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

Authors: Saket Shrotri[1], Sukhraj Kaur[1], Rahul Dhargalkar[1], Najla PV[1], and Vinita Gowda[1#].

Affiliation: [1]Tropical Ecology and Evolution (TrEE) Lab, Department of Biological Sciences, Indian Institute of Science Education and Research (IISER) Bhopal, Bhopal, Madhya Pradesh, India, 462066.

[#]Corresponding author: gowdav@iiserb.ac.in

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ABSTRACT

Seasonally flowering communities often exhibit higher flowering synchrony than what can be attributed to environmental factors alone. Flowering synchrony can either increase competition for pollinators or improve pollination through facilitation. Consequently, analysing a community's flowering patterns can help identify its ecological constraints. In this study, we characterised the flowering phenology of a seasonal, herbaceous community (Kaas plateau) in Western Ghats, India, known for its endemic flora and mass flowering displays. Over three years, we addressed the following questions: (a) Is flowering seasonality shaped by environmental factors? (b) Is there evidence for flowering synchrony within the community? (c) Are plant-pollinator interactions specialised?

Our results show that flowering seasonality was shaped by long dry seasons and subsequent rainfall patterns. Based on the floral abundance, we categorised the flora into mass flowering and non-mass flowering species. To incorporate flowering abundance in defining flowering synchrony, we introduced two novel synchrony indices, which identified community-wide flowering asynchrony, despite having mass flowering species. Finally, the plant-pollinator networks identified native bees as dominant pollinators and the prominence of generalised interactions. We also noted sub-seasonal temporal shifts in pollination networks that matched flowering abundances within the community.

This is the first study to exhaustively characterise 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. Our results suggest that competition for pollinators probably drives flowering asynchrony within these seasonal herbaceous communities, rather than pollination facilitation.

KEYWORDS

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

1. INTRODUCTION

Flowering phenology refers to the timing and pattern of flower production and it can greatly impact the reproductive success of plants. Individuals of the same species are often under an adaptive selection to synchronise their flowering phenology, resulting in intraspecific synchrony (Gentry, 1974; Bawa et al., 1985; Rathcke and Lacey, 1985; Kudo, 2006; Elzinga et al., 2007). This is because synchronous flowering of conspecifics can improve their floral display resulting in higher pollinator visitation, cross-pollen deposition, and reduced rates of heterospecific pollen transfer (HPT; Ashton, 1969; Augspurger, 1983; Ashton et al., 1988; Sakai et al., 1999).

In contrast, numerous plant communities have demonstrated that interspecific flowering synchrony is also common and far exceeds synchrony predictions based on abiotic factors like environmental seasonality (Parrish and Bazzaz, 1979; Schemske, 1981; Rathcke, 1983; Ims, 1990; Dante et al., 2013; Nagahama and Yahara, 2019). Studies have also indicated that species with synchronised flowering may also exhibit similar floral traits, like floral colour (Bergamo et al., 2020). Synchrony in floral colour enhances visual cues, attracting a greater number of pollinators and ultimately improving the reproductive success of the species (Tepedino and Stanton, 1981; Gumbert et al., 1999; Camargo et al., 2023). However, flowering synchrony between two species will be favoured by positive selection only if pollinator sharing does not compromise their reproductive assurances (Aizen and Vázquez, 2006; Sargent and Ackerly,

2008). Consequently, if trait-based synchrony enhances pollination efficiency (Rathcke, 1983; Kudo et al., 2008; Gurung et al., 2018; Bergamo et al., 2020) and improves the reproductive fitness of the species involved (Bergamo et al., 2020), both synchronous flowering among heterospecific species and their associated floral traits such as floral colour are likely to undergo strong adaptive selection.

Mass flowering (MF) is an extreme example of synchronous flowering within a landscape or community (Ashton et al., 1988; Appanah, 1993). Although this phenomenon is acknowledged in various ecosystems, its ecological characteristics remain understudied. MF species are often fewer in number compared to the non-mass flowering species (nMF), which aligns with the commonly recognized '*few common, many rare*' species-abundance distribution pattern (Polechová and Storch, 2008). The extravagant floral displays of MF species can increase pollinator recruitment to the landscape (Augspurger, 1983; Sakai, 2002). However, community-wide studies focussing on floral colour as a functional trait that influences pollinator visitation, and hence flowering phenology remain notably scarce (Bosch et al., 1997; Oleques et al., 2017; Bergamo et al., 2020; Albor et al., 2022). The pollinator-mediated facilitation hypothesis suggests that the presence of MF species can lead to an increase in pollination of nMF species if they share floral characteristics and pollinator groups (Bergamo et al., 2020). Thus, we propose that the nMF species within a community can improve reproductive fitness by synchronising their flowering with MF species.

