risk of seed mortality during dormancy.

A new index of synchrony was developed based on the Freitas index (Freitas & Bolmgren 2008) but addressed the issue of sensitivity to the duration of the phenophase, which was lacking in the Freitas index. This was done by calculating the observed overlap to the maximum possible overlap between two sets of individuals given a duration of an activity. This index is independent of the scale of observation of phenology be it actual count, Fournier scale or percentage scale. The Freitas index showed a correlation of 0.8 to the Augspurger index while the actual values being 2.2 to 3.0 fold lower than the Augspurger index. In contrast, the index developed here showed a correlation of 0.69 to Freitas index and are yet on average, 4.5 fold lower than the actual values of the Freitas index. This index was further used to examine the correlation between parameters in this chapter, and the differences between groups in the next chapter.

The results indicated a wide variation in phenology parameters. The vegetative phases had the broadest range of duration with some having activity for about a month to others that were active for 8-9 months of the year. The flowering duration was much shorter, going to a maximum of 3 months while fruiting lasted till a maximum of 7 months. A

similar extent of activity has been observed in dry forests of India (Kushwaha & Singh 2005), Africa (Sun *et al.* 1996) and Mexico (Cortes-Flores *et al.* 2017; Luna-Nieves *et al.* 2017). In terms of frequency of activity, most species have an annual cycle of flushing and senescing. However, about 25 percent of species did flush and senesce more than once a year, and very few species were leaf exchanging. One-tenth of the species, in contrast, did not flush and senesce every year. This may be because these species flushed and senesced very few leaves at a time or for a very short period and were therefore difficult to detect. In contrast, flowering and fruiting frequency were much more supra-annual with only about 15-30 percent of species showing regular annual cycles. Only one species showed sub-annual flowering and fruiting. The high percentage of supra-annual behaviour was driven by interannual variation in flowering and fruiting at the individual level than a consistent activity at the population level. A severe limitation of water or nutrients in these seasonally dry forests might have influenced such behaviour. The intensity of vegetative phases turned out to be much lower than the reproductive stages. This might be because reproductive phases occur for a shorter duration than the vegetative phases, which are spread out over time. Skewness in phenology activity has been rarely reported in the literature, but even among them, most studies describe a positively skewed flowering pattern as observed in this study. Thomson (1980) explained a positively skewed flowering pattern might be favoured by selection in competition for pollinators. Interannual variation in phenology is an essential indicator of climate change. Although studies report variation in the timing of flushing and senescing to range between 7-10 days (Williams *et al.* 1997), the observed range is much higher, about 25-30 days with some species going as high as 50-60 days. This might again be attributed to the variation in rainfall and soil water availability in the study site.

Start and stop dates, and thereby the duration of the activity period is influenced by environmental factors and available resources. It is reasonable to expect the duration of activity to be fixed given a constant resource. Therefore, if environmental factors influence the timing of a phenophase, hastened or delayed, stop dates are expected to show a corresponding change. However, long term monitoring of phenology has revealed an increase in the overall duration of a phase with start dates being hastened and stop dates being delayed (Jeong *et al.* 2011). Here I found a significant relationship between start and stop dates for all phases which supports the assumption that duration is

conserved and that species that enter activity early stop early and correspondingly those who start later stop later in the season.

The relationship between the timing of flushing and the other parameters indicated that species that flush around the spring equinox have a short, synchronous, high intensity activity with low variation between years than species flushing closer to the rains. This pattern might be explained by the fact that species' flushing is under strong cue of light availability (van Schaik, Terborgh & Wright 1993). This strong cue drives the synchronous, short duration but high intensity flushing. Additionally, since light availability is relatively invariant between years compared to rainfall, species cueing to light showed lower interannual variation than species cueing to water availability, thereby flushing near the rains. As opposed to flushing, senescing showed a reverse pattern as the species that are more dependent on the water are more strongly influenced by seasonal drought and shed their leaves early in the dry season within a short duration but highly synchronous activity with high intensity. Flowering is a resource intensive process. Lack of water, resources, and shortage of maturation time for fruits to develop and disperse by the start of the rains might be driving the short duration, low intensity flowering in species flowering near the rains. Such a pattern of flowering has been observed by other authors like Bhat (1992), Crimmins, Crimmins and Bertelsen (2013) and Borges, Henrique and Prado (2014).

The phenology parameters like duration, frequency, synchrony, intensity, and interannual variation have been investigated independently in separate studies, but their relationships have rarely been explored. As described earlier, the synchrony index has both duration and intensity components such that it decreases with duration and increases with intensity. Also, given fixed resources, the intensity of a phenophase is expected to be negatively related to the duration. The relationship between duration, synchrony and intensity holds for flushing. Duration is also negatively related to flowering and fruiting intensity. Limitations in available resources impose constraints on duration, synchrony, and intensity for species with varying frequency. For example, for species that have activity more than once a year, the resource is distributed across each bout. Hence duration and intensity per bout are expected to be reduced. Also, species with activity

more than once a year might not be under a strong cue or in case of flowering, for example, might get more mating opportunities than species with activity once a year. Hence, duration, synchrony and intensity are expected to be negatively related to the frequency. The intensity was found to be negatively related to frequency. Indeed, Bawa, Kang and Grayum (2003) showed a negative relationship between frequency and duration. However, I found a positive relationship between frequency and duration and synchrony. However, this relationship might be interpreted with the caveat that frequency here represent the mean number of event per individual per year and not the true inherent frequency of the species. Interannual variation is the variability in the timing of a phenophase across years. A longer duration, higher frequency, lower synchrony, and lower intensity will contribute to higher interannual variation by description. These relationships hold for flushing and flowering. Fruiting synchrony and intensity is also related but not duration and frequency. However, that might be to do with extended maturation time for some fruits. There is no theoretical prediction or empirical data about the relationship of skewness to other phenology parameters. Here I find species to be positively skewed and the more the skewness, the longer the duration and the greater the frequency. Positively skewed species also have lower synchrony, intensity, and interannual variation. The underlying process behind such relationship need to be further explored.

The exclusive examination of phenological parameters in a multivariate space is the first report of such analysis that may help us determine coordinated changes in phenology parameters for different phenological strategies. When examining variation in phenology between species in multivariate space, there was no consistent parameter that explained most of the variation across all four phases. However, there were three major axes – the synchrony/intensity axis, the duration/skewness axis, and the interannual variation axis. Along with a few other parameters, these three sets explained different proportions of the variation across the four phases. This lack of similarity in parameter groupings across the phenophases indicate that different phases might be affected differently by environmental cues or constraints. For example, between flushing and senescing, although intensity and synchrony are always coordinated and positively related, they are negatively related to duration on PC1 in flushing; but no such relationship of intensity and synchrony with duration exist on PC1 in senescing. Around spring equinox for example, duration of

flushing for species in the study site might be decreased along with increase in intensity and synchrony of flushing. However, if some other factors result in an increase in senescing intensity and synchrony, a corresponding change in duration of senescence cannot be predicted.

Phenology parameters of one phase may influence the parameters of other phases. Studies have shown that light availability changes can trigger flushing and flowering (Wright & Calderon 2018; Adole *et al.* 2019). It is also postulated that it is energetically efficient to transport photosynthates directly from leaves to flowers rather than storing them and translocating them later (van Schaik, Terborgh & Wright 1993). Thus, the timing of flushing can be expected to be related to the timing of flowering. I found the relationship to be true for flushing, flowering, and fruiting. In contrast, the timing of senescing was negatively related to flushing. However, this is expected because species that are more dependent on water availability for maintaining activity is the first to be affected by drought and hence drop their leaves earlier than species which cue to light for flushing. Most of the species showed a positive lag between flushing and flowering, indicating species flowered after flushing. The lag ranged between 0 days to 4.5 months while very few species had a negative lag. Singh and Kushwaha (2006) showed a similar lag between vegetative and reproductive phase. This indicated that species are using current resources from newly flushed leaves rather than last year's resources. It also supported the theoretical prediction by van Schaik, Terborgh and Wright (1993) about being energetically more efficient to transport photosynthates to flowers. Flushing and flowering phenology were not only related in time, but the duration, intensity, and skewness of the phases were also related to each other owing to the same cue. Another explanation might be because the longer duration of flushing can accumulate more photosynthates to support flowering for a longer time. Flushing synchrony and intensity was positively related to each other. This has to do with the amount of water stress experienced by species in the study site. Flushing and senescing skewness was related to each other. Finally, predictably, flowering frequency, synchrony and interannual variation were positively related to those of fruiting.

This study described the seasonal variation in phenology of vegetative and reproductive phenophases and comprehensively explored the intricate relationships between phenology parameters within and between phenophases. Most of the relationships previously existed as theoretical predictions with some rare studies that looked at some of these relationships in isolation. These results provide some unique insights into these predictions supporting most of them. However, there were a few of them that were found contrary to the expectation that needs further exploration. Although species showed a lot of variation in different phenology parameters, species can be grouped into categories based on some common factors. Then, the species within each group are expected to be more similar in their phenology characteristics than between species in another group. This categorisation of species and understanding the differences between groups form the basis of the next chapter. However, this study has a couple of caveats. Firstly, the ensemble behaviour represented by percent species does not consider the variation in size and abundance of the species and thereby might not represent the actual behaviour at the community level. This is addressed in Chapter 3. Secondly, a phylogenetic correction was not considered. Phylogeny has been shown to constrain phenology of species (Bawa, Kang & Grayum 2003). Further exploration is required with consideration of phylogeny to reevaluate these relationships.

Tables and figures

Table 1: Relationships between the synchrony indices for the four phases – a) Flushing, b) Senescing, c) Flowering and d) Fruiting. The values represent Pearson's correlation, and the symbol * represents significance value, $p < 0.05$. The synchrony indices are as follows: Current = the index of synchrony developed and described in this study, Freitas = an index of synchrony described in Freitas and Bolmgren (2008), Augspurger = an index of synchrony described in Augspurger (1983), Vec len = vector length (r) from circular statistics describing a measure of angular concentration, and Circ SD = circular standard deviation of mean angles of individuals.

a) Flushing

	Current	Freitas	Augspurger	Vec len	Circ SD
Current	1.00				
Freitas	0.85*	1.00			
Augspurger	0.23*	0.63*	1.00		
Vec len	0.40*	0.22	0.09	1.00	
Circ SD	-0.39*	-0.21	-0.10	-0.99*	1.00

b) Senescing

	Current	Freitas	Augspurger	Vec len	Circ SD
Current	1.00				
Freitas	0.91*	1.00			
Augspurger	0.61*	0.77*	1.00		
Vec len	0.74*	0.55*	0.27*	1.00	
Circ SD	-0.76*	-0.58*	-0.30*	-0.98*	1.00

c) Flowering

	Current	Freitas	Augspurger	Vec len	Circ SD
Current	1.00				
Freitas	0.85*	1.00			
Augspurger	0.45*	0.80*	1.00		
Vec len	0.50*	0.26*	0.05	1.00	
Circ SD	-0.50*	-0.25*	-0.06	-0.99*	1.00

d) Fruiting

	Current	Freitas	Augspurger	Vec len	Circ SD
Current	1.00				
Freitas	0.85*	1.00			
Augspurger	0.67*	0.94*	1.00		
Vec len	0.64*	0.30*	0.15	1.00	
Circ SD	-0.61*	-0.29*	-0.15	-0.98*	1.00

Table 2: Variation in the phenology parameters across the four phenophases. Results presented in the format Mean ± Standard Error (Minimum - Maximum). IAV stands for interannual variation.

Variable	Flushing	Senescing	Flowering	Fruiting
Duration	82±5 (36-282)	109±5(31-245)	42±2(30-97)	125±5(44-223)
Frequency	1.1±0.0 (0.4-1.7)	1.1±0.0 (0.4-1.7)	0.6±0.0 (0.1-1.4)	0.5±0.0 (0.1-1.1)
Synchrony	0.0100±0.0032 (0.0001-0.2399)	0.0023±0.0004 (0.0001-0.0193)	0.043±0.0058 (0.0009-0.2838)	0.0141±0.002 (0.0001-0.0627)
Intensity	16±1 (6-61)	10±1 (5-32)	35±2 (7-75)	49±2 (20-83)
Skewness	2.4±0.1 (0.6-3.3)	1.8±0.1 (0.2-3.2)	3.2±0 (2.3-3.5)	2.2±0.1 (0.9-3.3)
Kurtosis	6±0 (1-11)	4±0 (0-10)	10±0 (5-12)	6±0 (1-11)
IAV	21±1 (7-49)	35±1 (8-55)	11±1 (0-50)	19±2 (1-53)

Table 3: Relationship between the timing of the phenophase and the supplementary phenology parameters. The numbers represent the angular linear correlation (r_{al}) of the supplementary parameters to the timing of the corresponding phenophase. The symbols represent the level of significance (p): * =0.05, ** = 0.01, and *** = 0.001

Parameters	**Flushing**	**Senescing**	**Flowering**	**Fruiting**
Duration	0.11***	0.01	0.07**	0.00
Frequency	0.17***	0.31***	0.02	0.03
Synchrony	0.21***	0.02	0.17***	0.12***
Intensity	0.32***	0.04	0.09**	0.03
Skewness	0.11***	0.03	0.01	0.04
Interannual variation	0.06*	0.11***	0.03	0.15***

Table 4: Relationship between the supplementary phenology parameters across phenophases. The parameter pairs represented as the phenophases followed by the corresponding parameter. For example, Flushing - Flowering duration means the relationship between the duration of flushing and the duration of flowering. The values represent Pearson's correlation between phenology parameters across phenophase. The symbol * represent the correlation coefficient significant at $p < 0.05$

Parameter pair	**r**
Flushing - Flowering duration	0.41*
Flushing - Senescing synchrony	0.43*
Flushing - Flowering synchrony	0.39*
Flushing - Senescing intensity	0.51*
Flushing - Senescing skewness	0.32*
Flushing - Flowering skewness	0.30*
Senescing - Flowering duration	0.26*
Senescing - Flowering skewness	0.38*
Flowering - Fruiting frequency	0.57*
Flowering - Fruiting synchrony	0.35*
Flowering - Fruiting interannual variation	0.33*

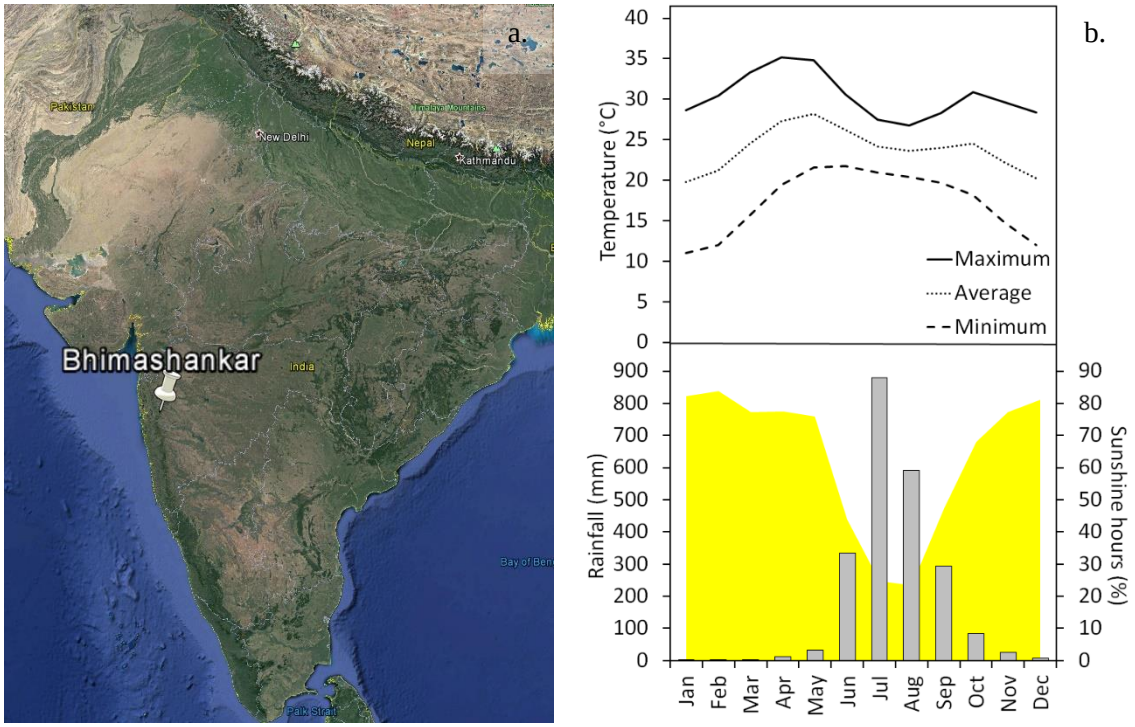


Figure 1: Location of the study site and the seasonality of temperature, light, and water availability at the site. Panel (a) shows the location of the study site in India. Panel (b) Line graphs on the top depict the annual variation in temperature, the bar graph on the bottom depicts the rainfall per month (in mm), and the shaded area depicts the variation in solar insolation expressed as the percentage of sunshine hours.

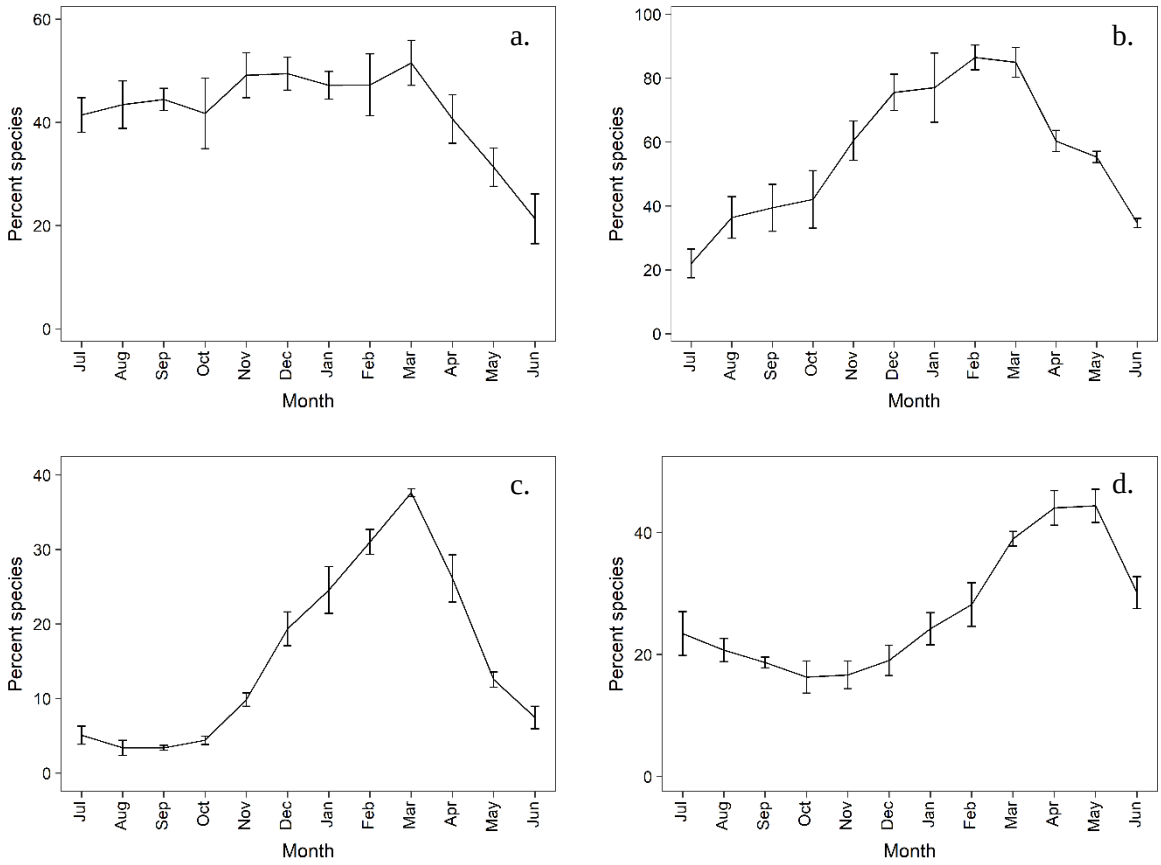


Figure 2: Seasonal variation in the percent species in activity across the year for a) Flushing, b) Senescing, c) Flowering and d) Fruiting phenophases. The error bars represent the standard error of the mean, with n = 4 years of data.

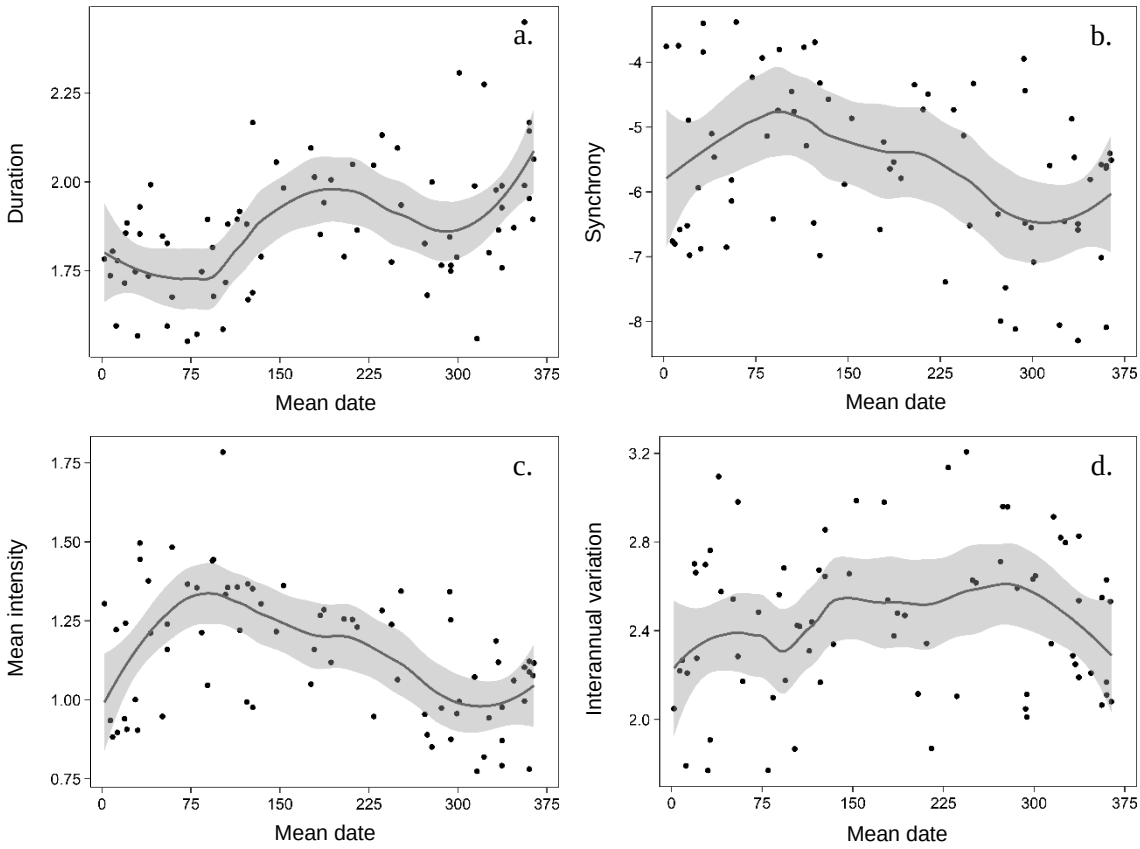


Figure 3: Relationship between the timing of flushing and the phenology parameters of a) duration, b) synchrony, c) intensity and d) interannual variation. The timing is represented as the day of the year, and the y-axis is the transformed values of the corresponding parameters. The shaded area represents 95 percent confidence interval.

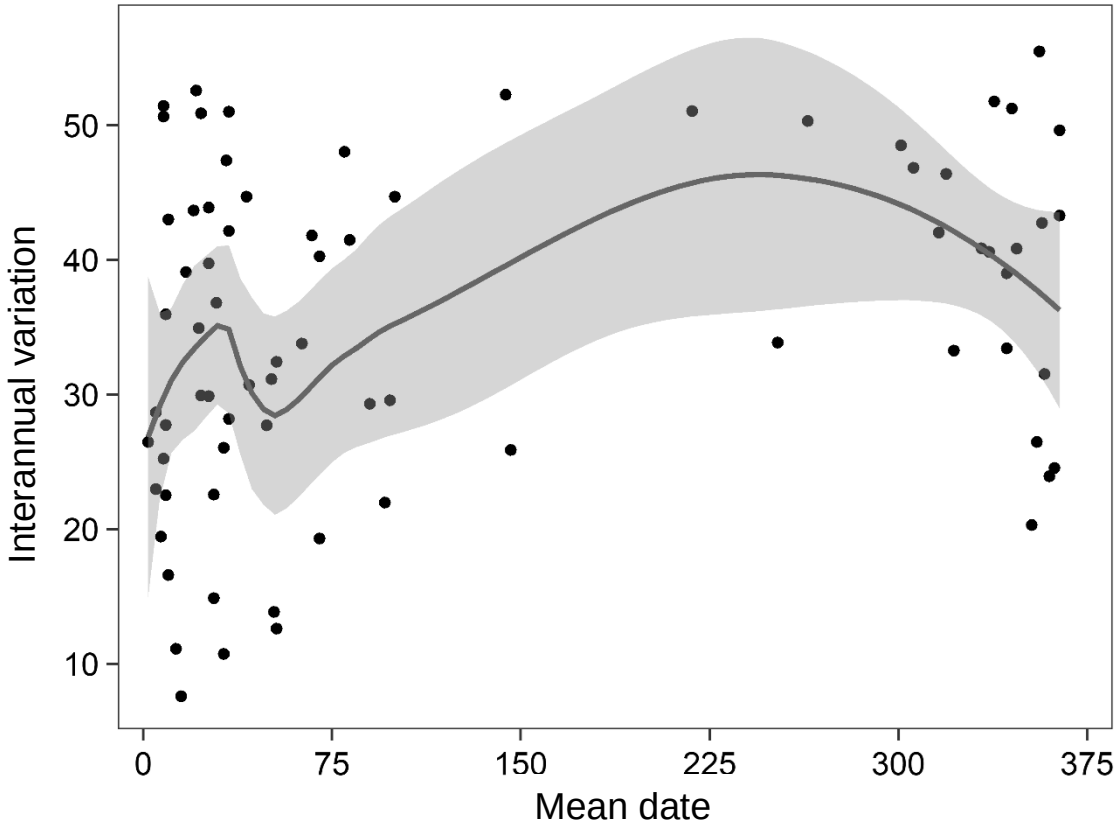


Figure 4: Relationship between the timing of senescing and the interannual variation. The timing is represented as the day of the year, and the y-axis is the transformed value of the parameter. The shaded area represents 95 percent confidence interval.

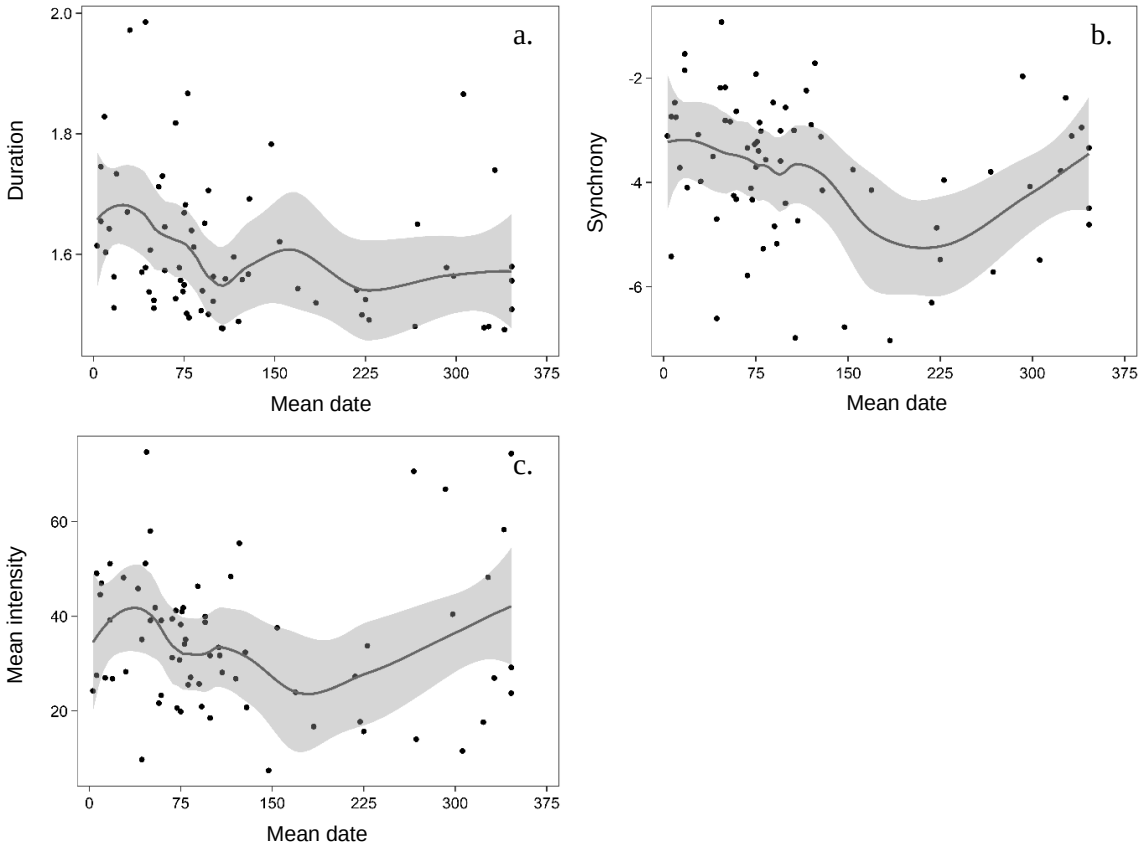


Figure 5: Relationship between the timing of flowering and the phenology parameters of a) duration, b) synchrony and c) intensity. The timing is represented as the day of the year, and the y-axis is the transformed values of the corresponding parameters. The shaded area represents 95 percent confidence interval.

