Title: Long-term citizen science data reveals environmental controls on tropical tree flowering at the regional scale

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OPEN RESEARCH STATEMENT

Data are already published and publicly available, with those items properly cited in this submission. SeasonWatch data is publicly archived as Ramaswami (2022).

Abstract

Tropical tree reproductive phenology is sensitive to changing climate, but inter-individual and interannual variability at the regional scale is poorly understood. While large-scale and long-term datasets of environmental variables are available, reproductive phenology needs to be measured in-site, limiting the spatiotemporal scales of the data. We leveraged a unique dataset assembled by SeasonWatch, a citizen-science phenology monitoring programme in India to assess the environmental correlates of flowering in three ubiquitous and economically important tree species - jackfruit, mango and tamarind - in the south-western Indian state of Kerala. We explored the possibility of predicting (i) the flowering status of a tree at any given time, knowing recent environmental conditions, (ii) the environmental conditions that predict the onset of flowering and (iii) explored spatiotemporal patterns in these predictors to aid future hypotheses for changing phenology patterns. We used 165006 phenology observations spread over 19591 individual trees over 9 years, environmental predictors for the fortnight preceding each observation derived from remotely sensed observations (ERA5-LAND) to model the environmental correlates of flowering using two statistical approaches - machine learning and generalised linear mixed models. We found strong influences of temperature and rainfall variables on phenophase presence - soil moisture and minimum temperature had high importance values under machine learning models of presence/absence and had strong effects in the onset of flowering. The effect of time-varying environmental factors, minimum temperature, soil moisture and solar radiation, were also modified by static predictors like elevation, aspect, and

urbanisation. Taken together, our results show the pervasive influence of climate on tropical tree reproductive phenology and its variability among years and individuals. Our results become increasingly important in the face of large heterogenous change in the climate of this landscape and other tropical regions. We demonstrate the potential and limitations of citizen-science observations in making and testing predictions at scale for predictive climate science in tropical landscapes.

INTRODUCTION

Tree reproductive phenology is altered by a changing climate, affecting species interactions and ecosystem functions and services (Cleland et al. 2007, Mora et al. 2015). Flowering in trees is triggered by environmental cues like rainfall events, dry spells, and photoperiod, and is therefore sensitive to a changing environment (Chapman et al. 2005, Chang-Yang et al. 2016, Pau et al. 2018). Changes in onset, persistence, and quantity of reproductive phenophases can alter flower and fruit availabilty in the landscape, affecting interactions with other species like pollinators, frugivores, and seed dispersers (Visser and Both 2005, CaraDonna et al. 2014, Morellato et al. 2016). Consequently, for wild populations of trees, changes in phenology can influence regeneration dynamics and population persistence. Changing phenology can also have socio-cultural impacts, through altering food production and creating mismatches in cultural understanding of tree behaviours (Mora et al. 2015, Morellato et al. 2016). While landscape-level phenological shifts in temperate regions have been studied over decades, large gaps remain in ecological documentation and predictions for shifts in the reproductive phenology of tropical trees.

Phenology of tropical and temperate trees respond to different sets of environmental factors (Pau et al. 2011, Abernethy et al. 2018). For example, in temperate landscapes, distinct growing seasons correspond to rapid phenological onset responses like spring “green-up” or synchronised flowering (Elmendorf et al. 2019, Li et al. 2021). On the other hand, in tropical landscapes where trees grow and reproduce year-round, environmental cues for phenological change are more

spatially and temporally diffuse (Parmesan 2007, Chen et al. 2018, Abernethy et al. 2018). Temperature, precipitation, and solar radiation (e.g. cold days, dry spells, total accumulated rainfall and soil moisture) have been demonstrated to affect the onset and persistence of flowering phenology in tropical trees (Brearley et al. 2007, Pau et al. 2013, Diez et al. 2014, Wright and Calderón 2018). Furthermore, climate change has resulted in altered rainfall and temperature regimes as well as extreme events in tropical environments, increasing inter-annual variability (Mora et al. 2013). Interannual rainfall variability - high rainfall years and drought years including cycles like the El Niño Southern Oscillation and the Indian Ocean Dipole - can result in interannual variability in tree phenophase onset and intensity (Medway 1972, Zimmerman et al. 2007, Chang-Yang et al. 2016, Chapman et al. 2018, Dunham et al. 2018, Pau et al. 2018). There is a growing understanding of the influence of environmental factors on leaf phenology of tropical species, but information on reproductive phenology is lacking (Chaturvedi et al. 2021, Devi et al. 2023). To predict future phenological shifts in the tropics, an important first step is to understand the extent of environmental controls on tropical tree reproductive phenology.

Environmental cues could affect phenology with a lag time, interact with habitat factors and affect individuals differently, necessitating large-scale and long-term data. An example of a long-term phenology dataset is from Japan where the flowering of cherry blossoms (*Prunus jamasakura*) has been documented since the 9th century creating strong baselines to assess contemporary change in flowering phenology with changing environmental cues (Aono and

Kazui 2008, Allen et al. 2014). In the tropics, phenology of even ubiquitous species have rarely been recorded systematically, hindering the potential to make large-scale predictions of climate impacts of tree-associated ecosystem services (Piao et al. 2019, McDonough MacKenzie et al. 2020). In tropical species, at least six years of data is necessary to accurately detect phenology in regularly flowering species, with much more for noisy species (Bush et al. 2017). Reproductive phenology could also be affected by spatial factors that influence water availability - like elevation and the aspect of the slope - as well as the degree of urbanisation. For instance, even within the same year (similar climatic cues), trees in North America, Europe and China have been found to flower earlier in cities than in surrounding non-urban habitats, likely due to urban heat island effects (Neil and Wu 2006). Tropical tree phenology also exhibits large variation among individuals, necessitating large spatial samples besides long-term data for a process-based understanding(Satake et al. 2013, CaraDonna et al. 2014, Li et al. 2021). A recent review of reproductive phenology studies from the Neotropics showed that across 218 datasets, the majority of datasets lasted 2 years or less, and only 10.4% monitored > 15 individuals per species (Mendoza et al. 2017). In the absence of robust datasets, potentially high intraspecific variation in reproductive phenology makes it difficult to parametrise models that span spatial scales of environmental change.

Citizen science allows access to longitudinal data across large spatial scales that is difficult to achieve through other sampling techniques. Citizen science data has led to novel understanding of phenological patterns in other taxa - observations of migratory bird populations across North

America have been useful in documenting phenological shifts, spatial differences in sensitivities to changing climate, as well as disentangling drivers of change (Hurlbert and Liang 2012, Kelly et al. 2016, Haas et al. 2022). Other efforts, like the USA National Phenology Network, have helped quantify advancing spring behaviours of plant species in North America (Schwartz et al. 2012, Brunsdon and Comber 2012). SeasonWatch, a citizen science phenology monitoring programme has been collecting data on several phenophases for common, widespread tree species across India (Ramaswami et al. 2019, 2021). Each week, observers record flowering, along with other phenophases, on specific trees consistently using a uniform protocol that records both presence and intensity of a phenophase (Fig 1a). This dataset, with substantial contributions since 2014, provides a unique opportunity to build baselines for phenology in the Indian subcontinent. In the past, some analyses of these data have revealed patterns of change in at least one species - Cassia fistula - over the time period of observation (Ramaswami and Quader 2018, Ramaswami et al. 2021). These common species, spread across ecoregions and habitats, can add to phenological understanding beyond focussed, localised studies.

