Mass flowering and flowering asynchrony characterise a seasonal herbaceous community in the Western Ghats

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ABSTRACT

Seasonally flowering communities often exhibit higher flowering synchrony than what can be attributed due to environmental factors alone. In contrast, competition is known to favor asynchrony in flowering phenology. Here we analyse the flowering pattern of a seasonal, herbaceous community (Kaas plateau) in Western Ghats, India to identify environmental constraints that may facilitate flowering synchrony and we address the questions: (a) Is flowering seasonality correlated with environmental factors? (b) Is there evidence for flowering synchrony within the community? (c) Do plant-pollinator interactions shift with flowering phenology?

Flowering patterns were significantly influenced by environmental seasonality. We recorded flowering phenology of 76 herbaceous species and categorized them into mass flowering (MF) and non-mass flowering (nMF), based on flowering density. Two novel synchrony indices proposed here temporal overlap (SI_{temp}) and synchrony in abundance (SI_{abd}) both revealed low synchrony values for the community. We also noted an absence of synchrony among MF species and between MF - nMF species of the same floral colour group, thus suggesting that competition and not facilitation is shaping flowering asynchrony within this seasonally herbaceous community. Finally, we also noted sub-seasonal temporal shifts in pollination networks that matched flowering abundances within the community.

In this study we exhaustively characterised the flowering phenology of plants from a laterite plateau in the Western Ghats. We show that despite seasonality, both mass flowering and flowering asynchrony emerged as the defining characteristics of this habitat. We therefore propose that establishing flowering synchrony is a critical first step towards assessing competition for pollinators within the community.

KEYWORDS

community structure, Kaas plateau, laterite plateau, native bees, plant-pollinator networks, sky island, synchrony index, tropical community

1. INTRODUCTION

Flowering phenology—the timing and pattern of flower production—plays a pivotal role in the reproductive success of plants. Among individuals of the same species, selection often favours synchrony in flowering to maximize pollinator attraction (Gentry, 1974; Bawa et al., 1985; Rathcke and Lacey, 1985; Kudo, 2006; Elzinga et al., 2007) and facilitate cross-pollination while minimizing heterospecific pollen transfer (HPT; Ashton, 1969; Augspurger, 1983; Ashton et al., 1988; Sakai et al., 1999). However, at the community level, flowering patterns may be shaped by contrasting evolutionary pressures. For instance, flowering synchrony among co-occurring species may emerge due to common environmental triggers (e.g., seasonal rainfall) or adaptive strategies that amplify floral displays, thereby enhancing pollinator attraction through facilitation (Parrish and Bazzaz, 1979; Ims, 1990; Sakai et al., 1999; Nagahama and Yahara, 2019). On the contrary, asynchrony (or staggered flowering) may be favored since it reduces competition for pollinators, particularly in communities with high niche overlap (Schemske, 1981; Aizen and Vázquez, 2006; Lasky et al., 2016). While synchrony is often expected in communities with strong climatic seasonality, the interplay between these opposing forces—facilitation versus competition—is critical in order to understand and predict phenological patterns that shape plant communities.

Mass flowering (MF) is an extreme example of synchronous flowering. Historically, the term

'mass flowering' has been applied to describe an event of high flowering density both within a species (Baker, 1959; Augspurger, 1983; Gentry, 1974) and within a community (Ashton et al., 1988; Appanah, 1993; see Box 1). Here, we define 'mass flowering' as a species-specific event, where simultaneous flowering of multiple individuals of a species, over a wide area results in a high flowering density within the landscape. This definition aligns with the previous definitions by Baker (1959), Augspurger (1983) and Gentry (1974; Box 1), while distinguishing mass flowering from other high-density flowering events in a landscape that could arise from the synchronous flowering of multiple sympatric species (Box 1).

Another important but understudied pattern in communities exhibiting synchronous flowering is the convergence of floral traits, particularly in floral colour. When species with similar floral hues synchronise their flowering, their visual signals to pollinators can be amplified. For instance, MF species may facilitate pollination in non-mass flowering (nMF; low flowering density) species through trait matching—a premise formalised in the pollinator-mediated facilitation hypothesis (Bergamo et al., 2020). Thus, in a community with a few MF species, nMF species may benefit by co-flowering with MF species and therefore a higher synchrony may be expected between MF and nMF species resulting in a co-ordinated, amplified floral display (Tepedino and Stanton, 1981; Augspurger, 1983; Gumbert et al., 1999; Sakai, 2002; Bergamo et al., 2020). We checked if floral colour-mediated synchrony between MF and nMF species may be present within our study site, and we predicted that co-flowering species with shared floral colours may show higher flowering synchrony to optimise pollinator attraction. High-altitude laterite plateaus ('sky islands') of the Western Ghats, India, provide an ideal model to explore these dynamics. These seasonal ecosystems host a unique herbaceous flora with exceptional endemism (Lekhak and Yadav, 2012) and conspicuous mass-flowering events

(Figure 1). The short, intense monsoon imposes stringent environmental filters, potentially synchronizing flowering across species (Lasky et al., 2016). However, the coexistence of MF and nMF species raises questions about how competition and facilitation interact under such constraints. We investigated the flowering phenology of 76 herbaceous species (~90% of the plateau's flora) over three years and addressed the following questions:

(a) To what extent do climatic factors explain community-wide flowering seasonality?

(b) Do MF species synchronize with each other and with nMF species, and are there patterns of floral synchrony by floral color?

(c) How do plant-pollinator networks shift temporally in response to flowering phenology?

2. METHODS

2.1. Study area: geography and climate

We conducted all phenological and pollinator observation studies at Kaas plateau (कास पठार, 17°43'12.4" N, 73°49'28.1" E; Figure 1a) between 2018 and 2020. Kaas is a high-altitude lateritic plateau situated at 1250 m a.s.l. in the Northern Western Ghats, India (Lekhak and Yadav, 2012). We identify these plateaus as 'sky islands' owing to their prominent cliff edges, steep slopes, and isolated biotic communities separated by surrounding valleys (Figure 1b). Sky islands of the Western Ghats are characterised by rocky outcrops with minimal soil substrate (Watve, 2013). They experience extreme environmental conditions such as a prolonged dry season lasting seven months from November to May, followed by a wet season from June to October, which marks the Indian monsoon. Hence, these plateaus primarily support herbaceous plant species, many of which are endemic and exhibit flowering during the monsoonal or post-monsoonal period

(Figure S1).

2.2. Flowering phenology

We conducted periodic flowering censuses between August to November at 15-day intervals in 2018 and 10-day intervals in 2019 and 2020 using seven transects (20 x 2 m^2; Figure 1a). We quantified the flowering abundance of all herbaceous taxa by counting the total number of flowering individuals present within the transect. In this study, we established a classification metric for the Kaas landscape, identifying a species as mass flowering (MF) if its flowering density exceeded ~560 individuals across our total sampled area of 280 m^2 per census (unit time). This translates to ≥ 2 flowering individuals per m^2 per census, which we define as a mass flowering species (MF) or a species with 'high flower density' in our study community (Box 1). Species that did not meet this threshold were classified as non-mass flowering (nMF or species with 'low flower density'; Table S1). This metric recognizes mass flowering as a high flower density event, irrespective of whether it occurs in a temporally short, or long flowering period [Gentry's type 3 and 4 (1974)].

To test whether species may be synchronised by their floral colour, we categorised all recorded species into three groups based on their floral spectral reflectance (Figure S2). However, these groups are named after the colours perceived by human vision, such as Whites (WH), Pinks and Purples (PK-PL), and Yellows (YL). Although we did not perform spectral analyses for all the species, the three colour categories were defined using cumulative spectral data from a total of 13 species (Figure S2). The spectral reflectance values for Whites (WH) range from approximately 400 to 700 nm with high reflectance across the spectrum, Pinks and Purples (PK-PL) show distinct peaks in the 400-500 nm and 600-700 nm ranges, and Yellows (YL) exhibit

high reflectance in the 500-600 nm range (Figure S2).