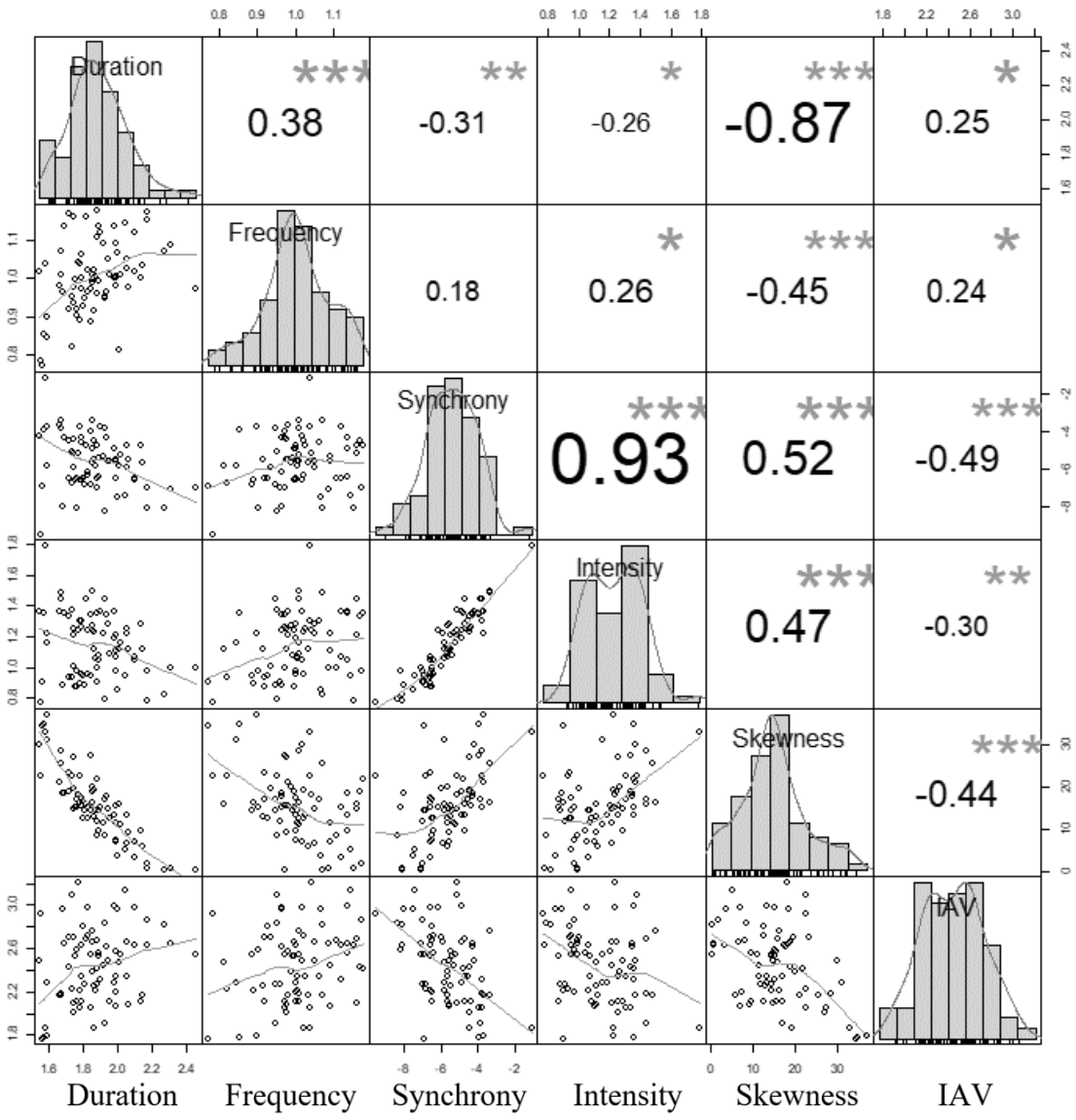


Figure 6: Relationships between the flushing supplementary phenology parameters. The rows represent the following parameters in sequence: the flushing duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

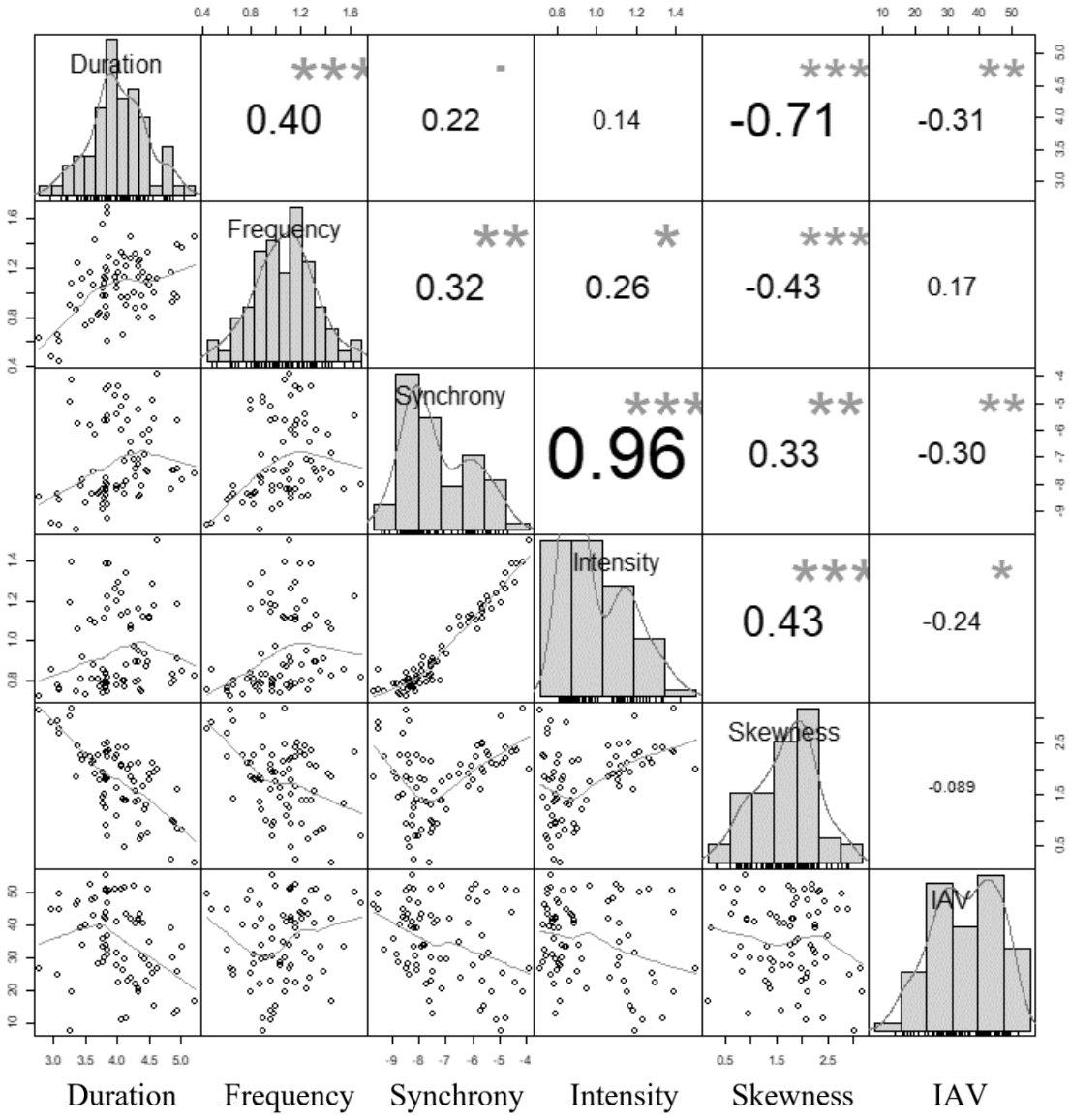


Figure 7: Relationships between the senescing supplementary phenology parameters. The rows represent the following parameters in sequence: the senescing duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

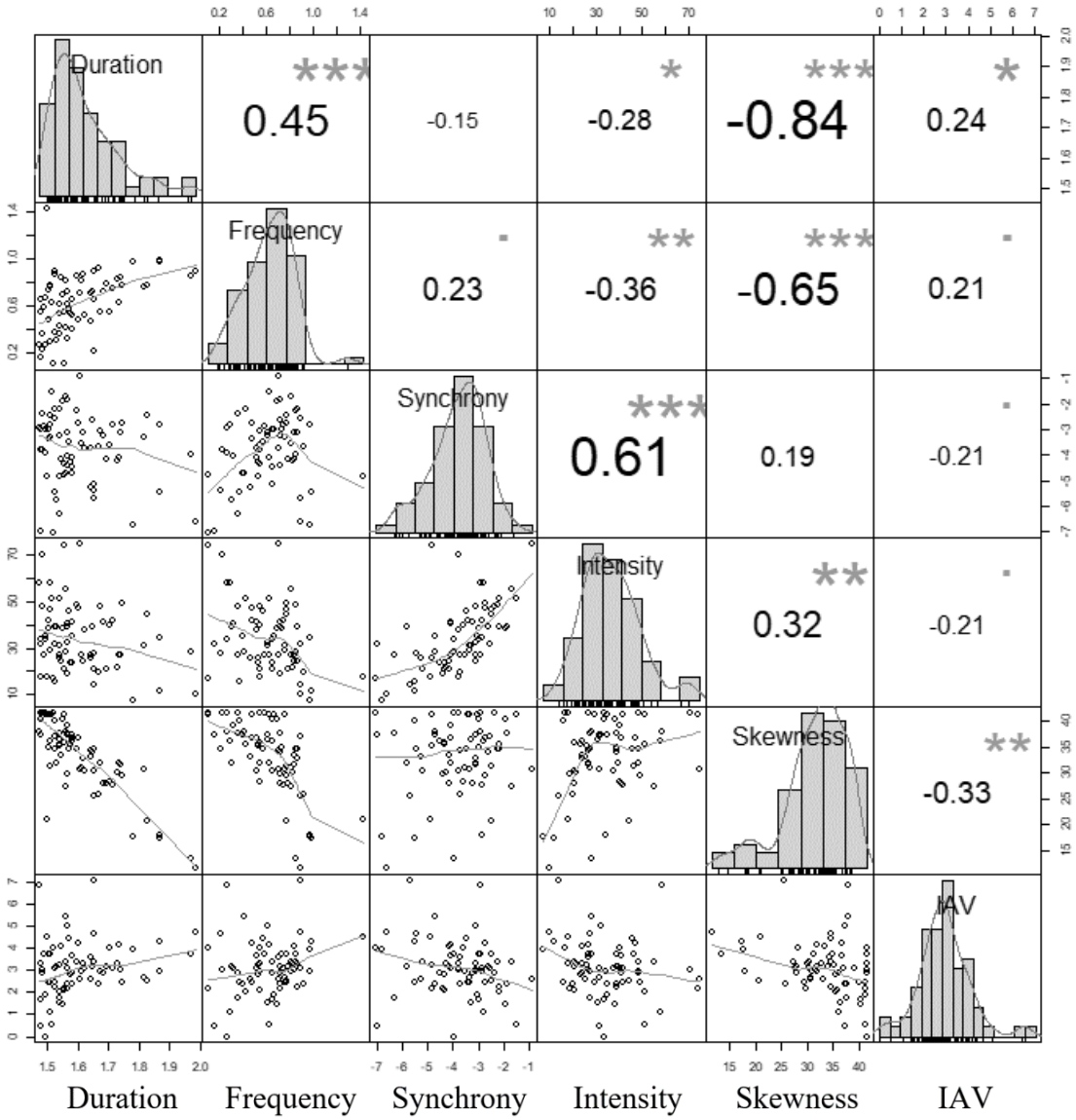


Figure 8: Relationships between the flowering supplementary phenology parameters. The rows represent the following parameters in sequence: the flowering duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

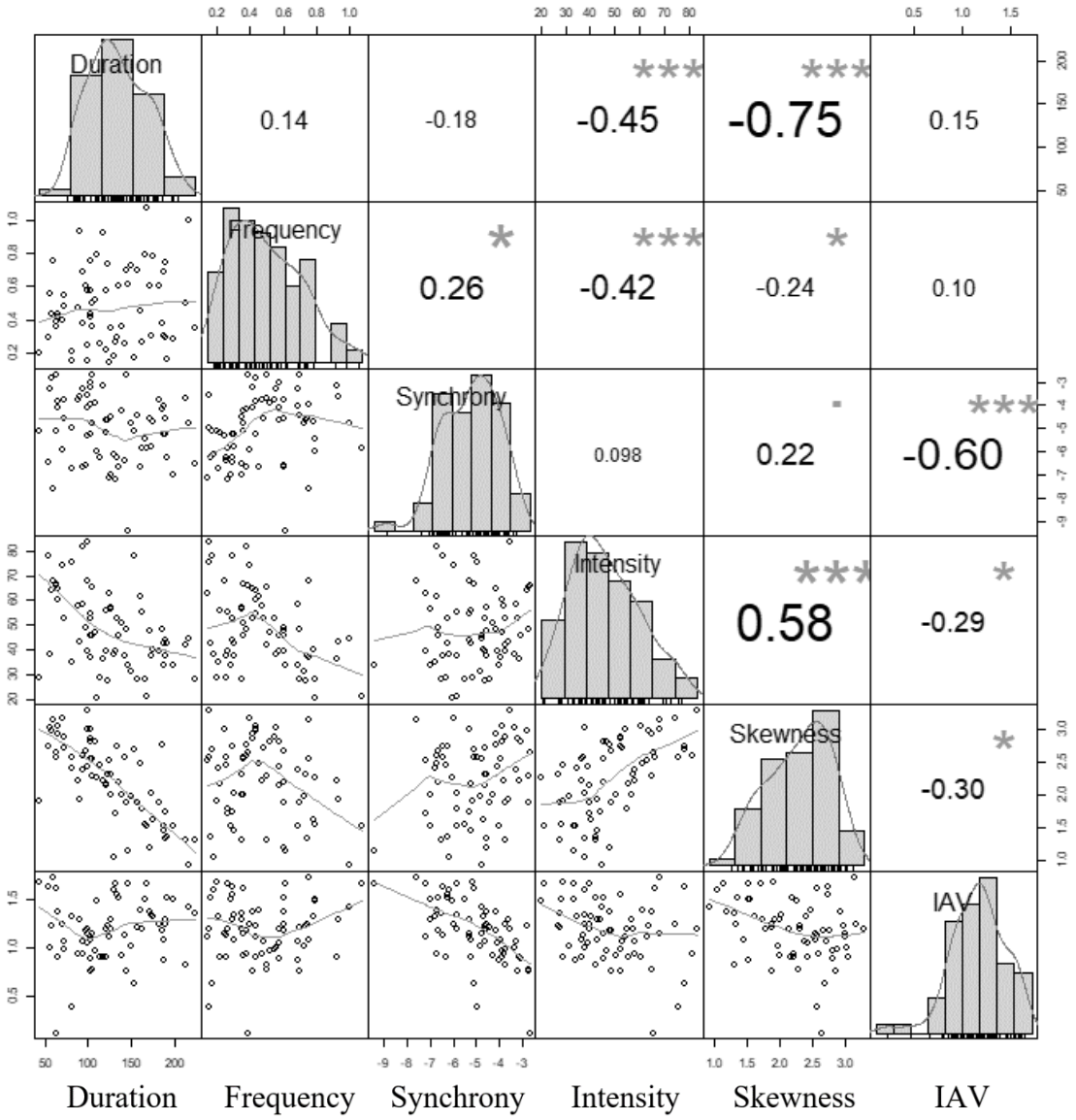


Figure 9: Relationships between the fruiting supplementary phenology parameters. The rows represent the following parameters in sequence: the fruiting duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

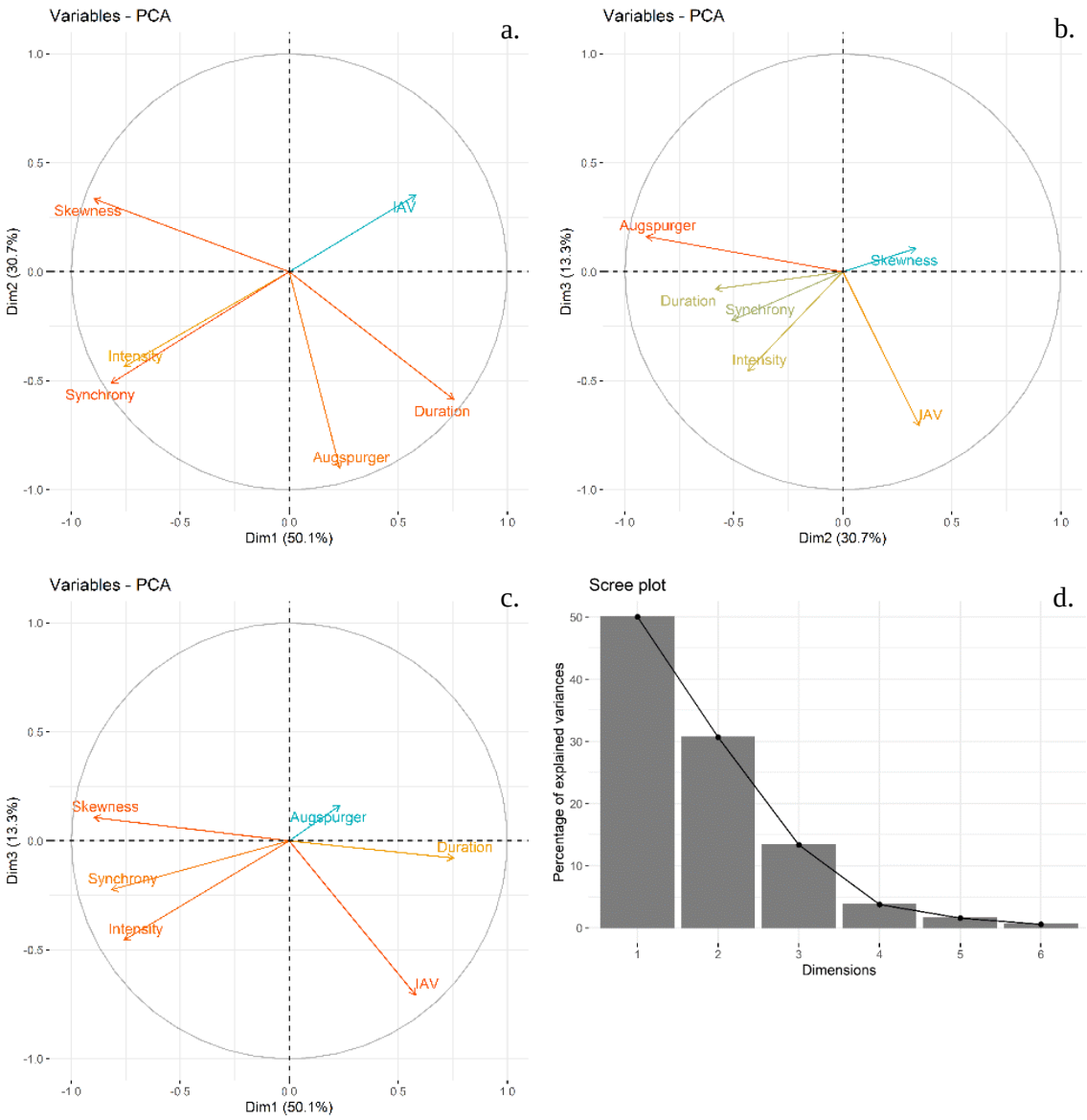


Figure 10: Results for principal component analysis of flushing phenology parameters: a) biplot for components 1 and 2, b) biplot for components 2 and 3, c) biplot for components 1 and 3 and d) scree plot.

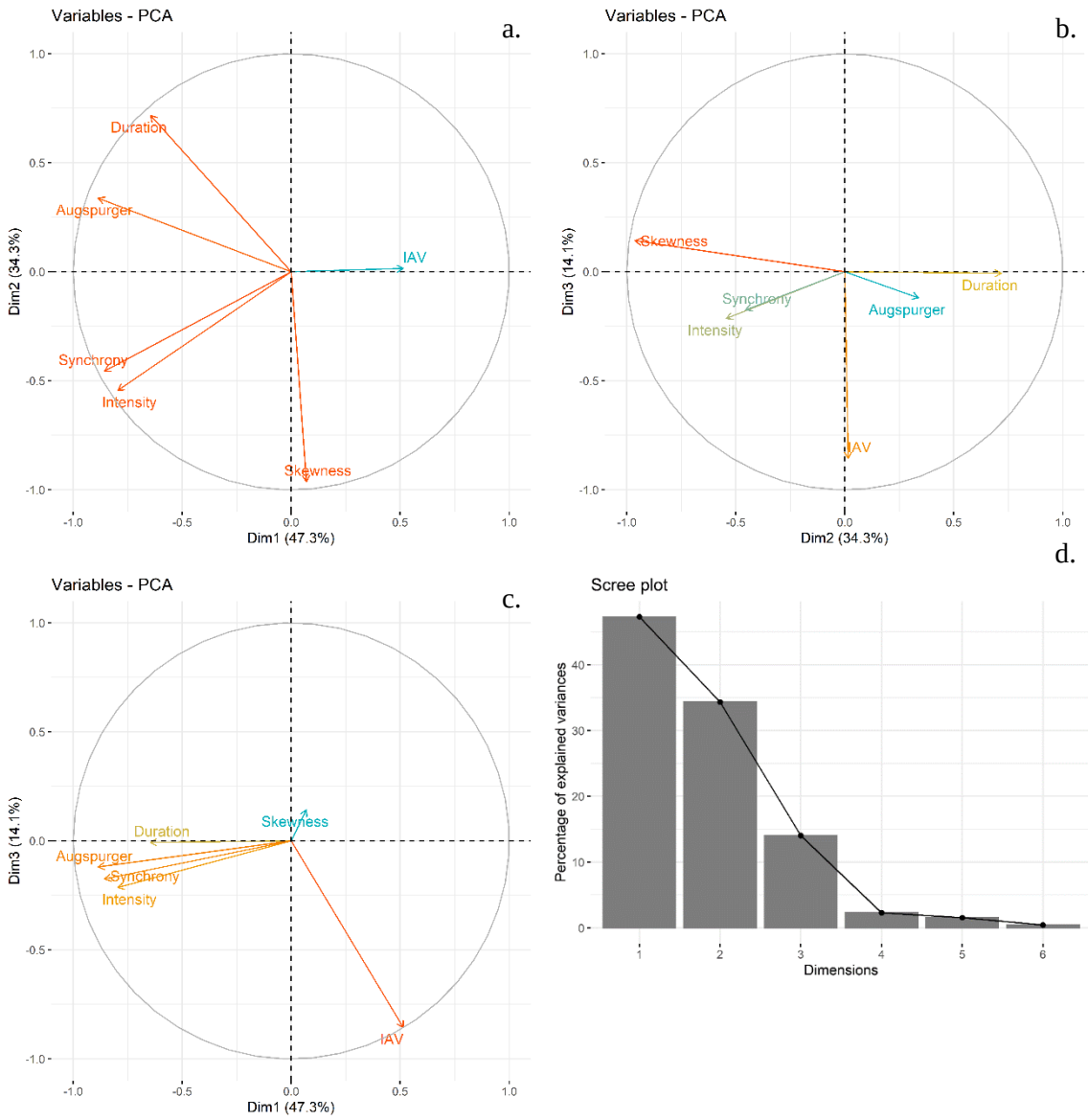


Figure 11: Results for principal component analysis of senescing phenology parameters: a) biplot for components 1 and 2, b) biplot for components 2 and 3, c) biplot for components 1 and 3 and d) scree plot.

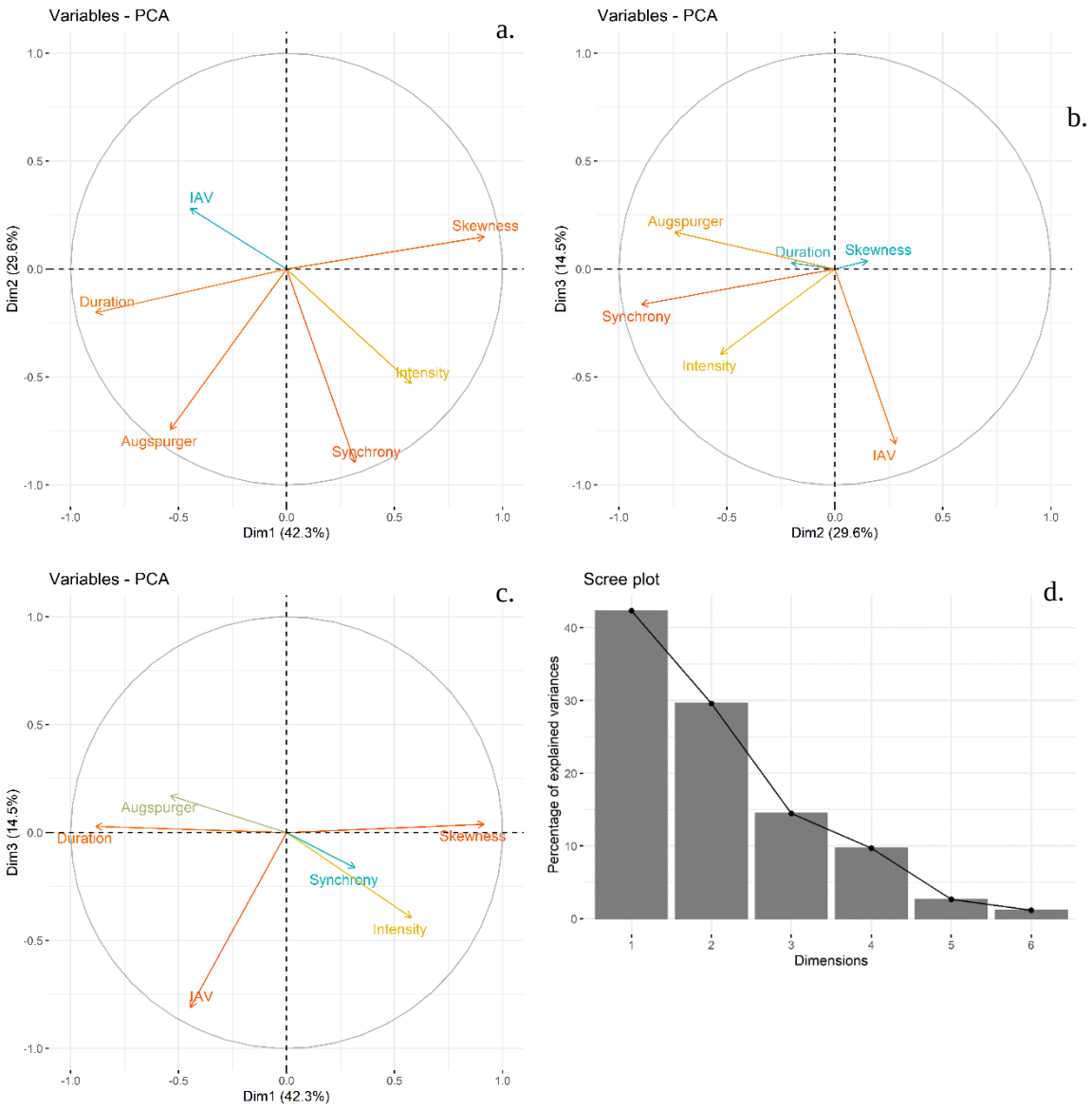


Figure 12: Results for principal component analysis of flowering phenology parameters: a) biplot for components 1 and 2, b) biplot for components 2 and 3, c) biplot for components 1 and 3 and d) scree plot.

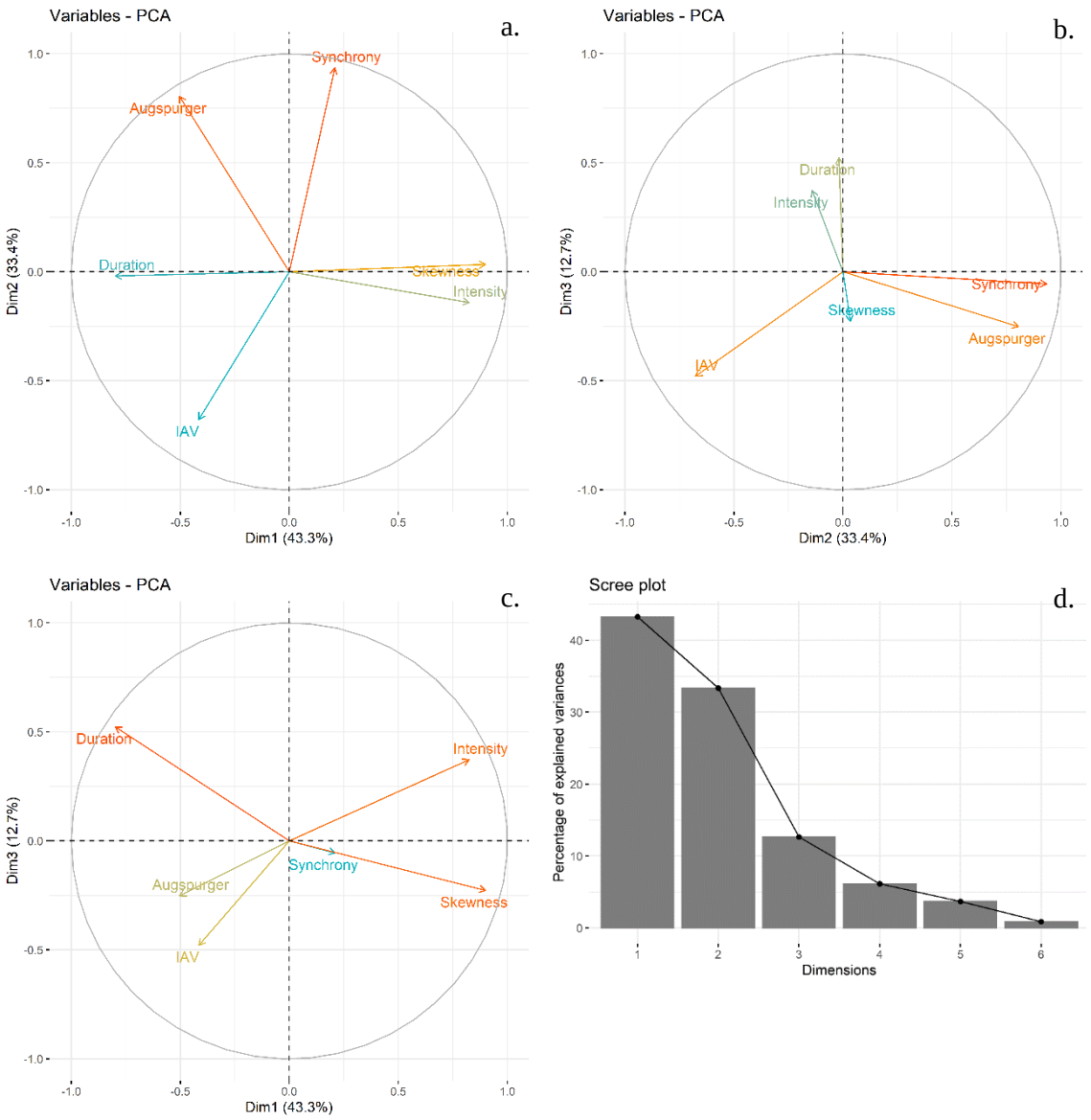


Figure 13: Results for principal component analysis of fruiting phenology parameters: a) biplot for components 1 and 2, b) biplot for components 2 and 3, c) biplot for components 1 and 3 and d) scree plot.