Here, we investigated the environmental correlates of flowering in common tree species in India at the individual tree scale using SeasonWatch data. We used 165006 phenology observations across 19591 individual trees over 9 years from tree species in the southwestern Indian state of Kerala, and correlated these with remotely-sensed environmental variables using machine learning and generalised linear mixed model approaches. We asked (i) to what extent can recent environmental conditions predict the probability of observing flowering on a given tree at a

given time? (ii) to what extent do recent environmental conditions and habitat factors predict the onset of flowering on individual trees? (iii) how are climatic correlates of phenology changing across the landscape assessed? We focussed on flowering of three species with the greatest number of individuals and observations across Kerala - jackfruit (*Artocarpus heterophyllus*), mango (*Mangifera indica*) and tamarind (*Tamarindus indica*). Jackfruit, mango, and tamarind are common trees, with fruits widely used in Indian cuisine and are commercially important fruit-bearing trees. Flowering phenology of these species is thus vital for predicting fruit crop sizes which directly affects human livelihoods and well-being.

We expected (i) temporally variable temperature and precipitation patterns to influence the onset of flowering, (ii) temporally static, but spatially variable habitat factors - elevation, aspect, and degree of urbanisation, to modify the effects of temperature and precipitation, and iii) environmental correlates of flowering to be species-specific. (iv) We also predict that these environmental correlates are experiencing high spatiotemporal variation in Kerala in the study period.

METHODS

STUDY AREA, SPECIES AND SEASONWATCH DATA

We analyzed phenology and environmental data from the south western Indian coastal state of Kerala. Bounded between 8° 18’ N, 12° 48’ N, 74° 52’ E and 72° 22’ E, Kerala lies along the Arabian Sea with a tropical monsoon climate. The total population of the state is over 3 million, spread over an area of 38,863 km^2. The state receives an average annual rainfall of over 3000mm

via two major branches of the Indian monsoon system - the southwest (June-September) and northeast (October-December) monsoon. Across all SeasonWatch data (SeasonWatch Citizen Scientist Network, 2022, Ramaswami (2022)), 263,288 observations across species and categories, and 93.23% of observations of top 3 species are from Kerala. Moreover, these data span a large range of the existing environmental variability in the state in rainfall, temperature, elevation, lat/long, and solar radiation. This information density and spread, especially for repeat observations, makes it an ideal dataset to answer these questions.

We analyzed flowering phenology in three of the most frequently observed species in the SeasonWatch dataset - *Artocarpus heterophyllus* (henceforth "jackfruit"), *Mangifera indica* (henceforth "mango") and *Tamarindus indica* (henceforth "tamarind") from January 2014 - July 2022. All three tree species are grown across the state in orchards, homes, and also occur wild. The fruits of all three species are commercially and culturally important. Observations to SeasonWatch comprise estimates of the presence and quantity of a given phenophase. Observers register one or more trees from a list of suggested species with the project and record phenology on a weekly basis. The standard protocol for reporting a phenophase involves dividing the canopy of a tree into thirds, reporting a phenophase as 'none' if it is not observed, as 'few' if a phenophase is observed only in 1/3rd of the canopy, and as 'many' if a phenophase is observed on more than 1/3rd of the canopy (Fig 1a). Observers are children or adults, participating from diverse habitats such as school campuses, urban and rural residential areas, and forests. As in other citizen science projects, there is likely to be inter-observer variability in reporting

phenophases as well as bias towards observing familiar species with conspicuous flowers or fruits. At present, the project minimises biases and errors through workshops and training as well as one-on-one follow-up and troubleshooting. Moreover, the flowering phases of the common trees chosen for analysis are distinctly observable with the naked eye, and familiar to participants, lending confidence to community data. The data distribution across species and years is provided in Table 1, Fig S1 and Fig S2.

ENVIRONMENTAL DATASETS

To generate a set of predictors for flowering, we summarised environmental datasets from various sources within the state boundary of Kerala. We derived seven potential spatiotemporal predictors of flowering from remotely sensed data - three related to temperature (minimum, maximum and mean), three to precipitation (total precipitation, soil moisture and the number of consecutive dry days), and solar radiation. We used daily measurements of precipitation, temperature, solar radiation and soil moisture for the entire soil column from the ERA5-Land dataset at the 11.1 km spatial resolution. Using Google Earth Engine, we summarised these layers to arrive at the specific predictors for the fortnight (14 days) preceding each observation (Table 2). We calculated these values also at monthly and quarterly timescales and found that they were highly correlated to the fortnightly value (Fig S3) and hence used this finest temporal resolution (fortnight) for the analysis.

Along with spatiotemporal predictors, we calculated spatial factors - elevation, aspect and degree of urbanisation - at each tree location that might potentially act as modifiers for the temporal

predictors (Table 2). We used a Digital Elevation Model created from the Shuttle Radio Topography Mission (SRTM) at the 30 m resolution to calculate elevation, slope and aspect at the tree location. Further, we used the NASA nightlights layer from 2016 at the 500 m resolution as a proxy for the degree of urbanisation (Sutton et al. 2001). We chose this metric as the ambient light, one of the proxies for degree of urbanisation, also has a direct ecological relevance on the physiology of plant life.

DATA CLEANING AND ANALYSIS

We cleaned and processed the SeasonWatch dataset to maximise inclusion of data points. SeasonWatch datasets include two types of data - repeat observations of the same tree ("regular") or single observations of a tree, usually during a coordinated event ("casual").
We included all observations of both kinds that we were able to reliably assign and validate locations (see Appendix S2). We assembled a final dataset of 165006 observations across 19596 trees; 7927 trees of jackfruit, 9919 of mango and 1750 of tamarind across the state of Kerala (Fig 1, Table S1). The SeasonWatch raw data are ordinal with "none", "few" and "many" - three levels possible for each observation. The observations also include separate categories for buds and open flowers. For every observation of a tree, we recoded the observed phenophase from (none/few/many) to (yes/no; binary); by coding an observation as "1" if it was recorded as "few" or "many" for buds or flowers, and "0" otherwise. We chose to combine the bud and the flowering observations to minimise observation errors in these species where flowers are small

and can be difficult to distinguish from buds, especially for taller canopies. Our choice of binary variable also reduces potential user subjectivity in the categorising of “few” and “many”.