2.3. Environmental parameters

Due to the absence of local weather stations within 100 km of the study site, environmental data were retrieved from the NASA POWER database (https://power.larc.nasa.gov) for January 2018–December 2020 with ½° latitude, ⅝° longitude resolution. We obtained daily variations in five environmental parameters: Rainfall (mm), maximum (T_{max}), minimum (T_{min}) and average (T_{avg}) temperature at two metres (°C), relative humidity at two metres (%), and surface soil wetness (proportion). To account for delayed climatic effects on flowering phenology, we employed Generalized Additive Models for Location, Scale, and Shape (GAMLSS; Rigby and Stasinopoulos, 2005) with cubic spline smoothing and forward stepwise selection (GAIC criterion). Each model assumed a Negative Binomial Type I (NBI) distribution to accommodate overdispersed floral count data with excess zeros and the RS algorithm (Stasinopoulos and Rigby, 2008) was used to obtain the estimates of the environmental predictors.

Five separate models were constructed to evaluate the independent effects of rainfall, maximum/minimum temperatures, average temperature, relative humidity, and soil wetness. Lagged environmental predictors (optimum lags were determined via cross-correlation analysis) were incorporated to assess delayed impacts. To mitigate multicollinearity among parameters, each climatic variable was analyzed independently. Environmental data were temporally aligned with floral census intervals (10-day resolution) prior to analysis. All analyses were conducted in R v4.4.1 (R core team, 2022).

2.4. Flowering synchrony

We quantified flowering synchrony using the phenological data collected in 2020. Due to limitations of previously proposed synchrony indices (Box 1), we propose two new synchrony indices to measure temporal synchrony (i.e., flowering overlap) and synchrony in abundance (synchrony of flowering intensity) between two species (see Box 1 for a detailed explanation). Synchrony in flowering time (SI_{temp}), that we modified from Primack (1980) to quantify flowering synchrony among species and defined as the ratio of the flowering overlap between species1 and species2 to the total flowering duration of the two species (Box 1). This is calculated as

$$SI_{temp} = \frac{F_o}{(F_1 + F_2) - F_o} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1$$

where, F_1 and F_2 represent the total flowering duration (number of days in flowering) for species1 and species2, respectively, and F_o represents the temporal overlap (number of days when two species co-flower) in flowering. SI_{temp} ranges from 0 to 1, where zero represents no temporal overlap, while 1 represents a complete overlap of flowering duration between two species (i.e., when $F_o = F_1 = F_2$; Box 1). We quantified SI_{temp} between all species-pairs recorded in the phenology census.

Whenever $F_o \neq 0$, i.e., $SI_{temp} > 0$ for a species-pair, we calculated the synchrony in flowering abundance (SI_{abd}) between them. This metric provides an index for the relative flowering abundances of two co-flowering species. In this study, flowering abundance is calculated as the number of individuals in flowering phenophase in the observed area, however this index is free of this definition. SI_{abd} is calculated as the sum of the proportions, where each proportion is the

abundance of the less abundant species divided by the abundance of the more abundant species at any given census. This sum is then averaged across all census readings where both species were recorded (n; Box 1). SI_{abd} is calculated as

$$SI_{abd} = \frac{\sum_{i=1}^{n} \frac{abundance\ of\ species\ x}{abundance\ of\ species\ y}}{n} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ 2$$

The value of SI_{abd} also ranges from 0 to 1, where one represents an equal flowering abundance of the two species when they co-flower. Synchrony values below 0.4 were considered asynchronous, while values above 0.6 were considered synchronous, and values between 0.4 and 0.6 were characterised as intermediate. These ranges were also verified against one published study (Oleques et al., 2017) where the entire dataset was available in the appropriate format. We analysed flowering synchrony: (a) among all species in the community, using data from 2018, 2019, and 2020; (b) among MF and nMF species pairs; (c) among three floral colour groups (WH, PK-PL, and YL); and (d) between nMF and MF species of each floral colour group. Analyses (b), (c), and (d) were restricted to the 2020 dataset, which provided a comprehensive phenological census covering the entire flowering season (May to November). In contrast, the datasets from 2018 and 2019 included only partial flowering phenology (August to November). The species *Eriocaulon sedgwickii* (Eriocaulaceae) was excluded from synchrony-analysis due to its consistently high flowering abundance throughout the season, which resulted in a prominent outlier effect. Synchrony indices were calculated and analysed using R v4.4.1 (R core team, 2021).

2.5. Plant-pollinator network

To capture temporal shifts in plant-pollinator interactions during the flowering season, we

conducted manual pollinator observations on a total of 46 flowering species (~ 52% of total species recorded in the phenology transects) between August 2018 and October 2019. Observations were carried out between 0600 hrs to 1600 hrs using a total of 339 observation slots of 10–20-minutes. A floral visitor was identified as a pollinator only when it came in contact with the reproductive structures of the flower. During each observation slot, we recorded the taxonomic identity of the visiting pollinator type, the total number of visits in a single visitation bout, and the number of flowers in the observation plot. To characterise broad plant-pollinator patterns within the community we grouped pollinators into seven categories: bees, flies, beetles, butterflies, wasps, moths, and ants.

We divided the flowering season into three sub-seasons based on floral abundance and diversity: (a) pre-peak (August to mid-September) with low abundance and diversity, (b) peak (mid-September to early October) with the highest abundance and diversity, and (c) post-peak (mid-October to November) with moderate to low abundance and diversity. We then calculated pollinator visitation rates (number of visits per flower per hour) for every plant-pollinator pair within each sub-season. These rates were used to construct interaction matrices, with plant species as rows (lower trophic level) and pollinators as columns (higher trophic level). We constructed three sub-seasonal networks using the *bipartite* package (Dormann et al., 2009) in R (version 4.4.1) and created a single cumulative network for the entire flowering season to understand the landscape-wide nature of plant-pollinator interactions. For all networks, we calculated the following indices: links per species (LPS), Shannon's diversity index (H'), degree of specialisation (H_2'), and network modularity. We also computed the mean number of shared partners and niche overlap among plant species, as well as species strength and specialisation index (d') for pollinator types. Finally, we tested the significance of the network indices by

comparing the observed network values to a null model (Vázquez and Aizen, 2003) using 10,000 iterations with a 95% confidence interval.

3. RESULTS

3.1. Environmental seasonality and effect of environmental factors

Based on climatic and environmental seasonality, we identified three distinct seasons: cold-dry (November to February), hot-dry (March to May), and the wet season (June to October, which coincides with the Indian monsoon; Figure 2a). During the three-year study period (2018 to 2020), daily temperatures fluctuated from 9.4 to 38.7 °C in the cold-dry season and 14 to 44 °C in the hot-dry season. Temperature fluctuations were lowest during the wet season (ranging from 14.6 to 32.8 °C), compared to other seasons. Peak rainfall was recorded in July and August, with an average annual precipitation of ~ 2500 mm (Figure 2a). GAMLSS analysis showed that rainfall, temperature, humidity and soil wetness are significant climatic predictors of flowering phenology (Table 1; Table S1):

(a) Rainfall (model 1): Immediate precipitation positively influenced flowering ($\beta = 0.0082$, $p = 0.002$), while a 170-day lag showed strong negative effects ($\beta = -0.1324$, $p < 0.0001$).

(b) Temperature (model 2 and 3): T_{max} had a negative effect on flowering ($\beta = -1.0636$, $p < 0.0001$), whereas T_{min} had a positive effect ($\beta = 1.9474$, $p < 0.001$). T_{avg} showed a negative effect ($\beta = -0.9975$, $p = 0.0035$), with no lagged associations.