Chapter 3: Variation in vegetative and reproductive phenology between plant functional groups

Introduction

Plant species can be grouped into categories sharing some specific traits. Such groups are hereby defined as plant functional groups. There can be various plant functional groups based on their growth habit and biotic interactions, but the most well-known and well-studied among them are groups based on leaf shedding habit – the evergreen and deciduous species. Although there is a lot of variation between species in their vegetative and reproductive phenology, one can expect similarities in phenology between species belonging to a particular group and differences between species of different groups. However, even for the most well-known evergreen and deciduous categories, such similarities and differences have seldom been addressed in a comprehensive manner (Kushwaha & Singh 2005). Another important aspect is that there exists a lot of variation between species within groups. Such variation has received even less attention (Williams, Bunyavejchewin & Baker 2008). In this study, I looked at the variation in phenology between some of these functional groups. I then examined the variation between species in each group as a continuous trait for the most well-known evergreen and deciduous species.

Plant growth habits involve two functional groups for woody species: life form – trees, lianas and shrubs, and the canopy strata group – canopy, sub-canopy, and understory. Although different characteristics define these groups, their phenology is influenced by similar limitations of light and water. Trees and lianas have deeper roots and can access deep soil water. Some trees also have the capacity for water storage in their stems and roots (Borchert 1994). Shrubs, in contrast, are typically shallow rooted and do not have the capacity for stem water storage (Becker & Castillo 1990). Plants in the upper canopy layer have access to greater availability of light. In contrast, plants in the sub-canopy and understory layer are more limited by light. Therefore, plants in the sub-canopy and understory layers often flush when the canopy layer sheds leaves (Justiniano & Fredericksen 2000) and exhibits less seasonal flowering and fruiting than plants in the upper canopy (Opler, Frankie & Baker 1980; van Schaik, Terborgh & Wright 1993).

Thus, species belonging to different life forms and those from different canopy strata are expected to show variation in their vegetative and reproductive phenology.

Broad-leaved evergreen and deciduous species are important and dominant plant functional types in dry tropical forests. These leaf habit categories represent different water use and conservation strategies. Evergreen species maintain photosynthesis under low soil moisture and can utilize the greater availability of sunshine in the drier parts of the year for their growth and reproduction (van Schaik, Terborgh & Wright 1993; Eamus 1999). Deciduous species are fast-growing and avoid drought by dropping their entire canopy, thus eliminating transpirational water loss during dry periods. Therefore deciduous species have a greater dependency on water for activity and typically flush and flower closer to the onset of the rains (Elliott, Baker & Borchert 2006). Studies have shown deciduous species to shed leaves during the cool dry season in response to water stress and flush at the end of the dry season (Williams-Linera 1997; Kushwaha & Singh 2005). In contrast, evergreen species initiate bud break in the middle of the dry season around the spring equinox (Kushwaha & Singh 2005). However, Williams-Linera (1997) did not find differences in the timing of reproductive phenophases between evergreen and deciduous species. Not only in timing but studies have also found evergreen species flush, flower and fruit for longer durations than deciduous species (Kushwaha & Singh 2005; Borges, Henrique & Prado 2014; Lacerda *et al.* 2018). Hence evergreen and deciduous species are expected to differ in their vegetative and reproductive phenology.

Several studies highlight the importance of examining continuous traits rather than discrete functional groups (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004; Williams, Bunyavejchewin & Baker 2008). One important reason for this is that studying variation between groups hides a lot of variation that exists between species in each group. For example, different deciduous species can range in leafless duration from a week to greater than six months. Similarly, in evergreen species, maximum canopy loss can vary from zero to >75% of the total canopy. As evergreen and deciduous leaf habit categories are ecologically important functional groups, researchers have tried to quantify leaf shedding behaviour as a continuous trait. Deciduousness, the shedding of leaves in the dry season, is an indicator of seasonal drought experienced by trees in tropical dry forests (Singh & Kushwaha 2016). Several measures of deciduousness have been used across different studies. These include the duration of leafless period (Kushwaha & Singh

2005; Williams, Bunyavejchewin & Baker 2008), the maximum amount of leaf loss (Williams *et al.* 1997; Williams, Bunyavejchewin & Baker 2008) and some annual canopy cover measures including leaf area index (Blackburn & Milton 1995; Ryu *et al.* 2014) and average canopy (Williams *et al.* 1997; Condit *et al.* 2000). These studies have described wide variation of these continuous measures of deciduousness and their relationships to other parameters like flushing and flowering duration (Kushwaha & Singh 2005), intensity (Borges, Henrique & Prado 2014) etc.

Flowering is a resource-intensive process and is influenced by the availability of individual resources, other flowering individuals in the population and pollen vectors (Fenner 1998). A trade-off exists between the investment of resources in a single flower and the number of flowers produced during a season (Sargent *et al.* 2007). Thus, flower size is expected to be inversely related to the flowering intensity. Between plant sexual systems, dioecious species are known to have generalist pollinators and can be expected to be seasonal in their flowering time (Ibarra-Manriquez & Oyama 1992; Kang & Bawa 2003; Ramirez 2005). They are also likely to be more synchronous in flowering between individuals. Within dioecious species, males are expected to flower earlier and longer than females (Forero-Montana & Zimmerman 2010). Availability of other flowering individuals potentially contributes to individuals' reproductive success for cross-pollinating species (Marquis 1988). Thus, rarer species are expected to be more synchronous and flower with greater intensity to ensure reproductive success than highly abundant species. Plants pollinated by particular insect groups are expected to flower when their pollinators are most abundant to ensure maximum reproductive success (Kang & Bawa 2003).

Zoochorous species may fruit at any time of year (Janzen 1967) depending upon disperser availability. However, animal dispersers usually more active in the wet season (Smythe 1970). Zoochorous species generally have large fleshy fruits to attract dispersers (Primack 1987). Fleshy fruits can be kept attractive for a longer time in the wet season (Batalha & Mantovani 2000). Thus, zoochorous species are expected to fruit in the wet season. Dry periods dehydrate pericarp of autochorous fruits (Batalha & Martins 2004). Additionally, high wind speeds and bare branches facilitate dispersal by the wind in the dry season (Augspurger & Franson 1987). Thus, autochorous and anemochorous species tend to fruit in the dry season (Batalha & Martins 2004). Zoochorous species with large fleshy fruits

are expected to take more time to mature than smaller fruits with low reserves (Primack 1987).

Apart from the evergreen-deciduous categories, the other functional groups only notably have theoretical predictions and some empirical observations. To get a thorough resolution of these predictions, I explored the variation in phenology between the following plant functional groups for the corresponding phenophases. I looked at the differences in timing and the differences in the supplementary parameters described in Chapter 2. For the growth habit category with differences in access to light and water, I expected trees and lianas to flush and flower in the early dry season utilising maximum sunlight, while the shrubs would show activity near the rains. Subcanopy and understory layer is more limited by light than water, hence expected to be dominated by species primarily cueing to light and flush and flower earlier in the dry season than the canopy layer. Evergreen species that are relatively less water-limited should flush and flower in the early dry season with maximum sunlight. Deciduous species which are highly water-limited are expected to show activity near the rains. Evergreen species are also likely to show activity for a longer duration, lower synchrony, lower intensity, and lower interannual variation than deciduous species. The conservative resource accumulating evergreen species are expected to use current year's resources and hence flower after flushing while the fast-growing, exploitative resource accumulating deciduous species are expected to use previous year's resources and hence flower before flushing. In the plant sexual system groups, dioecious and polygamous species are expected to flower for longer duration and be more synchronous between individuals than other hermaphrodite species. Within dioecious species, males are expected to flower earlier and for a more extended period than females. Differences in timing between pollinator groups are expected to coincide with the timing of availability of pollinators. Finally, for dispersal syndrome, I expect anemochorous and autochorous species disperse in the dry season while zoochorous species do so in the wet season.

I also examined leaf shedding phenology as a quantitative trait to understand the continuous nature of variation in leaf shedding habit and its relationship to other phenology parameters. Here I expected that species with lower deciduousness would flush and flower earlier in the dry season than species with higher deciduousness. They are expected to show activity for a longer duration, have lower synchrony, lower

intensity, and lower interannual variation than those with higher deciduousness. Finally, I explored the relationship between mate availability and flower and fruit investment with reproductive phenology. I expected species with lower abundance to be more synchronous in flowering timing than species with higher abundance. I also expect that owing to limited resources, species with larger flowers and fruits have activity for shorter duration and lower intensity than species with lower investment per flower or fruit.

Materials and Methods

The same data used to study variation in phenology between species was used to look at the variation in phenology between plant functional groups. Plant species were classified into different functional groups based on various plant traits, strategies, and biotic interactions. The following functional groups were recognised: A) Plant growth habit groups that included trees, lianas, and shrubs. I defined woody plant species with an adult height of less than 3m as a shrub, plants that used other plants as vertical support to grow towards the canopy as lianas and the rest as trees. The canopy strata include the canopy, sub-canopy, and understory species. I defined plant species with leaves directly exposed to the sun as belonging to the canopy layer while species that occur in the shade and not grow more than a height of 3m as the understory layer. Sub-canopy species occupy between the canopy and the understory. B) Leaf habit groups that include the evergreen and deciduous species. I defined species as being deciduous if at least three individuals of a species for at least more than one year were completely devoid of any leaf for at least one month of the year. Others were identified as evergreen species. C) Plant sexual system groups that include hermaphrodite, monoecious, polygamous, and dioecious species. D) Pollination syndrome groups that include the species pollinated by melittophily (bee), diverse insects, bee/psychophily, psychophily (butterfly), phalaenophily (moth), cantharophily (beetle), myophily (fly), anemophily/melittophily and anemophily/diverse insects. E) The dispersal syndrome groups include the species dispersed by endozoochory, ectozoochory, autochory and anemochory. Plant sexual system, pollination and dispersal syndrome were identified by integrating information from the literature, species flower and fruit traits and personal observations. Details of the relevant literature are given in the appendix.

Three indices of deciduousness were used together to calculate an index of deciduousness. These were calculated per individual per year, averaged across years to get an individual mean and then averaged across all individual to get a species mean. These include a) Average canopy loss – the reduction in total canopy averaged across all months in a year, b) Maximum canopy loss – the maximum loss of total canopy across all months in a year, and c) Duration of deciduousness – the duration in days when an individual was completely leafless. A PCA was done with these three parameters to get an overall index of deciduousness.

Lag of flushing and flowering was calculated as the difference in days between the timing of flushing and the timing of flowering. Here positive lag indicates flowering after flushing while negative lag indicates flowering before flushing. One-way ANOVA and Pearson's correlation was used to understand differences in lag between evergreen and deciduous species and examine the relationship to deciduousness, respectively.

Length of flower and fruit (in cm) for each species was collected from literature and previous work done in the lab. Flower and fruit number for each species was estimated by creating five categories based on an estimated number of flowers or fruits in a cubic meter of the canopy volume at 100 percent intensity and then assigning each species to one of these five groups. Finally, the flower and fruit display size were calculated by multiplying flower/fruit size and the corresponding estimate of the number. For calculation of mate availability, the total number of mature individuals for each species from plots in the three habitats was multiplied by the total area of each habitat in the study site to give the total number of individuals. For dioecious species, the number of females was used as the number of mates available. The total number of mates, expressed as the fraction of the total number of individuals in a habitat, was considered as the mate availability for a species.

Rayleigh's test for uniformity was used to test if the timing of a phenophase for species in a group is uniform throughout the year or not. If different from a uniform distribution, a mean angle representing peak activity for each group was calculated using circular statistics. Difference between the mean angle of groups was tested using Watson-Williams test from the package "circular" in R. The relationship between dates and deciduousness was calculated using circular-linear correlation from "Directional"

package in R. Relationship of deciduousness to linear parameters was calculated using Pearson's correlation. One-way ANOVA was used to test for differences in the linear phenology parameters and PCs between the functional groups.

Results

Species in the study site were categorized into growth habits based on life forms and location in the canopy strata, leaf shedding habit, sexual system, pollination, and dispersal syndromes (Table S1). Of the 75 species, 48 were trees, 14 were lianas, and 13 were shrubs. Flushing, flowering, and fruiting in shrubs were uniformly distributed throughout the year (Table 1). In lianas, flushing was also uniformly distributed. Flowering and fruiting in shrubs and all the phases of trees peaked in the middle of the dry season. Senescing in all the life forms also peaked in the middle of the dry season. However, there was no significant difference in timing between any of the phases (Table 1). In the context of supplementary parameters, shrubs flushed for a longer duration (116 ± 16 days) than trees (77 ± 5 days) and lianas (68 ± 7 days). Shrubs flowered more frequently and at a significantly lower intensity than trees (Table S2). There was no difference between life forms for any of the phenophases in multivariate space.

50 species belonged to the canopy layer, 21 in the sub-canopy and only 4 were understory species. The number of understory species was too low and was discounted from further analysis. The sub-canopy species flushed in the early dry season and senesced in the middle of the dry season. Flowering and fruiting were uniform throughout the year. The canopy layer also showed activity in the middle of the dry season (Table 2). When comparing canopy strata groups, while there was no difference in senescing timing, the sub-canopy layer flushed more than 4.5 months earlier than the canopy layer. The canopy layer had significantly higher flowering synchrony (0.05 ± 0.01) than the sub-canopy (0.03 ± 0.01) layer (Table S3). The flowering of the sub-canopy layer differed significantly from the canopy layer in multivariate space ($F = 5.66$, $p = 0.02$).

There was an almost comparable number of evergreen and deciduous species in the study site. The evergreen group had 44 species while the deciduous group had 31 species. Both the groups had vegetative and reproductive phases distributed non-uniformly throughout

the year. All the phases for both the groups peaked in the dry season (Table 3). However, evergreen species flushed more than 5 months earlier, flowered about a month earlier and fruited about 2 weeks earlier than deciduous species. There was no difference in the timing of senescence. There was no difference in the lag of flushing and flowering between evergreen (36 ± 6 days) and deciduous (30 ± 10 days) species ($F = 0.37$, $p = 0.55$). Species with a mixture of terminal and axillary inflorescence where lag of flushing and flowering cannot be predicted had a much lower lag (6 ± 10 days) than species where flowering was either dependent (41 ± 13 days) or independent (38 ± 7 days) of flushing ($F = 3.3$, $p = 0.04$). Deciduous species had significantly higher flushing frequency, synchrony, and intensity than evergreen species (Table 4). Deciduous species also showed higher senescing synchrony, intensity, and lower interannual variation than evergreen species. Deciduous species had higher synchrony than evergreen species. Evergreen and deciduous species differed in flushing ($F = 7.09$, $p = 0.01$) and senescing phenology ($F = 88.54$, $p < 0.001$) but not in flowering and fruiting phenology in a multivariate space.

The three measures of deciduousness, namely, average canopy loss, maximum canopy loss and duration of deciduousness, showed a wide range of leaf loss behaviour (Fig. 1). Species lost from almost no canopy to more than 50 percent of the canopy throughout the year on average. While some species lost no canopy at all, some lost their entire canopy at some point of time. Those species that lost their entire canopy remained leafless for a period that ranged from a couple of days to about 4.5 months of the year. A principal component analysis was performed with these three deciduousness measures. PC1 accounted for 92% of the variance, while PC2 accounts for 7% of the variance (Fig. 2). The average canopy loss and maximum canopy loss loaded equally on PC1 (0.98 and 0.97 respectively) while the duration of deciduousness had the highest loading on PC2 (0.37). Thus, PC1 explained most of the variation is henceforth referred to as the index of deciduousness. The timing of flushing ($r_{al} = 0.78$, $p < 0.001$), and flowering ($r_{al} = 0.37$, $p = 0.001$) was significantly related to deciduousness of species. The flushing timing was negatively related to the deciduousness indicating species with lower deciduousness flushed earlier in the dry season while those with higher deciduousness flushed later in the dry season as expected. Although there was no difference in the lag of flushing and flowering between evergreen and deciduous species when examined as discrete

categories, the quantitative index of deciduousness was significantly correlated to the deciduousness of species (r_{al} = 0.32, $p < 0.001$). Species with higher deciduousness had higher flushing frequency, synchrony, and intensity than species with lower deciduousness. Interannual variation in flushing was not related to deciduousness (Fig. 3). Timing of senescing was also not related to the deciduousness (r_{al} = 0.12, p = 0.36). Only PC2 was positively related to senescing frequency. Senescing synchrony and intensity were positively related to deciduousness, while interannual variation was negatively related to deciduousness (Fig. 4). In flowering, only PC2 was positively related to frequency, and synchrony (Fig. 5). In fruiting, only PC2 was related to frequency (Fig. 6).

There was no relationship between flower size (r = -0.11, p = 0.35) or display size (r = -0.09, p = 0.48) to flowering intensity. However, display size was positively related to the timing of flowering (r_{al} = 0.33, $p < 0.001$). Display size was positively related to the flowering synchrony (r = 0.44, p = 0.0001). Flower size (r = -0.26, p = 0.03) and display size (r = -0.28, p = 0.02) was negatively related to interannual variation (Fig. 7). Between the plant sexual system groups, 42 species were hermaphrodite, 10 were monoecious, 7 were polygamous, and 15 were dioecious species. Monoecious and polygamous species flowered uniformly throughout the year. While hermaphrodite species flowering peaked 22nd March, dioecious species peaked significantly earlier on 21st February (F = 5.93, p = 0.0182). Monoecious species had a longer flowering duration (57 ± 10 days) than hermaphrodite (43 ± 2 days), polygamous (35 ± 1 days) or dioecious species (38 ± 2 days) contrary to expectation (F = 3.03, p = 0.04). There was no difference in synchrony between sexual systems (Table S4). There was no difference between sexual systems in flowering phenology in multivariate space (F = 2.00, p = 0.12). In dioecious species, males flowered either at the same time or earlier and for either the same or longer duration than the females (Table S5).

Flowering synchrony was not related to the mate availability (r = 0.03, p = 0.84). However, mate availability was positively related to flowering frequency (r = 0.32, p = 0.0051) and negatively to the flowering intensity (r = -0.27, p = 0.0239) of the species (Fig. 7). Most of the pollinator groups had a very low number of species and did not have a distribution of flowering dates different from uniform (Table 5). Bee, butterfly, beetle,

and species pollinated by other diverse insects had a significant angular concentration. While all peaked in the dry season, beetle pollinated species peaked earliest on the 15th of February, butterfly and diverse insect groups peaked on 12th and 15th of March respectively and the bee pollinated species peaked last on 2nd of April ($F = 4.18$, $p = 0.01$). There was no difference between the groups in the other parameters or flowering in multivariate space ($F = 1.21$, $p = 0.31$).

There were 5 anemochorous species, 14 autochorous species and 55 zoochorous species. Among the zoochorous species, 26 were ectozoochorous while 29 were endozoochorous species. Fruit stop dates were used as the date of dispersal. Autochorous and anemochorous species had peak dispersal in the dry season on 11th of April and 3rd of June respectively as expected. Ectozoochorous species also had peak dispersal in the dry season on 2nd of May. However, endozoochorous species which have thick fleshy fruits had peak dispersal significantly later, in the middle of the wet season on the 13th of September ($F = 6.39$, $p < 0.001$) (Table 6). Autochorous (0.02 ± 0.01) and anemochorous (0.03 ± 0.01) species had significantly higher synchrony than endozoochorous (0.01 ± 0.003) and ectozoochorous (0.01 ± 0.002) species (Table S6). There was no difference between dispersal syndrome groups in fruiting phenology in multivariate space ($F = 1.13$, $p = 0.34$). Endozoochorous and ectozoochorous species did not fruit for a significantly longer duration than autochorous and species ($F = 0.77$, $p = 0.52$). Fruit size ($r = 0.17$, $p = 0.16$) was not related to fruiting duration but fruit display size is positively related to fruiting duration ($r = 0.33$, $p = 0.0059$) as expected.

Discussion

The species in the study site covers a range of growth habits, leaf habit and biotic interactions. This provided a unique opportunity to understand the variation in phenology between groups based on these categories. The wide variation in the quantitative index of deciduousness and its relationships with vegetative and reproductive phenology is an important finding of this study. The results provide support for the insolation-limitation hypothesis as described in Chapter 2 (van Schaik, Terborgh & Wright 1993; Sun *et al.* 1996). I also examined the relationship of some species' reproductive characteristics and phenology and differences between groups of different biotic interactions. These have

mostly been addressed through theoretical predictions and received little attention with scant empirical evidence in past studies

Plant growth habits – life-forms and canopy strata are under the similar influence of limitations in light and water availability. Trees and lianas have the best access to soil water, and some even have water storage in trunks in roots. Additionally, those trees and lianas in the canopy do not have limitations in light availability. In contrast, those in the sub-canopy are limited by light and not so by water. Shrubs in the understory are limited by both light and water. Shrubs flushed, flowered, and fruited uniformly throughout the year. They also flushed for a longer duration and flowered more frequently with lower intensity than trees and lianas. In terms of vertical strata, sub-canopy species flushed very early in the dry season, and very close to the start of senescing for species in the canopy layer. Species in the canopy flushed in the middle of the dry season. Although, Opler, Frankie and Baker (1980) and Ramirez (2002) reported a predominant wet season flushing, flowering and fruiting, Marques, Roper and Salvalaggio (2004) described aseasonality in vegetative and reproductive phenology of shrubs. The proportion of shrubs that are highly dependent on water might explain this range of behaviour. If the shrubs have comparable proportions of species cueing to light and water, shrubs' overall behaviour will be aseasonal. In contrast, they will show activity near the rains if all the shrubs are highly dependent on water availability for their activity.

Evergreen and deciduous species have a contrasting capacity of resource acquisition and utilisation for their growth and reproduction (Eamus 1999) and thereby experience variable water stress under seasonal drought. This, coupled with the insolation-limitation hypothesis, entails the expectation that evergreen species would flush and flower with maximum sunlight while deciduous species being dependent on water would show activity near the rains. Indeed, several studies have shown evergreen species to flush 1-3 months before deciduous species (Williams-Linera 1997; Kushwaha & Singh 2005; Nanda *et al.* 2011). By contrast, evergreen species in the study site flushed more than 5 months and flowered more than 1.5 months before the deciduous species. Deciduous species also showed higher flushing frequency, synchrony, and intensity than evergreen species. The high seasonality in precipitation and the long and extreme dry season in the study site might drive such variation between evergreen and deciduous species. No difference in the lag of flushing and flowering could be detected between evergreen and

deciduous species unlike expected. The fact that both the groups showed a positive lag, flowering about a month after flushing might be because of lack of any photosynthate storage by both evergreen and deciduous species.

A wide range of deciduousness behaviour was observed in different parameters of deciduousness. For example, the duration for the leafless period in deciduous species ranged from 2 days to about 4.5 months and among evergreen species some barely lost and canopy while others lost as high as more than 70 percent of the canopy. This considerable variation would be lost by just categorising species into evergreen and deciduous groups. Among the three familiar indices of deciduousness, average canopy loss explained most of the variation between species and the first principal component accounting for 92 percent of the variance was selected as the index of deciduousness. Although I did not find a difference in the lag of flushing and flowering between evergreen and deciduous species, the lag was related to the deciduousness of the species (r_{al} = 0.32, p = 0.0008). PC1 in flushing and PC2 in senescing, flowering, and fruiting showed similar relationships with the other phenology parameters like in the evergreen and deciduous categories. Thus, quantification of deciduousness demonstrated a gradient of leaf loss behaviour due to a wide range of water stress from seasonal drought experienced by species in the study site.

Limited resources allotted for reproductive phenology imposes a trade-off between flower size and flowering intensity. I did not observe any relationship between flower size or display size and flowering intensity. However, species with larger display sizes flowered later in the dry season, were more synchronous between individuals, and showed little interannual variation than species with smaller display sizes. Dioecious species flowered a month earlier than hermaphrodite species. Avoiding competition for pollinators with some copiously flowering hermaphrodite species might have resulted in this temporal separation (Mosquin 1971). As opposed to dioecious species expected of having the longest flowering duration to maximise outcrossing, monoecious species showed the longest flowering duration. In dioecious species, males are expected to flower earlier and longer than females to optimise competition for females (Lloyd & Webb 1977; Bawa & Beach 1981; Bullock & Bawa 1981). Indeed Forero-Montana and Zimmerman (2010) showed such a variation in two dioecious species. While most species did not show any difference, in only a few species, males flowered earlier and longer than females. This

lack of variation might be because I did not have enough resolution of field observation to detect a difference between male and female flowering. Rarer species in the study site did not show more synchronous flowering than more abundant species as expected, but they had lower frequency and higher flowering intensity. High intensity flowering can also be a compensation for rarer species to increase their mating opportunity. The number of species in most pollination syndrome groups except for those pollinated by bees or other diverse insects was insufficient to get any significant results. Among those two groups, species pollinated by other diverse insects flowered about three weeks earlier than bee-pollinated species. Overall, the timing of flowering for species with different pollination syndromes did not correspond to the timing of peak abundance of the pollinators. This might be because of a combination of factors including the overall lack of pollinator specialization across species in the study site. There was no difference in any other phenology parameters.

Autochorous and anemochorous species dispersed in the dry season while zoochorous species dispersed in the wet season. They also had higher synchrony than zoochorous species. This might have to do with developing and maturing together to attract large number of animal dispersers. The timings were consistent with the timing of availability of respective dispersal agents (Smythe 1970; Augspurger & Franson 1987). Indeed Batalha and Martins (2004) showed a similar dry and wet season fruiting pattern among the different dispersal syndrome groups. I did not find a difference in fruiting duration between ctozoochorous, ctozoochorous, autochorous and anemochorous species unlike expected. This might have to do with the fact that there was no consistent difference in fruit size across dispersal syndrome groups. However, fruit display size was positively related to fruiting duration, supporting the notion that large fleshy fruit would take more time to mature than smaller fruits.

The results presented here represent a comprehensive effort to understand variation across all phenology parameters among different plant functional groups. The study confirmed several theoretical predictions and, in some cases, provided a stark contrast between species in some of the categories that have not been reported before. Here I also developed a continuous measure of deciduousness that highlighted the wide variation in behaviour between species within each group, thus indicating that continuous quantitative estimates may be more appropriate than discrete categories. More importantly, I found

that these quantitative measures of deciduousness were functionally relevant and related to many other phenology parameters, thus describing species' response to seasonal drought, and helping predict their behaviour under a changing environment. The wide range of variation between species was explored in Chapter 2. Going up a level, this chapter explored the variation between groups of species sharing some common characteristics. Going further up a level of organisation, variation in community weighted phenology across three habitats with contrasting light, and soil water availability will be explored in the next chapter.

Tables and figures

Table 1: Difference in the timing of phenophases between the life forms. The first three rows describe the number of species belonging to each group, followed by the mean angular concentration of the four phases. The dates are represented as the day of the year ± standard deviation (in days). 'Uniform' denotes that the group has failed the Rayleigh's test for uniformity and hence the species are uniformly distributed throughout the year. The last two rows indicate the F-statistics and the significance values (p) for Watson-Williams test (the equivalent of one-way ANOVA in circular statistics) calculated only for the values with a significant angular concentration.

Life forms	**Species**	**Flushing**	**Senescing**	**Flowering**	**Fruiting**
Trees	48	74 ± 68	41 ± 38	73 ± 56	94 ± 59
Lianas	14	Uniform	49 ± 45	58 ± 43	96 ± 47
Shrubs	13	Uniform	61 ± 55	Uniform	Uniform
F			0.20	0.50	0.00
p			0.82	0.48	0.95

Table 2: Difference in the timing of the phenophases between species belonging to different canopy strata. The first two rows describe the number of species belonging to each group, followed by the mean angular concentration of the four phases. The dates are represented as the day of the year ± standard deviation (in days). 'Uniform' denotes that the group has failed the Rayleigh's test for uniformity and hence the species are uniformly distributed throughout the year. The last two rows indicate the F-statistics and the significance values (p) for Watson-Williams test (the equivalent of one-way ANOVA in circular statistics) calculated only for the values with a significant angular concentration.

Canopy strata	Species	Flushing	Senescing	Flowering	Fruiting
Canopy	50	81 ± 70	43 ± 40	70 ± 51	94 ± 54
Sub-canopy	21	301 ± 59	47 ± 42	Uniform	Uniform
F		**8.68**	0.27		
p		<0.01	0.61		

Table 3: Difference in the timing of the vegetative and reproductive phenophases between the evergreen and deciduous species. The first two rows describe the number of species belonging to each group, followed by the mean angular concentration of the four phases. The dates are represented as the day of the year ± standard deviation (in days). The last two rows indicate the F-statistics and the significance values (p) for Watson-Williams test (the equivalent of one-way ANOVA in circular statistics).

Leafing habit	**Species**	**Flushing**	**Senescing**	**Flowering**	**Fruiting**
Evergreen	44	317 ± 47	49 ± 44	60 ± 53	89 ± 57
Deciduous	31	112 ± 62	42 ± 40	95 ± 51	102 ± 67
F		**89.14**	0.84	**22.71**	**3.97**
p		< 0.0001	0.36	< 0.0001	0.05

Table 4: Differences in the supplementary phenology parameters across the four phenophases between the evergreen and deciduous species. Each phase shows the F-statistics and the significance values (p) for one-way ANOVA between the groups.

Parameter	**Flushing**		**Senescing**		**Flowering**		**Fruiting**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Duration	0.01	0.91	2.11	0.15	0.59	0.44	0.28	0.60
Frequency	**12.52**	<0.001	2.85	0.10	1.37	0.25	0.06	0.81
Synchrony	**24.43**	<0.001	**130.45**	<0.001	**4.15**	0.05	0.07	0.79
Intensity	**38.15**	<0.001	**140.42**	<0.001	0.00	0.97	0.60	0.44
Interannual variation	0.01	0.91	**6.03**	0.02	0.66	0.42	0.02	0.88

Table 5: Differences in the timing of flowering between the different pollination syndrome groups. The first nine rows describe the number of species belonging to each group, followed by the mean angular concentration of flowering phenology. The dates are represented as the day of the year ± standard deviation (in days). 'Uniform' denotes that the group has failed the Rayleigh's test for uniformity and hence the species are uniformly distributed throughout the year. The last two rows indicate the F-statistics and the significance values (p) for Watson-Williams test (the equivalent of one-way ANOVA in circular statistics) calculated only for the values with a significant angular concentration.

