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TITLE: The ecology of tree reproduction in an African medium altitude rainforest

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ABSTRACT

The occurrence of flowering and fruiting in tropical trees will be affected by a variety of factors, linked to availability of resources and suitable climatic triggers, that may be affected by increasing global temperatures. Community-wide flowering and fruiting of 2,526 trees in 206 plots were monitored over 24 years in the Budongo Forest Reserve (BFR), Uganda. Factors that were assessed included: the size of the tree, access to light, the impacts of liana load, effects of tree growth and variation between guilds of trees. Most flowering occurs at the end of the long dry season from February to April. Trees that had access to more light flowered and fruited more frequently. Pioneer and non-pioneer light demanding species tended to reproduce more frequently than shade-bearing species. Trees that grew faster between 1993-2011 also fruited more frequently. When examining all factors, growth rate, tree size, and crown position were all important for fruiting, while liana load but not growth rate was important in reducing flowering. Trees in BFR show a large decline in fruiting over 24 years, particularly in non-pioneer light demanders, shade-bearers, and species that produce fleshy fruits eaten by primates. The decline in fruit production is of concern and is having impacts on primate diets and potential recruitment of mahogany trees. Whether climate change is responsible is unclear but flowering of the guilds/dispersal types which show declines is correlated with months with the coolest maximum temperatures and we show temperature has been increasing in BFR since the early 1990s.

Key Words: Budongo Forest Reserve, crown position, climate impacts, guild, phenology, tree size, tropical forest

Word Count: 5015 words

Tweetable abstract: Flowering and fruiting of trees, providing fruit for primates, declines dramatically in tropical forest - warming temperatures may be to blame

A COMPLEX SET OF FACTORS POTENTIALLY AFFECT FLOWERING AND FRUITING of tropical trees but these are poorly understood. Factors such as climatic cues have been suggested to trigger flowering but whether a tree flowers and then subsequently produces fruit will also be affected by available resources which in turn will be affected by competition with neighbouring trees or with factors that affect the availability of light and of nutrients from the soil. To date, much research of the impact of climate change on flowering and fruiting has focused on the timing during the seasons of phenology of temperate/boreal zone plants (Root *et al.* 2005; Parmesan, 2006) with relatively few studies heralding from the tropics (*e.g.* Corlett & LaFrankie, 1998; Wright & Calderón, 2006). Further, there is a paucity of knowledge on how ecological processes operating at local scales might confound or obscure phenological responses of tropical trees to global climate change.

Tropical trees may be sensitive to increasing temperatures; exhibiting lower growth rates (Feeley *et al.* 2007; Clark *et al.* 2003), photosynthesising over a narrower range of temperatures compared to temperate species (Cunningham and Reid 2002; 2003), and changing allocations of root and above-ground biomass (Reichart and Borchert, 1984; Körner, 1991). Climate changes are expected to affect a number of proximate cues for tropical tree phenologies such as: onset of rain in seasonal climates (Sakai *et al.* 2006), drought in aseasonal climates (Ashton *et al.* 1998), cold snaps (van Schaik *et al.* 1993), increasing temperature (Wright and van Schaik, 1994; Thomas and Vince-Prue 1997), and soil moisture (Wright and Calderón, 2006). In addition, invariant cues that will not be affected directly by climate change such as seasonal changes in solar irradiance (Borchert *et al.* 2005; Kinnaird, 1992), changes in day length (Cleland *et al.* 2007), and changes in timing of sunrise and sunset (Kinnaird and O'Brien, 2007) have been shown to affect phenology, but their impacts may be affected if climate change increases cloud cover for instance, and thereby reduces light level or duration.

Ecological factors that might also affect flowering and fruiting of tropical trees include species level differences in life-history (e.g. guilds and dispersal mechanisms), availability of light, age or size of tree, and competition from lianas (Wright *et al.* 2015). The role of these factors in determining phenology in tropical forests has rarely been studied, partly because most sites monitor large trees and often a subset of trees such as those important as food for primates.