Besides the above-mentioned biotic or ecological selection pressures, climatic and environmental factors also play a crucial role in shaping the flowering phenology of communities up to a certain extent. Specifically in seasonal climates, species may face strong environmental constraints to synchronise their flowering due to short favourable windows

(Elzinga et al., 2007; Lasky et al., 2016). In this study, we address both abiotic and biotic factors that may shape the strong annual flowering seasonality on one of the high-altitude laterite plateaus of the Western Ghats which are also identified as ‘sky islands’. These plateaus are known for their highly endemic herbaceous flora (Lekhak and Yadav, 2012) and mass-flowering events (Figure 1). We investigated the flowering phenology of 76 herbaceous species (~ 90% of the taxa) on the Kaas plateau, over three consecutive years. First, we assessed whether environmental factors could explain the overall flowering seasonality of the herbaceous species at Kaas. Next, we examined the presence of flowering synchrony by testing if mass flowering species synchronised with each other and with non-mass flowering species. Finally, using network analyses, we explored any temporal shifts in plant-pollinator interactions within the Kaas community.

2. METHODS

2.1. Study area: geography and climate

We conducted all phenological and pollinator observation studies at Kaas plateau (□□□ □□□□, 17°43'12.4" N, 73°49'28.1" E) 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 S1). 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 1).

2.2. Environmental parameters

Due to the absence of open-source weather stations within 100 km of the study site (the nearest being 125 km away in Pune, Maharashtra), we retrieved weather data for Kaas from the NASA POWER (Prediction of Worldwide Energy Resources) project database (https://power.larc.nasa.gov). We obtained daily variations in five environmental parameters from January 2018 to December 2020, with a resolution of ½° latitude and ⅝° longitude. These parameters included average temperature at two metres (°C), precipitation (mm), specific humidity at two metres (%), relative humidity at two metres (%), and surface soil wetness (proportion). We conducted two time-series analyses to evaluate the correlation between (a) rainfall and other environmental parameters to determine if rainfall could serve as a representative variable for regional seasonality, and (b) rainfall patterns and trends in flowering phenology. For the first comparison, we used daily values of all environmental parameters over three years (2018 to 2020), converting each into a time series vector using the *ts* function in R (version 4.3.0). For the second comparison, we averaged rainfall data over the same intervals as the phenology data for the corresponding years and then converted it into a time series at an annual frequency. We performed cross-correlation analysis (CCA) using the *ccf* function to compute the degree of correlation and the pairwise temporal lag between the two time-series. All statistical analyses and plots were built using R (version 4.3.0; R core team, 2021).

2.3. 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

S1). Within each transect, we identified all herbaceous plant taxa and quantified their flowering abundance by counting the total number of flowering individuals. In this study, we established a classification metric for the Kaas landscape, in which a species was identified as mass flowering (MF) if its flowering density exceeded 500 individuals across the total sampled area of 280 m^2 (i.e., ≥ 2 flowering individuals per m^2). Species that did not meet this threshold were classified as non-mass flowering (nMF; Table S1).

To test if species may be synchronised by their floral colour traits since it is the simplest means by which large floral displays can be achieved, we categorised all recorded species into three groups based on their spectral reflectance of flowers. However, these groups are named after the colours perceived by human vision, such as Whites (WH), Pinks and Purples (PK-PL), and Yellows (YL; Figure S2). While we did not perform spectral analyses for all the species, the three colour categories were established based on cumulative spectral data from a total of 13 species (Figure S2).

2.4. Flowering synchrony

We quantified flowering synchrony using the phenological data collected in 2020. We used both flowering time and flowering abundance to assess the interspecific pairwise synchrony (see Note S1 for a detailed explanation). Synchrony in flowering time (SI_{temp}) was defined as the ratio of the flowering overlap between species1 and species2 to the total flowering duration of the two species. This is calculated as

$$\square\square_{\square\square\square\square} = \frac{\square_{\square}}{(\square_1 + \square_2) - \square_{\square}} \quad \ldots\ldots\ldots\

overlap of flowering duration between two species (i.e., when $F_o = F_1 = F_2$; Note S1). 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. 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; Note S1). SI_{abd} is calculated as

$$\square\square_{\square\square\square} = \frac{\sum_{\square=1}^{\square} \frac{\square\square\square\square\square\square\square\square\square\ \square\square\ \square\square\square\square\square\square\square\square\ \square}{\square\square\square\square\square\square\square\square\square\ \square\square\ \square\square\square\square\square\square\square\square\ \square}}{\square} \quad \ldots\ldots\ldots\

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 phenology transects) between August 2018 and October 2019. Observations were carried out between 0600 hrs to 1600 hrs using 15-minute observation slots. 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 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 4.3.0) 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

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. The highest rainfall was recorded in July and August, with an average annual precipitation of ~ 2500 mm (Figure 2a). The cross-correlation analysis revealed statistically significant correlations between rainfall and all other environmental parameters ($p < 0.0001$ for all comparisons; Table 1). Trends in average temperature preceded rainfall by 77 days or with a positive lag of 0.2108 (r-value = 0.518; Table 1), while specific and relative humidity showed zero lag with rainfall (i.e., real-time change; r-value = 0.51 and 0.4982, respectively). Surface soil wetness lagged behind rainfall by 32 days or with a negative lag of - 0.0876 (r-value = 0.484; Table 1). We observed a significant positive correlation between rainfall and flowering phenology at a negative lag of - 0.164 (i.e., rainfall patterns preceded flowering trends by 60 days, r-value = 0.7066; $p < 0.0001$; Table 1; Figure 2b).