We modelled the ecological predictors of flowering separately for each of the three species, as these species are physiologically and evolutionarily distinct (belonging to three different families - Moraceae, Anacardiaceae, and Fabaceae) and may therefore show diverse responses to the same environmental cues. We modelled the influence of environmental variables on probability of observing a phenophase at any given time, and the probability of its onset through two different modelling techniques: decision-tree-based classification through machine learning and generalised linear mixed models.

Analyses were performed using R version 4.1.3 and ArcGIS Pro version 3.0.2 (R Core Team 2022).

MACHINE LEARNING MODELS TO MODEL THE PROBABILITY OF FLOWERING AT ANY GIVEN TIME

For the entire set of observations, we used Random Forest models to classify the flowering occurrence observations based on environmental predictors. Random Forest classifier is a supervised learning algorithm that uses an ensemble of decision trees using majority voting to classify datasets into two categories; here the presence/absence of flowering (Breiman 2001). Random Forest classifiers have been used widely in ecological data analysis because of their flexibility and accuracy (Cutler et al. 2007). This approach allows for predicting the probability

of observing flowering in a tree given recent environmental conditions. For each of the three species, we ran separate models to classify flowering status according to the following model:

$$phenophase_{l,t} \sim precipitation_{l,t} + maximumtemperature_{l,t} + minimumtemperature_{l,t} + meantemperature_{l,t} + drydays_{l,t} + soilmoisture_{l,t} + solarradiation_{l,t}$$

Where precipitation, temperature, dry days, soil moisture, solar radiation are temporal predictors for the fortnight before the observation at location l and time t. We ran these models in R using the package *randomForest* (Liaw and Wiener 2002) for 500 decision trees. Tree-based methods are fairly insensitive to collinearity among predictors, allowing us to compare the full-range of temperature and precipitation variables simultaneously, as well as the full dataset, including repeat observations for the same tree. We calculated variable importance for each model using the Mean Decrease in Accuracy (MDA) metric which removes a predictor from the model, re-trains the model to make predictions, and evaluates the decrease in accuracy.

GENERALISED LINEAR MIXED MODELS TO MODEL THE ONSET OF FLOWERING

We further explored the effects of the environment on the onset of flowering in the three species using predictive modeling accounting for interactions between variables and variable collinearity. The onset of flowering is defined as the first observation in a timeseries where flowering is observed after a non-flowering observation. To model the onset of a phenophase, we subset dataset to observations of trees (at time t) that had been observed to have no flowering in

the preceding week ($t-1$). This reduced the dataset to 64333 observations, across 2448 trees (Table 1, Fig S2). This step excluded non-repeating observations on a tree, as well as all observations without an observation in the immediate preceding week, to maximise data quality. We then modelled the probability of observing flowering at time t as a function of environmental variables in the preceding fortnight. For each of the three species modelled, the time-varying predictors were identified by picking the most influential variables from the ML models that were ecologically distinct. Specifically, for each species, we picked most important variable in the temperature group (among minimum, maximum and mean), the most important variable in the precipitation group (among total precipitation, number of dry days and soil moisture), and solar radiation. This grouping was based on the idea that although temperature, precipitation and solar radiation are influenced by distinct processes, but are all known to elicit tree responses. By picking one of each, we also eliminate potential correlations among predictor variables that can violate mixed modelling assumptions.

To account for the modification of the influence of environmental variables based on habitat, we also modelled interactions with elevation, aspect and degree of urbanisation - three habitat variables that have a range of variation in Kerala. Although it is possible that each of these variables could potentially interact with the temporal variables, some of these are known to be correlated with each other (e.g. elevation and temperature). Since our study design did not explicitly account for these correlations, we chose to model only interactions that did not have known, high ecological correlation. Specifically, among the set of possibilities, we excluded

interactions between elevation and minimum temperature, aspect and precipitation (the Western Ghats range in Kerala affects rainfall patterns), degree of urbanisation and minimum temperature (known heat island effects in urban areas), degree of urbanisation and soil moisture (potentially associated with heat island effects). Further, to account for data structure in space and time, we included random effects of tree and the spatial grid in which it was located.

We modelled the onset of the phenophase using a generalized linear mixed model with a binomial family of errors using the *package* lme4 (Bates et al. 2015). Using a dataset of only consecutive measurements and accounting for interactions between variables and spatial and temporal autocorrelation using a generalised linear mixed model (GLMM), we modelled the probability of observing flowering given an absence of flowering in the previous week ("onset"). Although we picked variables for each species, the most influential temperature variable for all species was minimum temperature and the precipitation variable was soil moisture . So, we specified the onset model for each species as:

$$phenophase_{l,t} \sim minimum.temperature_{l,t} + soil.moisture_{l,t} + solar.radiation_{l,t} + elevation_l * soil.moisture_{l,t} + elevation_l * solar.radiation_{l,t} + aspect_l * minimum.temperature_{l,t} + aspect_l * soilmoisture_{l,t} + +urbanisation_l * solar.radiation_{l,t} + (1|TreeID) + (1|GridID)$$

Where minimum temperature, soil moisture and solar radiation are measured at the location l for the fortnight before the observation t, elevation, aspect and urbanisation are spatial predictors tied to the tree location l. The model includes two random effects on the intercept; $TreeID$ to account for repeated measures on the same tree and $GridID$ to account for spatial autocorrelation.

For all models, we mean-centred all predictor variables at 0 and scaled it to a distribution with standard deviation 1 for ease of comparing the effect sizes. We tested the fit of these models using conditional and marginal R^2 using packages *performance* and *sjPlot* (Lüdecke et al. 2021, Lüdecke 2023).

MODEL VALIDATION

With large datasets and many predictors, models can be overfit to the modelled data but unable to predict "new" observations. Traditional model diagnostics, like R^2 or likelihood, report the "fit" or amount of variance in the dataset used for modelling explained by the model, but not for "out-of-bag" data that has not been encountered by the model. For both of our modelling approaches, we used a cross-validation technique, leave-one-out cross-validation (LOOCV), to test the predictive power of our model. In this method, we ran each model 9 times, systematically leaving one year of observations out each time. We then used the model coefficients to predict these "new" observations and tested their accuracy, and then tested for reliability of predicted values.

We tested the predictive power of models by comparing the predicted data from the LOOCV models for each year vs actual observations using F1 scores based on true and false positives and negatives. F1 scores are good indicators of the distribution of correct and incorrect predictive classifications by taking the harmonic mean of precision and recall (Hossin and Sulaiman 2015, Grandini et al. 2020). Specifically, we calculated F1 scores as:

$$F1 = 2 * (Precision + Recall)$$

where

$$Precision = \frac{TP}{TP + FP}$$

and

$$Recall = \frac{TP}{TP + FN}$$

where TP is the number of true positives, FP is the number of false positives and FN is the number of false negatives for "out-of-bag" predictions. For GLMMS, in addition to F1 scores, we also calculated mean square error (MSE) of the observations and Pearson's correlation coefficient between predicted and observed values.