(c) Humidity (model 4): Relative humidity had a positive effect on flowering ($\beta = 0.1756$, $p = 0.0076$), with no lagged associations.

(d) Surface soil Wetness (model 5): Immediate soil moisture strongly promoted flowering ($\beta = 34.722$, $p < 0.0001$), contrasting with a negative effect of soil moisture at 20-day lag (β

= -21.497, $p < 0.0001$).

3.2. Flowering Phenology

Over three years, we recorded 76 angiosperm taxa on the Kaas plateau, encompassing 57 genera and 31 families (taxonomic details in Table S1). Although 33 taxa exhibited flowering in all three study years, species richness fluctuated between years, with 53 species in flower in 2018, 43 species in 2019, and 59 species in 2020 (Figure 3; Table S1). The peak flowering abundance also varied across the three years, with the total flowering abundance in 2020 (~ 10,000 individuals per 280 m^2) being almost three times higher than in 2018 (~ 2000 individuals per 280 m^2; Figure 2b). The community displayed a *'few common, many rare'* pattern of species distribution in all study years (Figure S3). Based on the criteria of flowering density, that is ≥ 2 flowering individuals per m^2, we classified 58 species (76.32 %) as nMF and 18 species (23.68 %) as MF species (Figure 3). The number of MF species recorded each year was - two species in 2018, 12 species in 2019, and 14 species in 2020 (Figure 3; Table S1). The species richness of the three colour groups was as follows: Whites (WH = 20 species), Pinks and Purples (PK = 18, PL= 17), and Yellows (YL = 21). While the peak flowering abundance of the community was observed to be September across the three years (Figure 2b), the peak flowering times of different floral colour groups varied within a year. The WH group showed two separated flowering peaks in August and September, the flowering peak of PK and PL was in September, and the flowering peak of YL was in September and October (Figure S4).

3.3. Flowering synchrony

We found that in all three study years, flowering phenology of the herbaceous community was

asynchronous (i.e., SI < 0.4), both in time (SI_{temp} in 2018: 0.3456 ± 0.008; in 2019: 0.3262 ± 0.01; in 2020: 0.2396 ± 0.007) and abundance (SI_{abd} in 2018: 0.143 ± 0.004; in 2019: 0.124 ± 0.006; in 2020: 0.2371 ± 0.007; Figure 4; Table 2). This asynchrony was also found among both MF and nMF species (Figure 4; Table 2). However, MF species exhibited significantly higher synchrony values than nMF species for both SI_{temp} (Kruskal Wallis chi-squared = 29.271, d.f. = 1, $p < 0.0001$) and SI_{abd} (Kruskal Wallis chi-squared = 27.828, d.f. = 1, $p < 0.0001$). Synchrony values within the three floral colour groups were below 0.4, suggesting low synchrony (Table 2).

3.4. Structure and function of pollination networks

We recorded 90 unique plant-pollinator interactions over approximately ~ 101 hours of total observation time. Of the 46 flowering species observed, 33 species (71.73 %) received visits from pollinators (Table S3), while 13 species (28.26 %) received no visits. Among the pollinators, bees (24 links), beetles (20 links), and flies (18 links) were the most frequent visitors (Figure S5). Bees had the highest species strength (10.9), followed by beetles (7.8), flies (7.2), wasps (2.7), ants (2.5), butterflies (1.1), and moths (0.7; Table S3). As the flowering season progressed, the number of species observed increased from 15 in the pre-peak to 25 in the peak season and then decreased to 20 in the post-peak season (Figure 5). A similar trend was observed in the number of links per species (LPS), which increased from pre-peak (1.4) to peak (1.69), and then decreased in the post-peak (1.56) network (Table S3). This shift in plant-pollinator interactions was also evident in the Shannon diversity (H') values, which increased from 2.9 in the pre-peak to 3.66 in the peak network, followed by a decrease to 3.37 in the post-peak network.

Flies were the most frequent floral visitors in the pre-peak season, with 11 links (Figure 5), while

bees became the dominant visitors during the peak (20 links) and post-preak (13 links) seasons. This shift in pollinator relevance was captured by the increasing species strength of bees from pre-peak (3.31) to peak (5.56) and post-peak (7.79) seasons (Table S2). The degree of specialised interactions (H_2') was highest in the pre-peak (0.67) network, as compared to the peak (0.56) and post-peak networks (0.57). This trend was supported by higher niche overlap among plants in the peak season (0.43) compared to post-peak (0.40) and pre-peak (0.36), and a greater number of shared pollinators in the peak season (1.02) compared to post-peak (0.92) and pre-peak (0.81; Table S3).

In the cumulative network (Figure S5), we identified five modules based on the predominant interacting pollinator: bee, beetle, fly, ant-wasp, and butterfly-moth. The modularity score of 0.365 was significantly lower than those of the randomly generated null model networks ($p < 0.001$). Additionally, null model networks revealed that the observed degree of specialisation ($H_2' = 0.437$; $p < 0.0001$) was significantly lower than expected by chance. At the individual node level (d'), the degree of specialisation ranged from low to moderate, with bees showing the most generalised interactions (d' = 0.23) and ants exhibiting relatively more specialised interactions (d' = 0.51; Figure S5; Table S3).

4. DISCUSSION

Flowering synchrony between two species is a temporal event, but the ecological effects of this synchrony can be affected by flowering abundances (Marquis, 1988; Elzinga et al., 2007). To emphasise the role of both temporal overlap and abundance values, we separated these factors and introduced two separate indices in this study (Box 1). In this study, we also present SI_{temp} and SI_{abd} as two robust metrics that were able to capture the flowering synchrony and the strength

of this synchrony of a community.

This study is novel for its multi-year investigations where we characterised the flowering phenology of a sky island community from the Northern Western Ghats. We identified a very short flowering phenology on the Kaas plateau, which lasts only five months. Overall, we noted shifts in flowering phenology at Kaas to match yearly shifts in various environmental parameters. For instance, rainfall and soil wetness demonstrated lagged effects (170 and 20 days, respectively), while flowering was more immediately affected by the temperature and humidity, suggesting that the flowering phenology of the Kaas community is water-dependent.

Using the synchrony index proposed in this study, we segregated the Kaas plant community into MF species (high flower density) and nMF species (low flower density), although we failed to detect any synchrony within the MF species or the nMF species. We also did not detect any synchrony between nMF-MF species pairs that shared the same floral colour. Therefore, competition and asynchrony, and not facilitation by synchrony between similar coloured nMF and MF species seems to be a key phenological characteristic of the plant community on the Kaas plateau.

4.1. Seasonality in a Sky Island Community

Our multi-year flowering-phenology study of the Kaas plateau is a targeted novel effort to initiate characterisation of the unique sky island community from the Northern Western Ghats. We identified a very short flowering phenology on the Kaas plateau, which lasts only five months. The flowering season on Kaas showed pronounced environmental seasonality, marked by a long dry season (March to May) and subsequent intense Indian monsoon (June to October). Overall, we noted shifts in flowering phenology at Kaas to match yearly shifts in various

environmental parameters. For instance rainfall and soil wetness demonstrated lagged effects (170 and 20 days, respectively), while flowering was more immediately affected by the temperature and humidity, suggesting that the flowering phenology of the Kaas community is water-dependent.