These designs preclude community-wide analyses of flowering and fruiting. In one of the rare studies that looked at community-wide phenology in Africa, Sun *et al.* (1996) measured the flowering and fruiting of trees in the Nyungwe Forest in Rwanda and extrapolated the results to community wide phenology patterns using plot data on the abundance of trees. They showed that larger seeded species tended to have more aggregated fruiting patterns but did not assess guilds of tree fruit types. However, they selected the 15-20 cm diameter at breast height (DBH) as a measure of an 'adult' tree and only sampled trees bearing fleshy fruits, because of their interest in frugivores. Plumptre (1996) showed that several species will not fruit until at a much larger DBH than 20 cm so that it is important to factor in DBH in any analysis of phenology data. Studies of tropical tree phenology have usually assessed the times of the year when flowering and fruit production occur (Chapman *et al.* 2005a; 2005b; 2012) or the frequency of flowering and fruiting over the years (Bush *et al.* 2017; Bush *et al.* 2018; Adamescu *et al.* 2018). This paper makes a community-wide ecological assessment of phenology of trees in plots from the Budongo Forest Reserve (BFR) in western Uganda, monitoring all species of trees larger than 10 cm DBH in plots, because community-level effects may be more closely aligned to functional change in the ecosystem than detailed mechanistic analyses of individual species where usually 'mature' individuals are selected for monitoring.

The BFR is one of the larger Forest Reserves in Uganda, situated on the escarpment above Lake Albert in the Western Rift Valley, a medium altitude semi-deciduous moist tropical forest dominated by *Cynometra alexandri, Celtis mildbraedii, Celtis zenkeri* and four mahogany species (*Khaya* and *Entandrophragma* species). It has been one of the main sources of hardwood for the country since 1925. Early management aimed to undertake selective logging after cycles of 60-80 years (Plumptre, 1996). In 1991, the Budongo Forest Project, which subsequently became the Budongo Conservation Field Station (BCFS), was established to monitor the impacts of the selective logging and to better understand the ecology of the forest including the role of frugivores in seed dispersal and forest regeneration (Plumptre, 2006; Plumptre and Reynolds, 1994; 1996). Unlike many sites where tree phenology is monitored in tropical forests, a plot-based approach to phenology was employed, monitoring all trees larger than 10 cm DBH in 7 m radius plots across two compartments in the forest. This provides a unique opportunity to assess how community-wide fruiting and flowering in the forest varies by tree size (Plumptre, 1995; Wright *et al.* 2005), its position in the canopy, with guild of tree, and with its growth rate to better understand the causes of variation in tree phenology within and between species. A decline in fruiting has been reported from the forest (Babweteera *et al.* 2012; Plumptre, 2012) but the causes are not known and the decline is described in more detail here.

Analyses focused on four main questions:

1. What are the annual patterns in community-wide flower and fruit availability in Budongo Forest Reserve? This is important to understand the ecology of the forest and the feeding ecology of dependant species.
2. What are the differences in phenology between guilds of trees and their seed dispersal mechanisms? Guilds of species are more likely to show a similar functional response to changes in the environment.
3. How does phenology vary with respect to the size of a tree, its position in the forest and what impacts can lianas have on the phenophases? It is important to understand what ecological factors may be hindering reproduction in trees separately from changes in climate.
4. How has community-wide fruit and flower production varied over time? Understanding the long term trends in flower and fruit availability in the forest and how trends have varied over time is important for understanding broader ecological impacts, and possible impacts of climate change.

METHODS

DESIGN OF STUDY - Phenology data collection was initiated in the BFR in 1993 by BCFS. Five line transects were established in each of eight logging compartments in the forest (Plumptre, 1996) which were used for surveying primates (Plumptre & Reynolds, 1994; 1996) using a stratified random sampling method (Plumptre & Reynolds, 1994). At 100-metre intervals, seven-metre radius plots were established to measure the abundance of trees within the compartments. Phenology data were collected monthly in 206 plots in two compartments, N15 (100 plots) and N3 (106 plots), which have been monitored almost continuously from January 1993 to December 2016. A total of 2,526 trees were monitored from 125 species in 35 families. Initially 1,509 trees were marked for monitoring in January 1993. New trees which had reached 10 cm DBH were added for monitoring in 1997 (202 trees) and again in 2011 (812 trees) as individuals in the plots died and were replaced. Effectively, all trees greater than 10 cm DBH were monitored within an area of 3.17 hectares across both sites, allowing us to estimate flower and fruit availability per unit area. Trees were monitored visually rather than collecting fruit in traps because it provides a more direct assessment of the phenology and has been found to be more accurate (Morellato *et al.* 2010).