HOTSPOT ANALYSIS

To understand how environmental conditions might affect phenology in the coming years, we analysed spatiotemporal patterns of environmental variables that affect flowering in Kerala, with an intention to identify directional changes or spatial shifts. Hotspot analysis allows the identification of such spatiotemporal patterns using the entire timeseries of environmental data across the years measured. A hot spot/cold spot is defined as a location which has high (or low) value for an environmental variable, like temperature, precipitation or soil moisture, and is surrounded by other areas with similar values; a spatial cluster. With changing patterns in climate, these can shift in location and new hotspots and coldspots can emerge over time, with potential implications on phenology patterns that track environmental variables. Using fortnightly aggregated environmental variables from 2014-2022, we ran emerging hotspot analysis in ArcGIS Pro to identify statistically significant hot spots and their trends over time for minimum temperature, mean soil moisture and total solar radiation, the three variables used for the GLMM analysis, across Kerala. We used a combination of two statistical measures 1) the Getis-Ord Gi* statistic to identify hot spots and cold spots of climate measurements for each time step (i.e., fortnightly), and 2) the Mann Kendall trend test to examine how hot spots and cold spots have evolved over time (Mann 1945, Sen 1968, Kendall et al. 1987, Getis and Ord 1992). For further details on methods, refer Appendix S7.

RESULTS

Jackfruit, mango and tamarind trees exhibit differing patterns of flowering seasonality. Across the SeasonWatch dataset from 2014 to 2022, peak flowering in jackfruit and mango across

Kerala was observed in the first few weeks of the year (Fig 1). Tamarind, on the other hand, showed peak flowering in the middle of the year. In jackfruit and mango, most trees observed (~75%) were flowering at the observed peak, while the proportion of trees flowering at peak flowering was lower for tamarind. Across all three species, trees were observed to be flowering at all times of the year; no week had a zero proportion of trees flowering (Fig 1). The transition from least flowering to peak flowering was gradual, across several weeks to months, in both jackfruit and mango, but less so for tamarind. There was also substantial variation in the proportion of trees flowering in a week, shown by large standard deviations. These differences could be because of variation across years, sites or individuals.

PROBABILITY OF OBSERVING FLOWERING ON A TREE

Machine learning models with spatiotemporal predictors were able to classify flowering phenophases for the three species with substantial precision. The accuracy of a binary model by random chance would be 50%, leading to an F1 score of 0.5; models with higher F1 scores than randomly expected have predictive value. With 500 runs each, Random Forest models were able to predict the presence/absence of flowering in jackfruit, mango, and tamarind trees given the environmental conditions of the previous fortnight with F1 scores of 0.59, 0.62, and 0.26, respectively. These performance metrics describe the ability of the models to predict tree phenophases for an unobserved year based on environmental variables alone. We note that the distribution between flowering and no-flowering observations was about 2:1, potentially influencing the F1 score.

Random forest models identified environmental variables strongly correlated with flowering for each of the species. The mean importance of each of the factors, calculated using MDA, was different across species (Fig 2). For all three species, minimum temperature in the preceding fortnight was the most important predictor of flowering status. Among precipitation variables, soil moisture in the preceding fortnight had the strongest influence in classifying flowering status. Solar radiation also ranked among the top three variables for all three species. Across the 9 LOOCV runs, the relative importance of the variables had some variation (Table S2, S3, S4), but total precipitation and the number of consecutive dry in the previous fortnight consistently were ranked lowest across runs in all species (Fig 2). Some of the variation in importance was also potentially influenced by the difference in number of observations across the years, with 2014 being the lowest sample (Fig S1).

PROBABILITY OF FLOWERING ONSET ON A TREE

Similar to flowering status, the onset of flowering at the individual tree level across Kerala was predicted both by temperature, precipitation and solar radiation. Minimum temperature, soil moisture and solar radiation had significant effects on the onset of flowering in jackfruit and mango trees (Fig 3). For both these species, low minimum temperature and soil moisture were associated with high probability of flowering onset (Fig 3). Solar radiation had a weak positive effect on the probability of flowering in jackfruit and mango (Fig 3). For tamarind, however, only minimum temperature was a significant environmental predictor of flowering probability; soil moisture and solar radiation were not significant (Fig 3). These models were built using

4685 trees, 6220 trees and 1224 trees each of jackfruit, mango and tamarind respectively across the years.

Similar to the ML models of flowering status, GLMMs models of flowering onset had substantially better fits for jackfruit and mango than tamarind. The conditional R^2 for the models, a metric of model fit including random effects, for jackfruit, mango and tamarind were 0.312, 0.344 and 0.306. But marginal R^2, that only includes predictions using fixed effects, was 0.094, 0.110 and 0.029 for jackfruit, mango and tamarind, suggesting poor predictability from environmental variables alone, especially for tamarind. This suggests that fixed effects explained lower amount of variation in the data than random effects of site and individual. The ICC of the models were 0.241, 0.262 and 0.286 suggesting that random effects were not very clustered. To assess the predictive power of the model for out-of-bag data, we assessed the agreement between the predicted and observed values from the onset model for one year of the data that was withheld from modelling across 9 LOOCV runs. Coefficient across these runs were similar in magnitude and direction (Appendix S6). Pearson's correlation coefficients for predicted vs observed for jackfruit, mango and tamarind across these runs 0.061, 0.106, -0.001. The average mean square errors, respectively were 0.061, 0.059, 0.055. F1 scores were 0.031, 0.063 and 0.003.

INTERACTIONS BETWEEN VARIABLES IN PREDICTING ONSET

The onset of flowering in mango trees was modified by several spatial factors. We considered five interactions in the models as described above. Elevation, aspect and degree of urbanisation

were significant modifiers of the flowering onset probability in mango trees. Drier soils were associated with higher probability of flowering onset; this effect was stronger in lower elevations. Lower minimum temperatures were associated with higher probability of flowering onset; this effect was stronger in north and east-facing slopes, the leeward side. Increased solar radiation had a small effect on increasing the probability of flowering; however this effect was obscured in urban environments, shown by a negative interaction effect .

Interaction effects were also important in models of jackfruit flowering, but not for tamarind. Elevation was a significant modifier of the flowering onset probability in jackfruit trees. Solar radiation increased the probability of flowering in jackfruit trees, but trees at lower elevation were more sensitive to changes in solar radiation than those at higher elevation (Fig 4). No other interactions assessed were significant for flowering onset in jackfruit. No interactions were significant for onset of flowering in tamarind trees. However, the model was a poor fit, and therefore, the possibility of significant interactions with more data cannot be ruled out.

SPATIOTEMPORAL PATTERNS IN ENVIRONMENTAL VARIABLES

Locations across Kerala are experiencing heterogenous change in climatic conditions. Emerging hotspot analysis revealed spatiotemporal patterns in the three variables assessed, minimum temperature, soil moisture and solar radiation, in the time period when SeasonWatch data was collected. Aggregated across the state, these environmental variables did not show significant overall directional trend of change, defined as new or intensifying hotspot/coldspot, at the spatial scale assessed, from 2014-2022. Along the west to east elevational gradient in Kerala, minimum

temperature had persistent hotspots in coastal locations, while inland sites towards the east were persistent cold spots, potentially due to higher elevation (Fig 5). Emerging hotspot analysis for soil moisture revealed a persistent hotspot in the south centre of the state. This hotspot corresponds to the eastern parts of the districts of Ernakulam and Kottayam, and the western parts of Idukki. All areas show oscillating trends for solar radiation across the time period assessed, as expected.