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). 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 S3). 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 the flowering phenology of the herbaceous community was asynchronous (i.e., SI < 0.4), both in time (SI_{temp} = 0.2396 ± 0.007) and abundance (SI_{abd} = 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 30 hours of total observation time. Of the 46 flowering species observed, 33 species (71.73 %) received visits from pollinators (Table S2), 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 S2). 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 S2). 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-preak 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 S2).

In the cumulative network, 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 S2).

4. DISCUSSION

This study is novel for its multi-year investigations where we characterised the flowering phenology of a sky island community in the Northern Western Ghats (Figure 1; S1). The flowering period at Kaas plateau is short, lasts only five months, and is water-dependent, as noted by the flowering phenology that matched yearly shifts in rainfall patterns (Figure 2a,b; Table 2). We could segregate the community into MF and nMF species although no synchrony was recorded among MF and nMF groups (Figure 4), as well as in nMF-MF species pairs sharing the same floral colour, thus contradicting our predictions based on the pollinator-mediated facilitation hypothesis. The pollination network at Kaas plateau was dynamic and bees pollinated almost 60% of the plant species (Figure S5). In summary, our results suggest that the flowering asynchrony among interspecific species may be under selection to avoid pollinator

competition, which matches findings from most community-level studies (~ 72% of studies according to Feinsinger et al., 1986).

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 (Note S1). 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.

4.1. Seasonality in a Sky Island Community

The flowering season on Kaas showed pronounced environmental seasonality, marked by a long dry season and subsequent intense rainy season (Figure 2a). Two factors influenced flowering seasonality on the Kaas plateau, the passage of the hot-dry season from March to May-end, and the arrival of the wet season from June to October, representing the Indian monsoon. 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; McLaren & McDonald, 2005; Stevenson et al., 2008; Lasky et al., 2016), 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 dependence on rainfall (r-value: 0.7066; $p < 0.0001$; Table 1), rocky landscape with minimal soil layers, and hot-dry summers and winters.

Across the three years, we were able to document the flowering phenology of 25 species endemic to the Western Ghats which accounted for 34% (total = 76 species) of the diversity on the plateau (Table S1; Lekhak and Yadav, 2012; Gore et al., 2014; Gaikwad et al., 2015). Within

our study period from 2018 to 2020, the community-level flowering abundance showed a three-fold increase (Figure 2b), which suggests the presence of a supra-annual flowering pattern within Kaas (Medway, 1972; Frankie et al., 1974; Ashton et al., 1988; Sakai et al., 1999; Sakai, 2002). Our predictions can only be confirmed by future efforts to monitor the phenology, and we strongly recommend Kaas to be part of any long-term monitoring studies. Supra-annual variations in floral abundance are characteristic of seasonal tropical forests and are usually correlated with rainfall patterns linked to El Niño Southern Oscillation (ENSO) events, which is also known to be a major factor that affects India's monsoon (Sakai et al., 2005; Wright and Calderón, 2006; Detto et al., 2018).

4.2. Flora and flowering phenologies within the Kaas community

Flora of the Kaas plateau consisted of approximately five dominant plant families that contributed to 46% of the total number of species (species richness; Table S1). The remaining 54% of the species richness was represented by 26 plant families, each of which was represented by three or fewer species (Table S1). Similar patterns where the ~ 70 % species richness of a landscape is explained by 5-6 plant families have been observed across other tropical forests (Filgueiras, 2002; Royo and Carson, 2005; Oleques et al., 2017), suggesting possible phylogenetic clustering which has been noted in communities at higher elevation (Li et al., 2023).

Over the three years, we found that MF species constituted only about 24% of the total species richness (18 species from 11 plant families; Figure 3) while 58 species were nMF species (Table S1). Further, the same species rarely displayed MF in consecutive years (green asterisks in Figure 3), 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 (Figure S3), and their peak flowering marked the extravagant floral displays resulting in the 'super bloom' like events (Figure 1).

Studies from the Cerrado (Neves et al., 2017) and the tropical forests of Puerto Rico (Lasky et al., 2016) and Jamaica (McLaren and McDonald, 2005) have shown that temporal variations in flowering abundances, rather than taxonomic diversity, are common. We noted similar patterns in Kaas. For example, although peak flowering abundance in 2018 was reduced by 50%, species richness remained comparable to years (2019, 2020) when high flowering abundances were recorded (Figure 2b; 3). These shifts in flowering abundances and not taxonomic diversities across years suggest that flowering abundance will play a critical role in defining ecological dynamics, such as plant-animal interactions, since taxonomic diversity remains relatively stable across years.