DATA COLLECTED FROM MONITORED TREES - Each tree selected for phenology monitoring was visited once each month and the presence of flowers, unripe and ripe fruit were recorded on a 0-4 abundance scale. In the analyses, these scores were recoded to 1 or 0 for the presence or absence of the phenophase. Although unripe fruit data were recorded, we only analyse here the results of ripe fruit and flowering. From January 1998 observers also estimated the number of fruits by eye by counting a portion of the canopy and multiplying this by similar areas to estimate the total number in the canopy. All trees were marked for growth measurements by painting a line around the trunk at the point of measurement. DBH was recorded in 1992, 1997 and 2011 and used to calculate an average annual growth rate (GROWTH) between the earliest measurement and the re-measurement in 2011.

Tree Size Class: Tree species exhibit differences in their range of stem diameters. Understorey trees such as *Rinorea angustifolia*, and *Lasiodiscus mildbraedii* rarely reach 40 cm DBH, while large canopy species such as *Khaya anthotheca* and *Cynometra alexandrii* can exceed 200 cm DBH. In order to assess whether larger sized individuals tend to flower or fruit more frequently than small sized individuals (Plumptre, 1995) it was therefore necessary to standardise across the range of DBH values. Tree species where at least 30 individuals were monitored over the years were grouped into 5 classes of DBH based on relative sizes of the trees from the minimum sizes (10 cm) to the largest sizes for that species. This classified each species from small to large individuals on a 5-class scale (DBH.GROUP) and each individual was assigned to the size class 1-5 based on the cut-off values for its species. We also computed a binary class of DBH with classes 1-3 in one group and 4-5 in a second group (DBH2) to separate the largest trees from other trees.

Crown Position: We assessed the location of individual tree canopies with respect to the forest canopy using a Crown Position Score (CP), or Crown Exposure Index, in 1993, and 1997 (for trees added at that time): 1 = no direct light; 2 = side light from a gap; 3 = vertical overhead light but tree canopy below forest canopy level, 4 = tree canopy at forest canopy level; 5 = emergent tree above canopy (Dawkins, 1958; Alder & Synnott, 1992). Crown position is a proxy measure for light availability. We also grouped the CP classes into a binary group with classes 1-3 in one set and 4-5 in a second set (CP.GROUP) to separate trees at canopy level from other trees. A Fourier analysis (Bush *et al.* 2017) of the frequencies of flowering and fruiting by individual trees was made for the trees in the two CP.GROUP classes.

Liana impacts (LIANA): Similarly we recorded the position of lianas on the tree using a Liana Score (LIANA): 1 = no lianas on tree; 2 = lianas on bole of tree; 3 = lianas in branches and parts of tree crown; 4 = lianas covering crown of tree (Plumptre, 1996). Lianas will compete with a tree's ability to photosynthesise and we expected to find a reduction in phenophase with higher liana scores.

Data from 1997, 2001, 2002, 2003 and 2008 were not included in the analysis because of concerns about accuracy. So in all analyses these years were omitted. Occasional months (Dec 95, Nov 96, Oct 98, Jan & Feb 99, Sep, Oct & Dec 2000) were also not included because funding or illness had prevented data collection. A total of 18.5 years of data were therefore available for analysis.