Rainfall has also been reported to be critical in the flowering of herbaceous plants in arid and semi-arid landscapes like the tropical Cerrado (Neves et al., 2017), a few tropical seasonal communities (Reich & Borchert, 1984; Hamann, 2004; McLaren & McDonald, 2005; Wright and Calderón, 2006; Kushwaha and Singh, 2008; Stevenson et al., 2008; Lasky et al., 2016; Cortés-Flores et al., 2017), and the desert communities of Northern Oman (Ghazanfar, 1997). Although the Kaas plateau is not perceived as an arid landscape, we propose that the habitat is comparable to arid landscapes due to its strong environmental seasonality and dependence of herbaceous flowering on rainfall, relative humidity and surface soil wetness, as well as other geographic features such as rocky landscape with minimal soil layers.

We observed a three-fold increase in community-level flowering abundance between 2018 and 2020 shows that there is an inter-annual variation in flowering density and it is also suggestive of the presence of a supra-annual flowering pattern at Kaas Plateau, a phenomenon previously reported in some tropical systems (Medway, 1972; Frankie et al., 1974; Ashton et al., 1988; Sakai et al., 1999; Sakai, 2002). However, long-term monitoring (>20 years) is critical to confirm and characterise these patterns (Newstrom et al., 1994; Bawa et al., 2003). While supra-annual flowering has been prominently documented in Southeast Asian dipterocarp forests (Sakai et al., 1999; Sakai, 2002), community-level synchrony in herbaceous-dominated ecosystems like Kaas remains understudied, warranting a need for continued phenological studies on the laterite plateaus such as the Kaas plateau.

4.2. Flora and flowering phenologies within the Kaas community

Approximately five dominant plant families contributed to 46% of the species richness of Kaas plateau. The remaining 54% of the species richness was represented by 26 plant families, each of which was represented by three or fewer species. This pattern of a landscape's species richness being represented by a few dominant families has been reported in other tropical forests where upto 70% species richness has been noted to be explained by only 5-6 plant families (Filgueiras, 2002; Royo and Carson, 2005; Oleques et al., 2017). This pattern has also been shown to be suggestive of a phylogenetic clustering, which has also been noted in communities at higher elevation (Li et al., 2023). Future studies will test the presence of phylogenetic clustering among and within the different laterite plateaus of the Western Ghats, which will help to understand the origin and diversification of its flora.

Over the three years, we found that MF species constituted only about 24% of the total species richness (18 species from 11 plant families) while 58 species were nMF species. Further, MF by the same species was rarely observed in consecutive years, suggesting that factors such as resource limitation and predator satiation (Janzen, 1976; Augspurger, 1983) that also cause cyclical or periodicity in flowering patterns may play a critical role in the reproductive phenology of the mass flowering species at Kaas. The MF species showed higher flowering abundance than nMF species across all years, and their peak flowering marked the extravagant floral displays resulting in the 'super bloom' like events. The persistence of high flowering abundance of the MF species and nearly stable taxonomic diversity across years may play a critical role in shaping the plant-animal interactions in this landscape, which are being addressed in other studies on this plateau (Dhargalkar, 2019; Gangothri, 2022; Chandrachud, 2023).

4.3. Flowering synchrony

Given the brief flowering period in Kaas, we expected higher synchrony among the native herbaceous plants. Despite the strong association observed between environmental seasonality and the flowering season, our study did not detect interspecific flowering synchrony. In contrast, we noted a marked absence of flowering synchrony within the community and among MF and nMF species. This has also been observed in other community-wide studies of both herbaceous species and woody plants (~ 72% of studies according to Feinsinger et al., 1986) where an overall flowering asynchrony within the community due to interspecific competition for pollinators has been reported, although these studies lack computation of synchrony (Mosquin, 1971; Anderson and Schelfhout, 1980; Pleasants, 1980; Ashton et al., 1988; Pelayo et al., 2021). The pollinator-competition hypothesis suggests that flowering asynchrony among species that share floral traits and pollinators can minimise interspecific competition (Levin and Anderson, 1970; Mosquin, 1971; Stiles, 1977; Pleasants, 1980; Ashton et al., 1988; Moeller, 2004; Aizen and Rovere, 2010; Arroyo-Correa et al., 2024). We propose that the predominantly asynchronous flowering (among nMF, MF, or among floral colors) despite strong environmental seasonality indicates the presence of interspecific competitions among plants of the Kaas community.

4.4. Plant-pollinator interaction

The plant-pollinator networks revealed temporally dynamic interactions that matched temporal shifts in floral resources within the landscape. This was corroborated by the increase in Shannon diversity within the sub-seasonal networks (H'), indicating that an increase in floral resources matched an increase in the complexity of ecological interactions within the community, suggesting a putative cause and effect between the two. During the peak flowering season, we

observed lower node specialisation (lower *d'* values) and more links per pollinator type, both suggesting higher pollinator sharing. Bees emerged as the dominant, generalist floral visitors in a network otherwise lacking pollinator guilds. Thus, plant-pollinator interactions became more generalised with increased floral diversity and abundance during the peak flowering period at Kaas. Generalized plant-pollinator interactions have been recorded in European grassland communities (Ebeling et al., 2012; Venjakob et al., 2016; Fornoff et al., 2017), although studies reporting similar sub-seasonal shifts in interaction networks are limited.

The network analyses identified plant-pollinator interactions to be generalised in nature. Studies on pollen transfer have shown that generalised interactions, where the same pollinator species visit multiple plant species at the same time, can result in higher heterospecific pollen transfers (HPT). However, in a separate study in Kaas, we recorded strong floral constancy among foraging bees, where individual bees visited the same plant species for over ~ 30 consecutive visits thus probably promoting lower HPT rates (Shrotri et al., 2024). We therefore caution that the generalised plant-pollinator interactions detected, should not be interpreted as suggestive of higher HPT rates and lower plant reproductive fitness within this community (Ashman and Arceo-Gomez, 2013; Malecore et al., 2021).

5. CONCLUSION

The fragile ecosystems of high-altitude lateritic plateaus in India face immense pressure due to biodiversity loss, habitat destruction, and landscape modification (Watve, 2013). The observed asynchrony in flowering phenology and the absence of facilitative interactions between non-mass flowering and mass flowering species contradicted our predictions that synchrony would be common in these highly seasonal communities. While we detected the landscape-level shifts in

floral colour which is characteristic of the Kaas plateau, our study shows that this is merely a result of slightly higher flowering synchrony among MF species (in both SI_{temp} and SI_{abd}).

Annual plants display an unusual degree of phenotypic plasticity in flowering phenology and this plasticity is adaptive (Schmitt, 1983; Harder and Johnson, 2005; Franks et al., 2007; Blackman, 2017) and serves as a biological indicator of climate change (Gordo and Sanz, 2010; Menzel et al., 2006; 2020). Our study highlights the lack of phenological and ecological studies in the laterite plateaus which restricts its utility for climate change monitoring. Our study is a first step towards characterising these herbaceous communities to understand the ecological and evolutionary mechanisms behind their floristic diversity. Although the genetic basis for mass flowering is not clear, the molecular study in *Strobilanthes flexicaulis* (Acanthaceae) suggested that genetic traits that define periodicity and synchronicity in monocarpic, mass flowering species may be recently acquired from perennial polycarpic species (Kakishima et al., 2019). Our current study has now set the stage for future studies to carry out comparative studies that can explore the evolution and maintenance of the herbaceous communities within the Indian subcontinent and across continents.

6. TABLES

Table 1: Parameter estimates and goodness of fit statistics of the GAMLSS (NBI) process for five comparisons to test flowering response to environmental parameters at Kaas. Goodness of fit statistics: GD; global deviance; AIC; Akaike information criterion and SBC; Schwarz Bayesian Criterion. All predictors were significant at $p \leq 0.05$. Non-significant predictors were excluded and are given in Table S1.