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 predominant absence of flowering synchrony within the community and among MF and nMF species (Figure 4; Table 2). Our results align with other community-wide studies that have also reported an overall flowering asynchrony within the community, although these studies lack synchrony computations and comparisons among heterospecific species (Mosquin, 1971; Anderson and Schelfhout, 1980; Pleasants, 1980; Ashton et al., 1988; Pelayo et al., 2021). These studies and our findings from network analysis suggest that intra-annual

community asynchrony may be driven and maintained by interspecific competition for pollinators in the Kaas community.

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). Despite strong seasonality in flowering, there was no synchrony between nMF and MF species that shared similar floral colours (white, pink-purple, and yellow flowers; Table 2). This absence of synchrony suggests that colour-based facilitative interactions between nMF and MF species are absent in Kaas, and asynchrony may be a preferred strategy to optimise pollinator sharing.

4.4. Plant-pollinator interaction

The plant-pollinator networks revealed temporally dynamic interactions (Figure 5) 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'; Table S2), 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 (Figure 5b; Table S2), both suggesting higher pollinator sharing. Bees emerged as the dominant, generalist floral visitors in a network otherwise lacking pollinator guilds (Figure S5; Table S2). 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 in review). 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}; Table 2).

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: Results of time series analysis between rainfall and four environmental parameters and flowering phenology measured as abundance across three study years (2018-2020).

Environmental parameters correlated with rainfall	**Lag**	**Lag (in days)**	***r*-value**	***p*-value**
Rainfall ~ Average temperature	0.2108	77	0.518	< 0.0001
Rainfall ~ Specific humidity	0	0	0.510	< 0.0001
Rainfall ~ Relative humidity	0	0	0.4982	< 0.0001
Rainfall ~ Surface soil wetness	-0.0876	-32	0.4840	< 0.0001
Rainfall ~ Flowering abundance	-0.164	-60	0.7066	< 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. FIGURE LEGENDS

Figure 1: Landscape image depicting the shift in vegetation and flowering at the study site—Kaas plateau, over the flowering season (left panel) and within a year (right panel).

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. Mass flowering species (n = 18) are indicated on the Y-axis in bold-italics and marked by green asterisks (*) in the respective year(s) in which they displayed mass flowering.

Figure 4: Distribution of SI_{temp} and SI_{abd} 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.