For minimum temperature and soil moisture, pixels around the persistent hotspots, show varying and heterogenous trends in hotspots or coldspots. Mid-elevation sites in Kerala between the persistent coldspot and hotspot for minimum temperature have been classified as oscillating, sporadic or historical hot/coldspots, suggesting heterogenous change. One pixel in the east of Kerala also showed an intensifying cold spot. Similarly for soil moisture, areas around the persistent hotspot show sporadic or oscillating hotspots. No such patterns were discernible for solar radiation.

DISCUSSION

Altered temperature and precipitation patterns are expected to affect phenological responses of tropical tree species, but their variability across large spatial scales is rarely quantified and poorly understood. Combining a unique citizen science dataset from India, unparalleled in scale for tropical trees, with remotely sensed environmental variables, we show that flowering status and onset in three common tropical species is influenced by environmental variables in the preceding fortnight. Moreover, we show that the influence of these temporally varying environmental

factors are modified by elevation, slope and urbanisation. Finally, for widespread species, existing phenological information tends to be localised, making it difficult to measure variability across individuals and sites to make population-level predictions at the regional scale.

Our study, which spans large spatiotemporal scales, strengthens existing understanding on the influence of temperature, precipitation, and solar radiation on tropical tree reproductive phenology (Cook et al. 2012b, 2012a, Mendoza et al. 2017, Babweteera et al. 2018, Dunham et al. 2018). Across the three species, recent levels of minimum temperature had the highest influence on the observed flowering status of the tree at any given time, followed by either solar radiation or soil moisture (Fig 2). At the population scale, extremes in precipitation, including drought years, have been shown to reduce flowering and fruiting in tropical trees (Wright et al. 1999, Harrison 2000, Sakai and Kitajima 2019). Our results show that besides total precipitation, soil moisture is an important predictor for observable flowering phenophase at the individual scale, across these widespread species (Fig 2). Taken together, these results suggest that, although large variation exists, tropical tree phenology at the individual level responds to environmental conditions in the short term. Our study spans nine years of observations, more than the minimum recommended 6 years for tropical species (Bush et al. 2018), but we would like to note that given the geographic variation, this time series may not be sufficiently long. However, this dataset is, to the best of our knowledge, unprecedented in spatial and temporal scale for reproductive phenology in tropical tree species.

While the onset of flowering on tropical trees can be triggered by climatic factors, we show that habitat factors had modifying effects on their influence. Modelling the probability of flowering onset, we show that low minimum temperatures, dry soils, and higher levels of solar radiation are potential triggers for flowering in jackfruit and mango. This corresponds to the seasonal understanding of flowering in these species - with the start of flowering in late December or early January (Fig 1, Table S1). These results are also in concordance with other studies from the tropics, where cool temperatures, combined with drought conditions were found to trigger flowering in select forest species (Satake et al. 2019). Elsewhere, dry spells followed by single instances of precipitation have been found to trigger flowering (Wright et al. 2019). In both mango and jackfruit trees, lower minimum temperatures were associated with higher probability of the onset of flowering, and this effect was higher in north and east-facing sites, where there is lower light (Fig 4). This result is in concordance with another longitudinal study on forest trees monitored in Uganda where tree location, specifically in relation to light, increased the probability of flowering(Babweteera et al. 2018). However, this result is in contrast to results from the neotropics, where up to 12 weeks of consistent high solar irradiance predicted flowering in multiple forest species (Wright and Calderón 2018). Tropical tree leaf exchange and reproductive phenology are known to be altered in urban habitats (Neil and Wu 2006, Kabano et al. 2020). Our results from mango trees in Kerala shows that trees at lower elevations had higher probability of flowering in drier soils, and that the effect of solar radiation on flowering probability was obscured in more urban habitats (Fig 4). While interaction effects were different across species and not identifiable in some, our results from mango trees, with the largest number

of trees in the dataset, shows the potential of identifying these patterns along meaningful scales of variation. By assessing multiple modifiers simultaneously, our study makes novel contributions to predictive modelling of tree phenology in tropical habitats where multiple global and local drivers of change co-occur.

Our results on the onset of flowering phenology shows high variation among individuals and sites in three widespread tropical species. Tropical tree flowering patterns may not show discrete on/off signals that track the environment as many temperate species do. Reproductive strategies in tropical trees are often diverse and may have long-term evolutionary function in addition to short-term ecological response (Singh and Kushwaha 2006). Jackfruit, mango and tamarind trees showed diffuse and noisy patterns of flowering in Kerala, with this phenophase being reported as present in some proportion of trees in every week of the year in SeasonWatch (Fig 1, (Ramaswami et al. 2021)). Mixed models of flowering onset showed that environmental variables explained only ~10-15% of the variation, while including random effects of individuals and sites explained ~30-35% of the variation across all three species. Tree random effect was significant in the models for all three species, suggesting unexplained variation among the individual trees considered that requires further systematic inquiry. Since these are cultivated species, the differences in varieties among individuals has a known influence on phenological variation (Makhmale et al. 2016, Singh et al. 2021). However, information on variety of fruit is not recorded in SeasonWatch, and therefore our study could not test the extent of this effect . Random effect sizes could also be linked to energy reserves in the growing season, responding to

environmental correlates beyond the fortnightly time window that we considered (Babweteera et al. 2018). Further modelling that includes a forecasting framework and time lags would be an important future direction in tropical phenology research. Beyond the specific spatial factors included in the model, the site random effect explained a large amount of remaining variation. A potential contributor could be the spatial scale of environmental data; assessed variables are at the kilometre spatial scale whereas fine-scale heterogeneity in temperature and rainfall can influence trees (Scheffers et al. 2017). Further research on spatial and temporal drivers can faciliate mechanistic modelling and forecasting of pheonological responses in space and time.