Pollination syndrome	**Species**	**Timing of flowering**
Melittophily (Bee)	23	92 ± 51
Diverse insects	23	71 ± 65
Psychophily (Butterfly)	6	74 ± 45
Cantharophily (Beetle)	5	46 ± 38
F		**4.18**
p		0.01

Table 6: Differences in the timing of fruiting dispersal between the fruit dispersal syndrome groups. The first four rows describe the number of species belonging to each group, followed by the mean angular concentration of the fruiting dispersal time. Here, the fruit stop dates have been considered as the timing of dispersal. The dates are represented as the day of the year ± standard deviation (in days). The last two rows indicate the F-statistics and the significance values (p) for Watson-Williams test (the equivalent of one-way ANOVA in circular statistics).

Dispersal syndrome	**Species**	**Timing of dispersal**
Endozoochory	29	256 ± 65
Ectozoochory	26	122 ± 56
Autochory	14	101 ± 49
Anemochory	5	154 ± 20
F		**6.39**
p		<0.001

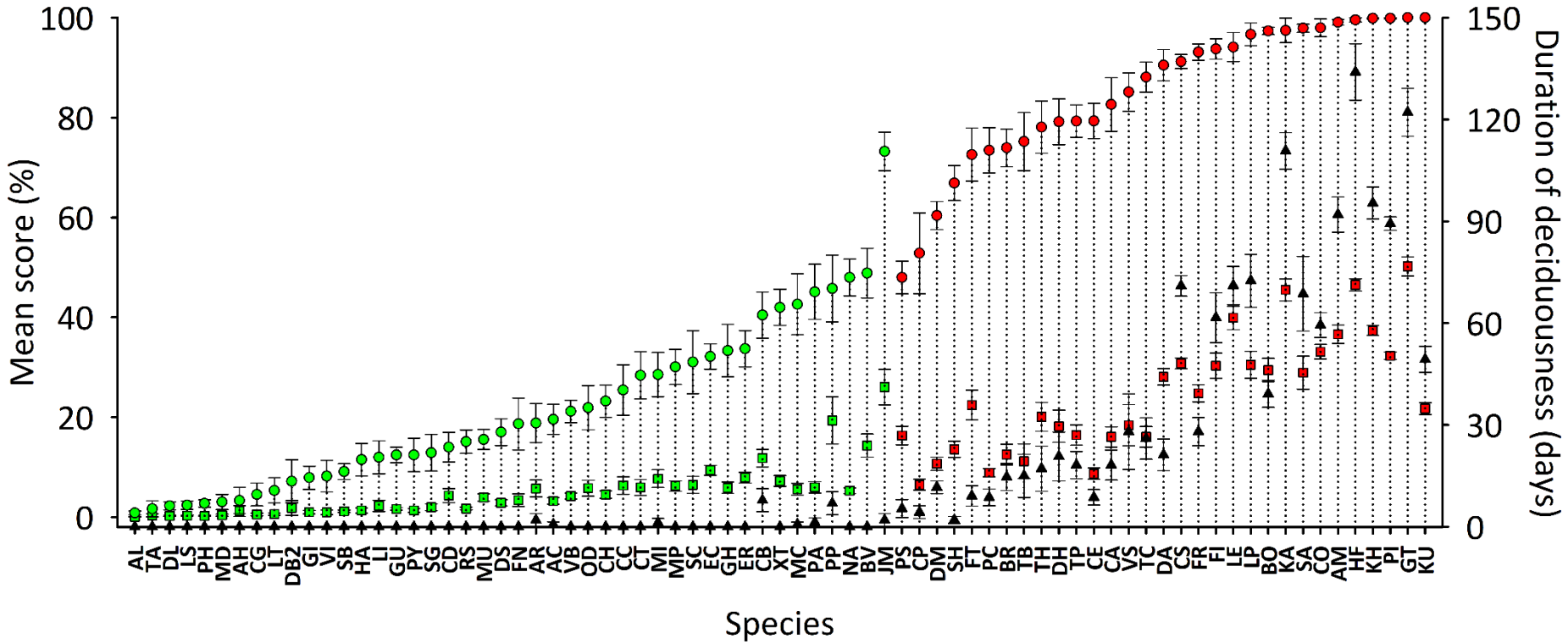


Figure 1: Variation in the three measures of deciduousness, namely, average canopy loss, maximum canopy loss and duration of deciduousness across species. The species are represented by codes (for details refer to Appendix: Table S1). The squares represent average canopy loss, the circles represent maximum canopy loss, and the triangles represent the duration of deciduousness. The squares and the circles in green are the evergreen species, and the ones in red are the deciduous species. The average canopy loss and the maximum canopy loss expressed in percentage and represented in the left y-axis while the duration of deciduousness is expressed in days and represented in the right y-axis.

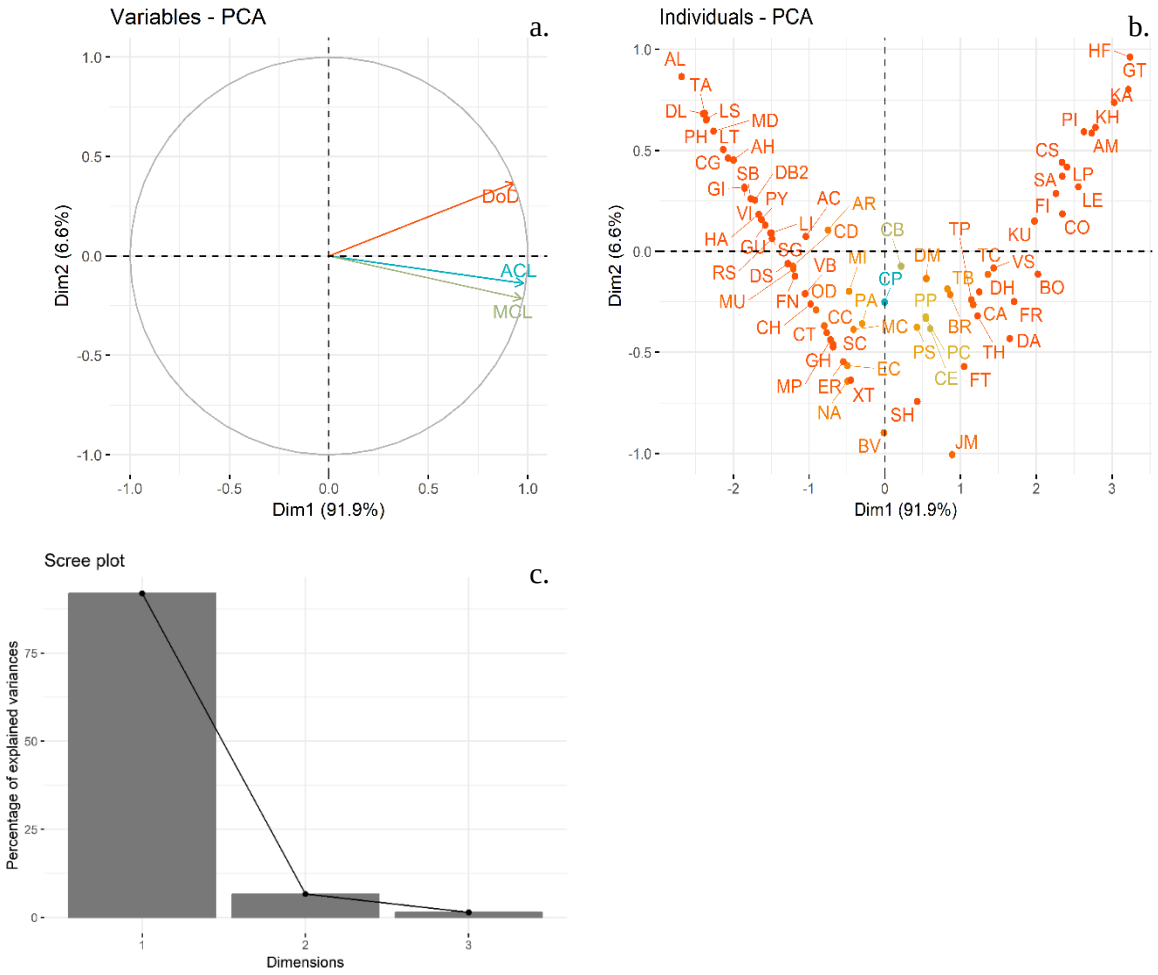


Figure 2: Principal component analysis of the three indices of deciduousness – average canopy loss (ACL), maximum canopy loss (MCL) and duration of deciduousness (DoD). Panel a) Biplot for components 1 and 2, b) Biplot for the individual species, and c) Scree plot. Note that in panel (b) the most evergreen species are on the top left corner while the most deciduous species are on the top right corner with intermediates in the middle.

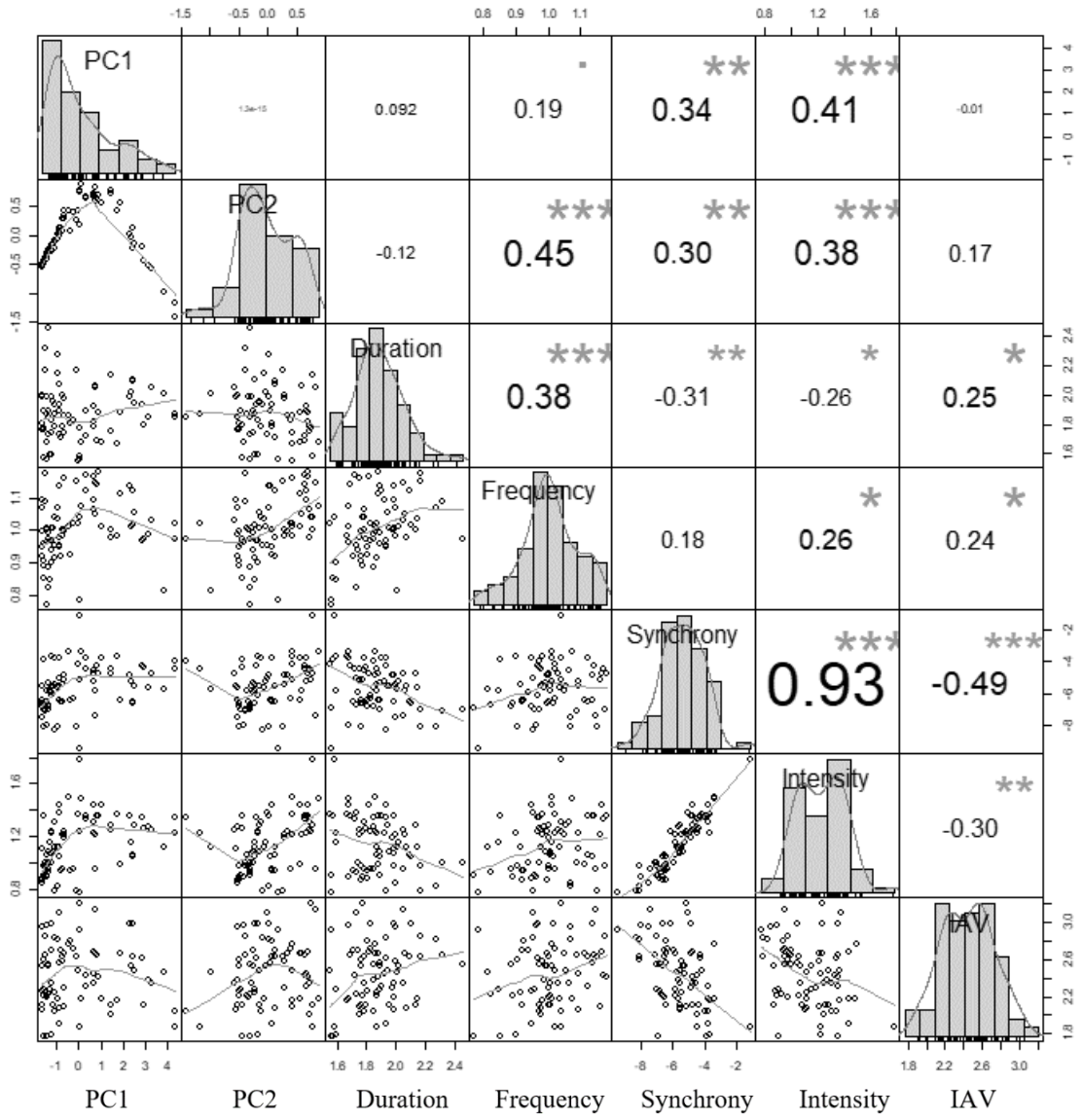


Figure 3: Relationship between canopy deciduousness with the flushing phenology parameters. The rows represent the following parameters in sequence – deciduousness PC1, deciduousness PC2, flushing duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

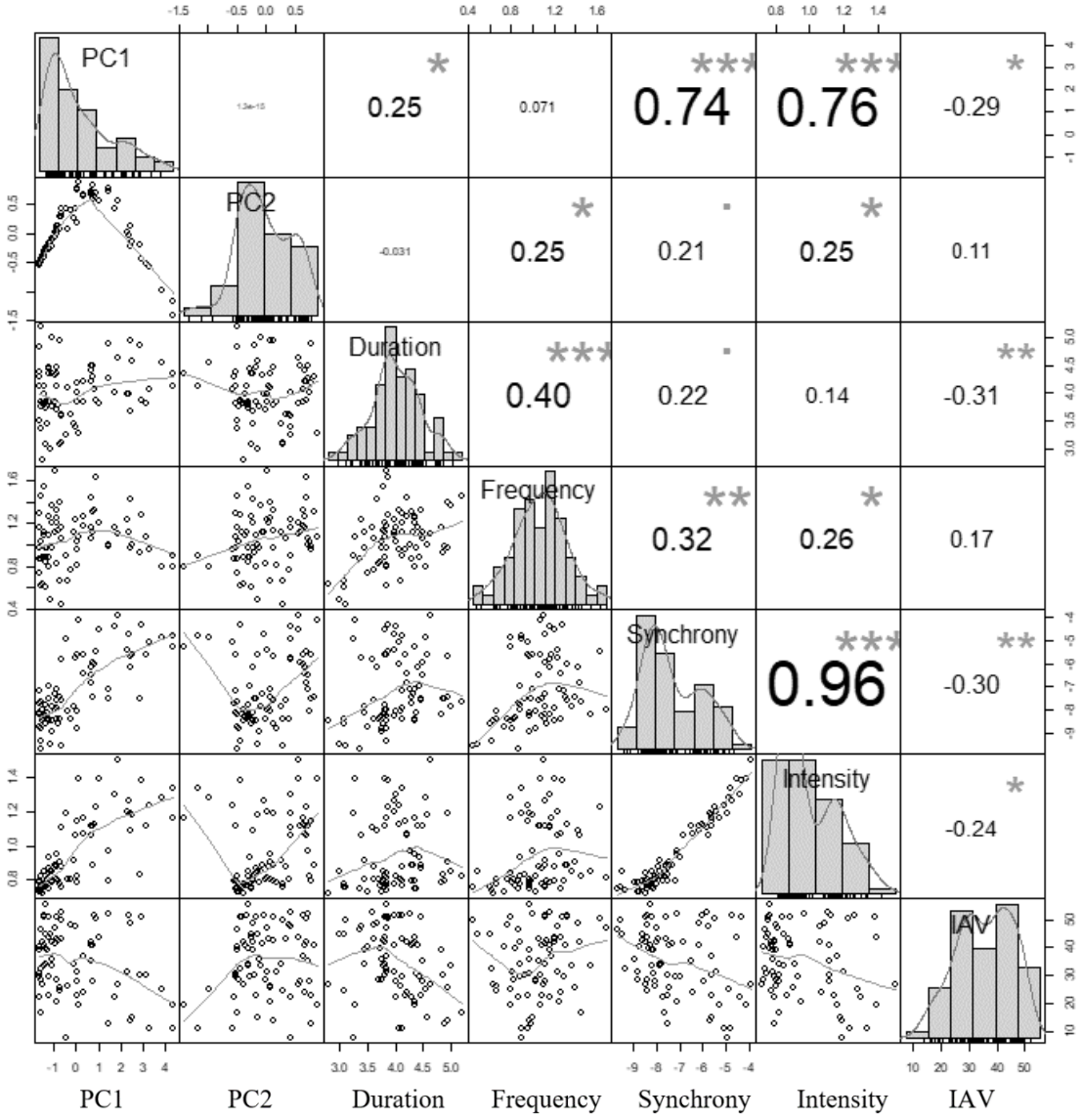


Figure 4: Relationship between canopy deciduousness with the senescing phenology parameters. The rows represent the following parameters in sequence – deciduousness PC1, deciduousness PC2, senescing duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

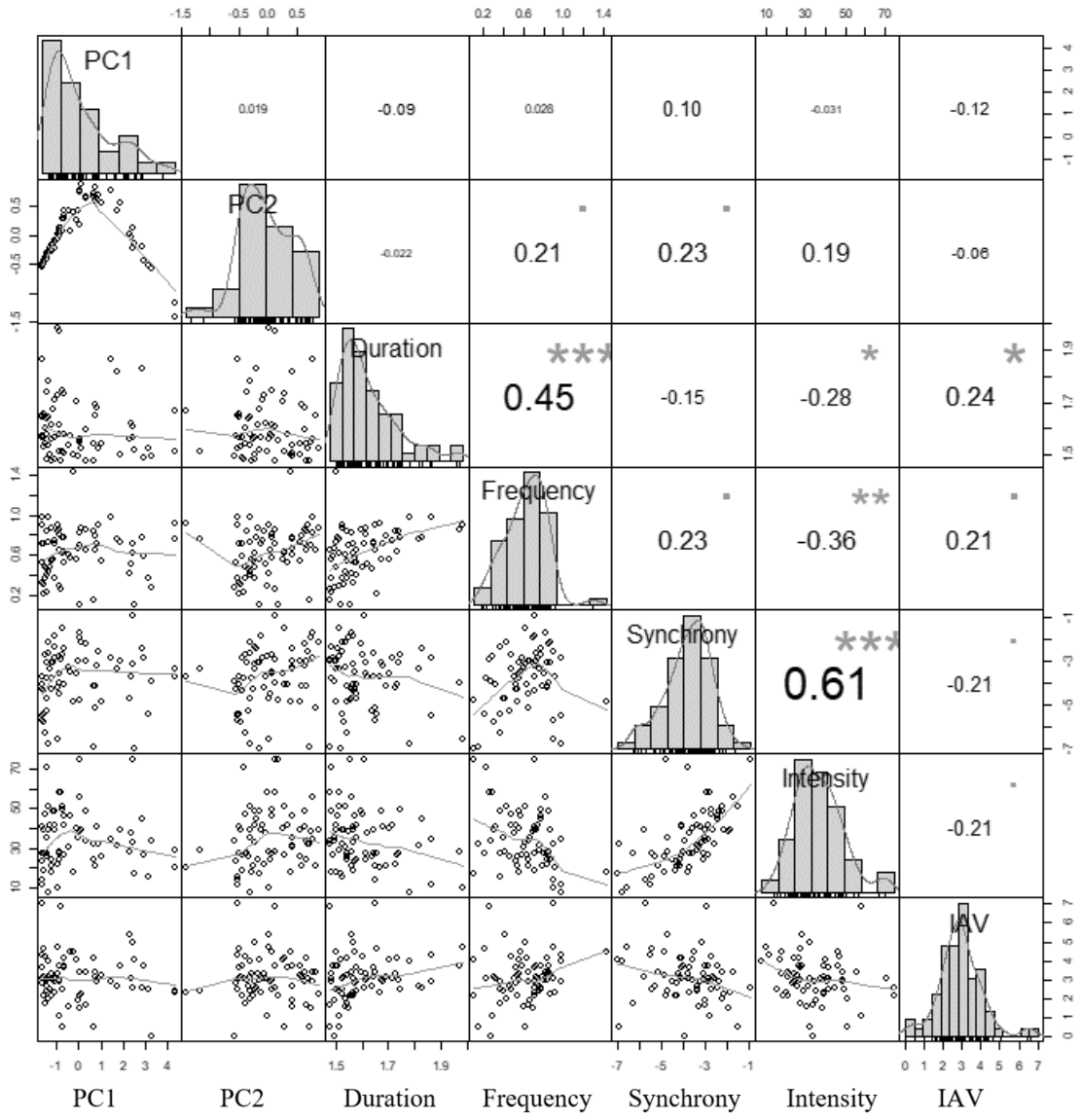


Figure 5: Relationship between canopy deciduousness with the flowering phenology parameters. The rows represent the following parameters in sequence – deciduousness PC1, deciduousness PC2, flowering duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

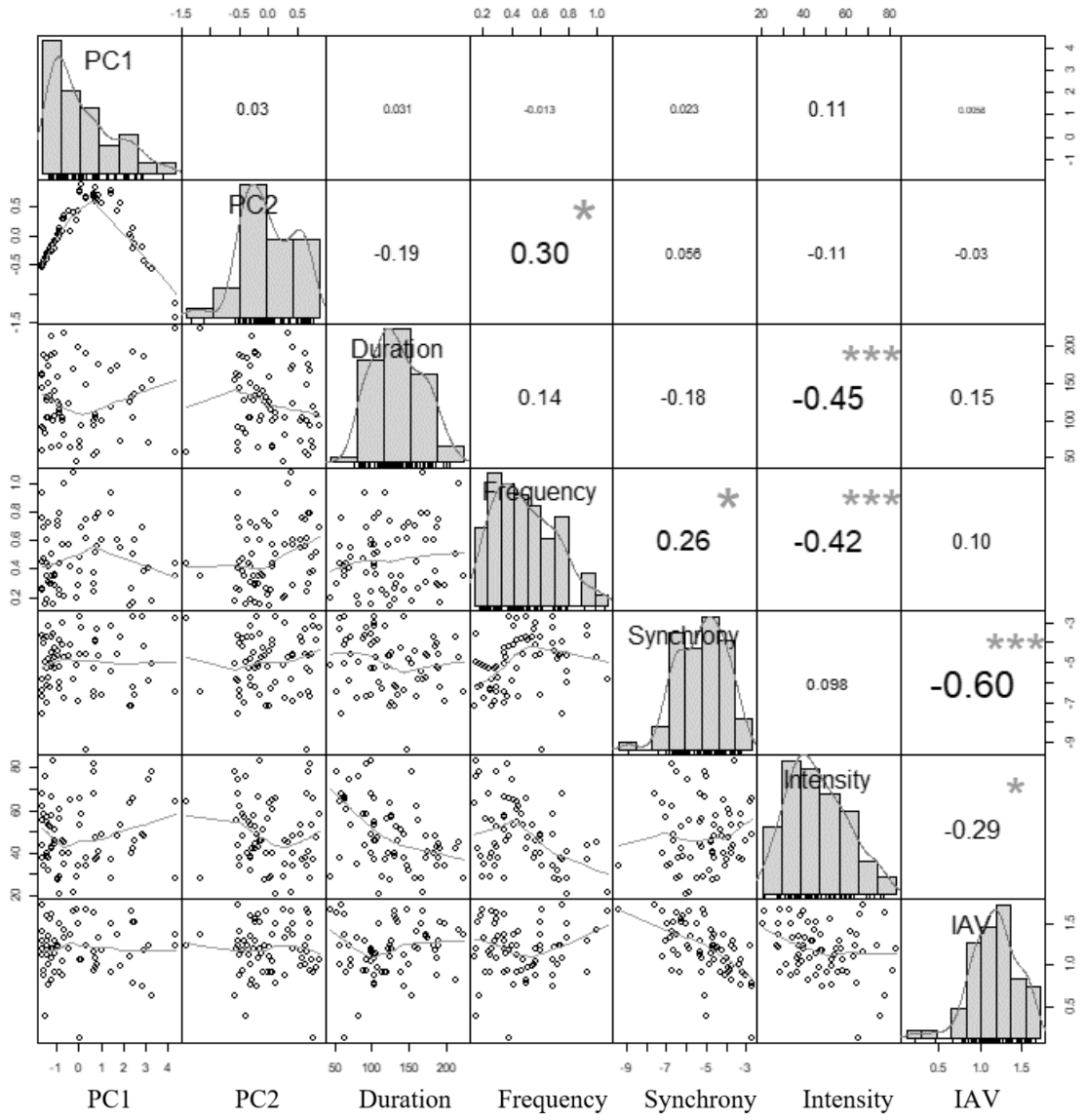


Figure 6: Relationship between canopy deciduousness with the fruiting phenology parameters. The rows represent the following parameters in sequence – deciduousness PC1, deciduousness PC2, fruiting duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

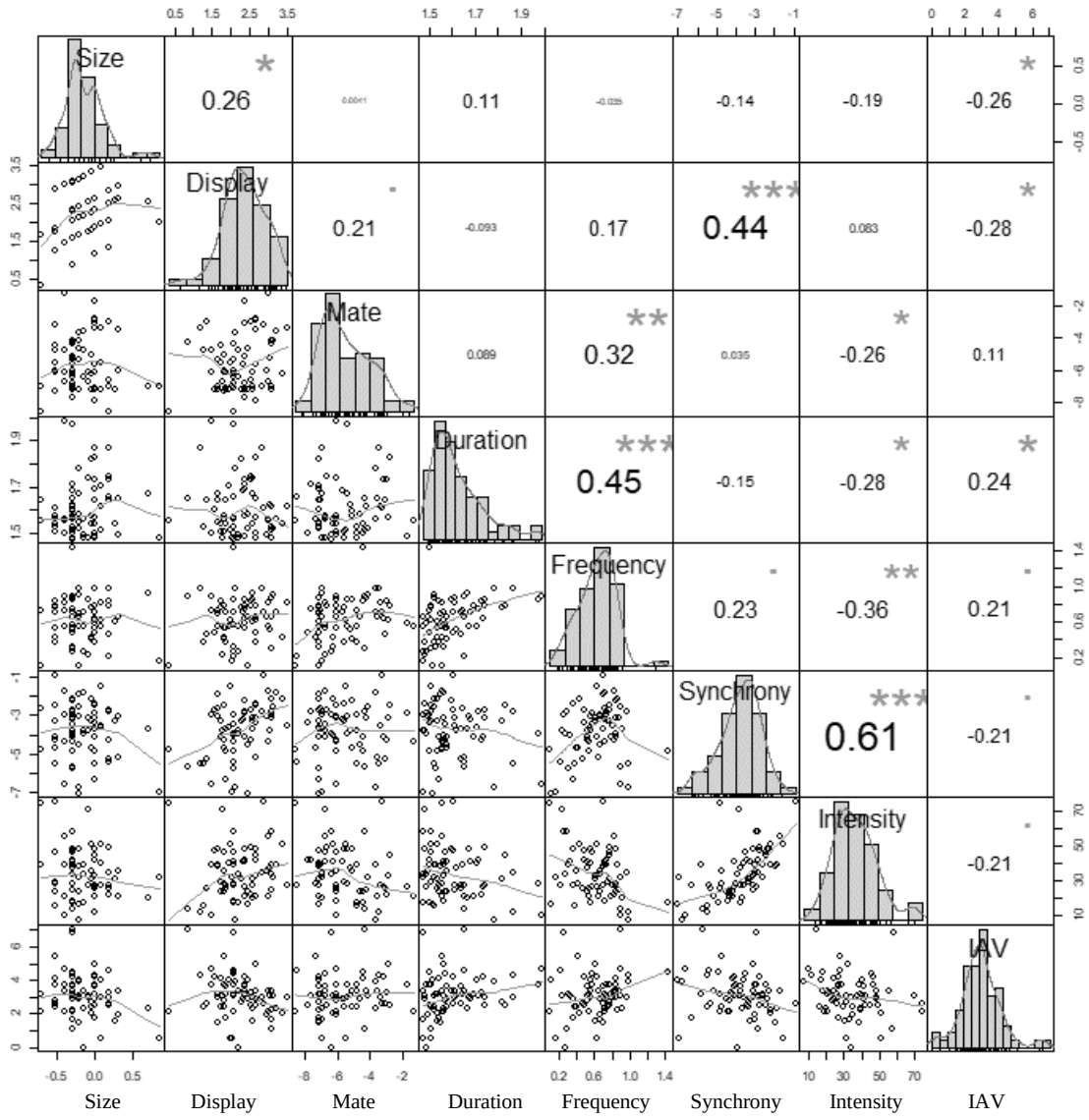


Figure 7: Relationship between flower size, display size and mate availability with the flowering phenology parameters. The rows represent the following parameters in sequence – flower size, display size, mate availability, flowering duration, frequency, synchrony, intensity, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1.

Chapter 4: Seasonal variation in community weighted phenology across three habitats with contrasting abiotic conditions, and the relationship of pollinators abundance to floral resource availability

Introduction

The effect of local microenvironment on the phenology of species have received little attention in past studies. An increasing number of studies report variation in phenology between plants in the forest edges and those in the interior (Laurance *et al.* 2003; Herrerias-Diego *et al.* 2006). These findings are especially relevant in a fragmented landscape with increasing human disturbance. However, we still do not have a clear understanding of how microenvironment affects plant phenology. Additionally, most insects exhibit seasonality in temperate and tropical forests, influenced by temperature, water, and food resources (Wolda 1988; Kishimoto-Yamada & Itioka 2015). Pollinators are declining worldwide, thereby resulting in large losses to seedling recruitment and agricultural productivity (Aizen *et al.* 2009; Gonzalez-Varo *et al.* 2013; Vanbergen *et al.* 2013). In this study, I examined variation in leafing, flowering, and fruiting phenology at the community level in three habitat types that differed in abiotic conditions, particularly, the availability of light and water. Additionally, I asked how flowering phenology and floral resources availability was related to the abundance of pollinators.

The phenology of species in seasonally dry forests is more diverse than tropical wet forest (Kushwaha, Tripathi & Singh 2011). However, very few studies have compared phenology for plants from wet and dry sites in the same region to understand the influence on microenvironments on phenology. Comparative phenology studies of dry and wet sites in tropical forests show that species in the wetter sites flush and flower earlier in the dry season than species in the drier sites (Frankie, Baker & Opler 1974; Opler, Frankie & Baker 1980; Murali & Sukumar 1993; Murali & Sukumar 1994). The drier sites have also been shown to have more pronounced peaks of shorter duration than the wetter sites (Frankie, Baker & Opler 1974). Borchert (1994) showed that relatively wetter sites retained leaves about a month longer than the dry sites. In contrast, in the riparian forests, most species were leaf exchanging and evergreen.