DISPERSAL TYPE AND TREE GUILD – Tree species were categorised by seed dispersal methods: Wind dispersal, Ballistic dispersal (fruits that tend to explode open), Auto dispersal (tend to fall from the tree – *e.g.* Beans in pods), and Animal dispersal. Animal dispersal was classified into three further groups: Large Fleshy fruits (larger than 2-cm long), Small Fleshy fruits (less than 2-cm) and Zoo-Capsules (hard berries that birds tend to disperse). Tree guilds were assigned using the classification of Hawthorne (1995) and Sheil (1996): 1 = pioneer; 2 = non-pioneer light demander (NPLD); and 3 = shade-bearers. A few other species that could not be confidently assigned to a guild were omitted from the analyses. A Fourier analysis using the methods of Bush *et al.* (2017) was used to estimate the cycle length of flowering and fruiting by individual trees. The dominant cycle length was also analysed for each fruit dispersal category and guild (Adamescu *et al.* 2018). Fourier analysis was only made on trees with at least 50 months of continuous data. This is below the recommended six years duration but the data precluded longer periods: short cycle lengths (but not necessarily cycles longer than 24 months) should be accurately identifiable from this time series.

CLIMATE DATA – Rainfall was measured at BCFS in a plastic rain gauge read at 8 am and recorded to the nearest millimetre. Maximum and minimum temperatures were recorded at the same time. These climate data were analysed to obtain average values for each month, average values for a seven day running mean and average values for each day across years. ENSO El Niño 4 (NINO4) Sea Surface Temperature (SST) values from 1993-2017 (https://climatedataguide.ucar.edu/climate-data/nino-sst-indices-nino-12-3-34-4-oni-and-tni) and Indian Ocean Dipole (IOD) SST values from 1993-2010 (http://www.jamstec.go.jp/frcgc/research/d1/iod/HTML/Dipole%20Mode%20Index.html) were compiled as they have been shown to influence African climate (Nicholson and Kim, 1997; Williams and Hanan, 2011). NINO4 measures the central-western Pacific Ocean temperatures and IOD measures the Indian Ocean temperatures, both known to affect climate and primary productivity in East Africa (Williams and Hanan, 2011).

Analyses were made in R version 3.4.3 (R Core Team, 2017) and focused on the following:

MONTHLY PHENOPHASE PATTERNS ACROSS THE YEAR – Community-wide patterns in annual flowering and fruiting of trees in Budongo were assessed by calculating the proportion of years for each month that individual trees flowered/fruited in that month between January 1993-December 2016. We selected trees that had at least 4 years of data using all the data for each individual estimate of proportion of years for each month that the tree flowered/fruited. Trees that died between 1993-2016 were removed from the analysis in case they were diseased when monitored and might have affected the analyses. These proportions were then summed and grouped by fruit dispersal type to assess the average number of trees of each dispersal type flowering and fruiting in each month of the year per hectare.

EFFECT OF TREE SIZE, CROWN POSITION, RATE OF GROWTH AND LIANAS ON PHENOLOGY – To assess the combined impacts of tree size, crown position, liana cover, guild, dispersal type and rate of growth on phenology we fitted a generalised linear mixed model (GLMM) to predict the proportion of years each individual tree fruited/flowered from the above factors using species as a random factor. We opted to use the proportion of years when each phenophase was shown because of the long time period of data (as opposed to predicting a 1/0 score for whether an individual tree flowered/fruited over the full time period). Effectively the GLMM assesses which factors predict more frequent flowering/fruiting across years and assumes that trees that are young or stressed will flower or fruit less frequently than those that are mature and less stressed.

$$P_{phenophase} \sim Dispersal\ type + Growth + DBH2 + CP + LIANA + GUILD + (1|Species)$$

where $P_{phenophase}$ = Proportion of years with phenophase

A binomial GLMM was made in the lme4 package (Bates *et al.* 2015) using the *glmer* function, weighted by the number of years of data for an individual tree and using a Logit link function. Anova tests were made between models selectively dropping variables to test for significant differences between models. Over-dispersion was assessed by calculating the sum of squared Pearson residuals/ (sample size – number of parameters) (Zuur *et al.* 2009). No over-dispersion was found for flowering (Ø = 0.71) and fruiting (Ø = 0.49) and we proceeded with the binomial model.