Our results become pertinent under existing and future climatic variability in the tropics, and the potential impacts on the reproductive phenology of commercially important tropical trees. Across Kerala, our results from emerging hotspot analyses show spatiotemporal patterning in climate variables associated with flowering phenology in common tree species (Fig 5). Although there were no directional patterns in change in variables (new or intensifying hot/cold spots), the years we assessed represent a short timescale. Our analysis of patterns over the last decade showed spatial variation in hotspots and coldspots for temperature and precipitation and their change over time. An important future direction for phenological studies would be to understand intraspecific variation across space and forecast phenological responses in these novel climates. However, even in the decade of assessment, we demonstrate low predictability in the direction climate responses in some regions (osciallating hotspots, sporadic hotspots). Such uncertainties across years could potentially influence tree responses to climate in these areas assessed. Global

climate phenomena such as the El Nino Southern Oscillation affect temperature and precipitation variability across the tropics, and often results in above-average temperatures or below-average precitpitation (Wright et al. 1999). The same is expected for the Indian subconitnent, along with influences on other climatic phenomena such as the Indian Ocean dipole affecting weather on the mainland Gadgil and Francis (2016). As spatiotemporal patterns in temperature and precipitation are altered by global climate change in tropical landscapes, forecasting phenological change is crucial. Across the Indian subcontinent, precipitation and temperature variability has increased in the past century and is projected to continue to increase (Power et al. 2013, Dahinden et al. 2017, Zhang and Fueglistaler 2019). Beyond the timescales of our study, Kerala, and much of the global tropics, is projected to move into a temperature and precipitation regime that has no analog globally, making it difficult to predict and plan for ecosystem responses (Dahinden et al. 2017). This makes it crucial to forecast and mitigate biotic responses to specific environmental correlates as well as combined effects. However, climate change predictions and action for the tropics are still largely at coarse spatial scales, making local forecasting and mitigation difficult (Dessai et al. 2009, Shepherd and Sobel 2020). As a result, climate policy for these regions are lacking in ecologically-derived understanding that prioritises the stability of ecosystem services.

Our study using repeat citizen-science data and individual based modelling at spatial and temporal scales of climate modelling, represents a significant first step in combining tropical ecology with climate science beyond broad generalisations. In some temperate landscapes, onset of leaf-out phenology can be remotely sensed and therefore measured at the large scale

(Czernecki et al. 2018). However, measurement of reproductive phenology, especially for species that have inconspicuous flowers and fruits, requires repeat on-ground measurements and is extremely difficult to organise at the large-scale. Citizen science may be one of the few ways to acquire such data, and we have leveraged such a unique dataset compiled by SeasonWatch to predict the onset of a reproductive phenophase (Abernethy et al. 2018, McDonough MacKenzie et al. 2020, Ramaswami et al. 2021). Broadly, we demonstrate the potential of citizen science observations in improving the state of our knowledge in climate science and infusing local ecology into climate-adaptive management. Predictive modelling informed by variation among individuals and sites is a crucial next step to phenology research as spatiotemporal patterns in climate variables change across tropical landscapes. Our study thus demonstrates the potential of citizen science in filling data gaps and providing fine-resolution predictions at the large-scale to aid locally relevant climate policies.

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DATA ACCESSIBILITY STATEMENT

All the data used in this manuscript are publicly accessible. The code used for accessing the geospatial data is archived in Google Earth Engine. The modified datasets, code for analysis and figures have been archived in GitHub and the repository will be made public upon acceptance.

Research ethics

The study did not deal with human subjects or data with personal identifiers. For SeasonWatch data, we followed ethical protocol that was agreed on by the SeasonWatch Citizen Scientist Network.

Author contributions

Funding for this work was acquired by GR and NA, while the study was conceptualised by GR and KA. Phenology data was collected by the SeasonWatch Citizen Scientist Network. KA cleaned and validated the phenology data while JM accessed and collated the geospatial data. KA, JM, CL and RR performed the analysis led by KA and supervised by GR and NA, with administrative support from HT. KA visualised the data and wrote the first draft; KA, JM and GR edited the manuscript with support from all authors.

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Conflict of Interest

The authors have no conflict of interest to declare.

TABLES

Table 1: Data distributions. *Description of the SeasonWatch dataset for jackfruit, mango and tamarind in Kerala from January 2014 to July 2022*

	Artocarpus heterophyllus	Mangifera indica	Tamarindus indica
Total number of observations	72,097	68,696	24,213
Total number of trees	7,927	9,919	1,750
Number of trees with single observations	6,270	8,128	1,277
Number of observations with no flowering at t-1	25,695	26,212	12,426
Number of trees in observations with no flowering at t-1	1,028	1,105	320

Table 2: Environmental data. *Variables, data sources and transformations*

Datasets	Data Source	Resolution	Transformations used	Variables derived
Flowering observations	SeasonWatch https://www.seasonwatch.in/	temporal: ~once every two weeks spatial: tree-level observations/spatial points		Flowering binary and ordinal
Precipitation	ERA5-Land https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview	temporal: hourly, aggregated to fortnightly spatial: 11.1 km grid	Sum	Total precipitation, DryDays
Temperature	ERA5-Land https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview	temporal: hourly, aggregated to fortnightly spatial: 11.1 km grid	Max, min, mean	Max temp, min temp, mean temp
Soil Moisture	ERA5-Land https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview	temporal: hourly, aggregated to fortnightly spatial: 11.1 km grid	Mean (of total column depth at each time step), Mean (hourly -> Daily -> Fortnightly)	Mean SM
Solar radiation	ERA5-Land https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview	temporal: hourly, aggregated to fortnightly spatial: 11.1 km grid	Sum (hourly -> daily -> Fortnightly)	SolarRad
elevation	SRTM https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1	temporal: no change spatial: 30 m grid	terrain functions	Elevation, slope, aspect
urbanisation	NASA nightlights https://earthobservatory.nasa.gov/features/NightLights	temporal: no change spatial: 0.5 km grid		urbanisation