Few studies have explored the diversity of pollinators in tropical forests of Neotropics (Bawa *et al.* 1985), Africa (Johnson 2004), Asia (Kato 1996; Momose *et al.* 1998; Sakai *et al.* 1999a; Itioka *et al.* 2001; Devy & Davidar 2003) and Australia (Hansman 2001). Bees followed by beetles, flies and small diverse insects constitute major pollinators of lowland tropical forests (Bawa *et al.* 1985; Corlett 2004). In the tropical forests of India, bees, beetles, and moths constitute the major groups of specialised pollinators (Devy & Davidar 2003). Thrips constitute major pollinators during general flowering in dipterocarp forests (Appanah 1993). In comparison, Neotropical forests have higher proportions of large solitary bees, butterflies and moths and nectarivorous vertebrates (Corlett 2004). There is very limited information about pollinators in the forest of Africa and Australia (Hansman 2001; Johnson 2004). Besides these major pollinators, there are minor, less efficient pollinators, including ants, bugs, cockroaches, and other insects.

While the seasonality of insects is dominated by temperature in the temperate region, variation in rainfall has been attributed to the seasonality of insects in the tropical region (Wolda 1988). Most insects exhibit seasonality in the tropical dry forests, peaking in either the dry or wet season (Kishimoto-Yamada & Itioka 2015). Bees have been shown to peak in the dry season (Janzen 1967; Kang & Bawa 2003), beetles in late dry/early wet season (Grimbacher & Stork 2009), flies in the wet season (Denlinger 1980) and butterflies and moths in late wet/early dry season (Haber & Frankie 1989; Kunte 1997). Overall, studies on insect abundance in the tropics have failed to capture any clear seasonality (Kishimoto-Yamada & Itioka 2015). However, unlike temporal variation in insect abundance, spatial variation is relatively better understood owing to studies on habitat fragmentation and edge effects. Bees and butterflies have been shown to prefer open habitats (Vu 2009; van Halder, Barbaro & Jactel 2011; Bailey *et al.* 2014) while beetles did not demonstrate any habitat preference of woodland or grassland (Rusch *et al.* 2012).

Nectar and pollen are critical food resources for many pollinators. Several studies have looked at the relationship between flowering and pollinator abundance. Studies have shown flowering to be positively related to pollinators (Fründ, Linsenmair & Blüthgen 2010; Fowler, Rotheray & Goulson 2016; Cohen *et al.* 2020). Mass flowering has been shown to attract pollinators from nearby areas (Appanah 1993). During periods of low flowering, pollinators either move to other areas or switch to other food sources (Momose

et al. 1998). However, apart from floral resources there can be other factors that may influence pollinator dynamics in the study site. Habitat fragmentation, canopy openness and human disturbance are important factors that might affect pollinators independent of phenology. Finally, in the seasonally dry forest, water availability may also affect the abundance of pollinators in the study site (Gallagher & Campbell 2017).

I examined the temporal variation in community weighted vegetative and reproductive phenology across three different habitats with varying light availability and soil moisture. I expected trees in the edge and closed habitats in my study site with relatively higher soil moisture, to flush and flower earlier in the dry season than trees in the open habitat where light is not limiting, but water availability is more constrained. I examined the variation in insect abundance to understand the difference between the three habitats with varying plant species composition, canopy structure and light and water availability. Finally, I examined the relationship between the abundance of pollinators and floral resources to understand if floral resources influence pollinators' abundance in these three habitats. I expect pollinator to follow floral abundance in the respective habitats.

Materials and Methods

There are three habitats in the study site (Fig. 1a). Open habitats mainly occur on the mountain crests. These are characterised by the lowest soil depth and soil moisture content. This is mostly a savannah habitat with less than 30 percent of tree cover. The trees are a mixture of deciduous and evergreen species with heights ranging between 5-8 metres. Edge habitats mainly occur in the slopes of hills and valleys. They have intermediate soil depth and soil moisture. The trees are mostly evergreen species with a few deciduous species with canopy height ranging between 10-15 metres. Closed forests occur in the valleys. They have the greatest soil depth and moisture content among the three habitats. These are all evergreen species with tall trees and canopy height ranging between 18-20m.

The study site's Google Earth image was classified into open, edge and closed habitats based on the colour of the surrounding area on the map, field experience, and knowledge of the study site. Points 200 m apart from each other were pinned and numbered. These were then randomised, and that random order was serially visited in the site. The sites

were then accepted as plot points based on their accessibility, canopy structure and disturbance. Nine such points were selected in each habitat, and a 20x20m plot was laid at these points. Thus, 27 plots were laid across the three habitats covering a total of 1.08 hectares (Fig. 1b). In each of the plots, height and girth of all individuals were measured, and mature individuals were selected from among them and marked. If there were more than ten mature individuals of a species in a plot, only ten randomly selected individuals were selected for phenology monitoring. Phenology of all selected individuals was monitored monthly from January, 2017 to December, 2018 using the same method described in Chapter 2.

The same plots used to monitor phenology was used to lay traps for pollinators. Two kinds of pollinator traps were used – pan traps and sticky traps. Plastic bowls of 15cm in diameter and 5cm of depth were used as pan traps. These were painted with fluorescent blue, yellow and white spray paint to get three colours of pan traps and filled with colourless and odourless soap water. Yellow acrylic sheets of size 15x15cm were covered with stick glue (Tanglefoot) and used as sticky traps. Two sets of pan traps of each colour were hung on trees at orthogonal corners with one set at the canopy layer and one set at the height of 1 m from the ground giving a total of 6 traps per plot. A sticky trap at the height of the canopy was hung at any of the other corners in each plot. Trapping was done for eight months at a monthly interval between October, 2017 to May, 2018. The collected insects were cleaned, identified at the order level, counted, and then stored in 70 percent ethanol.

The plot phenology data was error checked using the same steps as described in Chapter 2. The scores were averaged across all individuals to get a mean monthly score for each species in a plot. It was then weighted by the total basal area of all individuals of a species in a plot and then summed for all species in the plot to give a plot level phenophase score per month. The weighted scores were then normalised to the maximum for each plot in each year. This score was averaged across the nine plots to get a habitat score at a monthly resolution. Insect captures were checked for unusually high capture of a particular type (species), and the count for such types was not included in the analysis. Five of the captured insect orders were recognised plant pollinators, and these henceforth termed as potential pollinators were used in further analysis. These include – bees, wasps, lepidoptera (butterflies and moths), diptera (flies) and coleoptera (beetles).

Rayleigh's test for uniformity was used to test if the activity of a phenophase in a habitat is uniform throughout the year or not. If different from a uniform distribution, a mean angle representing peak activity for each habitat was calculated using circular statistics. Difference between the mean angle of habitats was tested using Watson-Williams test from the package "circular" in R. A generalized linear model (GLM) was used to understand variation in phenology across time and space. A GLM was also used to understand variation in insect abundance across time in the three habitats. Mean flowering and potential pollinator capture in the three habitats across eight months were square-root transformed to obtain a normal distribution. Pearson's correlation was used to examine the relationship between flower abundance and potential pollinator abundance.

Results

From the general linear model, used to examine the variation in phenology across time between the three habitats, I could not detect significant variation in flushing phenology in a particular habitat (Table 1). The habitats varied differently across time in their flushing phenology ($F = 5.00$, $p = 0.007$). In contrast, while senescing and flowering phenology showed significant variation across time, there was no difference in senescing across the three habitats while a difference in flowering phenology could not be detected. There was significant variation in fruiting phenology both across time and across habitats (Table 1).

While all habitats had peak flushing in the early dry season, open habitats peaked earliest in January while closed habitat peaked latest in February (Fig. 2c). There was also a secondary flushing peak in open habitats at the end of July which was not observed in the edge and closed habitats. There was no difference in senescing peak between habitats (Fig. 3c). In contrast, all habitats flowered (Fig. 4c) and fruited (Fig. 5c) in the dry season and edge habitats did so earlier than open or closed habitats. Visual inspection of the variation of phenophase intensity across time revealed that except in some dates, the pattern of the unweighted mean score was similar to the score weighted by number or basal area (Fig. 2-5) suggesting that the ultimate variation across time was driven by variation in the intensity of species in the three habitats and not by variation in species composition, number, and basal area across the three habitats.

The sticky traps used were not effective in capturing a substantial number of insects, nor had a diversity of capture as compared to the pan traps. Overall, the sticky trap results did not reveal anything different from the pan traps. So, only the pan trap data were used for further analysis. An initial generalized linear model with negative binomial distribution fitting was run with all the parameters that might lead to variation in pollinator capture. These included colour, height, date, and habitat. Plot id was used as a random factor. There was no significant effect of height, and the effect of colour was driven by a particular group of insects on a certain date. Hence both height and colour were ignored, and the data were reanalysed.

The habitats differed by date in the abundance of potential pollinators ($\chi^2 = 310.23$, $p<0.0001$). The abundance of pollinators was higher in open habitat post rains, in October and in the mid dry season in February (Fig. 6). In contrast, the edge habitat showed an increase in the abundance of pollinators from February to the end of the dry season in May. The closed forests showed high capture in December and then followed the trend of edge habitat, increasing till the end of the dry season.

Flies, butterflies, and moths dominated the capture across all the three habitats. All the potential pollinator groups varied by month across the three habitats (Table 2). The abundance of flies was higher at the end of the dry season than post rains, especially in edge and closed habitats. Butterflies remained high during the early to mid-dry season and then decreased in abundance. Bees showed an increase in the dry season, especially in the open habitat. Beetles were most abundant at the end of the wet season and then decreased in the dry season (Fig. 7a-c).

The effect of time, habitats, and floral abundance on the abundance of total pollinators and individual pollinator groups were analysed using a generalized linear model (Table 3). The overall pollinators showed a significant effect of floral abundance ($n = 216$, $F = 5.12$, $p = 0.0249$) and varied differently across time between habitats ($n = 216$, $F = 2.86$, $p < 0.001$). For the individual pollinator groups, others except for the bees and butterflies

also showed an effect of floral abundance (Table 3). In contrast, wasps varied with across time and with flowering while flies varied across time, habitat, and flowering. Only the beetles varied differently across with varying floral abundance. Overall pollinators (Fig. 8) and the individual pollinator groups, including flies and wasps, were negatively related to floral abundance. Bees, beetles, and lepidopterans did not show any relationship to floral abundance (Table 4).

Discussion

While the previous chapters dealt with variation in phenology between species and between groups of species, it did not reveal the actual pattern of seasonal variation at the community level. This study describes the community weighted pattern of phenology, both within and between years, and contrasts it among three different habitats with varying light and water microenvironment in a tropical dry forest. This community weighted pattern contrasts unweighted percent species phenology described in many studies and represents the variation in the amount of food resources for the primary consumers across time and habitats. Additionally, I also looked at the temporal and spatial variation in insect pollinator groups and to understand how variation in floral resources might be related to the abundance of pollinators.

Theoretical predictions based on light and water availability from closed to open habitats states that open habitats would be expected to have higher activity of vegetative and reproductive phenology than closed habitat (Lovejoy *et al.* 1986; Wright & van Schaik 1994; Aldrich & Hamrick 1998; Sizer & Tanner 1999). Additionally, I expected open habitats to have short sharp peaks occurring later in the dry season closer to rains than the closed habitats. Laurance *et al.* (2003) found only a few species to respond to distance from the edge but reported an overall lack of significant edge effect on vegetative and reproductive phenology. I found flushing phenology to vary differently between habitats across time. While edge and closed habitats showed a single flushing cycle in a year, generally peaking between January-March between habitats across two years; open habitats showed bimodal behaviour with one peak between November-January while another peak around June-July at the start of the rains. This bimodality in the open can be attributed to equivalent proportions of evergreen and deciduous species in the open which showed different flushing behaviour as described in Chapter 3. Senescing and flowering

phenology did not show any habitat effect. Senescence had a single peak between February-March across all habitats. Flowering had the most irregular pattern of all the phases. There was a major peak between January-February in both years across the three habitats, but there were some irregular minor bouts of flowering at different times across the habitats. For example, there was a second bout of flowering around October in the closed and another around June-July in the open habitat. However, the one in the closed was consistent in both the years but the one in the open was prominent in the first year but inconspicuous in the next. This irregularity might explain why a difference between habitats in flowering phenology could not be detected. Fruiting phenology had both month and habitat effect indicating considerable variation in fruiting intensity across time and across the three habitats. This inconsistency of flowering phenology at the habitat level might have to do with different proportion of species flowering at different time points across the year with no major synchronous flowering across species. Fruiting was generally high between February-June with a peak in April in the three habitats.

Comparison between an unweighted pattern of phenophase intensity, intensity weighted by number and intensity weighted by the total basal area of the species revealed that except in some dates, the pattern of an unweighted mean score was similar to score weighted by number or basal area. This similarity indicated that the ultimate variation is purely driven by variation in the intensity of species in the three habitats and not by variation in species composition, number, and basal area across the three habitats. This finding suggests that the role of local microenvironment, light, and water availability, might be putting similar constraints on different species that overwhelms the variation that might arise due to differences size and composition of species in these three habitats.

Like the plant species, their pollinators are also expected to be affected by the seasonality of water availability in the dry tropics (Kishimoto-Yamada & Itioka 2015). Some insects have also been shown to prefer open or closed habitats (Vu 2009). Of the two trap types used in the study, sticky traps had significantly lower capture and also captured lower diversity of insects. The abundance of pollinators varied between habitats across time. This was also true for individual pollinator groups except for wasps. Wasps only showed variation across time but did not differ between habitats. In terms of capture of pollinators across habitats, pollinators were higher in the open than in edge and closed habitats, but mainly so post rains (October) and in the mid dry season (February). In contrast, edge and

closed habitats kept increasing from February till May. This might be because of lack of long term variation pattern that we don't have the complete picture of insect seasonality across time. However, the increase in abundance from February to May might be rudimentary signs of pollinator abundance following the general increase in flowering in the dry season. Bees, beetles, moths, flies, and other small diverse insects are the major pollinators of tropical forests (Bawa *et al.* 1985; Devy & Davidar 2003; Corlett 2004). In contrast, primarily flies, and then butterflies and moths dominated capture in the traps across all the three habitats. Bees and beetles constituted only a small part of the capture. The abundance of flies was higher at the end of the dry season than during rains, unlike expected (Denlinger 1980), especially in the edge and closed habitats. Butterflies remained high from the early to mid-dry season and then decreased in abundance. This coincided with the timing of their maximum abundance (Kunte 1997). Bees showed an increase in the dry season, especially in the open habitat also as expected (Kang & Bawa 2003; Bailey *et al.* 2014). Beetles were most abundant at the end of the wet season and then decreased in the dry season.

Flowers providing pollen and nectar are essential food sources for the pollinators. Therefore, it is reasonable to expect and have also been shown that the abundance of pollinators is positively related to the abundance of floral resources (Cohen *et al.* 2020). Indeed, overall pollinators and individual pollinator groups excepting bees and butterflies varied with floral abundance. However, contrary to expectation, be it overall pollinators or individual pollinator groups, they either showed no relationship or was negatively related to floral abundance in their respective habitats. This negative relationship can either be because a) there was too much variation in pollinator abundance across time, which either cancelled out or gave a negative relationship overall; b) a lot of different pollinator species that behaved differently across time but was clubbed under the same group which overall gave a negative effect to the relationship with floral resources; or c) there were some other factors that affected pollinator abundance independently and had nothing to do with flowering. This requires long-term monitoring and further investigation to fully understand the effect of floral abundance on the abundance of pollinators.

This study gave unique insights into the seasonal variation of community level phenology, highlighting the contrasts between habitats with different microenvironments,

the likes of which have been rarely addressed in a water limited seasonally dry tropical forest. The results showed differences in annual cycles and interannual differences between open, and edge and closed habitats arising due to differences in species composition between the habitats. It also highlighted that the difference between habitats was mainly brought about by the variation in intensity between the habitats and not by differences in tree size, habitat structure and species composition. This emphasised the effect of environmental constraints in driving phenology in the dry forests superseding the variation between the species. Finally, the variation in abundance of pollinators across the habitats revealed the seasonality and habitat preference of the different pollinator groups. The negative relationship with the abundance of floral resources pointed to some other external factors driving pollinators' seasonality in the seasonally dry forest. This gives us preliminary insights into the overall pattern of pollinator abundance that may serve as a baseline information. Fully understanding the relationship between floral resources and pollinators definitely require long term monitoring.

Tables and figures

Table 1: Variation in vegetative and reproductive phenology across time in the open, edge and closed habitats. A GLM was done with time and habitats as predictors of phenology for each of the phenophases. F-statistics and the significance level (p-value) is depicted for each phenophase.

	Flushing		**Senescing**		**Flowering**		**Fruiting**	
Interaction	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Date	0.50	0.4782	**28.18**	<0.001	0.02	0.8980	**8.07**	0.0047
Habitat	2.75	0.0644	**7.25**	<0.001	0.31	0.7353	1.68	0.1873
Date * Habitat	**5.93**	0.0028	2.63	0.0726	1.22	0.2961	**11.76**	<0.001

Table 2: Variation in the abundance of total pollinators and pollinator groups across time and the open, edge and closed habitats. The values represent the χ^2-statistics (Type II Wald χ^2 tests), and the stars represent the significance level of the GLM. *** = 0.001, ** = 0.01, and * = 0.05.

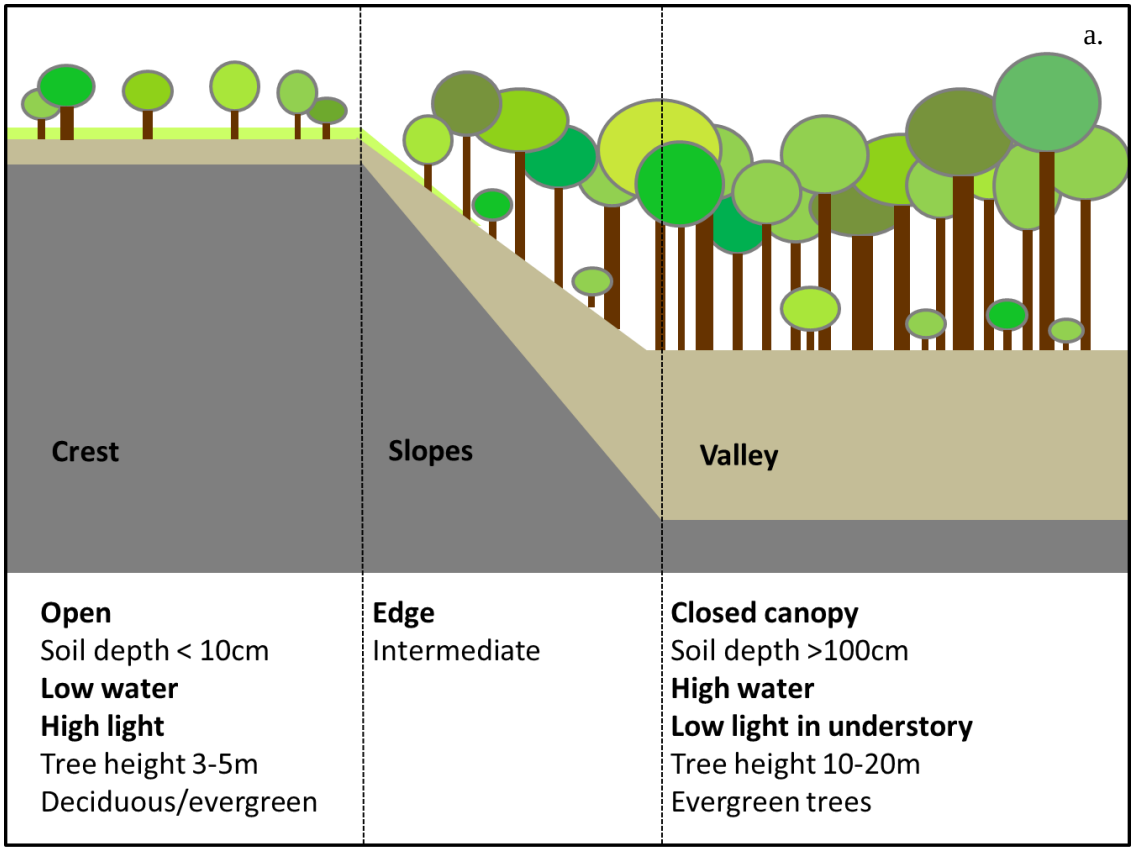
Parameters	**Total**	**Flies**	**Lepidoptera**	**Beetles**	**Bees**	**Wasps**
Date	791.13***	274.05***	142.17***	302.92***	169.13***	102.49***
Habitat	50.70***	15.45***	70.06***	31.22***	87.02***	2.71
Date * Habitat	310.23***	147.37**	74.31***	137.95***	25.12*	47.23***

Table 3: Variation in the abundance of total pollinators and pollinator groups across time in the open, edge and closed habitats with varying floral abundance as predictors. The values represent the F-statistics, and the stars represent the significance level of the GLM. *** = 0.001, ** = 0.01, and * = 0.05.

Parameters	**Total**	**Flies**	**Lepidopters**	**Beetles**	**Bees**	**Wasps**
Flower	5.12*	4.94*	1.24	7.32**	3.90	8.35**
Habitat	0.18	5.28**	12.70***	13.96***	21.38***	0.78
Date	7.41***	15.64***	8.25***	24.27***	6.53***	7.30***
Flower * Habitat	0.09	0.39	0.80	0.54	1.59	0.08
Flower * Date	0.99	1.22	0.97	3.98***	0.67	0.47
Habitat * Date	2.86***	2.36**	3.54***	8.90***	3.30***	2.69**
Flower * Habitat * Date	1.08	0.19	1.13	1.04	0.27	0.41

Table 4: Relationship between the floral abundance to the total pollinator abundance and the abundance of individual pollinator groups. The figures indicate Pearson's correlation and significance level (p-value).

Pollinator	**R**	**p**
Total	**-0.57**	0.0035
Diptera	**-0.56**	0.0069
Lepidoptera	0.22	0.3106
Coleoptera	-0.35	0.0955
Bees	-0.34	0.1031
Wasps	**-0.51**	0.0102



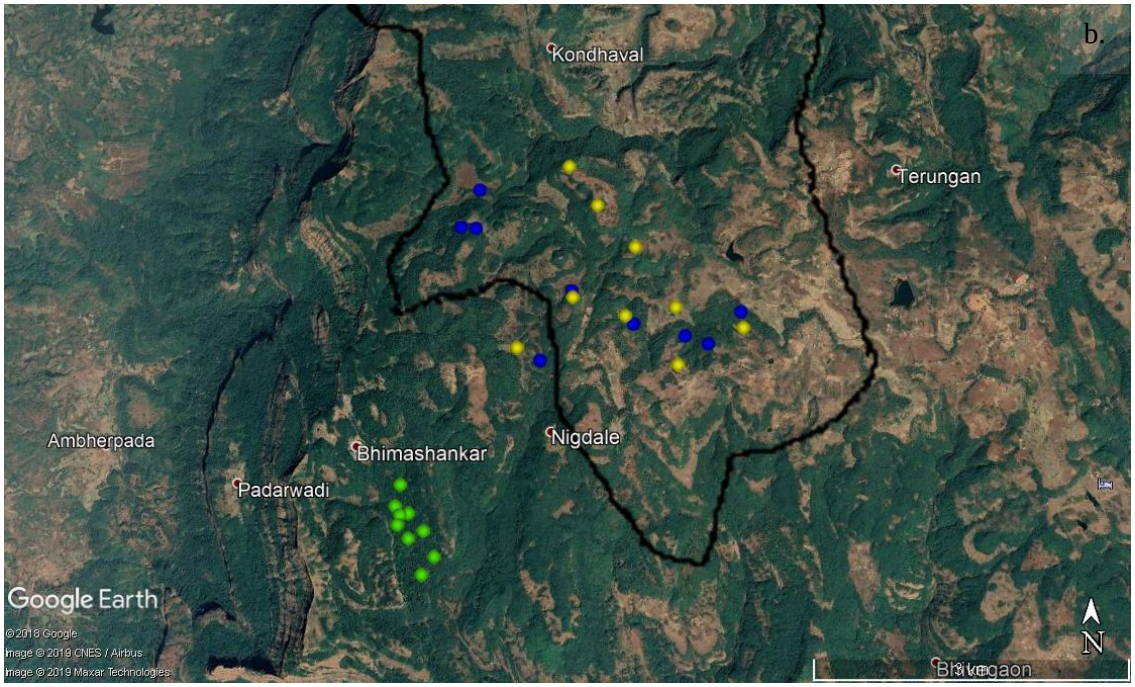


Figure 1: Schematic representation of the habitats and the location of the plots in the study site. Panel (a) represents the schematic diagram of the three habitats showing the differences in soil depth, relative soil water status and canopy height and light status. Panel (b) represent the plots on the satellite image of the study site. The yellow dots represent the open habitats, blue dots are the edge habitats, and the green dots are the closed habitats.

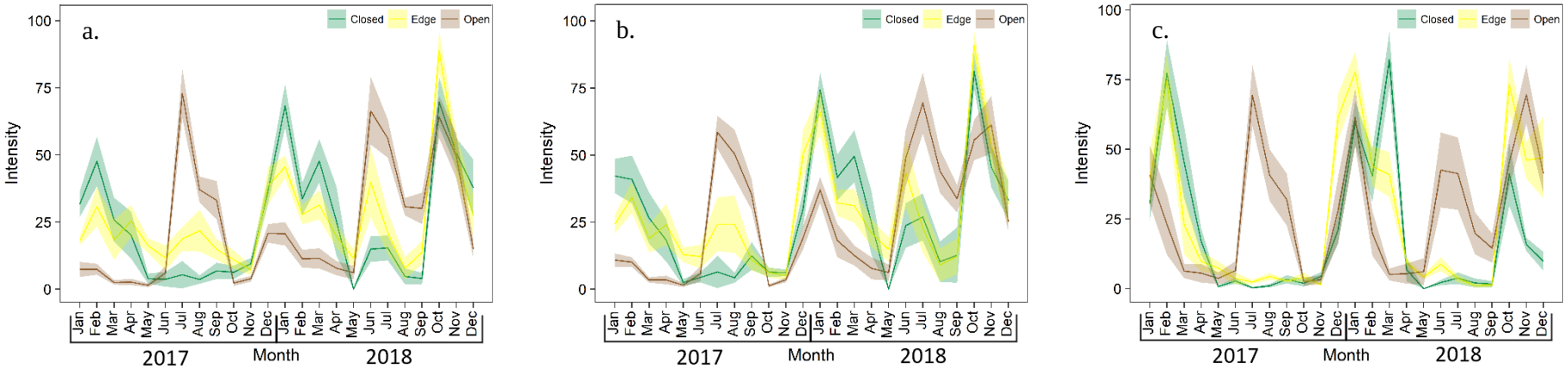


Figure 2: Variation in flushing phenology across time in the three habitats. Panel (a) represent unweighted mean intensity. Panel (b) represent mean intensity weighted by the number of individuals. Panel (c) represent mean intensity weighted by the cumulative basal area of each species, thus considering both number and basal area. The shaded portions represent standard error of n = 9 plots in each habitat.

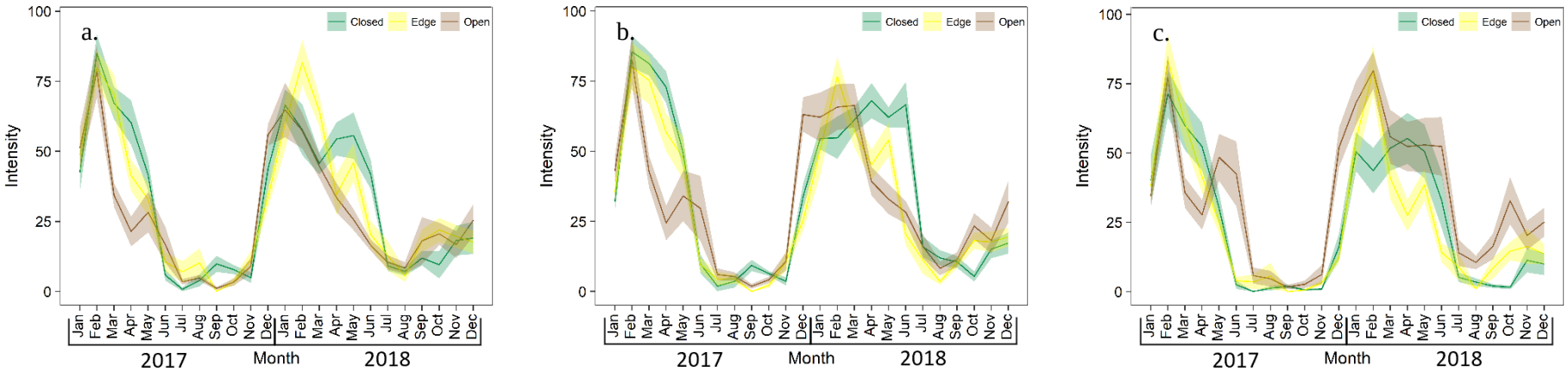


Figure 3: Variation in senescing phenology across time in the three habitats. Panel (a) represent unweighted mean intensity. Panel (b) represent mean intensity weighted by the number of individuals. Panel (c) represent mean intensity weighted by the cumulative basal area of each species, thus considering both number and basal area. The shaded portions represent standard error of n = 9 plots in each habitat.