Predictor	**β-estimate**	**S.E.**	***t*-value**	***p*-value**	**GD**	**AIC**	**SBC**
Model 1							
Intercept	3.2669	0.5529	5.909	**<0.0001**	500.6	556.1	609.2
Rainfall	0.0082	0.0024	3.482	**0.0021**			
lag17	-0.1324	0.0358	-3.698	**0.0012**			
Model 2							
Intercept	2.856	4.1929	0.681	0.499	539	581.8	629.2
T_{max}	-1.0636	0.1562	-6.81	**< 0.0001**			
T_{min}	1.9474	0.1952	9.977	**< 0.0001**			
Model 3							
Intercept	18.2985	4.1134	4.448	**< 0.0001**	571.4	600	631.4
T_{avg}	-0.9975	0.3261	-3.059	**0.0035**			
Model 4							
Intercept	-14.5076	2.3417	-6.195	**< 0.0001**	585	601	618.9
Relative humidity	0.1756	0.0636	2.763	**0.0076**			
Model 5							

Intercept	-12.159	1.587	-7.661	< **0.0001**	536.1	567.3	601.7
Surface soil wetness	34.722	3.689	9.411	< **0.0001**			
lag2	-21.497	4.354	-4.938	< **0.0001**			

Table 2: SI_{temp} and SI_{abd} values (mean ± s.e.) for: (a) the community (all species pairs), (b) MF and nMF pairs, and (c) all three floral colour groups.

(a) The community and (b) MF and nMF species pairs:

	Community	**MF-MF**	**nMF-nMF**	**nMF-MF species pairs**
Total species	59	14	45	59
SI_{temp}	0.2396 ± 0.0065	0.3658 ± 0.0309	0.2112 ± 0.008	0.2707 ± 0.011
SI_{abd}	0.2371 ± 0.007	0.4172 ± 0.0264	0.2716 ± 0.0099	0.159 ± 0.007

(c) Floral colour groups:

Floral colour	Total number of species	SI_{temp}	SI_{abd}	SI_{temp} for nMF-MF pairs	SI_{abd} for nMF-MF pairs
WH	16	0.2074 ± 0.0244	0.2944 ± 0.0203	0.2811 ±0.0558	0.1384 ± 0.0313

PK-PL	28	0.2456 ± 0.0298	0.2176 ± 0.0274	0.3089 ± 0.0331	0.1396 ± 0.0277
YL	15	0.2943 ± 0.029	0.2153 ± 0.0234	0.3218 ± 0.0518	0.2075 ± 0.0432

7. BOX

Box 1: Mass flowering and synchrony indices: addressing terminological and methodological gaps

Ambiguity in defining 'mass flowering':

The term '*mass flowering*' has long been entangled in ambiguity due to its context-specific origins and inconsistent application across ecological literature. Historically, the definition is rooted in tropical forest studies such as by Ashton et al. (1988) and Appanah (1993) that emphasised *supra-annual flowering*, describing mass flowering as intermittent, community-wide events tied to multi-year cycles. Similarly, Kelly & Sork (2002) framed mast seeding (and by extension, flowering) as "*synchronous intermittent production*" over decadal scales. These definitions, however, conflict periodicity with floral abundance, treating supra-annual cycles as a *sine qua non* of mass flowering. This paradigm is problematic for three reasons:

a. Contextual bias: Early studies focused on taxa like Dipterocarps or bamboos (Baker, 1959), where 'gregarious flowering' is inherently linked to multi-year cycles. This led to the generalization that *all* mass flowering must be supra-annual, despite evidence of annual high-density flowering in other systems (Gentry, 1974; Augspurger, 1983).

b. Neglect of empirical measures: Classic definitions assumed—but did not measure—high floral density as a hallmark of mass flowering. For example, Ashton et al. (1988) inferred mass flowering from synchronicity rather than abundance, while Baker (1959) misinterpreted "gregarious" flowering of bamboo (a phenomenon exclusively reported in monocarpic plants; Seifriz 1923) with "mass flowering" (a density-dependent phenomenon).

Critically, the supra-annual requirement is both biologically restrictive and empirically unsound. Many herbaceous systems, including the annually flowering species on laterite plateaus of Northern Western Ghats, show ‘mass flowering’. Ehrendorfer in Baker (1959) provided so-far the most accurate definition of mass flowering as *‘initiation of flowering by certain atmospheric conditions over wide areas.’* Enrendorfer’s definition does not convey any information about the flowering duration, periodicity or the nature of the species-specificity, which is later addressed by Gentry (1974) and Augspurger (1983).

To resolve this ambiguity, we redefine mass flowering as *intra-specific flowering characterized by empirically measured high floral density*, decoupled from assumptions about periodicity or synchrony. We propose a threshold of ≥ 2 flowering individuals/m² for herbaceous species, normalized to regional abundance baselines. This approach rejects supra-annual dogma by focusing on density rather than periodicity, it accommodates both annual and episodic flowering systems, aligning with empirical evidence from annually flowering grasslands (this study) and tropical herbs (Gentry, 1974) and also provide a replicable metric for identifying mass flowering across habitats.

Distinguishing mass flowering from flowering synchrony

Mass flowering and flowering synchrony represent distinct axes of phenological variation, yet they are interchangeably used in literature. In this study we refer to mass flowering *high floral density* (≥2 individuals/m²), which may or may not coincide with synchrony among species of a community. **Flowering synchrony** refers to *temporal overlap in flowering*, which can occur: a) intra-specifically: synchrony among individuals of the same species (a potential contributor to, but not synonymous with, mass flowering) and b) inter-specifically: synchrony across species at the community level—the focus of our study.

Inter-specific synchrony does not imply mass flowering, as co-flowering species may exhibit low floral densities. Conversely, a mass-flowering species may bloom asynchronously relative to others. For instance, on the Kaas Plateau, inter-specific synchrony (measured across 2018–2020) remained stable due to tight coupling with abiotic cues, whereas intra-specific mass flowering (high density) varied annually. This decoupling highlights the necessity of treating these phenomena as separate axes.

Methodological gaps in synchrony indices

Existing flowering synchrony indices have critical limitations that restrict their applicability across ecological studies. A prominent issue across multiple methods is the failure to incorporate flowering abundance, as seen in indices proposed by Pool and Rathcke (1979), Primack (1980), Augspurger (1983), and Gorchov (1990), which focus solely on temporal overlap or individual-level metrics. Other indices, such as those by Blomgren (1998) and Freitas & Bolmgren (2008), are constrained to specific scales (e.g., individual or paired comparisons, which is often not applicable to annual herbaceous plants) and lack community-level applicability. Additionally, methods like Mohoro (2002) and Dainou et al. (2012) require high temporal resolution data,

limiting their utility for broad-scale or multi-species analyses. Further shortcomings include subjective categorizations of flowering intensity (Michalski and Durka, 2007) and an inability to disentangle within-individual synchrony from population-level patterns (Marquis, 1988).

To address these gaps, we propose two synchrony indices: SI_{temp} (temporal synchrony) and SI_{abd} (synchrony in abundance; Figure B1). SI_{temp} quantifies temporal overlap relative to total flowering duration, resolving issues of skewed phenological distributions (Pool and Rathcke, 1979) and dependence on flowering duration (Augspurger, 1983). SI_{abd} explicitly incorporates flowering abundance by averaging relative abundance ratios only during the co-flowering periods. Both indices are designed for species with high heterogeneity in flowering duration and abundance, decoupling time and abundance to prevent dominance of one factor over the other. Unlike earlier methods, they are applicable across ecological scales (individual, population, community), temporal units (days, months), and community types (herbs, trees), circumventing limitations of taxonomic specificity and restrictive resolution requirements (Mohoro, 2002).