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FIGURES

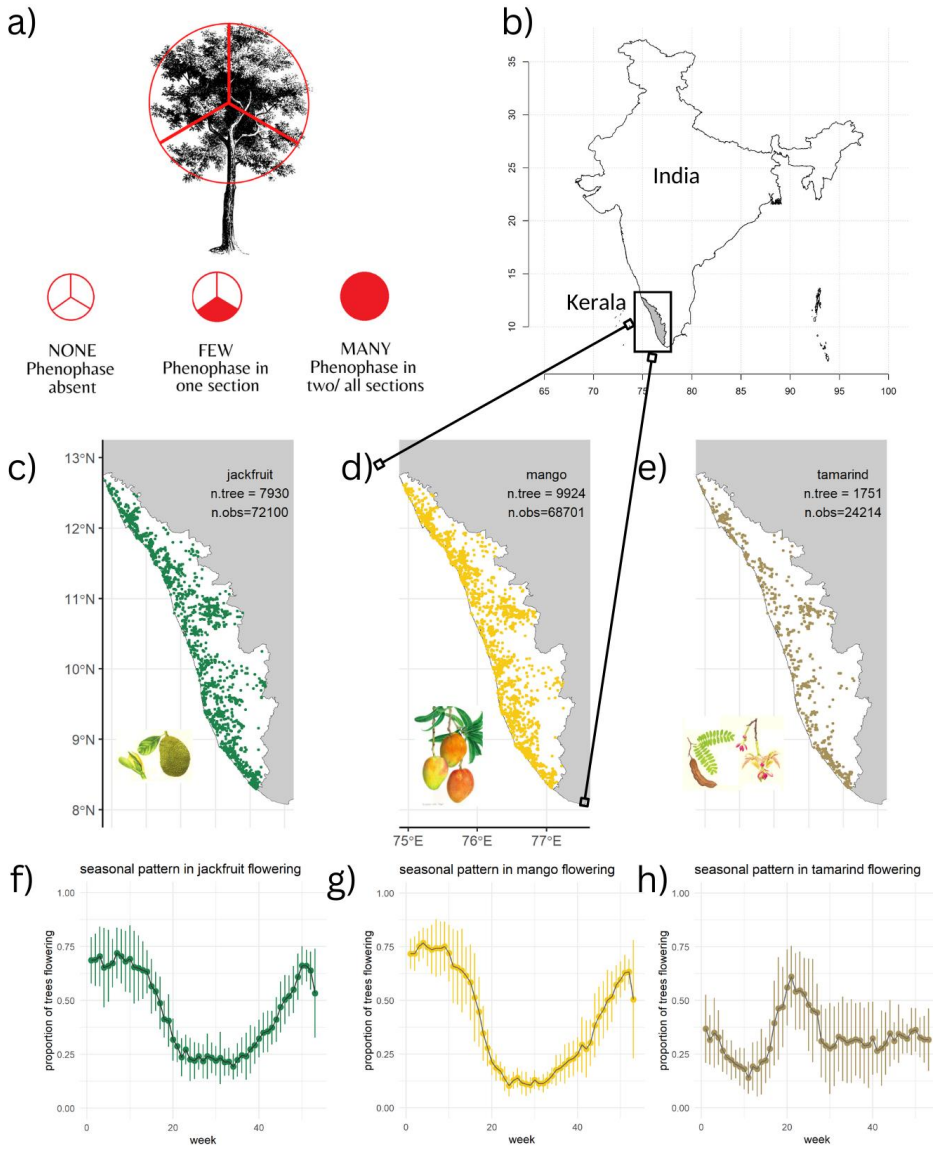

Figure 1: SeasonWatch protocol, species and map of observations. *a) SeasonWatch observation protocol for tree phenology - phenophase quantities 'none', 'few', 'many' roughly correspond to*

the presence of a phenophase in 0, 30%, and >30% of the tree canopy b) Outline of India with the state of Kerala marked in grey. c), d) and e) - map of observations of jackfruit, mango and tamarind trees across Kerala, considered in this study along with illustrations of flowering and fruiting phenophases in jackfruit, mango and tamarind respectively. Panels f), g) and h) show seasonal patterns in flowering of the three species in Kerala from 2014-2022. Dots represent mean proportion of trees flowering in that week and error bars represent standard deviation across the years of study. Image credits: a) Sayee Girdhari; illstration in c) Neelam Modi for SeasonWatch; illustration in d) fairchildgarden.org; illustration in e) Neelam Modi for SeasonWatch

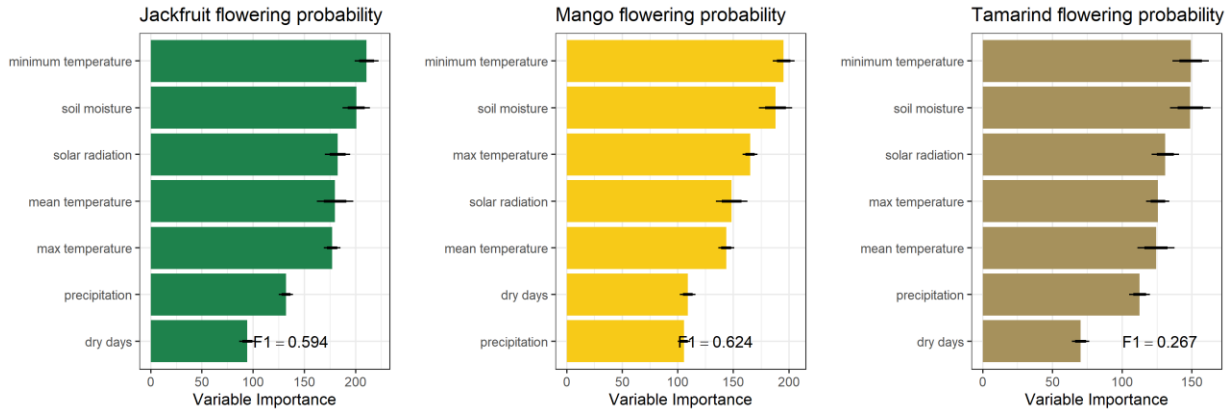

Figure 2: Variable importance from machine learning models of flowering occurrence *Mean Decrease in Accuracy from Random Forest models of the probability of observing flowering in a) jackfruit, b) mango, c) tamarind. Variable importance has been calculated at each LOOCV run, Length of the bars represent mean MDA across the runs and variables are ordered in their decreasing order of mean importance. Thick black error bars represent 1 standard deviation from the mean and the thin bars represent 1.96 standard deviation from the mean across the runs.*

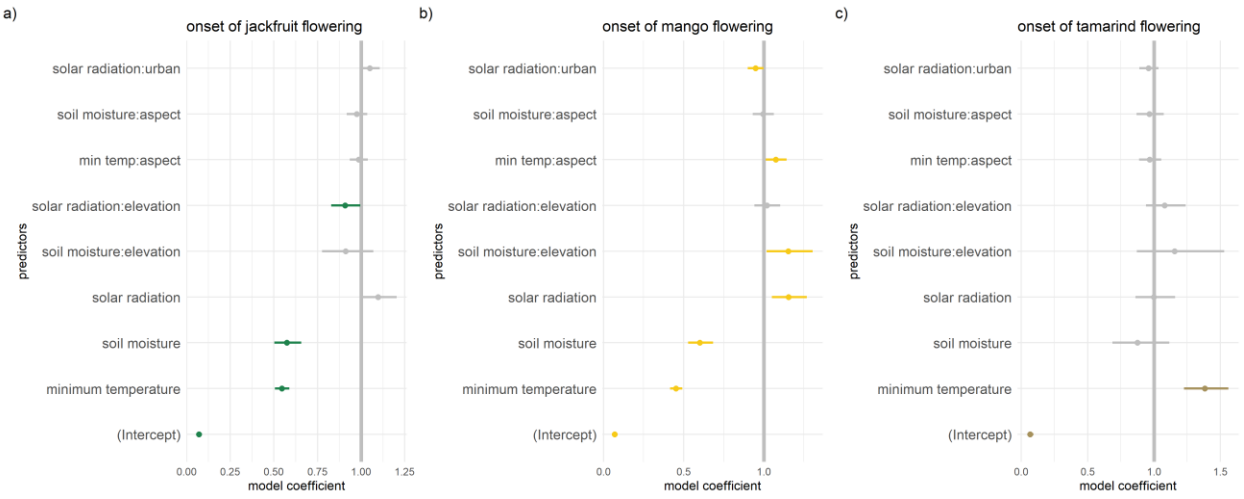

Figure 3: Model coefficients for flowering onset from GLMM models *Generalised linear mixed effect models (with a binomial family of errors) modelling flowering onset; i.e. the probability of observing flowering given no flowering at the previous timestep. Model includes most influential temperature variable, precipitation variable from the ML models and solar radiation. Model also includes all interactions barring known correlated combinations. Dots reporesent mean effect and the lines represent 95% confidence intervals of the estimate. The vertical grey line represents no-effect. Predictors with confidence intervals that do not overlap with the no-effect line are considered significant; others are represented with grey dots.*