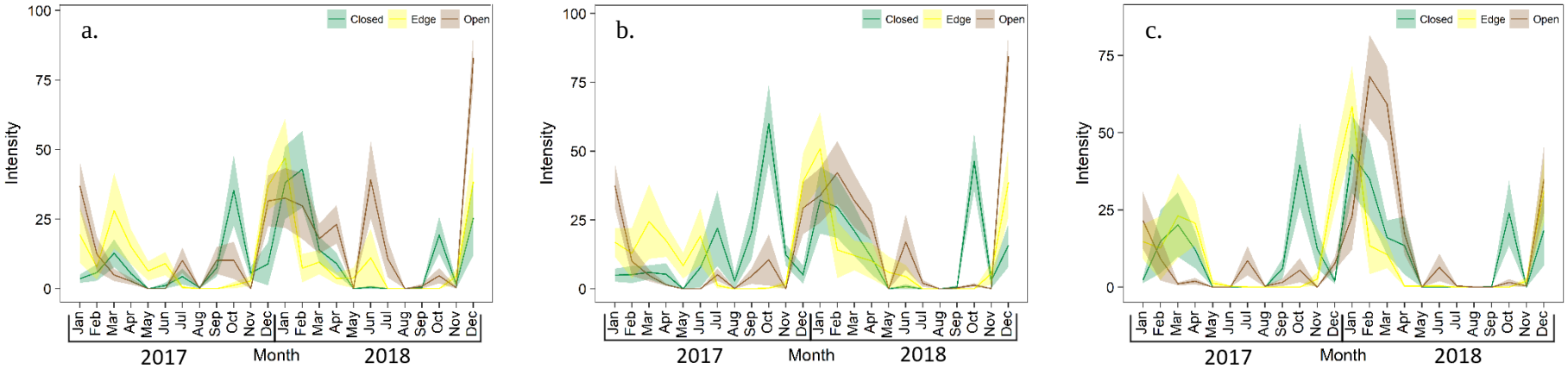


Figure 4: Variation in flowering phenology across time in the three habitats. Panel (a) represent unweighted mean intensity. Panel (b) represent mean intensity weighted by the number of individuals. Panel (c) represent mean intensity weighted by the cumulative basal area of each species, thus considering both number and basal area. The shaded portions represent standard error of n = 9 plots in each habitat.

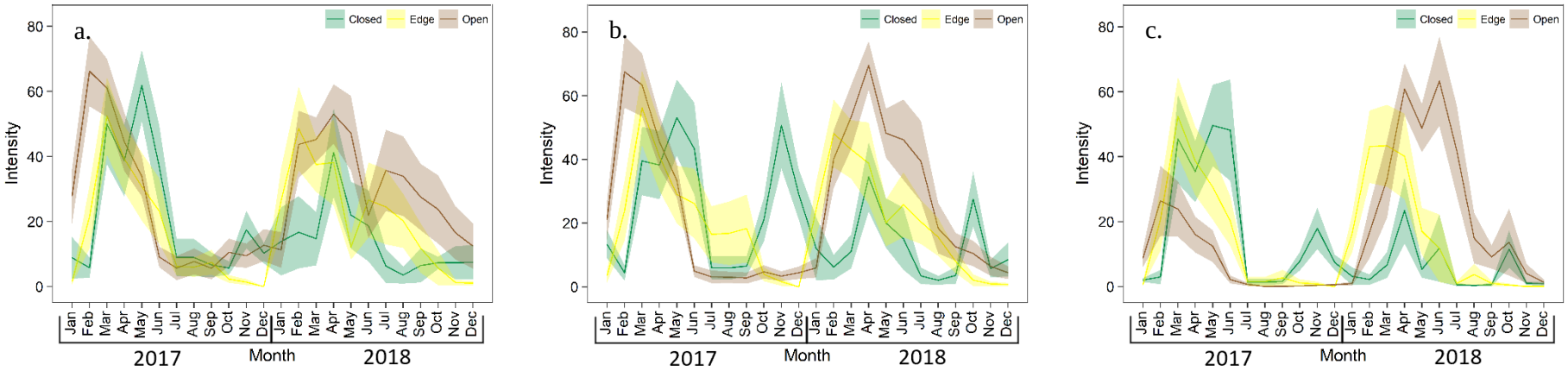


Figure 5: Variation in fruiting phenology across time in the three habitats. Panel (a) represent unweighted mean intensity. Panel (b) represent mean intensity weighted by the number of individuals. Panel (c) represent mean intensity weighted by the cumulative basal area of each species, thus considering both number and basal area. The shaded portions represent standard error of n = 9 plots in each habitat.

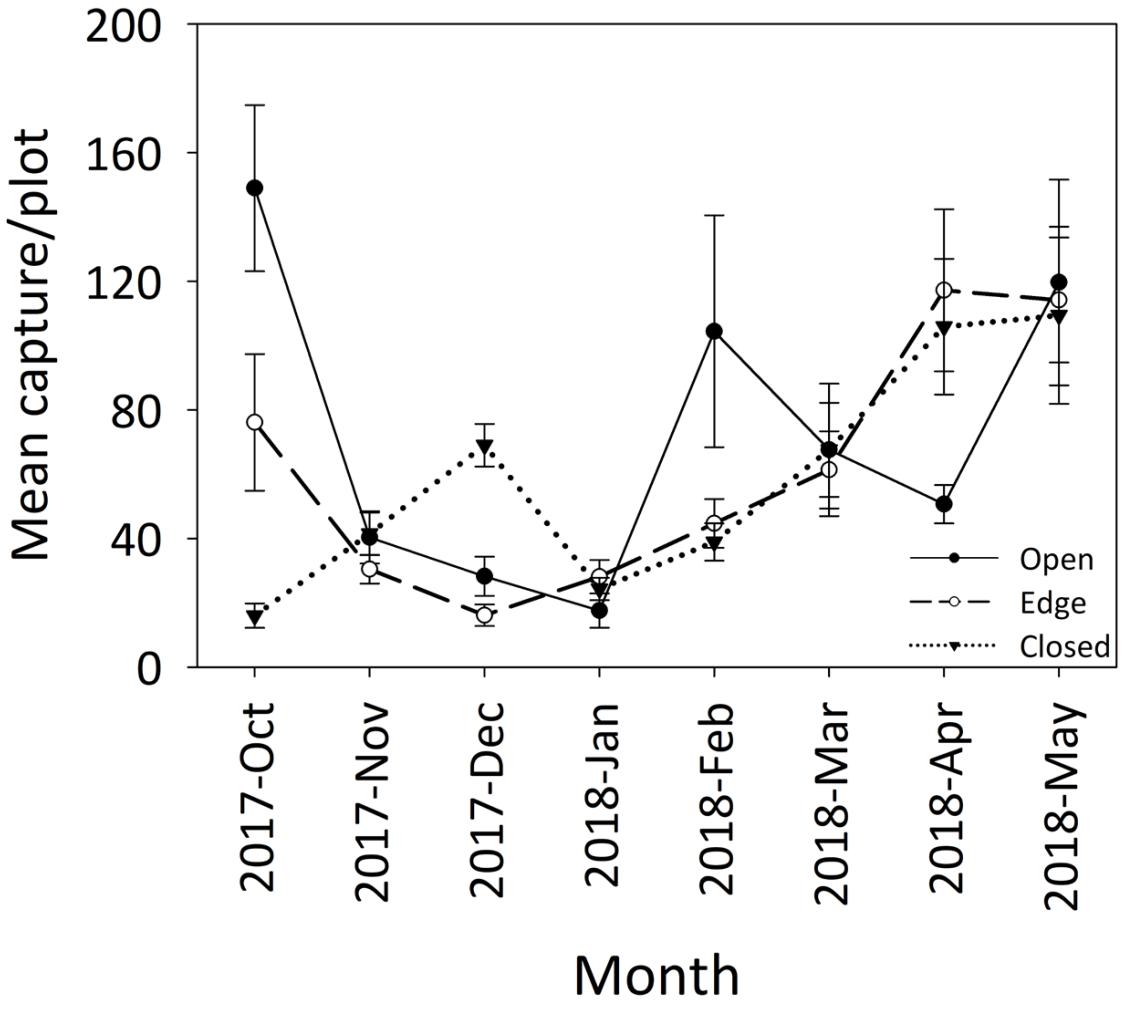


Figure 6: Variation in total potential pollinators across time in the three habitats for the pan traps. The error bars represent standard error of mean capture per plot (n = 9 plots).

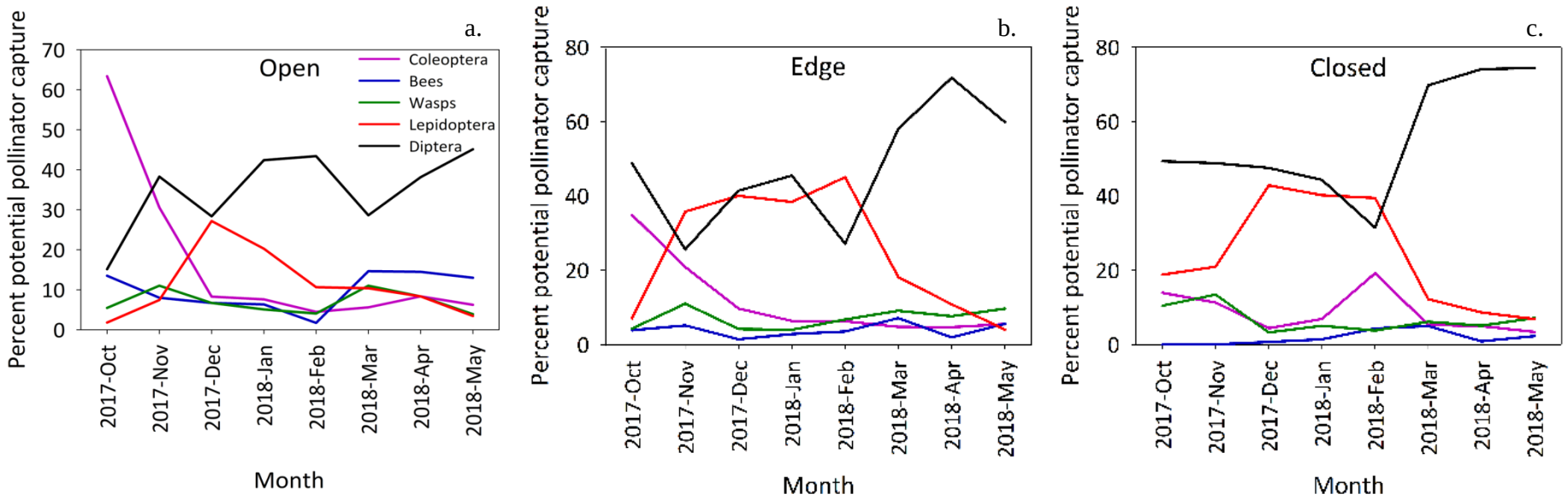


Figure 7: Variation in the abundance of individual insect groups across time in the three habitats: a) open, b) edge and c) closed habitats. Individual pollinator groups are presented as the percentage of total capture of potential pollinators.

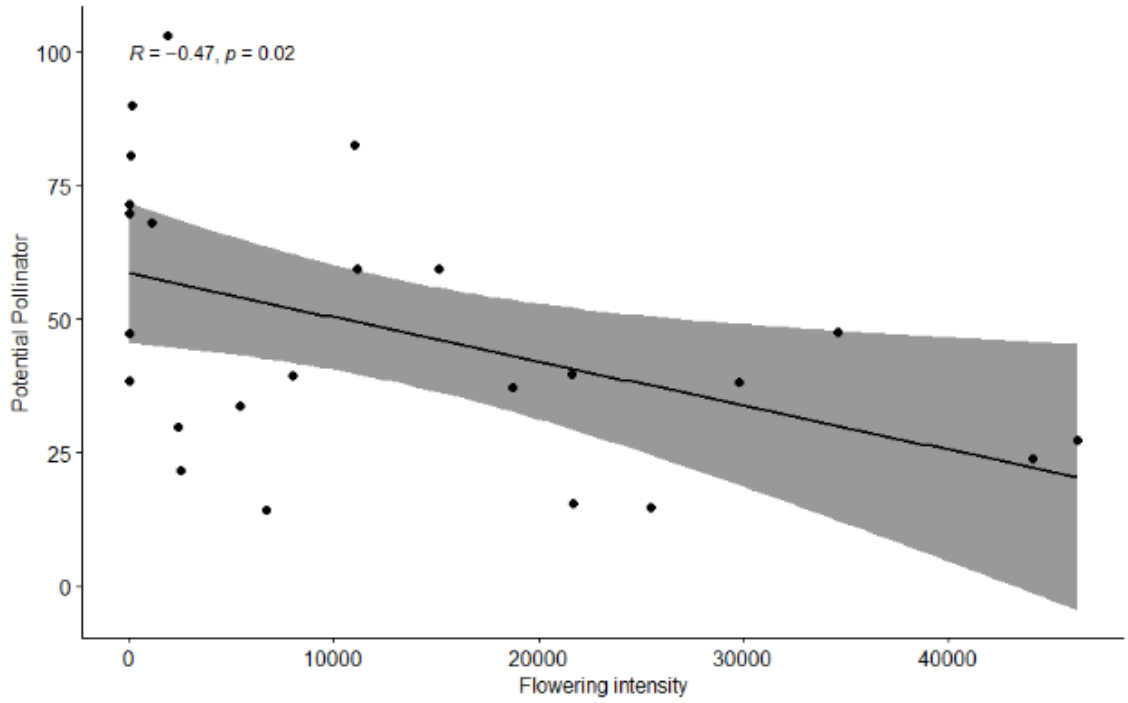


Figure 8: Relationship of the overall pollinator abundance from pan traps to the floral abundance in the habitats. The plot represents the relationship with pollinators across the eight sampling dates in three habitats. The flowering intensity was presented as the cumulative abundance of flowers across the nine plots in each habitat. Similarly, pollinator abundance was presented as cumulative capture of pollinators in the nine plots. The shaded area represents 95 percent confidence interval.

Chapter 5: Conclusions

Tropical dry forests experience a wide range of annual rainfall pattern and seasonality in solar insolation that bring about a broad diversity of phenology in plants. There has been a minimal exploration of this diversity. We have little understanding of how the interaction of limitations in light, water availability, and the plant's nutrient status affects its phenology. One way to simplify the variation is to study groups of species sharing common characteristics, termed as functional groups, and understand the variation between groups. However, even that has rarely received any attention. Furthermore, the past studies on phenology have mainly concentrated on the timing of the phenophase. Little attention has been paid to the variation in other phenology parameters like duration, frequency, synchrony, interannual variation etc. Even less attention has been paid to understanding the relationships between these parameters. The effect of local microenvironment on the phenology of species have also received little attention. Understanding such variations and the relationships between the parameters is crucial to predicting species' performance in a changing environment. The study site is a tropical dry forest with almost equal representation of evergreen and deciduous species, occurring in different habitats with a varying microenvironment. This variation of habitats and species characteristics provided a unique opportunity to understand the diversity of species behaviour in a tropical dry forest. This was the first comprehensive study attempting to understand the variation in phenology between species, not only in timing but also in the other parameters, attempting to understand the relationships between these parameters and the variation in phenology between habitats with a different microenvironment. Additionally, I also looked at the biotic interactions with pollinators to understand if the variation in floral resources affects pollinators' abundance in these habitats.

Synchrony is the measure of overlap in activity between individuals, best understood in case of flowering, as a measure of mating opportunities between pairs of individuals. Synchrony between a pair of individuals is determined not only by the duration of the overlap in flowering but also by the individuals' intensity of flowering. This was first captured in the index of synchrony developed by Freitas and Bolmgren (2008). However, their index treated shorter and longer durations equally and did not capture the dilution of mating opportunities associated with longer durations. The current index developed here

successfully captured the dilution effect, and the absolute values were more than four-fold lower than the Freitas index. The current index was highly correlated to the other synchrony measures. Additionally, it showed stronger correlations with other phenology parameters. The current synchrony index improved upon the previous indices, successfully capturing the variation in duration and intensity influencing synchrony. Thus, it was used as the measure of synchrony in the current study.

Variation in percent species across time showed an aseasonal flushing but highly seasonal senescing, flowering, and fruiting. An equal proportion of species had flushed from the beginning of the wet season to the middle of the dry season. This pattern is likely brought about by a mixture of a gradient of species having lower dependence on water and responding to light availability post rains to those highly dependent on water and flushing closer to the rains or post start of the rains. Senescing, flowering, and fruiting peaked in the middle of the dry season with the senescing and flowering happening around the spring equinox corresponding to peak light availability while fruiting peaked about a month later. These patterns demonstrated the interplay of light and water availability in influencing the phenology of species. Fruit peaking at the end of the dry season and dispersing by the start of the rains ensure optimal germination when water is available while avoiding the risk of seed mortality during dormancy.

There was a wide variation in all the phenology parameters. Except for flowering, which occurred for a maximum of 1.5 months, flushing, senescing, and fruiting usually lasted for 3-4 months. A similar extent of activity has been observed in dry forests of India (Kushwaha & Singh 2005), Africa (Sun *et al.* 1996) and Mexico (Cortes-Flores *et al.* 2017; Luna-Nieves *et al.* 2017). A fair number of species in all phases turned out to be having supra-annual behaviour. Although flushing and senescing may be attributed to observational oversights rather than the actual behaviour, flowering and fruiting supra-annual frequency was driven by interannual variation in flowering and fruiting at the individual level than a consistent activity at the population level. A severe limitation of water or nutrients in these fragmented habitats might have influenced such behaviour. Interannual variation in phenology is an essential indicator of climate change. The observed range reported here was much higher than reported elsewhere like Williams *et al.* (1997). This might be attributed to high variation in rainfall and soil water availability in the study site.

The supplementary phenology parameters had been investigated independently of each other in separate studies, and their relationships have rarely been explored. The synchrony index has both duration and intensity components such that it decreases with duration and increases with intensity. Also, given fixed resources, the intensity of a phenophase is expected to be negatively related to the duration. These relationships held for most cases but not so between duration and synchrony of flowering and fruiting Limitations in available resources impose constraints on duration, synchrony, and intensity for species with varying frequency. Duration, synchrony, and intensity are expected to be negatively related to the frequency. The intensity was found to be negatively related to frequency. I found a positive relationship between frequency and duration and synchrony, unlike expected. Longer duration, higher frequency, lower synchrony, and lower intensity will contribute to higher interannual variation. These relationships held for flushing and flowering. Fruiting synchrony and intensity is also related but not duration and frequency. However, that might be to do with extended maturation time for some fruits. Thus, most of the relationships supported theoretical expectations which had not been comprehensively explored before. However, I also found some relationships to be contrary to that expected. Such relationships like positive relationship between senescing duration and synchrony, and positive relationship between duration and frequency for all phases except fruiting require further exploration and explanation.

There was no consistent parameter across all four phases that explained most of the variation in phenology between species in multivariate space. Synchrony, intensity, and skewness explained most of the variation in flushing. Synchrony, intensity, and frequency similarly explained most variation in senescing. In flowering, start, mean, and stop dates explained most of the variation. Finally, in fruiting, duration, intensity, skewness, and interannual explained most of the variation in phenology between species. Phenology parameters of one phase influence the parameters of another. The flushing, flowering, and fruiting timing were related to each other, indicating light and water availability affected flowering and fruiting similarly. The relationship between flushing and flowering also supports the hypothesis that it is energetically efficient to transport photosynthates directly from leaves to flowers rather than storing them and translocating them later (van Schaik, Terborgh & Wright 1993). Most of the species showed a positive lag between flushing and flowering, indicating species are using current resources from newly flushed

leaves rather than last year's resources. Flushing and flowering phenology were not only related in time, but the duration, intensity, and skewness of the phases were also related to each other owing to the same cue. Another explanation might be because the longer duration of flushing can accumulate more photosynthates to support flowering for a longer time. Flowering frequency, synchrony and interannual variation were also positively related to those of fruiting.

Between the plant life-form categories, shrubs flushed, flowered, and fruited uniformly throughout the year. They also flushed for a much longer duration and flowered more frequently with lower intensity than trees and lianas. An equivalent proportion of shrub species cueing to light and water might explain this range of behaviour. In terms of vertical strata, sub-canopy species flushed very early in the dry season, post rains, and very close to the start of senescing for species in the canopy layer. The evergreen and deciduous species showed contrasting vegetative and reproductive phenology with differences between groups much higher than reported elsewhere. For example, the evergreen species in the study site flushed more than 5 months before the deciduous species. High levels of water stress in the study site might drive such considerable variation between evergreen and deciduous species. I found that the species with larger display sizes flowered later in the dry season were more synchronous between individuals and showed little interannual variation than species with smaller display sizes. Dioecious species flowered earlier than hermaphrodite species, probably to avoid competition for pollinators with some copiously flowering hermaphrodite species. Monoecious species showed the longest flowering duration. Within dioecious species, males flowered earlier and longer than females. This lack of variation might be because I did not have enough resolution of field observation to detect a difference between male and female flowering. Rarer species had lower frequency and higher intensity of flowering than more abundant species. High intensity flowering can also be a compensation for rarer species to increase their mating opportunity. The timing of flowering by different pollinator groups did not correspond to the timing of peak availability of the pollinators. However, the timing of fruiting of different dispersal groups was consistent with the timing of availability of respective dispersal agents. The fruit display size was positively related to fruiting duration, indicating that the large fleshy fruits take more time to mature than smaller fruits.

Here I also developed a continuous measure of deciduousness of species that was not bimodal. This index highlighted the wide variation in behaviour between species within each group, which would be lost by just categorising species into evergreen and deciduous groups, thus indicating that continuous quantitative estimates may be more appropriate, rather than discrete categories. Average canopy loss explained most of the variation between species. More importantly, I found that these quantitative measures of deciduousness were functionally relevant and related to many other phenology parameters and the lag of flushing and flowering. Thus, deciduousness calculation demonstrated a gradient of leaf loss behaviour due to a wide range of water stress from seasonal drought experienced by species in the study site and helped predict their behaviour under a changing environment.

This study is among a handful that described the actual community weighted phenology pattern, both within and between years, and contrasted it among three different habitats with varying light and water microenvironment in a tropical dry forest. I found flushing phenology to vary differently between habitats across time. While edge and closed habitats showed a single activity cycle in a year, open habitats showed bimodal behaviour. This bimodality can be attributed to equivalent proportions of evergreen and deciduous species in the open which showed different flushing behaviour. Senescing and flowering phenology did not differ between habitats. Fruiting phenology had both date and habitat effect indicating considerable variation in fruiting intensity across time and the three habitats. Comparison between an unweighted pattern of phenophase intensity, intensity weighted by number and intensity weighted by the total basal area of the species revealed that the ultimate variation is purely driven by variation in the intensity of species in the three habitats. This finding suggested the role of local microenvironment, light, and water availability, might nullify the variation that might arise due to differences in size and composition of species in these three habitats. Here I found the abundance of overall pollinators to vary differently between habitats across time. The same was also valid for individual pollinator groups except for wasps. Here, primarily flies, and then butterflies and moths dominated capture across all the three habitats. Bees and beetles constituted only a tiny part of the capture in the study site. The abundance of some of the pollinator groups coincided with their timing of peak availability. Overall pollinators or individual pollinator groups either showed no relationship or were negatively related to floral abundance in their respective habitats. This negative relationship might indicate high

diversity in species' activity in each group or some other factors are affecting pollinator abundance independently and had nothing to do with flowering. These negative relationships require further investigation.

This study provides further insight into the seasonal variation in species' vegetative and reproductive phenology in a seasonally dry tropical forest. This study is the first comprehensive exploration of the intricate relationships between all the phenology parameters within and between phenophases. Most of the relationships previously existed as theoretical predictions with some rare studies that isolatedly looked at some of these relationships. The study provided some unique insights into these predictions supporting most of them. The study site species covers a range of growth habits, leaf shedding habit, and biotic interactions. These ranges of habits provide a unique opportunity to understand the variation in phenology between groups based on these habits. The broad range of species deciduousness and its effect on producing a wide variety of vegetative and reproductive phenology is the most critical finding of this study. The results provide essential support for the insolation-limitation hypothesis (van Schaik, Terborgh & Wright 1993; Sun et al. 1996). I also looked at the relationship of some species' reproductive characteristics and phenology and differences between groups of different biotic interactions. These have mostly been accounted through theoretical predictions and received little attention in past studies. This study is among a handful that describes the actual community weighted phenology pattern, both within and between years, and contrasts it among three different habitats with varying light and water microenvironment in a tropical dry forest. I also looked at the temporal and spatial variation in insect pollinator groups. I tried to understand how variation in floral resources affects variation in the abundance of pollinators. Among all the findings that supported past theoretical predictions, some were contrary to expectation. These findings like the negative relationship between frequency and duration and synchrony, or the negative relationship between floral abundance and the pollinator groups require further exploration.

The topological nature of the study site, the pattern of water availability across the year, the distribution of species and their diversity in phenology, and their growth habits and vegetative and reproductive attributes together, can not only help us reflect on its past but predict the changes that might incur to the forest in the future. The crest forest for example might be a recent forest in geological time scale, formed on the thin layer of soil

from the volcanic rocks that formed the deccan plateau. The low soil depth, the short sparse forest patches studded with rocky outcrops and natural grasslands, and a mixture of pioneer and climax tree species indicate that the study site might be in a stable middle successional stage unlikely to reach a climax vegetation type. Soils of the crest and the slopes are known to be well drained with high permeability. This coupled with the highly seasonal rainfall might point towards a soil with low water and nutrient content. Empirical field observations across years suggest that many of the species exhibit cases of alternate fruit bearing which might also be a result of low nutrient availability. Coupled with these, an overabundance of less efficient flower visitors like flies over highly efficient pollinators like bees and butterflies also might contribute to pollen limitation and low fruit set. On the other hand, climate change and anthropogenic disturbance might affect the entire forest dynamics in the study site. Increasing draught might result in drier site that might promote the evergreen species still maintaining their productivity while that of the deciduous species may be severely hampered. This might gradually shift the species composition towards a more evergreen forest and thus might also alter the dynamics of the pollinators, dispersers and primary consumers that depended on such species in the future.

Reanalysing this data with phylogenetic corrections would be the next step forward. Also, long term habitat level study of plant phenology and the variation in pollinator abundance would be necessary to capture the interannual variation in these habitats more accurately and associate it with the pollinators' abundance. These long-term studies are necessary to understand the responses of both plant and pollinator communities in a changing environment. Studies in phenology can, not only help us reflect upon the responses of plants to environmental cues and biotic constraints but also predict how these responses might change in a changing environment. This is important as it can give vital insights into how these species might have behaved in the past by altering their phenology, how species might have colonised new environmental niches and altered their ranges, and ultimately how such changes in phenology have altered the interaction of the species with the primary consumers that depend on them.

References

Adole, T., Dash, J., Rodriguez-Galiano, V. & Atkinson, P.M. (2019) Photoperiod controls vegetation phenology across Africa. *Communications Biology*, **2,** 13.

Aide, T.M. (1992) Dry Season Leaf Production: An Escape from Herbivory. *Biotropica,* **24,** 532-537.

Aide, T.M. (1993) Patterns of Leaf Development and Herbivory in a Tropical Understory Community. *Ecology,* **74,** 455-466.

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, **103,** 1579-1588.

Aldrich, P.R. & Hamrick, J.L. (1998) Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science*, **281,** 103-105.

Anderson, D., Nordheim, E., Moermond, T., Bi, Z. & Boesch, C. (2005) Factors influencing tree phenology in Tai National Park, Cote d'Ivoire. *Biotropica*, **37,** 631-640.

Appanah, S. (1993) Mass flowering of dipterocarp forests in the aseasonal tropics. *Journal of Biosciences*, **18,** 457-474.

Aronson, J., Kigel, J., Shmida, A. & Klein, J. (1992) Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia,* **89,** 17-26.

Augspurger, C.K. (1983) Phenology, Flowering Synchrony, and Fruit-Set of 6 Neotropical Shrubs. *Biotropica,* **15,** 257-267.

Augspurger, C.K. & Franson, S.E. (1987) Wind Dispersal of Artifical Fruits Varying in Mass, Area, and Morphology. *Ecology,* **68,** 27-42.

Bach, C.S. (2002) Phenological patterns in monsoon rainforests in the Northern Territory, Australia. *Austral Ecology*, **27,** 477-489.

Bailey, S., Requier, F., Nusillard, B., Roberts, S.P., Potts, S.G. & Bouget, C. (2014) Distance from forest edge affects bee pollinators in oilseed rape fields. *Ecology and Evolution*, **4,** 370-380.

Bajpai, O., Pandey, J. & Chaudhary, L.B. (2017) Periodicity of different phenophases in selected trees from Himalayan Terai of India. *Agroforestry Systems,* **91,** 363-374.

Bassett, I., Holmes, R. & MacKay, K. (1961) Phenology of several plant species at Ottawa, Ontario, and an examination of the influence of air temperatures. *Canadian Journal of Plant Science,* **41,** 643-652.

Batalha, M.A. & Mantovani, W. (2000) Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. *Revista Brasileira de Biologia,* **60,** 129-145.

Batalha, M.A. & Martins, F.R. (2004) Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Australian Journal of Botany,* **52,** 149-161.

Bawa, K.S. & Beach, J.H. (1981) Evolution of Sexual Systems in Flowering Plants. *Annals of the Missouri Botanical Garden*, **68,** 254-274.

Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E. & Grayum, M.H. (1985) Reproductive Biology of Tropical Lowland Rain Forest Trees. II. Pollination Systems. *American Journal of Botany,* **72,** 346-356.

Bawa, K.S., Kang, H.S. & Grayum, M.H. (2003) Relationships among time, frequency, and duration of flowering in tropical rain forest trees. *American Journal of Botany,* **90,** 877-887.