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

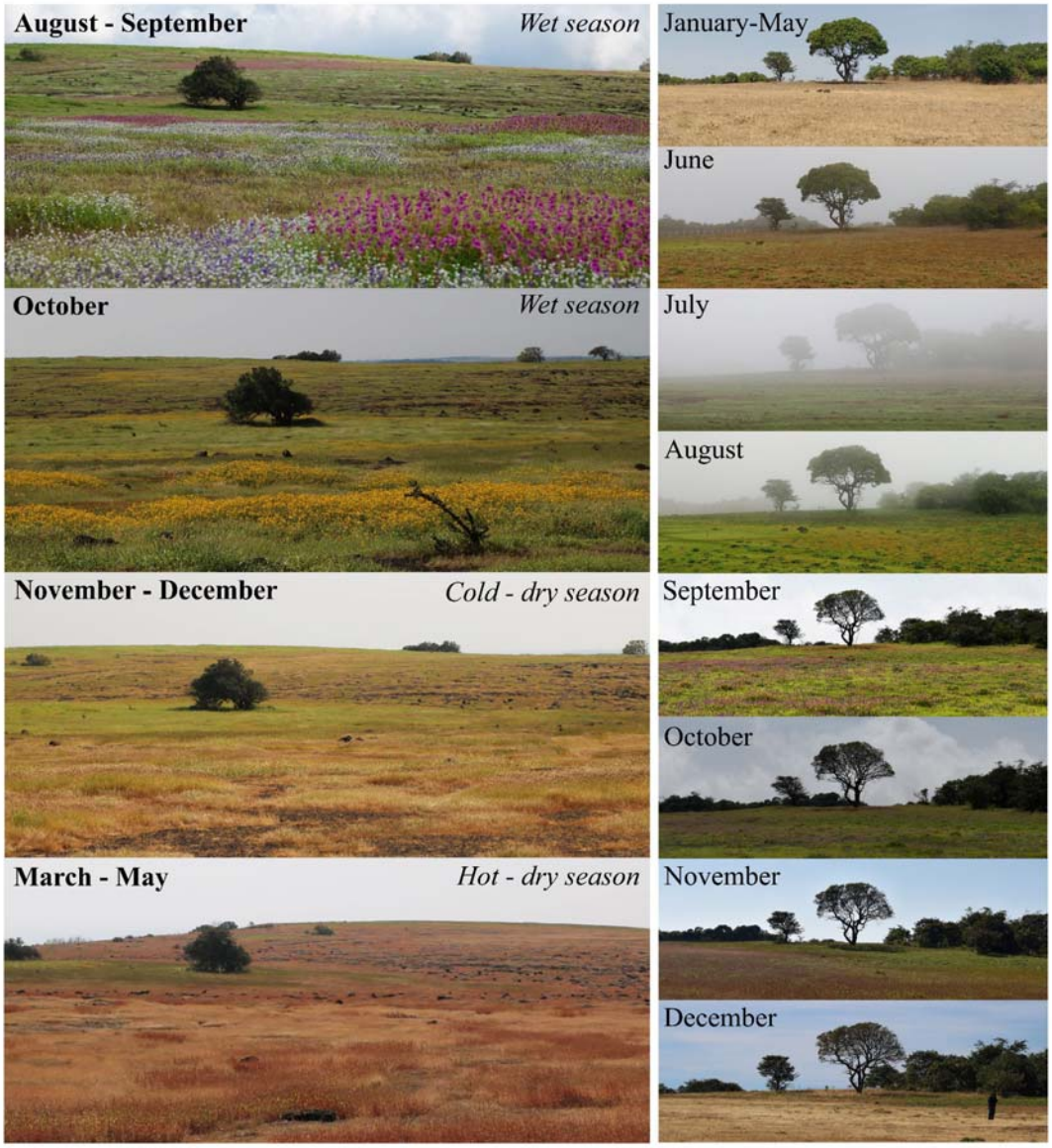


Figure 2

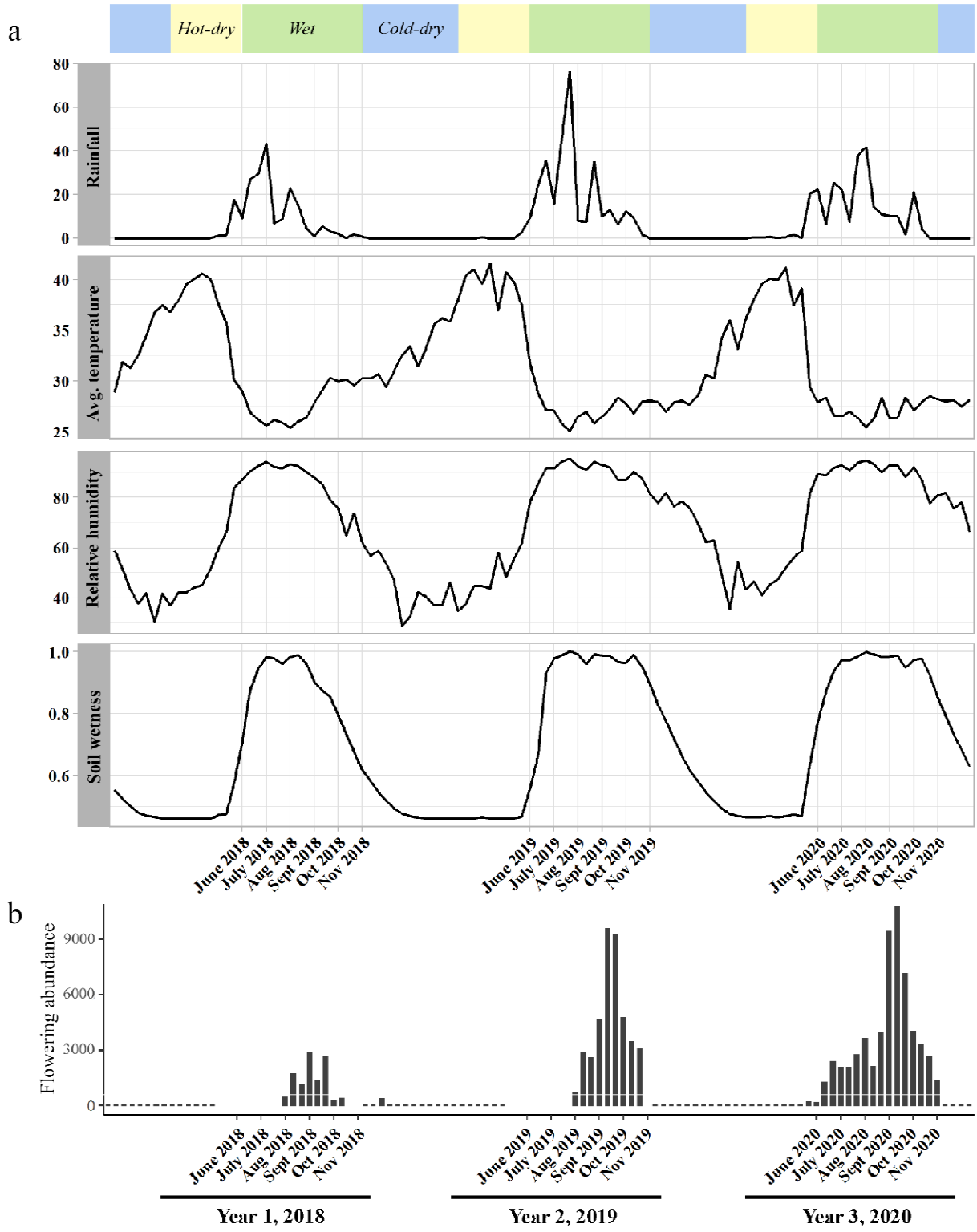

a
Hot-dry
Wet
Cold-dry
Rainfall
Avg. temperature
Relative humidity
Soil wetness
June 2018
July 2018
Aug 2018
Sept 2018
Oct 2018
Nov 2018
June 2019
July 2019
Aug 2019
Sept 2019
Oct 2019
Nov 2019
June 2020
July 2020
Aug 2020
Sept 2020
Oct 2020
Nov 2020
b
Flowering abundance
Year 1, 2018
Year 2, 2019
Year 3, 2020