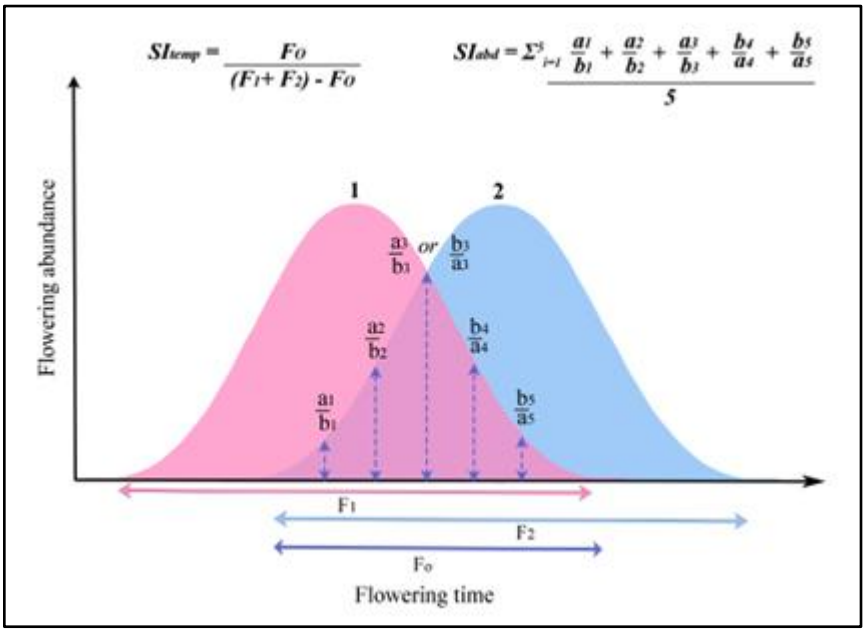


Figure B1: Hypothetical curve of flowering abundance versus time for two species (1 and 2). Species overlap in their flowering time for five censuses, as marked by the dashed lines. F_1 and F_2 represent the total flowering duration for species1 and species2, respectively; and F_o represents the temporal overlap in flowering (i.e., number of days both species are flowering simultaneously).

7. FIGURE LEGENDS

Figure 1: Study site and habitat: (a) Map demarcating the boundary of Kaas plateau, with the locations of phenology transects marked in red (n = 7). The inset map displays peninsular India, highlighting the geographical location of the study site (red circle). (b) A typical sky island habitat of Northern Western Ghats, Maharashtra, India, with distinct geographical isolation from the surrounding vegetation.

Figure 2: Trends in environmental parameters and flowering phenology across years 2018 to 2020. (a) Daily variations in four environmental parameters - rainfall (mm), average temperature (°C), relative humidity (%), and soil wetness (proportion). Coloured boxes demarcate the seasonal boundaries of wet, hot-dry, and cold-dry seasons. (b) Multi-year trends in total flowering abundance of the study community.

Figure 3: Multi-year trends (2018 to 2020) in flowering phenology of 76 herbaceous species on Kaas plateau, including a) 18 mass flowering (MF) species and b) 58 non-mass flowering (nMF) species. Species names are given as six letter codes and can be referred to Table S2 for their full forms.

Figure 4: Distribution of SI_{temp} (temporal synchrony) and SI_{abd} (synchrony in abundance) values

for: (a) all the species-pairs in the study community, and (b) species-pairs with nMF and MF groups. Mean distribution is shown by the red line. For definition and formulae of the synchrony indices, please refer to Box 1.

Figure 5: Sub-seasonal plant-pollinator visitation networks for: (a) pre-peak, (b) peak, and (c) post-peak seasons. Total number of nodes in the network are shown by values above the two trophic levels that are flowering species and pollinator groups. The thickness of the links represents the strength of the interaction (here visitation frequency). The colour of the floral colour hue is shown for each plant species and the size of the coloured rectangles represents the relative importance of the species in the network (that is the number and strength of its interactions with other species). The mass flowering species are denoted by the (*) symbol.

8. FIGURES

Figure 1

Figure 2

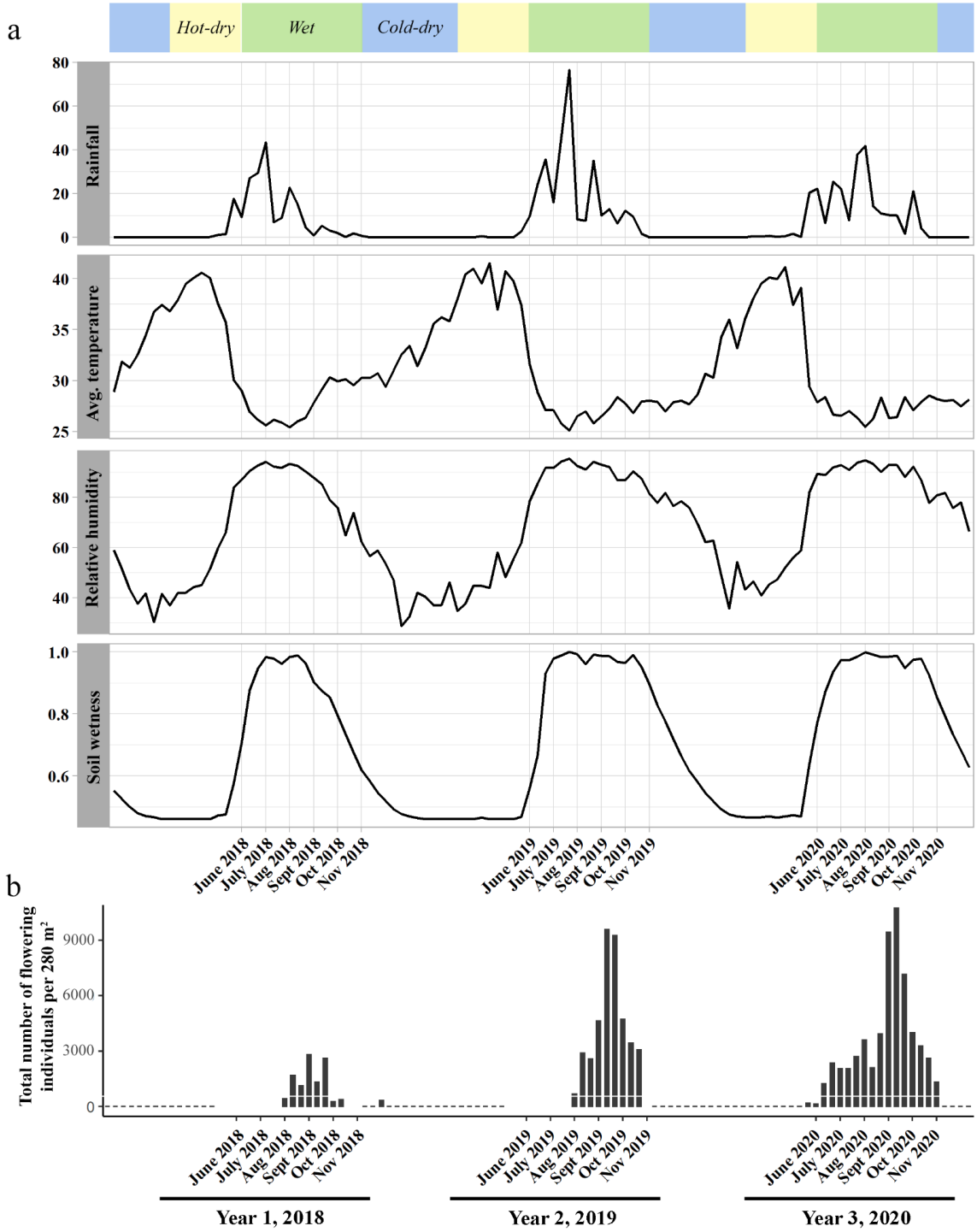

a
Hot-dry
Wet
Cold-dry
Rainfall
Avg. temperature
Relative humidity
Soil wetness
June 2018
July 2018
Aug 2018
Sept 2018
Oct 2018
Nov 2018
June 2019
July 2019
Aug 2019
Sept 2019
Oct 2019
Nov 2019
June 2020
July 2020
Aug 2020
Sept 2020
Oct 2020
Nov 2020
b
Total number of flowering individuals per 280 m²
Year 1, 2018
Year 2, 2019
Year 3, 2020