Becker, P. & Castillo, A. (1990) Root Architecture of Shrubs and Saplings in the Understory of a Tropical Moist Forest in Lowland Panama. *Biotropica,* **22,** 242-249.
Bentos, T.V., Mesquita, R.C.G. & Williamson, G.B. (2008) Reproductive Phenology of Central Amazon Pioneer Trees. *Tropical Conservation Science,* **1,** 186-203.
Bhat, D.M. (1992) Phenology of Tree Species of Tropical Moist Forest of Uttara-Kannada District, Karnataka, India. *Journal of Biosciences*, **17,** 325-352.
Blackburn, G.A. & Milton, E.J. (1995) Seasonal variations in the spectral reflectance of deciduous tree canopies. *International Journal of Remote Sensing,* **16,** 709-720.
Boinski, S. & Fowler, N.L. (1989) Seasonal Patterns in a Tropical Lowland Forest. *Biotropica*, **21,** 223-233.
Borchert, R. (1994) Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology*, **75,** 1437-1449.
Borchert, R., Meyer, S.A., Felger, R.S. & Porter-Bolland, L. (2004) Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography,* **13,** 409-425.
Borchert, R., Robertson, K., Schwartz, M. & Williams-Linera, G. (2005) Phenology of temperate trees in tropical climates. *International Journal of Biometeorology,* **50,** 57-65.
Borges, M.P., Henrique, C. & Prado, B.D. (2014) Relationships between leaf deciduousness and flowering traits of woody species in the Brazilian neotropical savanna. *Flora,* **209,** 73-80.
Bullock, S.H. & Bawa, K.S. (1981) Sexual Dimorphism and the Annual Flowering Pattern in Jacaratia Dolichaula (D. Smith) Woodson (Caricaceae) in a Costa Rican Rain Forest. *Ecology,* **62,** 1494-1504.
Bullock, S.H. & Solismagallanes, J.A. (1990) Phenology of Canopy Trees of a Tropical Deciduous Forest in Mexico. *Biotropica,* **22,** 22-35.
Calle, Z., Schlumpberger, B.O., Piedrahita, L., Leftin, A., Hammer, S.A., Tye, A. & Borchert, R. (2010) Seasonal variation in daily insolation induces synchronous bud break and flowering in the tropics. *Trees-Structure and Function,* **24,** 865-877.
Chapman, C., Wrangham, R., Chapman, L., Kennard, D. & Zanne, A. (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology,* **15,** 189-211.
Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007) Shifting plant phenology in response to global change. *Trends in Ecology & Evolution,* **22,** 357-365.
Cohen, H., Philpott, S.M., Liere, H., Lin, B.B. & Jha, S. (2020) The relationship between pollinator community and pollination services is mediated by floral abundance in urban landscapes. *Urban Ecosystems***,** 16.
Coley, P. & Barone, J. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics,* **27,** 305-335.
Condit, R., Watts, K., Bohlman, S., Perez, R., Foster, R. & Hubbell, S. (2000) Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science,* **11,** 649-658.
Corlett, R. (2004) Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biological Reviews,* **79,** 497-532.
Cortes-Flores, J., Hernandez-Esquivel, K.B., Gonzalez-Rodriguez, A. & Ibarra-Manriquez, G. (2017) Flowering phenology, growth forms, and pollination

syndromes in tropical dry forest species: Influence of phylogeny and abiotic factors. *American Journal of Botany,* **104,** 39-49.
Crimmins, T.M., Crimmins, M.A. & Bertelsen, C.D. (2013) Spring and summer patterns in flowering onset, duration, and constancy across a water-limited gradient. *American Journal of Botany,* **100,** 1137-1147.
de Bie, S., Ketner, P., Paasse, M. & Geerling, C. (1998) Woody plant phenology in the West Africa savanna. *Journal of Biogeography,* **25,** 883-900.
de Lampe, M.G., Bergeron, Y., McNeil, R. & Leduc, A. (1992) Seasonal Flowering and Fruiting Patterns in Tropical Semi-Arid Vegetation of Northeastern Venezuela. *Biotropica,* **24,** 64-76.
de Oliveira, C.C., Zandavalli, R.B., de Lima, A.L.A. & Rodal, M.J.N. (2015) Functional groups of woody species in semi-arid regions at low latitudes. *Austral Ecology,* **40,** 40-49.
de Vasconcelos, S.F., de Araujo, F.S. & Lopes, A.V. (2010) Phenology and dispersal modes of wood species in the Carrasco, a tropical deciduous shrubland in the Brazilian semiarid. *Biodiversity and Conservation,* **19,** 2263-2289.
Demaree, G. & Rutishauser, T. (2011) From "Periodical Observations" to "Anthochronology" and "Phenology" - the scientific debate between Adolphe Quetelet and Charles Morren on the origin of the word "Phenology". *International Journal of Biometeorology,* **55,** 753-761.
Denlinger, D.L. (1980) Seasonal and Annual Variation of Insect Abundance in the Nairobi National Park, Kenya. *Biotropica,* **12,** 100-106.
Devy, M.S. & Davidar, P. (2003) Pollination systems of trees in Kakachi, a mid-elevation wet evergreen forest in Western Ghats, India. *American Journal of Botany,* **90,** 650-657.
Eamus, D. (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology & Evolution,* **14,** 11-16.
Elliott, S., Baker, P.J. & Borchert, R. (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography,* **15,** 248-257.
Elzinga, J., Atlan, A., Biere, A., Gigord, L., Weis, A. & Bernasconi, G. (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology & Evolution,* **22,** 432-439.
Fenner, M. (1998) The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics,* **1,** 78-91.
Forero-Montana, J. & Zimmerman, J. (2010) Sexual dimorphism in the timing of flowering in two dioecious trees in a subtropical wet forest, Puerto Rico. *Caribbean Journal of Science,* **46,** 88-95.
Fowler, R.E., Rotheray, E.L. & Goulson, D. (2016) Floral abundance and resource quality influence pollinator choice. *Insect Conservation and Diversity,* **9,** 481-494.
Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative Phenological Studies of Trees in Tropical Wet and Dry Forests in Lowlands of Costa-Rica. *Journal of Ecology,* **62,** 881-919.
Freitas, L. & Bolmgren, K. (2008) Synchrony is more than overlap: measuring phenological synchronization considering time length and intensity. *Revista Brasileira de Botânica,* **31,** 721-724.
Fründ, J., Linsenmair, K.E. & Blüthgen, N. (2010) Pollinator diversity and specialization in relation to flower diversity. *Oikos,* **119,** 1581-1590.

Fuchs, E.J., Lobo, J.A. & Quesada, M. (2003) Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree Pachira quinata. *Conservation Biology,* **17,** 149-157.
Funch, L.S., Funch, R. & Barroso, G.M. (2002) Phenology of gallery and montane forest in the Chapada Diamantina, Bahia, Brazil. *Biotropica,* **34,** 40-50.
Gallagher, M.K. & Campbell, D.R. (2017) Shifts in water availability mediate plant-pollinator interactions. *New Phytol,* **215,** 792-802.
Ghadage, M., Theurkar, S. & Patil, S. (2014) Ecological and Biogeographical Features of Khed Tahasil, Pune District, MS, India. *Res. J. Recent Sci.,* **3 (ISC-2013),** 33-37.
Gonzalez-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyorgyi, H., Woyciechowski, M. & Vila, M. (2013) Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology & Evolution,* **28,** 524-530.
Grimbacher, P. & Stork, N. (2009) Seasonality of a Diverse Beetle Assemblage Inhabiting Lowland Tropical Rain Forest in Australia. *Biotropica,* **41,** 328-337.
Griz, L.M.S. & Machado, I.C.S. (2001) Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology,* **17,** 303-321.
Haber, W.A. & Frankie, G.W. (1989) A Tropical Hawkmoth Community: Costa Rican Dry Forest Sphingidae. *Biotropica,* **21,** 155-172.
Hansman, D.J. (2001) Floral biology of dry rainforest in north Queensland and a comparison with adjacent savanna woodland. *Australian Journal of Botany,* **49,** 137-153.
Haugaasen, T. & Peres, C. (2005) Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica,* **37,** 620-630.
Herrerias-Diego, Y., Quesada, M., Stoner, K.E. & Lobo, J.A. (2006) Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree Ceiba aesculifolia. *Conservation Biology,* **20,** 1111-1120.
Hudson, I.L. & Keatley, M.R. (2009) *Phenological research: methods for environmental and climate change analysis*. Springer, Dordrecht.
Ibarra-Manriquez, G. & Oyama, K. (1992) Ecological Correlates of Reproductive Traits of Mexican Rain-Forest Trees. *American Journal of Botany,* **79,** 383-394.
IPCC (2001) *Climate change 2001: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, Cambridge.
Itioka, T., Inoue, T., Kaliang, H., Kato, M., Nagamitsu, T., Momose, K., Sakai, S., Yumoto, T., Mohamad, S.U., Hamid, A.A. & Yamane, S. (2001) Six-year population fluctuation of the giant honey bee Apis dorsata (Hymenoptera : Apidae) in a tropical lowland dipterocarp forest in Sarawak. *Annals of the Entomological Society of America,* **94,** 545-549.
Janzen, D.H. (1967) Synchronization of Sexual Reproduction of Trees within Dry Season in Central America. *Evolution,* **21,** 620-&.
Jeong, S.-J., Ho, C.-H., Gim, H.-J. & Brown, M.E. (2011) Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. *Global Change Biology,* **17,** 2385-2399.
Johnson, S.D. (2004) An overview of plant–pollinator relationships in southern Africa. *International Journal of Tropical Insect Science,* **24,** 45-54.
Justiniano, M.J. & Fredericksen, T.S. (2000) Phenology of tree species in Bolivian dry forests. *Biotropica,* **32,** 276-281.

Kang, H. & Bawa, K.S. (2003) Effects of successional status, habit, sexual systems, and pollinators on flowering patterns in tropical rain forest trees. *American Journal of Botany,* **90,** 865-876.
Kato, M. (1996) Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany,* **83,** 732-743.
Kinnaird, M.F. (1992) Phenology of Flowering and Fruiting of an East-African Riverine Forest Ecosystem. *Biotropica,* **24,** 187-194.
Kishimoto-Yamada, K. & Itioka, T. (2015) How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomological Science,* **18,** 407-419.
Kunte, K.J. (1997) Seasonal patterns in butterfly abundance and species diversity in four tropical habitats in northern Western Ghats. *Journal of Biosciences,* **22,** 593-603.
Kushwaha, C. & Singh, K. (2005) Diversity of leaf phenology in a tropical deciduous forest in India. *Journal of Tropical Ecology,* **21,** 47-56.
Kushwaha, C., Tripathi, S. & Singh, K. (2011) Tree specific traits affect flowering time in Indian dry tropical forest. *Plant Ecology,* **212,** 985-998.
Lacerda, D.M.A., Rossatto, D.R., Ribeiro-Novaes, E. & de Almeida, E.B. (2018) Reproductive phenology differs between evergreen and deciduous species in a Northeast Brazilian savanna. *Acta Botanica Brasilica,* **32,** 367-375.
Laurance, W., Merona, J., Andrade, A., Laurance, S., D'Angelo, S., Lovejoy, T. & Vasconcelos, H. (2003) Rain-forest fragmentation and the phenology of Amazonian tree communities. *Journal of Tropical Ecology,* **19,** 343-347.
Lieberman, D. (1982) Seasonality and Phenology in a Dry Tropical Forest in Ghana. *Journal of Ecology,* **70,** 791-806.
Lieth, H. (2013) *Phenology and seasonality modeling*. Springer Science & Business Media.
Liuth, H.S., Talora, D.C. & Amorim, A.M. (2013) Phenological synchrony and seasonality of understory Rubiaceae in the Atlantic Forest, Bahia, Brazil. *Acta Botanica Brasilica,* **27,** 195-204.
Lloyd, D.G. & Webb, C.J. (1977) Secondary sex characters in plants. *The Botanical Review,* **43,** 177-216.
Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation to canopy closure in southern Appalachian trees. *Am J Bot,* **95,** 1395-1407.
Lovejoy, T.E., Bierregaard, R.O.J., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S.J., Powell, A.H., Powell, G.V.N., Schubart, H.O.R. & Hays, M.B. (1986) *Edge and other effects of isolation on Amazon forest fragments*. Sunderland, Mass. (USA): Sinauer Associates.
Luna-Nieves, A.L., Meave, J.A., Morellato, L.P.C. & Ibarra-Manriquez, G. (2017) Reproductive phenology of useful Seasonally Dry Tropical Forest trees: Guiding patterns for seed collection and plant propagation in nurseries. *Forest Ecology and Management,* **393,** 52-62.
Machado, I.C.S., Barros, L.M. & Sampaio, E.V.S.B. (1997) Phenology of Caatinga Species at Serra Talhada, PE, Northeastern Brazil. *Biotropica,* **29,** 57-68.
Marques, M.C.M., Roper, J.J. & Salvalaggio, A.P.B. (2004) Phenological patterns among plant life-forms in a subtropical forest in southern Brazil. *Plant Ecology,* **173,** 203-213.
Marquis, R.J. (1988) Phenological Variation in the Neotropical Understory Shrub Piper Arielanum: Causes and Consequences. *Ecology,* **69,** 1552-1565.

McLaren, K.P. & McDonald, M.A. (2005) Seasonal Patterns of Flowering and Fruiting in a Dry Tropical Forest in Jamaica1. *Biotropica*, **37,** 584-590.
Momose, K., Yumoto, T., Nagamitsu, T., Kato, M., Nagamasu, H., Sakai, S., Harrison, R.D., Itioka, T., Hamid, A.A. & Inoue, T. (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany*, **85,** 1477-1501.
Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C. & Zipparro, V.B. (2000) Phenology of Atlantic Rain Forest Trees: A Comparative Study. *Biotropica*, **32,** 811-823.
Morris, J.B. (2008) Characterization of butterfly pea (Clitoria ternatea L.) accessions for morphology, phenology, reproduction and potential nutraceutical, pharmaceutical trait utilization. *Genetic Resources and Crop Evolution*, **56,** 421-427.
Mosquin, T. (1971) Competition for Pollinators as a Stimulus for the Evolution of Flowering Time. *Oikos*, **22,** 398-&.
Murali, K.S. & Sukumar, R. (1993) Leaf Flushing Phenology and Herbivory in a Tropical Dry Deciduous Forest, Southern India. *Oecologia*, **94,** 114-119.
Murali, K.S. & Sukumar, R. (1994) Reproductive Phenology of a Tropical Dry Forest in Mudumalai, Southern India. *Journal of Ecology*, **82,** 759-767.
Nanda, A., Prakasha, H., Murthy, Y.K. & Suresh, H. (2011) Phenology of leaf flushing, flower initiation and fruit maturation in dry deciduous and evergreen forests of Bhadra Wildlife Sanctuary, Karnataka, southern India. *Our Nature*, **9,** 89-99.
Nanda, A., Suresh, H.S. & Krishnamurthy, Y.L. (2014) Phenology of a tropical dry deciduous forest of Bhadra wildlife sanctuary, southern India. *J Ecological processes*, **3,** 1.
New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21,** 1-25.
Newstrom, L.E., Frankie, G.W. & Baker, H.G. (1994) A New Classification for Plant Phenology Based on Flowering Patterns in Lowland Tropical Rain Forest Trees at La Selva, Costa Rica. *Biotropica*, **26,** 141-159.
Newton, P.N. (1988) The structure and phenology of a moist deciduous forest in the Central Indian Highlands. *Vegetatio*, **75,** 3-16.
Ongole, S., Teegalapalli, K., Byrapoghu, V., Ratnam, J. & Sankaran, M. (2021) Functional traits predict tree-level phenological strategies in a mesic Indian savanna. *Biotropica***,** 10.
Opler, P.A., Frankie, G.W. & Baker, H.G. (1980) Comparative Phenological Studies of Treelet and Shrub Species in Tropical Wet and Dry Forests in the Lowlands of Costa Rica. *The Journal of Ecology*, **68,** 167-188.
Ouédraogo, D.-Y., Doucet, J.-L., Daïnou, K., Baya, F., Biwolé, A.B., Bourland, N., Fétéké, F., Gillet, J.-F., Kouadio, Y.L. & Fayolle, A. (2018) The size at reproduction of canopy tree species in central Africa. *Biotropica*, **50,** 465-476.
Pau, S., Wolkovich, E., Cook, B., Davies, T., Kraft, N., Bolmgren, K., Betancourt, J. & Cleland, E. (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17,** 3633-3643.
Primack, R.B. (1980) Variation in the Phenology of Natural Populations of Montane Shrubs in New Zealand. *The Journal of Ecology*, **68,** 849-862.
Primack, R.B. (1987) Relationships among Flowers, Fruits, and Seeds. *Annual Review of Ecology and Systematics*, **18,** 409-430.
Ramirez, N. (2002) Reproductive phenology, life-forms and habitats of the Venezuelan Central Plain. *American Journal of Botany*, **89,** 836-842.

Ramirez, N. (2005) Plant sexual systems, dichogamy, and herkogamy in the Venezuelan Central Plain. *Flora,* **200,** 30-48.
Rathcke, B. & Lacey, E.P. (1985) Phenological Patterns of Terrestrial Plants. *Annual Review of Ecology and Systematics,* **16,** 179-214.
Reich, P.B. (1995) Phenology of Tropical Forests - Patterns, Causes, and Consequences. *Canadian Journal of Botany-Revue Canadienne De Botanique,* **73,** 164-174.
Reich, P.B. & Borchert, R. (1984) Water Stress and Tree Phenology in a Tropical Dry Forest in the Lowlands of Costa Rica. *The Journal of Ecology,* **72,** 61-74.
Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America,* **94,** 13730-13734.
Rivera, G., Elliott, S., Caldas, L.S., Nicolossi, G., Coradin, V.T.R. & Borchert, R. (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees-Structure and Function,* **16,** 445-456.
Rusch, A., Valantin-Morison, M., Roger-Estrade, J. & Sarthou, J.P. (2012) Local and landscape determinants of pollen beetle abundance in overwintering habitats. *Agricultural and Forest Entomology,* **14,** 37-47.
Ryu, Y., Lee, G., Jeon, S., Song, Y. & Kimm, H. (2014) Monitoring multi-layer canopy spring phenology of temperate deciduous and evergreen forests using low-cost spectral sensors. *Remote Sensing of Environment,* **149,** 227-238.
Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A. & Nakashizuka, T. (1999a) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia (vol 86, pg 1414, 1999). *American Journal of Botany,* **86,** 1741-1741.
Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A. & Nakashizuka, T. (1999b) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany,* **86,** 1414-1436.
Sargent, R.D., Goodwillie, C., Kalisz, S. & Rees, R.H. (2007) Phylogenetic evidence for a flower size and number trade-off. *American Journal of Botany,* **94,** 2059-2062.
Scheiter, S., Kumar, D., Corlett, R.T., Gaillard, C., Langan, L., Lapuz, R.S., Martens, C., Pfeiffer, M. & Tomlinson, K.W. (2020) Climate change promotes transitions to tall evergreen vegetation in tropical Asia. *Global Change Biology,* **26,** 5106-5124.
Segrestin, J., Navas, M.L. & Garnier, E. (2019) Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. *New Phytologist,* **225,** 740-753.
Selwyn, M. & Parthasarathy, N. (2006) Reproductive traits and phenology of plants in tropical dry evergreen forest on the coromandel coast of India. *Biodiversity and Conservation,* **15,** 3207-3234.
Shukla, R.P. & Ramakrishnan, P.S. (1982) Phenology of Trees in a Sub-Tropical Humid Forest in Northeastern India. *Vegetatio,* **49,** 103-109.
Singh, K.P. & Kushwaha, C.P. (2006) Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Annals of Botany,* **97,** 265-276.
Singh, K.P. & Kushwaha, C.P. (2016) Deciduousness in tropical trees and its potential as indicator of climate change: A review. *Ecological Indicators,* **69,** 699-706.
Sizer, N. & Tanner, E.V.J. (1999) Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation,* **91,** 135-142.
Smythe, N. (1970) Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *The American Naturalist,* **104,** 25-35.

Somanathan, H. & Borges, R.M. (2000) Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India. *Biological Conservation,* **94,** 243-256.
Somanathan, H., Borges, R.M. & Chakravarthy, V.S. (2004) Does Neighborhood floral display matter? Fruit set in carpenter bee-pollinated Heterophragma quadriloculare and beetle-pollinated Lasiosiphon eriocephalus. *Biotropica,* **36,** 139-147.
Sparks, T. & Menzel, A. (2002) Observed changes in seasons: An overview. *International Journal of Climatology,* **22,** 1715-1725.
Sun, C., Kaplin, B.A., Kristensen, K.A., Munyaligoga, V., Mvukiyumwami, J., Kajondo, K.K. & Moermond, T.C. (1996) Tree Phenology in a Tropical Montane Forest in Rwanda. *Biotropica,* **28,** 668-681.
Sundarapandian, S.M., Chandrasekaran, S. & Swamy, P.S. (2005) Phenological behaviour of selected tree species in tropical forests at Kodayar in the Western Ghats, Tamil Nadu, India. *Current Science,* **88,** 805-810.
Thomson, J.D. (1980) Skewed Flowering Distributions and Pollinator Attraction. *Ecology,* **61,** 572-579.
Tooke, F. & Battey, N. (2010) Temperate flowering phenology. *Journal of Experimental Botany,* **61,** 2853-2862.
Torres, C. & Galetto, L. (2011) Flowering phenology of co-occurring Asteraceae: a matter of climate, ecological interactions, plant attributes or of evolutionary relationships among species? *Organisms Diversity & Evolution,* **11,** 9-19.
van Halder, I., Barbaro, L. & Jactel, H. (2011) Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important? *Journal of Insect Conservation,* **15,** 591-601.
van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993) The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics,* **24,** 353-377.
Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, M.P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunis, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N.E., Roberts, S., Ryabov, E.V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P.C., Stone, G.N., Termansen, M., Wright, G.A. & Insect Pollinators, I. (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment,* **11,** 251-259.
Vu, L.V. (2009) Diversity and similarity of butterfly communities in five different habitat types at Tam Dao National Park, Vietnam. *Journal of Zoology,* **277,** 15-22.
Walter, H. & Burnett, J.H. (1971) *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver and Boyd.
Wang, C., Tang, Y. & Chen, J. (2016) Plant phenological synchrony increases under rapid within-spring warming. *Scientific Reports,* **6**.
Williams-Linera, G. (1997) Phenology of deciduous and broadleaved-evergreen tree species in a Mexican tropical lower montane forest. *Global Ecology and Biogeography Letters,* **6,** 115-127.
Williams, L.J., Bunyavejchewin, S. & Baker, P.J. (2008) Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. *Oecologia,* **155,** 571-582.

Williams, R.J., Myers, B.A., Eamus, D. & Duff, G.A. (1999) Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica,* **31,** 626-636.
Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A. & Eamus, D. (1997) Leaf phenology of woody species in a North Australian tropical savanna. *Ecology,* **78,** 2542-2558.
Wolda, H. (1988) Insect Seasonality: Why? *Annual Review of Ecology and Systematics,* **19,** 1-18.
Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature,* **428,** 821-827.
Wright, S.J. & Calderon, O. (2018) Solar irradiance as the proximate cue for flowering in a tropical moist forest. *Biotropica,* **50,** 374-383.
Wright, S.J. & van Schaik, C.P. (1994) Light and the Phenology of Tropical Trees. *The American Naturalist,* **143,** 192-199.
Yu, R., Huang, J., Xu, Y., Ding, Y. & Zang, R. (2020) Plant Functional Niches in Forests Across Four Climatic Zones: Exploring the Periodic Table of Niches Based on Plant Functional Traits. *Front Plant Sci,* **11,** 841.

Appendix

Table S1: List of species in the study site and the plant groups they belong to. In the table headers, Code refers to 2 letter abbreviations used to refer to a species quickly; Species is the corresponding accepted scientific name according to The Plant List (TPL) [http://www.theplantlist.org/]; Family is the plant family the species belong to. The species functional group associations including life form, strata, leaf habit and sexual system was based primarily on field observation and previous work done in the lab. Life form and sexual system were also confirmed from literature when available. Pollination syndrome was assigned based on floral traits like size, colour, smell, reward, position in the canopy etc. along with actual observation of insect visitation in the field and then corroborated with that reported in the literature. Similarly, dispersal syndrome was also assigned based on fruit traits like size, colour, fleshiness etc. and then corroborated with that reported in the literature. The corresponding references for pollination and dispersal syndrome are given as superscripts.

Code	Species	Family	Life form	Strata	Leaf habit	Sexual system	Poll. synd.	Disp. synd.
AC	*Actinodaphne gullavara* (Buch.-Ham. ex Nees) M.R.Almeida	Lauraceae	T	C	E	D	ME[6]	EN[26]
AH	*Artocarpus heterophyllus* Lam.	Moraceae	T	S	E	M	PH[6]	EC[26]
AL	*Aglaia lawii* (Wight) C.J.Saldanha	Meliaceae	T	S	E	P	DI[3]	EC[26]
AM	*Embelia basaal* (Roem. & Schult.) A.DC.	Primulaceae	S	S	D	P	DI	EN[26]
AR	*Atalantia racemosa* Wight ex Hook.	Rutaceae	T	S	E	H	PS[13]	EC[26]
BO	*Casearia tomentosa* Roxb.	Salicaceae	S	C	D	H	DI[3]	AT[26]
BR	*Bridelia retusa* (L.) A.Juss.	Phyllanthaceae	T	C	D	M	DI[12]	EN[26]
BV	*Maytenus rothiana* Lobr.-Callen	Celastraceae	S	U	E	H	DI[12]	AT[26]
CA	*Careya arborea* Roxb.	Lecythidaceae	T	C	D	H	ME[12]	EC[26]

Table S1 continued…

Code	Species	Family	Life form	Strata	Leaf habit	Sexual system	Poll. synd.	Disp. synd.
CB	*Carallia brachiata* (Lour.) Merr.	Rhizophoraceae	T	C	E	H	DI[20]	EC
CC	*Carissa carandas* L.	Apocynaceae	S	C	E	H	PS[3]	EN[26]
CD	*Psydrax dicoccos* Gaertn.	Rubiaceae	T	C	E	H	ME[6]	EN[26]
CE	*Celtis timorensis* Span.	Cannabaceae	T	S	D	M	AN/DI[28]	EN[26]
CG	*Cassine glauca* (Rottb.) Kuntze	Celastraceae	T	C	E	H	DI[12]	EN[26]
CH	*Macaranga peltata* (Roxb.) Müll.Arg.	Euphorbiaceae	T	C	E	D	DI[6]	EN[7]
CO	*Colebrookea oppositifolia* Sm.	Lamiaceae	S	C	D	D	AN/ME[15]	AT[26]
CP	*Murraya koenigii* (L.) Spreng.	Rutaceae	T	S	D	H	ME[2]	EN[26]
CS	*Catunaregam spinosa* (Thunb.) Tirveng.	Rubiaceae	T	C	D	H	ME[3]	EC[26]
CT	*Callicarpa tomentosa* (L.) L.	Lamiaceae	T	S	E	H	PS[6]	EN[26]
DA	*Woodfordia fruticosa* (L.) Kurz	Lythraceae	S	C	D	H	ME[21]	AT[26]
DB2	*Dysoxylum gotadhora* (Buch.-Ham.) Mabb.	Meliaceae	T	S	E	H	DI[10]	AT[26]
DH	*Grewia tiliifolia* Vahl	Malvaceae	T	C	D	H	ME[12]	EN[26]
DL	*Dimorphocalyx glabellus* var. *lawianus* (Hook.f.) Chakrab. & N.P.Balakr.	Euphorbiaceae	T	S	E	M	DI[20]	AT[26]
DM	*Diospyros montana* Roxb.	Ebenaceae	T	C	D	D	ME[12]	EC[26]
DS	*Diospyros sylvatica* Roxb.	Ebenaceae	T	C	E	D	CA[6]	EC[26]
EC	*Elaeagnus conferta* Roxb.	Elaeagnaceae	L	C	E	H	ME/PS[11]	EC[26]

Table S1 continued…

Code	Species	Family	Life form	Strata	Leaf habit	Sexual system	Poll. synd.	Disp. synd.
ER	*Embelia ribes* Burm.f.	Primulaceae	L	S	E	D	DI[5]	EN[26]
FI	*Flacourtia indica* (Burm.f.) Merr.	Salicaceae	T	S	D	D	ME[1]	EN[26]
FN	*Ficus nervosa* B.Heyne ex Roth	Moraceae	T	C	E	M	WA[22]	EC[26]
FR	*Ficus racemosa* L.	Moraceae	T	C	D	M	WA[22]	EC[26]
FT	*Ficus tsjahela* Burm. f.	Moraceae	T	C	D	M	WA[22]	EC[26]
GH	*Glochidion hohenackeri* (Müll.Arg.) Bedd.	Phyllanthaceae	S	S	E	M	DI[11]	AT[26]
GI	*Garcinia indica* (Thouars) Choisy	Clusiaceae	T	C	E	P	CA[6]	EC[26]
GT	*Smilax ovalifolia* Roxb. ex D.Don	Smilacaceae	L	C	D	D	DI[3]	EN[26]
GU	*Gnetum ula* Brongn.	Gnetaceae	L	C	E	D	DI[20]	EC[26]
HA	*Ancistrocladus heyneanus* Wall. ex J.Graham	Ancistrocladaceae	L	S	E	H	ME/PS	AN[26]
HF	*Heterophragma quadriloculare* (Roxb.) K.Schum.	Bignoniaceae	T	C	D	H	ME[24]	AN[26]
JM	*Jasminum malabaricum* Wight	Oleaceae	L	C	E	H	PS[3]	EN[26]
KA	*Strobilanthes callosa* Nees	Acanthaceae	S	C	D	H	ME/PS[13]	AT[26]
KH	*Zanthoxylum rhetsa* DC.	Rutaceae	T	C	D	P	ME[1]	EC[23]
KU	*Sterculia guttata* Roxb. ex G.Don	Sterculiaceae	T	C	D	M	CA[3]	AT[26]
LE	*Gnidia glauca* (Fresen.) Gilg	Rutaceae	T	C	D	H	CA[24]	AN[26]
LI	*Leea indica* (Burm. f.) Merr.	Vitaceae	S	S	E	H	ME[8]	EN[26]
LP	*Lagerstroemia parviflora* Roxb.	Lythraceae	T	C	D	H	ME[12]	AN[26]

Table S1 continued…

Code	Species	Family	Life form	Strata	Leaf habit	Sexual system	Poll. synd.	Disp. synd.
LS	*Litsea josephi* S.M.Almeida	Lauraceae	T	C	E	D	DI[11]	EN[26]
LT	*Lepisanthes tetraphylla* Radlk.	Sapindaceae	T	S	E	M	ME/PS[14]	AT[26]
MC	*Caesalpinia cucullata* Roxb.	Leguminosae	L	C	E	H	ME	AT[26]
MD	*Myristica dactyloides* Gaertn.	Myristicaceae	T	C	E	D	PH[6]	EC[26]
MI	*Mangifera indica* L.	Anacardiaceae	T	C	E	P	MY[25]	EC[26]
MP	*Mallotus philippensis* (Lam.) Müll.Arg.	Euphorbiaceae	T	C	E	D	AN/DI[13]	AT[26]
MU	*Memecylon umbellatum* Burm. f.	Melastomataceae	T	C	E	H	ME[14]	EN[26]
NA	*Diploclisia glaucescens* (Blume) Diels	Menispermaceae	L	C	E	D	ME[27]	EC[26]
OD	*Olea dioica* Roxb.	Oleaceae	T	C	E	P	MY[11]	EN[26]
PA	*Heynea trijuga* Roxb. ex Sims	Meliaceae	T	S	E	H	DI	EN[7]
PC	*Premna coriacea* C.B.Clarke	Lamiaceae	L	C	D	H	ME[12]	EN[4]
PH	*Garcinia talbotii* Raizada ex Santapau	Clusiaceae	T	S	E	D	DI	EC[26]
PI	*Pavetta indica* L.	Rubiaceae	S	U	D	H	PS[17]	EN[26]
PP	*Piper trichostachyon* (Miq.) C. DC.	Piperaceae	L	S	E	D	DI	
PS	*Ixora nigricans* R.Br. ex Wight & Arn.	Rubiaceae	S	U	D	H	PS[11]	EN[7]
PY	*Oxyceros rugulosus* (Thwaites) Tirveng.	Rubiaceae	L	C	E	H	ME/PS	EN[19]
RS	*Rourea minor* (Gaertn.) Alston	Connaraceae	L	C	E		ME[28]	EN[26]
SA	*Terminalia tomentosa* Wight & Arn.	Combretaceae	T	C	D	H	ME[18]	AN[26]

Table S1 continued…

Code	Species	Family	Life form	Strata	Leaf habit	Sexual system	Poll. synd.	Disp. synd.
SB	*Symplocos beddomei* C.B.Clarke	Symplocaceae	T	C	E	H	CA[11]	EN[26]
SC	*Syzygium cumini* (L.) Skeels	Myrtaceae	T	C	E	H	AN/ME[12]	EC[26]
SG	*Syzygium gardneri* Thwaites	Myrtaceae	T	C	E	H	DI[6]	EC[26]
SH	*Acacia concinna* (Willd.) DC.	Leguminosae	T	S	D	H	ME/PS[16]	AT[26]
TA	*Mallotus resinosus* (Blanco) Merr.	Euphorbiaceae	S	U	E	H	DI	EC[7]
TB	*Terminalia bellirica* (Gaertn.) Roxb.	Combretaceae	T	C	D	H	ME[12]	EC[26]
TC	*Terminalia chebula* Retz.	Combretaceae	T	C	D	H	ME[12]	EC[26]
TH	*Ziziphus rugosa* Lam.	Rhamnaceae	L	C	D	H	ME[12]	EN[26]
TP	*Allophylus cobbe* (L.) Raeusch.	Sapindaceae	S	S	D	P	ME/PS	EN[26]
VB	*Ventilago bombaiensis* Dalzell	Rhamnaceae	L	C	E	H	DI	AT[26]
VI	*Pittosporum wightii* A.K.Mukh.	Pittosporaceae	T	S	E	H	DI[11]	EN
VS	*Meyna spinosa* Roxb. ex Link	Rubiaceae	T	C	D	H	DI[9]	EC
XT	*Xantolis tomentosa* (Roxb.) Raf.	Sapotaceae	T	C	E	H	ME	EC[26]

Abbreviations: Life form: T = Tree, L = Liana, and S = Shrub; Strata: C = Canopy, S = Sub-canopy, and U = Understory; Leaf habit: E = Evergreen, and D = Deciduous; Sexual system: H = Hermaphrodite, M = Monoecious, P = Polygamous, and D = Dioecious; Poll. Synd. stand pollination syndrome: ME = Melittophily (Bee), PS = Psychophily (Butterfly), PH = Phalaenophily (Moth), CA = Cantharophily (Beetle), MY = Myophily (Fly), DI = Diverse insects, ME/PS = Bee/Psychophily, AN/ME = Anemophily/Melittophily, and AN/DI = Anemophily/Diverse insects; Disp. synd. stand for dispersal syndrome: EN = Endozoochorous, EC = Ectozoochorous, AT = Autochorous, and AN = Anemochorous species.