INTER-ANNUAL VARIATION IN PHENOPHASE PATTERNS – The number of trees flowering or fruiting each year was calculated for trees which had been monitored between 1993 and 2016. Anomaly values were calculated for the forest as a whole comparing the value in each month with the mean value of that month across all years to assess if any general patterns could be detected for the forest as a whole. Anomaly scores were calculated for all trees, the three most common guilds and different dispersal types. In order to assess whether climate may be affecting flowering and fruiting, anomaly scores were correlated with the rainfall, maximum and minimum temperatures and the NINO4 and IOD SST values (Wright and Calderón, 2006) with up to a 12 month lag using Pearson correlations.

RESULTS

MONTHLY PHENOPHASE PATTERNS ACROSS THE YEAR – On average 13.3 trees flowered each month per hectare of forest but only 5.2 trees/ha produced ripe fruit each month. However variation in monthly flowering was large: flowering peaked in March (Fig. 1) with high numbers of trees also flowering in February and April. This occurs at the end of the long dry season from

December to early March (Fig. 1) when many trees lose their leaves and produce a flush of new leaves. Fruiting was more consistent across the year although it declines in the June-August short dry season when temperatures were lower (Fig. 1). On average fewer trees per hectare produced ripe fruit than flowered over the year indicating that many flowering events do not set fruit or that unripe fruit may be aborted before reaching maturity. Maximum temperature peaks in the long dry season (Dec-Feb) and is coolest in July-August while minimum temperatures show the opposite pattern (Fig. 1). Rainfall is bi-modal when analysed at monthly intervals but varies significantly within months of the year and these fluctuations (calculated using a running 7-day mean) are consistent between years (Fig. 1). To what extent these regular fluctuations within months of the year may act as triggers for flowering and fruiting is unknown.

DISPERSAL TYPE AND TREE GUILD –Fourier analysis of the frequency of phenophase for individual trees showed major variation between trees with different dispersal methods. Wind dispersed species had very consistent flowering times at annual intervals, while auto, and animal (capsules and small fleshy fruits) dispersed species flowered at both 12 and 18 month intervals (Fig. 2). Although flowering annually, fruiting of trees with wind dispersal occurred over a large range of intervals. This may be partly due to the fact that their fruits can stay on a tree for several months slowly dispersing the seeds so that no clear dominant cycles are identified despite the fact that flowering has a dominant 12 month cycle. Large fleshy-fruit producing trees tended to fruit at 18 month intervals. Fruits with ballistic dispersal methods tended to fruit at a sub-annual frequency (6 months).

Box plots of the frequency of flowering and fruiting across fruit dispersal type and guild show large variations between these functional types (Fig. S1. Supplementary Material). A Fourier analysis of flowering and fruiting frequencies by guild type did not produce any clear patterns between species (Fig. S2. Supplementary Material).

EFFECT OF TREE SIZE, CROWN POSITION AND LIANAS ON PHENOLOGY –

Tree size: Larger individuals within species flowered more frequently with higher proportions of trees flowering in group 4 and 5 classes compared with classes 1-3 (Table 1). Large trees also fruited more frequently (Table 1). This pattern was also found when comparing the average estimated number of fruits per fruiting event per tree (Fig. S3 Supplementary material), indicating that both the frequency of fruiting and the numbers of individual fruits increases as DBH increases across species. Analysing the most abundant tree species separately, we found an increase in the proportion of trees fruiting and in the average number of fruits per tree in a fruiting event with increasing DBH size class (Table 2).

Crown Position: The proportion of trees flowering or fruiting increased with larger crown position scores (Table 1). Trees at canopy level (score 4/5) fruited more frequently also. A Fourier analysis of the variation in flowering and fruiting cycles for trees in CP.GROUP score 1 or 2 did not show any clear patterns with crown position (Fig. S4 Supplementary material).

Liana score: There was no clear difference in the proportion of years in which a tree flowered with increasing liana load but there was a trend for decreasing fruiting with liana score (Table 1).