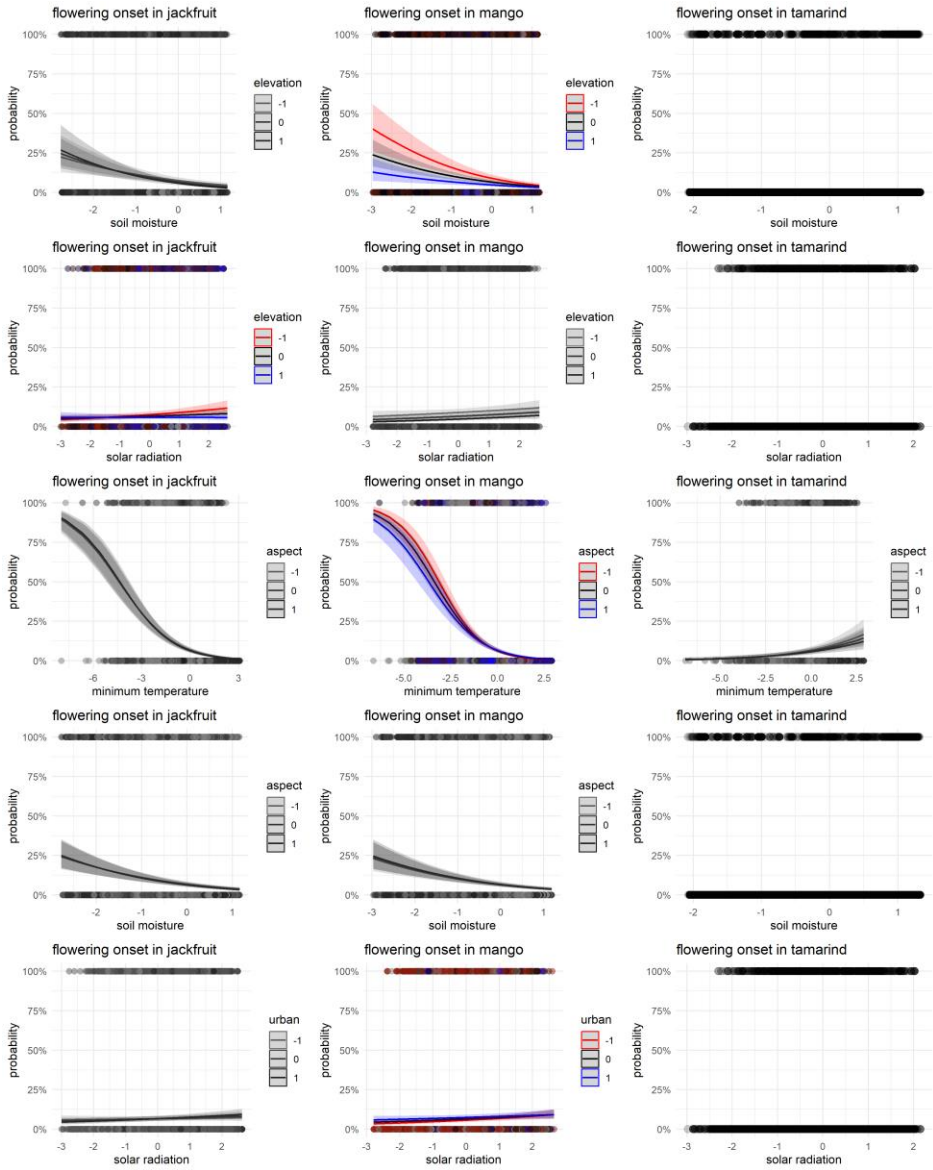

Figure 4: Predicted responses of flowering phenology of jackfruit, mango and tamarind trees (left to right) to interactions between static and time-varying environmental predictors. *Mean and interaction effects derived from generalised linear mixed models of each species using binary response variables. Flowering probability is represented as a function of each time-*

varying environmental variable at three levels of the static variable - mean value and mean+/- 1 sd for the range of observed values, with the low value represented as red, mean as black and high as blue. Lines represent binary model predictions and the ribbons around the lines represent 95% confidence intervals. Dots represent observed values of flowering. For main effects that are significant and interactions that are not significant, lines and points are represented in grey. For main effects that are not significant, only the data is plotted and not the predicted lines.

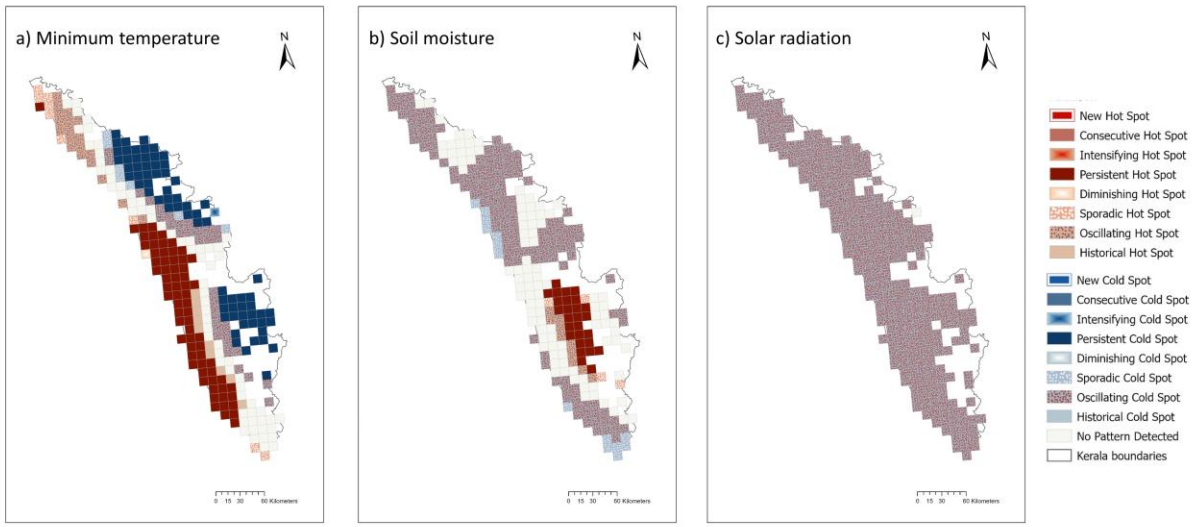

Figure 5 - Hotspot analysis of environmental data using spatiotemporal data from 2014-2022. *Hotspot analyses for a) minimum temperature within a fortnight, b) soil moisture within the fortnight and c) solar radiation within the fortnight within each grid of 11 km x 11 km spatial resolution*

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