Table S2: Differences in the supplementary phenology parameters between the life forms – trees, shrubs, and lianas, across the four phenophases. Each phase shows the F-statistics and the significance values (p) for one-way ANOVA between the groups.

Parameters	**Flushing**		**Senescing**		**Flowering**		**Fruiting**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Duration	**6.92**	<0.01	2.08	0.13	1.13	0.33	1.45	0.24
Frequency	0.50	0.61	0.15	0.86	**4.30**	0.02	2.76	0.07
Synchrony	1.15	0.32	1.74	0.18	0.87	0.43	1.22	0.30
Intensity	1.34	0.27	1.25	0.29	**4.38**	0.02	0.41	0.67
Interannual variation	0.15	0.86	0.15	0.86	2.53	0.09	1.03	0.36

Table S3: Differences in the supplementary phenology parameters across the four phenophases between the species belonging to different canopy strata – canopy, sub-canopy, and understory. Each phase shows the F-statistics and the significance values (p) for one-way ANOVA between the groups.

Parameter	**Flushing**		**Senescing**		**Flowering**		**Fruiting**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Duration	0.39	0.53	0.30	0.58	0.26	0.61	0.01	0.93
Frequency	0.54	0.47	0.17	0.68	0.09	0.76	0.62	0.43
Synchrony	3.42	0.07	1.60	0.21	**6.24**	0.02	0.65	0.42
Intensity	1.86	0.18	2.91	0.09	1.26	0.27	0.15	0.70
Interannual variation	1.53	0.22	0.35	0.55	1.79	0.19	0.17	0.68

Table S4: Differences in the supplementary flowering phenology parameters between groups of different plant sexual systems – hermaphrodite, monoecious, polygamous, and dioecious species. It shows the F-statistics and the significance values (p) for one-way ANOVA between the groups.

Parameters	**F**	**p**
Duration	**3.03**	0.04
Frequency	2.52	0.07
Synchrony	0.40	0.75
Intensity	1.36	0.26
Interannual variation	0.41	0.75

Table S5: Differences in the timing and duration of flowering between males and females of dioecious species. The first column is the species code (for details refer to supplementary table S1). The next two columns indicate the mean angular concentration of flowering, as the day of the year ± standard deviation (in days) for the males and the females of each species. The fifth and the sixth column similarly indicate the mean duration of flowering, as the number of days ± standard error (in days) for the males and the females of each species. The two p-value columns indicate the significance level of the difference between the males and females for the corresponding parameters. 'NS' stands for non-significant, * and ** represents $p < 0.05$ and $p < 0.01$, respectively.

Species	**Timing**		**p**	**Duration**		**p**
	Male	**Female**		**Male**	**Female**	
AC	354 ± 12	13 ± 13	NS	45 ± 2	37 ± 2	**
CH	55 ± 16	61 ± 17	*	61 ± 3	35 ± 1	**
CO	43 ± 12	47 ± 8	NS	43 ± 4	38 ± 2	NS
DM	79 ± 13	76 ± 8	NS	32 ± 1	31 ± 0	NS
DS	74 ± 17	78 ± 10	NS	33 ± 2	31 ± 0	NS
ER	318 ± 43	321 ± 41	NS	30 ± 0	30 ± 0	NS
FI	114 ± 55	105 ± 47	NS	36 ± 3	37 ± 3	NS
GT	342 ± 14	340 ± 13	NS	38 ± 4	32 ± 1	NS
GU	63 ± 14	59 ± 14	NS	43 ± 2	39 ± 2	NS
LS	299 ± 13	307 ± 15	NS	37 ± 4	34 ± 3	NS
MP	340 ± 16	343 ± 15	NS	48 ± 5	36 ± 2	**
NA	89 ± 14	82 ± 12	NS	33 ± 2	35 ± 3	NS
PH	31 ± 23	29 ± 22	NS	49 ± 3	38 ± 2	**

Table S6: Differences in the supplementary phenology parameters of fruiting between groups of different dispersal syndromes – endozoochory, ectozoochory, autochory, and anemochory. It shows the F-statistics and the significance values (p) for one-way ANOVA between the groups.

Parameters	**F**	**p**
Duration	0.77	0.52
Frequency	1.67	0.18
Synchrony	**3.12**	0.03
Intensity	0.33	0.81
Interannual variation	1.03	0.39

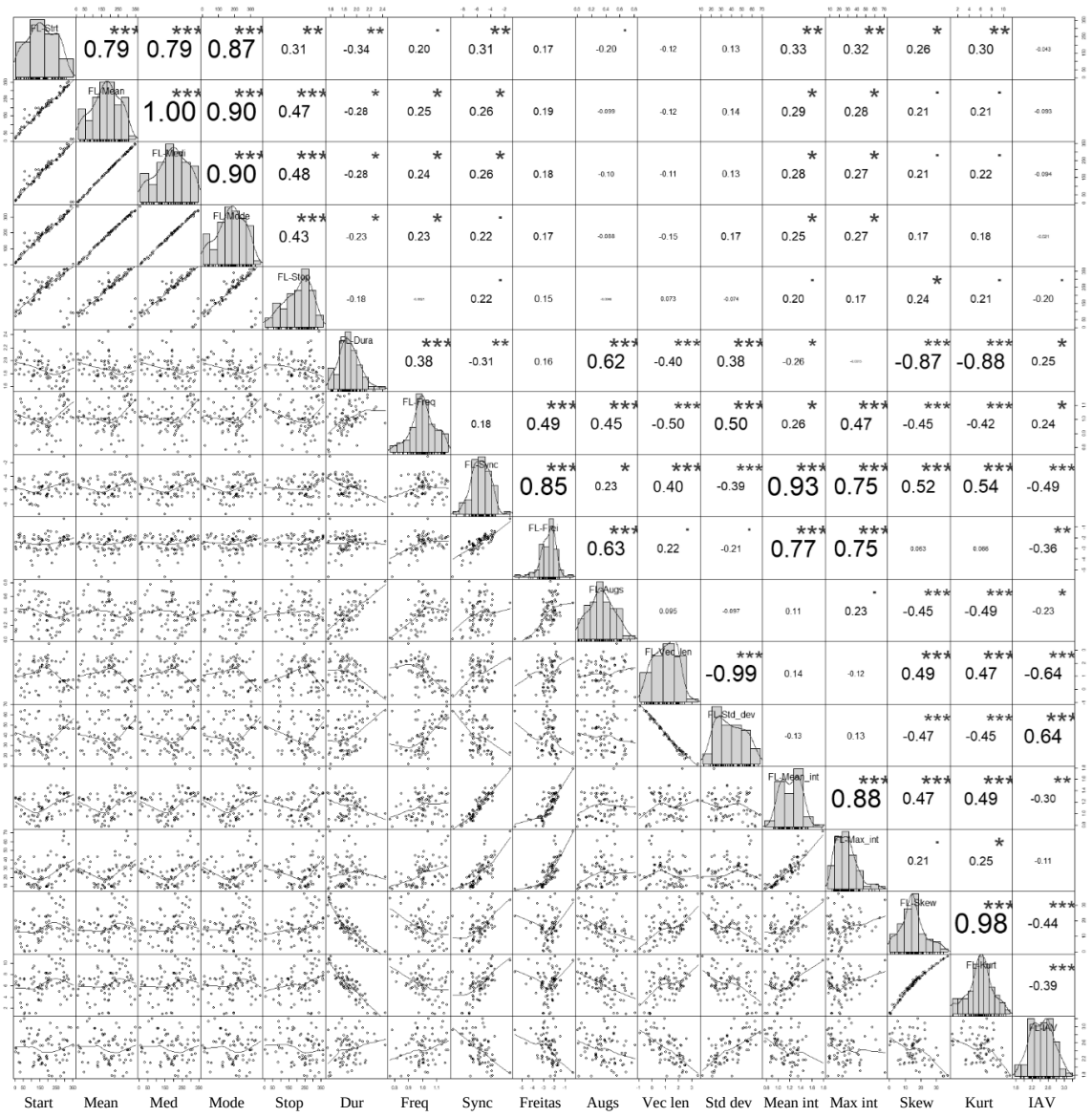


Figure S1: Relationships between the flushing phenology parameters. The rows represent the following parameters in sequence: phenophase start timing, mean timing, median timing, mode timing, stop timing, duration, frequency, current synchrony index, Freitas index, Augspurger index, vector length (r) from circular statistics, circular standard deviation, mean intensity, maximum intensity, skewness, kurtosis, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1

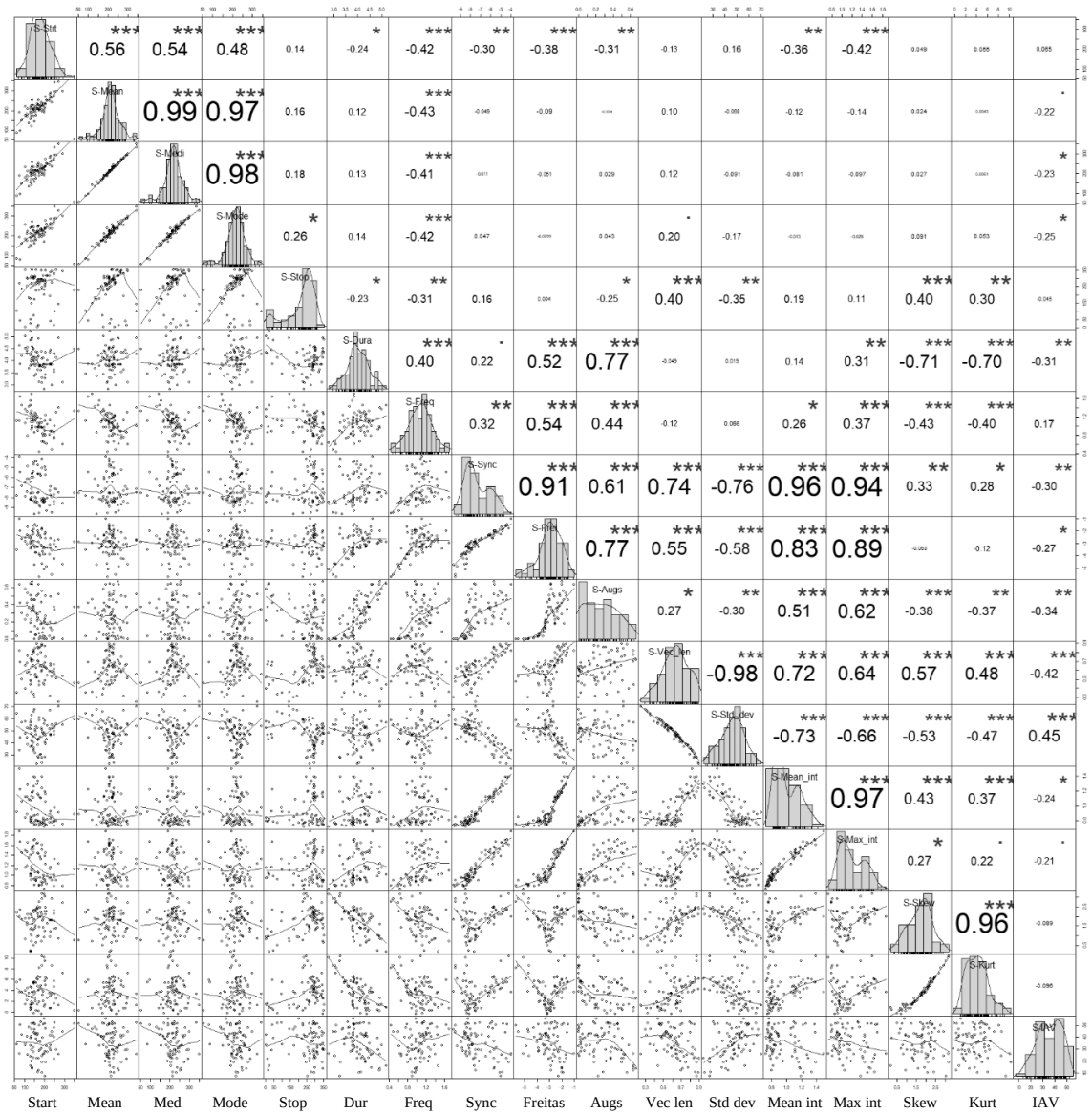


Figure S2: Relationships between the senescing phenology parameters. The rows represent the following parameters in sequence: phenophase start timing, mean timing, median timing, mode timing, stop timing, duration, frequency, current synchrony index, Freitas index, Augspurger index, vector length (r) from circular statistics, circular standard deviation, mean intensity, maximum intensity, skewness, kurtosis, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1

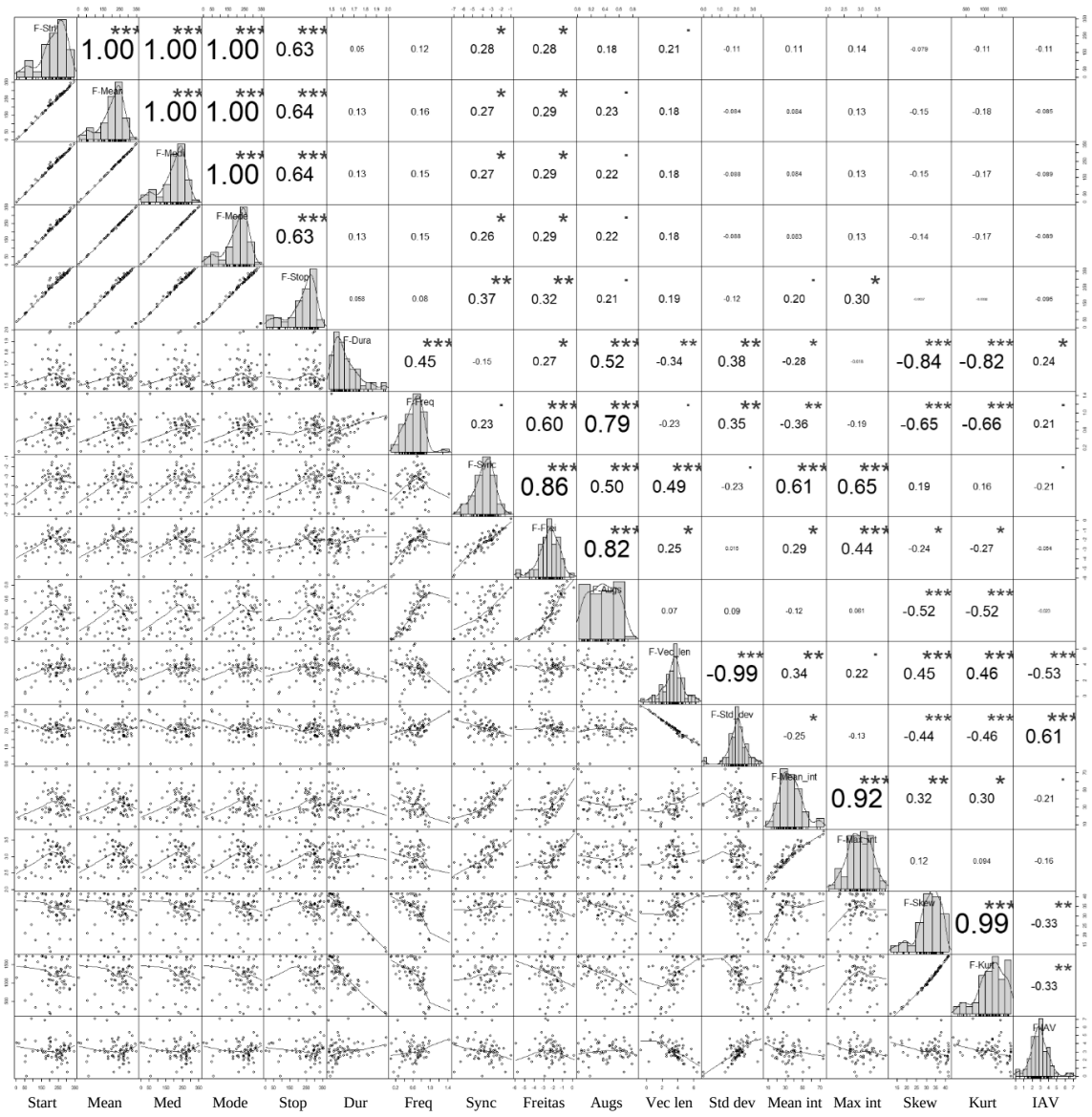


Figure S3: Relationships between the flowering phenology parameters. The rows represent the following parameters in sequence: phenophase start timing, mean timing, median timing, mode timing, stop timing, duration, frequency, current synchrony index, Freitas index, Augspurger index, vector length (r) from circular statistics, circular standard deviation, mean intensity, maximum intensity, skewness, kurtosis, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1

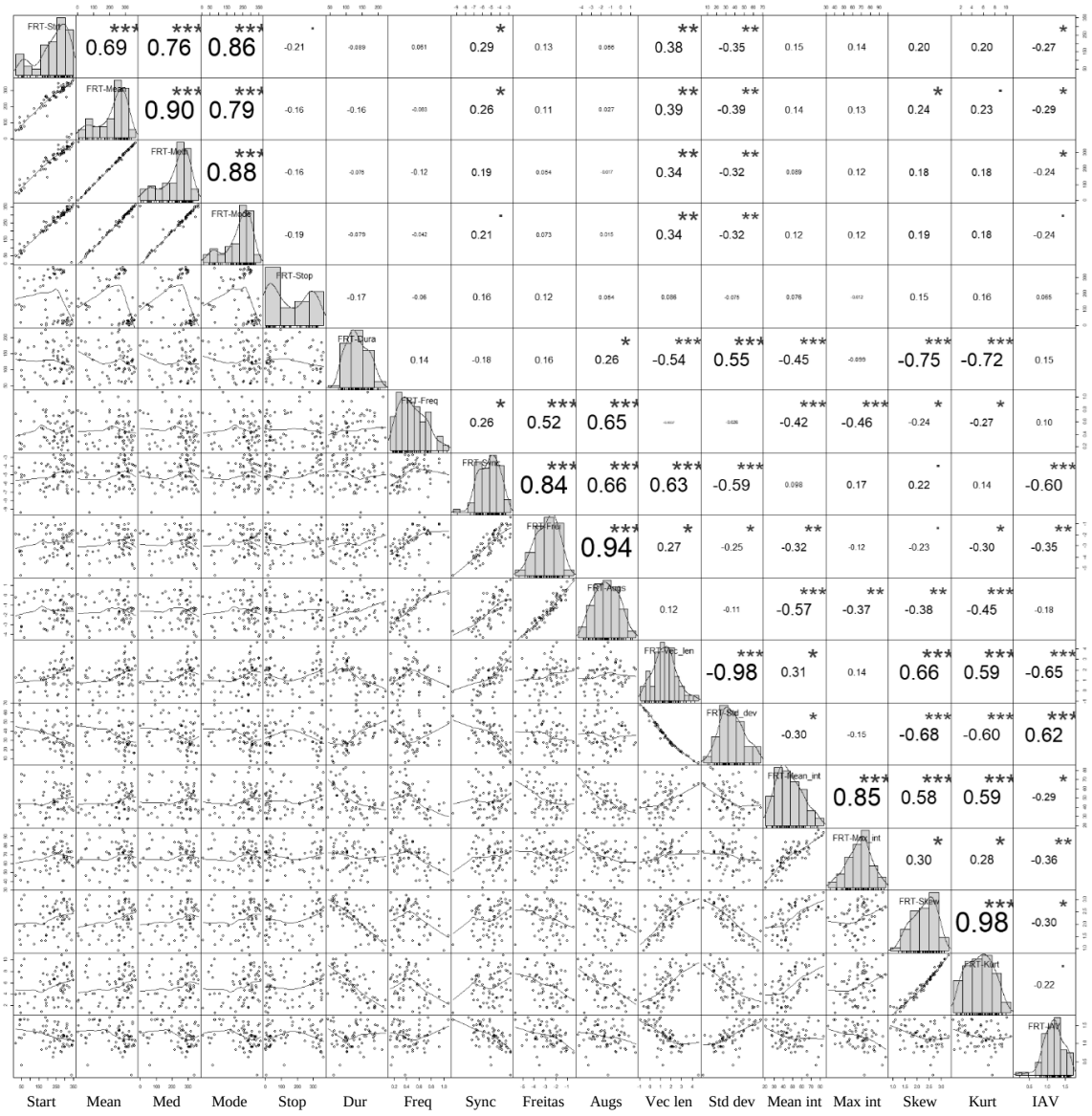


Figure S4: Relationships between the fruiting phenology parameters. The rows represent the following parameters in sequence: phenophase start timing, mean timing, median timing, mode timing, stop timing, duration, frequency, current synchrony index, Freitas index, Augspurger index, vector length (r) from circular statistics, circular standard deviation, mean intensity, maximum intensity, skewness, kurtosis, and interannual variation. The histogram in the diagonal represents the frequency distribution of each parameter. The bivariate scatter plots along with the fitted line are displayed on the bottom of the diagonal. The values are Pearson's correlation between each set of parameters and the significance level as stars are on the top of the diagonal. Each significance level is associated to a symbol: *** = 0.001, ** = 0.01, * = 0.05, and . = 0.1

Appendix References

1. Balachandran, C., Chandran, M.D.S. & Ramachandra, T.V. (2014) Keystone food resources for honey bees in South Indian west coast during monsoon. *Current Science,* **106,** 1379-1386.
2. Bhatnagar, S., Rathore, L., Vishnoi, G., Khan, A. & Kumar, B. (2018) Record of insect pollinators on the inflorescence of Murraya koenigii in Rajasthan. *Journal of Agriculture Ecology,* **5,** 38-41.
3. Corlett, R. (2004) Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biological Reviews,* **79,** 497-532.
4. David, J.P., Manakadan, R. & Ganesh, T. (2015) Frugivory and seed dispersal by birds and mammals in the coastal tropical dry evergreen forests of southern India: A review. *Tropical Ecology,* **56,** 41-55.
5. Deepthikumary, K.P. & Sreekala, A. (2019) Reproductive Biology of Embelia ribes: An Important Medicinal Plant of the Western Ghats. *International Journal of Science and Nature,* **10 (1),** 41-47.
6. Devy, M.S. & Davidar, P. (2003) Pollination systems of trees in Kakachi, a mid-elevation wet evergreen forest in Western Ghats, India. *American Journal of Botany,* **90,** 650-657.
7. Ganesh, T. & Davidar, P. (2001) Dispersal modes of tree species in the wet forests of southern Western Ghats. *Current Science,* **80,** 394-399.
8. Jain, A., Kunte, K. & Webb, E.L. (2016) Flower specialization of butterflies and impacts of non-native flower use in a transformed tropical landscape. *Biological Conservation,* **201,** 184-191.
9. Layek, U., Bhakat, R. & Karmakar, P. (2015) Foraging behavior of Apis florea fabricius during winter and spring-summer in Bankura and Paschim Medinipur districts, West Bengal. *Global Journal of Bio-science and Biotechnology,* **4,** 255-263.
10. Mohandass, D., Campbell, M.J., Chen, X.S. & Li, Q.J. (2018) Flowering and fruiting phenology of woody trees in the tropical-seasonal rainforest, Southwestern China. *Current Science,* **114,** 2313-2322.
11. Mohandass, D., Hughes, A.C. & Davidar, P. (2016) Flowering and fruiting patterns of woody species in the tropical montane evergreen forest of southern India. *Current Science,* **111,** 404-416.

12. Murali, K.S. & Sukumar, R. (1994) Reproductive Phenology of a Tropical Dry Forest in Mudumalai, Southern India. *Journal of Ecology*, **82,** 759-767.
13. Narmadha, N. & Varunprasath, K. (2018) Status of butterfly species in Pallassena village, Palakkad district, Kerala. *Journal of Entomology and Zoology Studies*, **6(3),** 320-329.
14. Nayak, K. & Davidar, P. (2010) Pollination and breeding systems of woody plant species in tropical dry evergreen forests, southern India. *Flora*, **205,** 745-753.
15. Quamar, M.F. & Bera, S.K. (2016) Pollen analysis of spider web samples from Korba District, Chhattisgarh (central India): an aerobiological aspect. *Aerobiologia*, **32,** 645-655.
16. Raju, A. & Rao, S.P. (2002) Reproductive Ecology of Acacia concinna (Shikakai) and Semecarpus Anacardium (Marking nut), with a note on pollinator conservation in the Eastern Ghats of Visakhapatnam district, Andhra pradesh. *Proceedings of the National Seminar on Conservation of Eastern Ghats, Tirupati, India*, pp. 22-24.
17. Raju, A.S., Rao, M.M., Ramana, K.V., Rao, C.P. & Sulakshana, M. (2016) Pollination ecology and fruiting behavior of Pavetta indica L.(Rubiaceae), a keystone shrub species in the southern Eastern Ghats forest, Andhra Pradesh, India. *Journal of Threatened Taxa*, **8,** 9155-9170.
18. Raju, A.S., Rao, S.P. & Kumari, P.K. (2003) The role of Apis florea in the pollination of some plant species in Andhra Pradesh, India. *Korean Journal of Apiculture*, **18,** 37-42.
19. Reddy, M.S. & Rao, B.R.P. (2007) Liana diversity in Eastern Ghats. *Proceedings of National Seminar on Conservation of Eastern Ghats-2007. Environment Protection Training and Research Institute, Hyderabad*, pp. 70-76.
20. Richard, P.S.S., Muthukumar, S.A. & Malleshappa, H. (2014) Melissopalynological studies from Kalakad-Mundanthurai Tiger Reserve (KMTR), southern western Ghats, India. *Indian Forester*, **140,** 1153-1159.
21. Saklani, S. & Mattu, V. (2017) Melissopalynological investigations on honey samples of Kangra hills, Himachal Pradesh, India. *International Journal of Entomology Research*, **2,** 41-51.
22. Satheesan, S.K. & Santhosh, S. (2019) Fig Pollinators (Hymenoptera: Agaonidae: Agaoninae) of India. *ENVIS Newsletter*, **25,** 26-27.

23. Sinu, P.A., Unni, A.P. & Jose, T. (2020) Biotic Seed Dispersal Mechanisms of Tropical Rain Forests–Bats, Fishes, and Migratory Birds. *Reproductive Ecology of Flowering Plants: Patterns and Processes*, pp. 299-334. Springer.
24. Somanathan, H., Borges, R.M. & Chakravarthy, V.S. (2004) Does Neighborhood floral display matter? Fruit set in carpenter bee-pollinated Heterophragma quadriloculare and beetle-pollinated Lasiosiphon eriocephalus. *Biotropica,* **36,** 139-147.
25. Sung, I.-H., Lin, M.-Y., Chang, C.-H., Cheng, A.-S., Chen, W.-S. & Ho, K.-K. (2006) Pollinators and their behaviors on mango flowers in southern Taiwan. *Formosan Entomol,* **26,** 161-170.
26. Tadwalkar, M.D., Joglekar, A.M., Mhaskar, M., Kanade, R.B., Chavan, B., Watve, A.V., Ganeshaiah, K.N. & Patwardhan, A.A. (2012) Dispersal modes of woody species from the northern Western Ghats, India. *Tropical Ecology*, **53,** 53-67.
27. Thomas, S.G., Rehel, S.M., Varghese, A., Davidar, P. & Potts, S.G. (2009) Social bees and food plant associations in the Nilgiri Biosphere Reserve, India. *Tropical Ecology,* **50,** 79-88.
28. van Dulmen, A. (2001) Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. *Plant Ecology*, **153,** 73-85.