Factors predicting phenology: The GLMM for flowering identified DBH.GROUP, CP, and LIANA as significant factors predicting the proportion of years in which trees flowered but GROWTH, Dispersal type and GUILD were not significant at any level. The results show that the larger DBH (within a species range of DBH values), and the presence of the tree crown in the canopy or above were good predictors of increased flowering frequency but lianas covering the crown (score 4) could decrease flowering frequency (Table 3).

The GLMM for fruiting identified GROWTH, DBH.GROUP, and CP as being significant variables explaining increasing proportion of years in which trees fruited but that Dispersal type, GUILD and LIANA were not significant (Table 3). Larger DBH sizes (relative to the spread for a species), crown presence in the canopy, and increasing rates of growth were significant predictors of increased frequency of fruiting per year (Table 3).

INTER-ANNUAL VARIATION IN PHENOPHASE PATTERNS – Anomaly scores for both number of individuals flowering (Fig. 3) and fruiting (Fig. 4), as well as number of species flowering and fruiting each month, show that there has been a general decline in individuals fruiting across years but less so with flowering individuals (Fig. 3). There has been a decline in flowering of shade-bearer species but not of the other two guilds (Fig. 3) and NPLD and shade-bearer species have shown more of a decline in fruiting over time than pioneer species (Fig. 4). Further analyses of anomaly scores between dispersal types and across guilds for only large trees of each species show that it is the decline in flowering (Fig. S5 Supplementary Material) and fruiting (Fig. S6) of trees producing fleshy fruits (large or small) that is contributing to the overall decline and this holds if only large trees are considered (Fig. S7 & S8 Supplementary Material).

Analysis of the rainfall in BFR shows that when comparing the first six years of data with the last six years of data that rainfall has become more strongly seasonal. Rainfall has increased in the wet seasons and dry periods have become longer in the dry seasons (Fig. 5). Rainfall also has increased in the later parts of each wet season recently but decreased in the December-February dry season. There is some indication that temperature has increased when comparing the same time periods but unfortunately the thermometer location was moved in the late 1990s so we cannot be sure whether the change is due to the move or real increases. Comparison of the period between 2000-2005 with 2011-2016 shows warmer maximum and minimum temperatures in recent times, particularly at the coolest time of year, although the December and early January maximum temperatures have been cooler (Fig. 5).

There were few significant correlations between NINO4/IOD values and numbers of individuals or species flowering in the three main guilds (only using data from large trees). There were significant correlations with actual climate variables at site, particularly maximum temperature or the difference between maximum and minimum temperature (Table 4). Making the same correlations with seed dispersal type also indicated that maximum temperature and temperature range in the day are important and correlate with no time lag for wind dispersed and fleshy fruiting species (Table 4). Wind dispersed species flowered when maximum temperature or temperature difference was large while small and large fleshy fruiting species flowered when maximum temperature or daily temperature differences were low (Table 4).

DISCUSSION

The flowering patterns of the BFR are very seasonal, linked to the semi-deciduous nature of the forest. Following the long dry season from December to February flowering peaks in March, which is slightly later than the January flowering peaks in the Nyungwe Forest to the south of Budongo. Here, though flowering peaks during the short dry season between December to February and not after the main dry season between June-August (Sun *et al.* 1996). The Nyungwe Forest study though only included trees producing fleshy fruits and in Budongo the flowering of large fleshy-fruit and zoo-capsule producing species, but not small fleshy-fruit producing trees, tends to occur when it is wetter also (Table 4). Fruiting of trees tends to peak in the wet seasons (March-May and September-November) but certain species do not follow this pattern. For example, wind dispersed species fruit at the end of the long dry season when many of the trees have lost their leaves so that the seeds have more chance of being dispersed far by the wind (Fig. 1). This confirms the broad patterns observed in the diets of primates studied at Budongo with more seed and pods eaten in the long dry season and fleshy fruits more commonly eaten in the wet seasons (Plumptre, 2006).