Figure 3

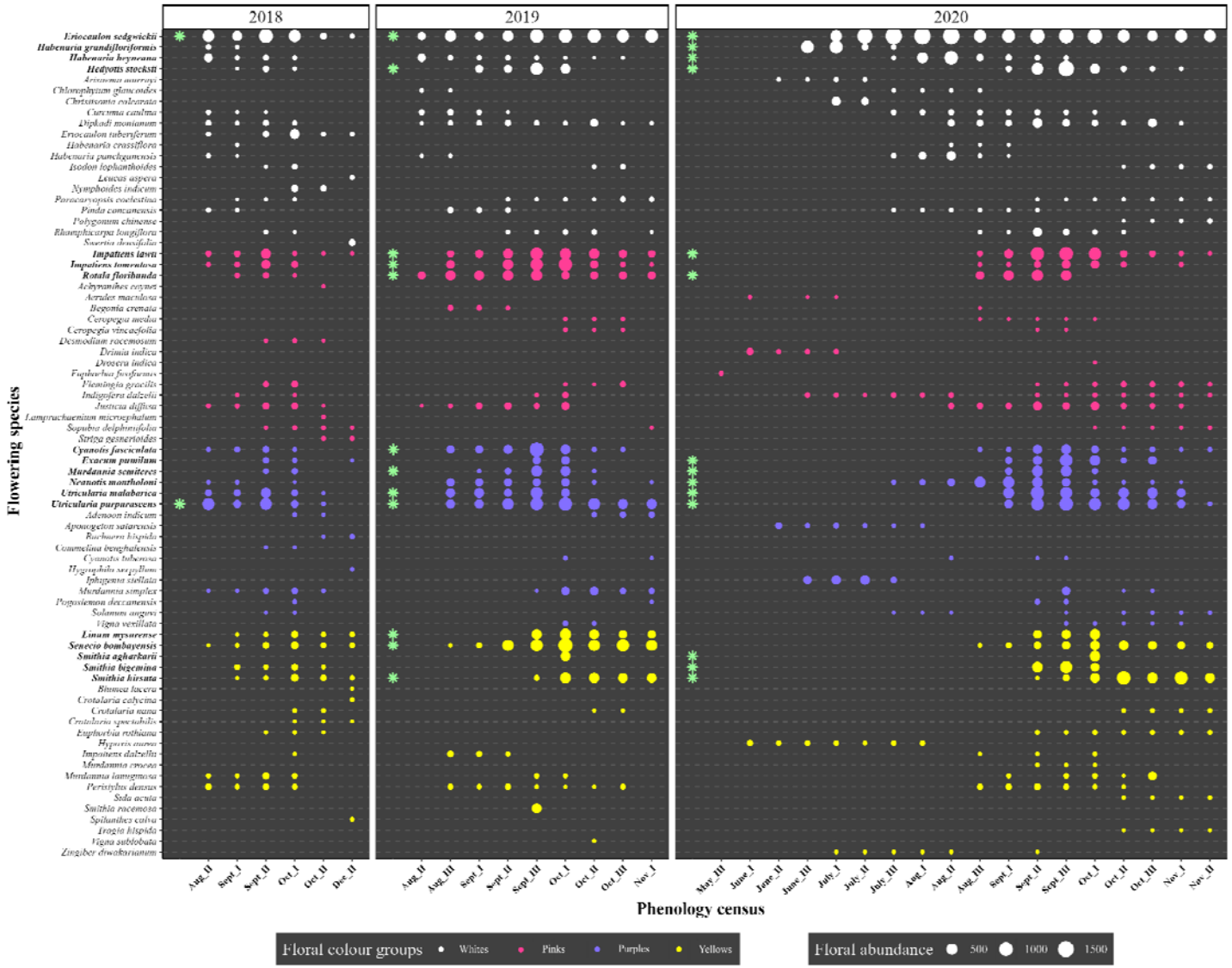

2018
2019
2020
Flowering species
Eriocaulon sedgwickii
Habenaria grandiflorriformis
Habenaria heyneana
Hedyotis stocksii
Arisaema murrayi
Chlorophytum glaucoides
Chrysoramis coleorata
Curcuma caulina
Diplodi moniamum
Eriocaulon tuberiferum
Habenaria crassiflora
Habenaria panchgumnosis
Isodon lophanthoides
Lesucas aspera
Nymphoides indicum
Paracarvopsis cochestina
Pinda concanensis
Polygonum chinense
Rhamphicarpa longiflora
Swertia densifolia
Impatiens ianii
Impatiens tomentosa
Rotala floribunda
Achyranthes aspera
Acrides maculosa
Begonia crenata
Ceropegia mealea
Ceropegia vincaefolia
Desmodium racemosum
Drimia indica
Droseria indica
Euphorbia fusiformis
Flemingia gracilis
Indigofera dalzelli
Justicia diffusa
Lamprachaenium microcephalum
Sopubia delphinifolia
Striga gesnerioides
Cyanotis fasciculata
Evacum pumilum
Murdannia semiteres
Neanotis monthoioni
Utricularia malabarica
Utricularia purpurascens
Adenosen indicum
Apoungeton satarensis
Ruellaria hispida
Commelina benghalensis
Cyanotis tuberosa
Hygrophila serpyllum
Ipnigenna stellata
Murdannia simplex
Pogostemon deccanensis
Solanum angusi
Vigna vexillata
Linum mysorense
Senecio bombayensis
Smithia agharkarii
Smithia bigemina
Smithia hirsuta
Biumea lacera
Crotalaria calycina
Crotalaria nana
Crotalaria spectabilis
Euphorbia rothiana
Hygrorhiza aurea
Impatiens dalzellii
Murdannia crocea
Murdannia lanugnosa
Peristylus densus
Sida acuta
Smithia racemosa
Spilanthes calva
Tragia hispida
Vigna subtobata
Zingiber diwakarianum
Aug_II
Sept_I
Sept_II
Oct_I
Oct_II
Dec_II
Aug_II
Aug_III
Sept_I
Sept_II
Sept_III
Oct_I
Oct_II
Oct_III
Nov_I
May_III
June_I
June_II
June_III
July_I
July_II
July_III
Aug_I
Aug_II
Aug_III
Sept_I
Sept_II
Sept_III
Oct_I
Oct_II
Oct_III
Nov_I
Nov_II
Phenology census
Floral colour groups
Whites
Pinks
Purples
Yellows
Floral abundance
500
1000
1500