Figure 3

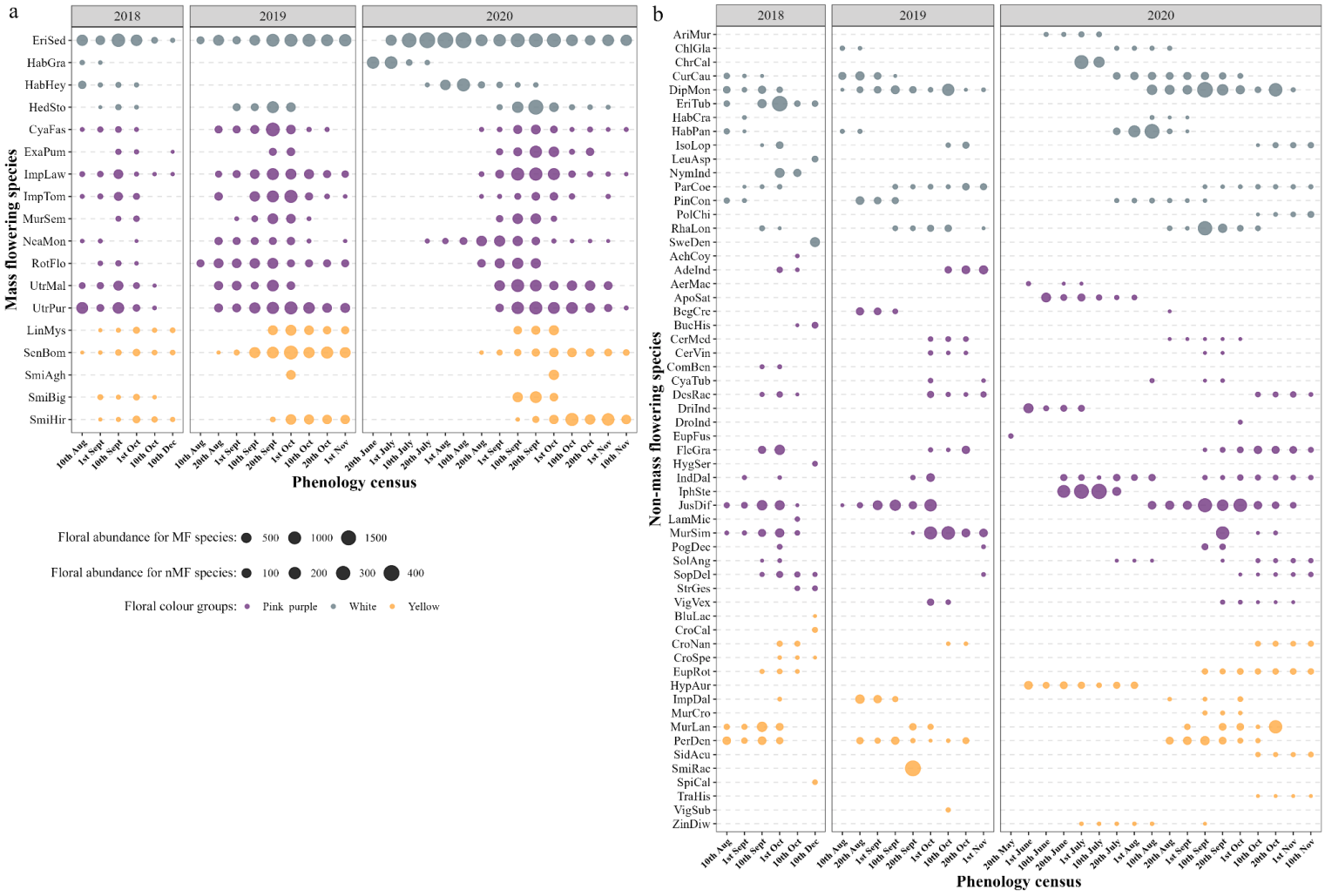

a
2018
2019
2020
Mass flowering species
EriSed
HabGra
HabHey
HedSto
CyaFas
ExaPum
ImpLaw
ImpTom
MurSem
NcaMon
RotFlo
UtrMal
UtrPur
LinMys
SenBom
SmiAgh
SmiBig
SmiHir
Phenology census
Floral abundance for MF species: 500 1000 1500
Floral abundance for nMF species: 100 200 300 400
Floral colour groups: Pink purple White Yellow
b
2018
2019
2020
Non-mass flowering species
AriMur
ChlGla
ChrCal
CurCau
DipMon
EriTub
HabCra
HabPan
IsoLop
LeuAsp
NymInd
ParCoe
PinCon
PolChi
RhaLon
SweDen
AchCoy
AdeInd
AerMac
ApoSat
BegCre
BucHis
CerMed
CerVin
ComBen
CyaTub
DesRac
DriInd
DroInd
EupFus
FleGra
HygSer
IndDal
IphSte
JusDif
LamMic
MurSim
PogDec
SolAng
SopDel
StrGes
VigVex
BluLac
CroCal
CroNan
CroSpe
EupRot
HypAur
ImpDal
MurCro
MurLan
PerDen
SidAcu
SmiRac
SpiCal
TraHis
VigSub
ZinDiw
Phenology census