Figure 4

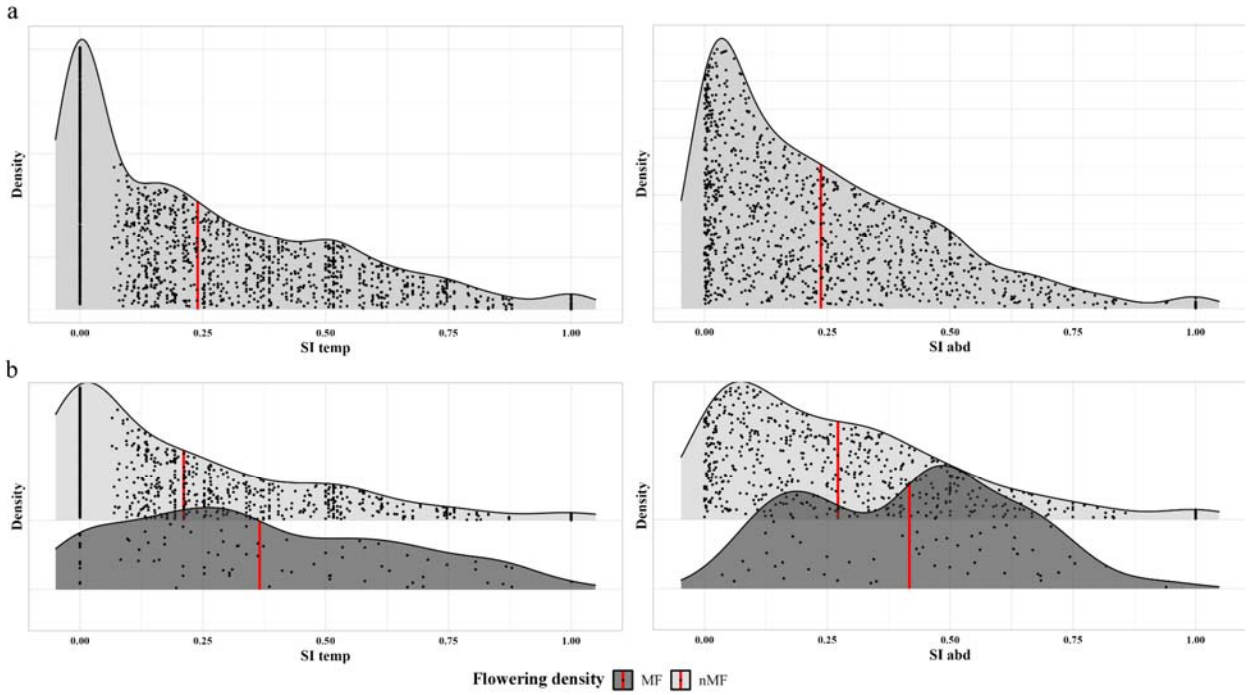
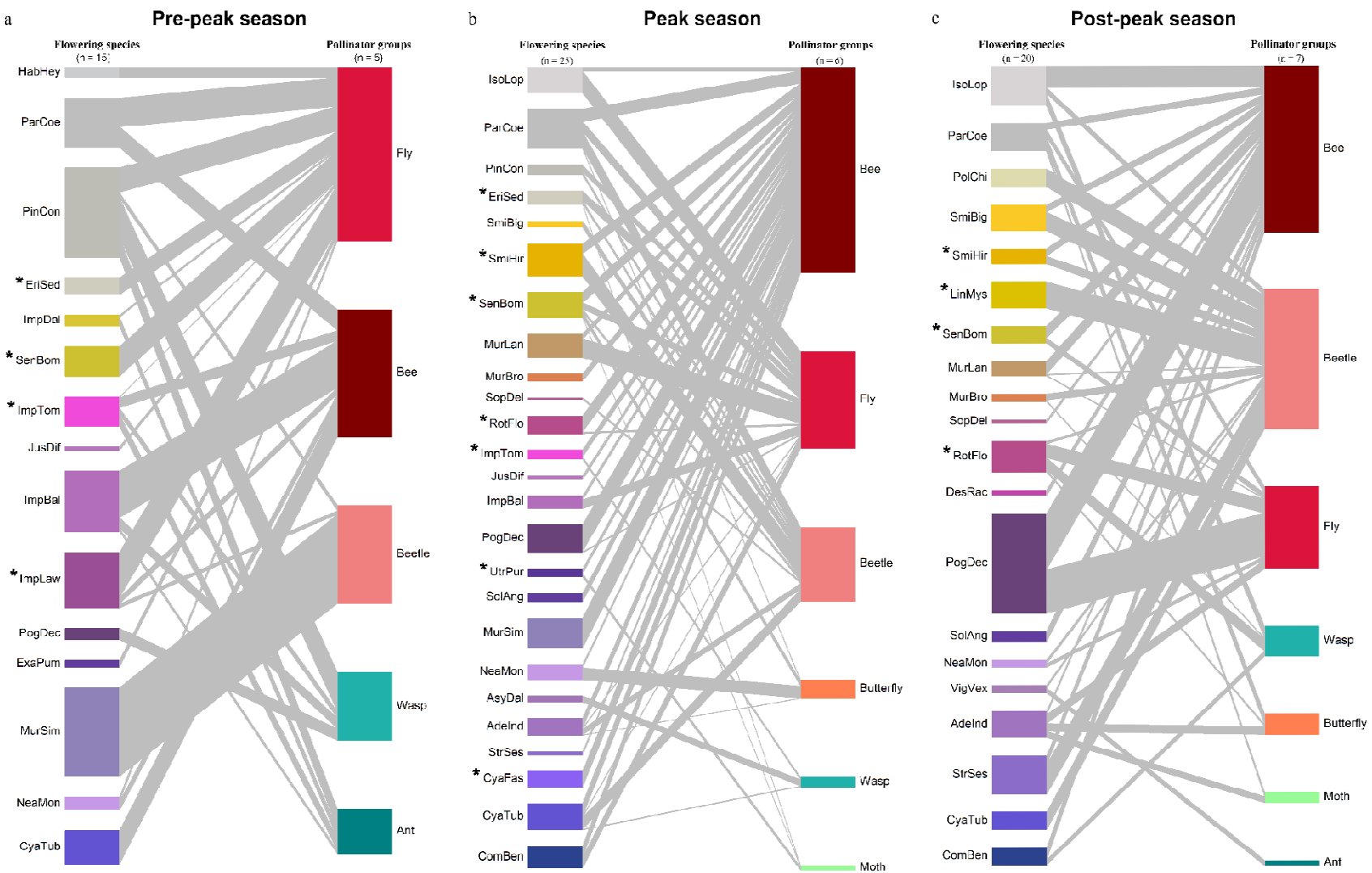

a
Density
0.00
0.25
0.50
0.75
1.00
SI temp
SI abd
b
Flowering density
MF
nMF

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 = 23)
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 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 that support the findings of this study are available on request from the corresponding author. The Editor-in-Chief has waived the required archiving due to privacy or ethical restrictions.

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 one note, two tables, and five figures.