Figure 4

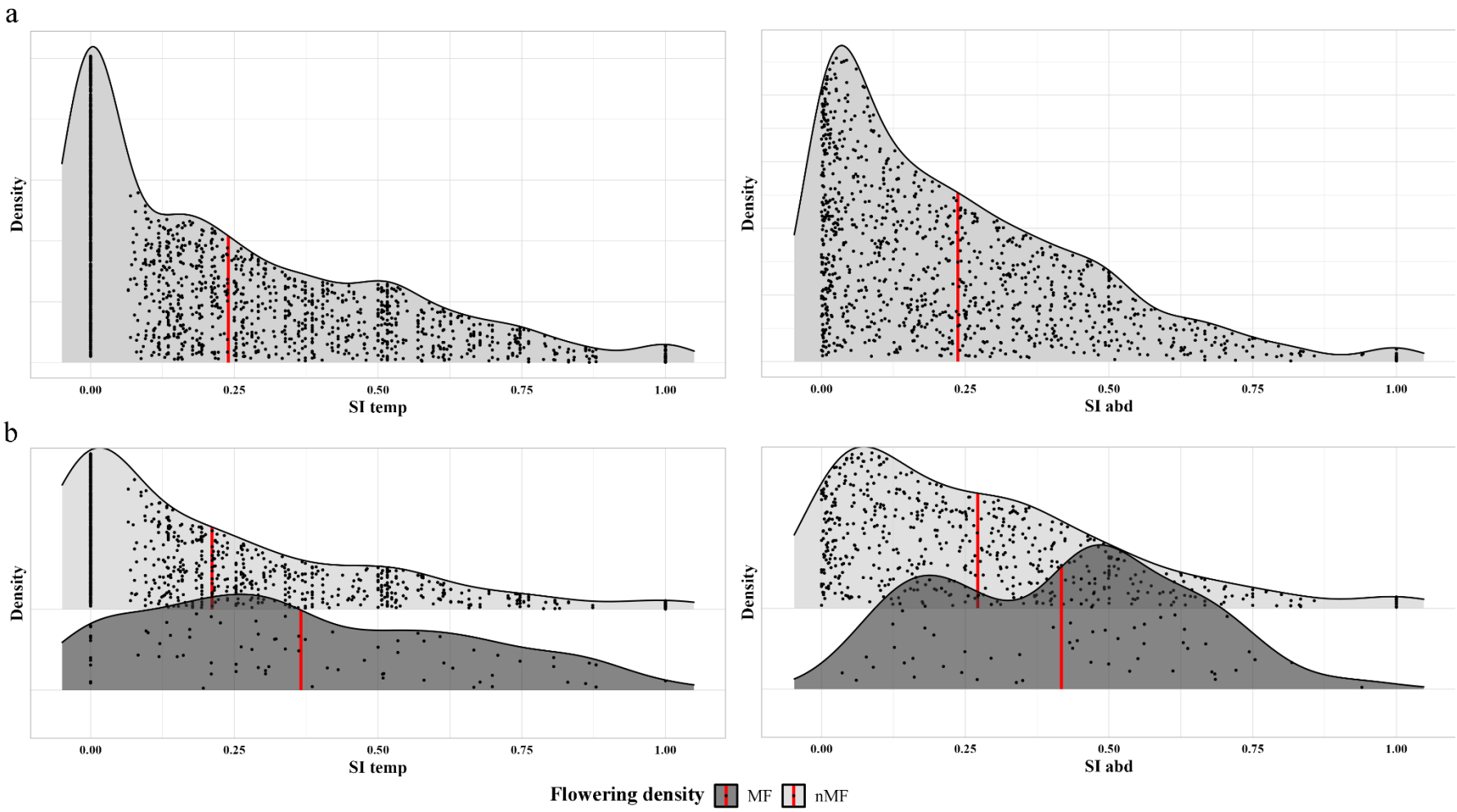
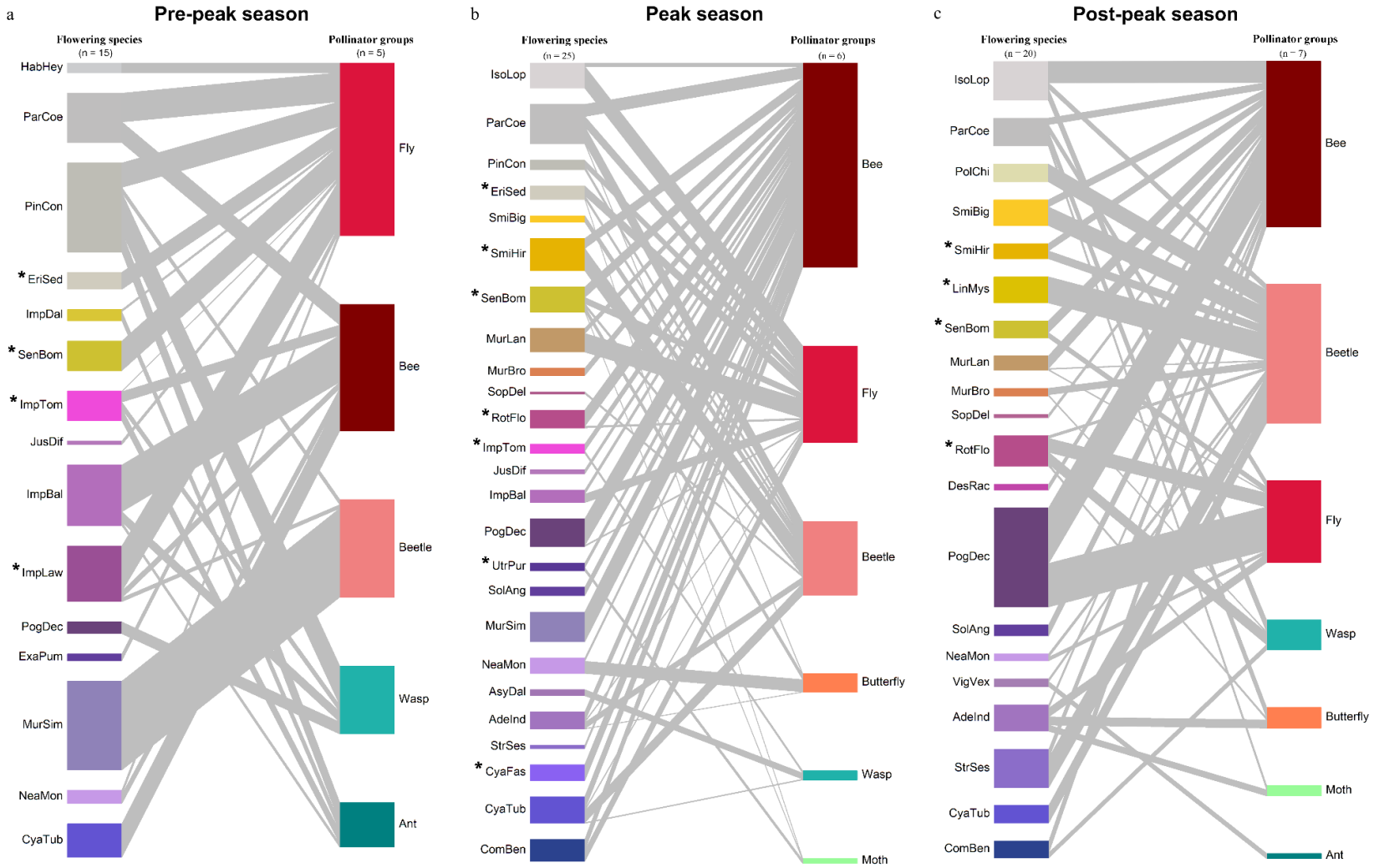

a
Density
0.00
0.25
0.50
0.75
1.00
SI temp
SI abd
b
Flowering density
MF
nMF

Figure 5


a
Pre-peak season
Flowering species
(n = 15)
Pollinator groups
(n = 5)
HabHey
ParCoe
PinCon
*EriSed
ImpDal
*SenBom
*ImpTom
JusDif
ImpBal
*ImpLaw
PogDec
ExaPum
MurSim
NeaMon
CyaTub
Fly
Bee
Beetle
Wasp
Ant
b
Peak season
Flowering species
(n = 25)
Pollinator groups
(n = 6)
IsoLop
ParCoe
PinCon
*EriSed
SmiBig
*SmiHir
*SenBom
MurLan
MurBro
SopDel
*RotFlo
*ImpTom
JusDif
ImpBal
PogDec
*UtrPur
SolAng
MurSim
NeaMon
AsyDal
AdeInd
StrSes
*CyaFas
CyaTub
ComBen
Bee
Fly
Beetle
Butterfly
Wasp
Moth
c
Post-peak season
Flowering species
(n = 20)
Pollinator groups
(n = 7)
IsoLop
ParCoe
PolChi
SmiBig
*SmiHir
*LinMys
*SenBom
MurLan
MurBro
SopDel
*RotFlo
DesRac
PogDec
SolAng
NeaMon
VigVex
AdeInd
StrSes
CyaTub
ComBen
Bee
Beetle
Fly
Wasp
Butterfly
Moth
Ant

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Author Contribution Statement

SS, SK and VG conceived and designed the study. VG and SS acquired the funds and administered the project. RD, NPV, SS and SK conducted the experiments and collected the field data. SS and SK performed the statistical analyses with inputs from VG. SS, SK and VG drafted the manuscript, provided conceptual advice and edited the manuscript. All authors gave final approval for publication and agreed to be held accountable for the contents.

10. DISCLOSURE STATEMENTS

The data and the R codes used in this study will be made available via Dryad repository upon acceptance of the paper. Acknowledgement of the forest divisions, Government of India that have provided the permits is expected as well as authors from TrEE lab, IISER Bhopal.

Conflict of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Open research

The data will be deposited in Dryad data repository once the manuscript is accepted for publication, or upon request by the reviewers.

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12. SUPPLEMENTARY INFORMATION

Attached as a separate file; contains three tables, and five figures.