We have assessed various ecological factors that could potentially affect flowering and fruiting of trees in BFR and which could influence results of phenology studies elsewhere in the tropics. The position of a tree with respect to the canopy (and hence its ability to receive light) was an important factor and once trees reach the canopy they flower and fruit more frequently. This is also related to the size of the tree (which may be linked to age although, since some trees in Budongo have not grown in 24 years, DBH and age do not correlate perfectly). Other studies have found that the size of the tree and the crown position affect flowering and fruiting with both increased size and increased light leading to greater reproduction (Plumptre 1996; Wright *et al.* 2005; Ouédrago *et al.* 2017). We had expected differences between tree guilds with pioneer species tending to grow fast, reproduce quickly, and invest less in wood density (Enquist *et al.* 1999) because they will die at a younger age than NPLD and shade-bearing species (Obeso 2002). Understorey species (shade-bearer) are presumably adapted to an environment below the canopy though, and would be expected to flower and fruit in such conditions and would not be so affected by crown position or size. However, guild type was not a significant predictor of the frequency of flowering or fruiting.

The growth rate of a tree also had a significant effect on fruiting frequency. Trees that grow faster will likely have more resources available for this growth and hence can also invest in fruit production once pollination has occurred. We had wondered if we would find a trade-off between growth and reproduction in individual trees (Obeso 2002) with those trees reproducing more frequently growing less fast but this was not the case for BFR. Where lianas covered the crown of a tree flowering frequency was reduced but liana load did not affect fruiting frequency significantly. The studies of Wright *et al.* (2005; 2015) found strong effects of lianas for some species with higher proportions of reproductive individuals with lighter liana loads. In BFR we know that trees with lianas in the crown grow more slowly and are more likely to die (unpublished data), and so expected a reduction in flowering and fruiting with increasing liana load.

We showed a marked decline in the fruiting of trees in BFR from the early 1990s with a decline but then recovery in flowering over the same time (Fig. 3). There was a peak in 2012 when considering all species but the causes of this is unknown. This decline is mostly found in the slower growing NPLD and shade-bearer species (Fig 3) and mostly those trees that produce fleshy fruit (Fig. S6). Chapman *et al.* (2012) documented decreasing fruit production between 1970 and 1984 from one dataset followed by increasing production between 1990 and 2002 from another set of trees measured in the same part of Kibale National Park in western Uganda, but it is unclear why there are these long term trends and differences between these two periods. Climate is likely to be an important factor in triggering flowering (Chapman *et al.* 2005b; Wright *et al.* 1999; Wright & Calderón 2006). We have shown that climate is changing in BFR with a trend of warming maximum and minimum temperatures and a greater seasonality in rainfall (Fig. 5), which follows predictions that have been made for climate change in the Albertine Rift (Seimon & Plumptre, 2012). Pioneer, NPLD and Wind dispersed species tended to flower when maximum temperatures were high while fleshy fruiting trees (Small and Large) and shade-bearers flowered in months when maximum temperatures were coolest (Table 4). More detailed experimentation is needed at a species level to assess what triggers flowering and fruiting but there is some evidence that the decline in fruiting of fleshy fruiting and shade-bearer species may be being affected by the warming temperatures at BFR.

We cannot be sure yet whether climate change is affecting the phenology of BFR but the large decline in fruiting is a concern as it is having impacts on the ability of primates to secure fruit in their diets. Studies of diets of monkeys have shown reduced fruit intake in 2012-2014 compared with 1993-1995 (Plumptre, 2006). Nyombi (2015) showed that fruit intake had markedly declined from 63% to 32% in blue monkeys (*Cercopithecus mitis*) and from 67% to 33% in red-tailed monkeys (*C. ascanius*). The diet of the monkeys is now predominantly leaves and other plant parts such as shoots and the bark. Recruitment of trees in the forest is therefore likely to be affected over time. Plumptre (1995) showed that mahoganies did not fruit until they attained large size (at least 50 cm DBH) and *Khaya anthotheca*, the most common mahogany species in BFR, fruited frequently between 1993 and 1997. However, of the 62 *Khaya* trees that have been monitored since 1997, only ten have fruited once in the past 20 years and none more than once. For the future production of timber in the forest this is of great concern. We need a better understanding of what causes trees to flower and fruit and hope this paper encourages further research on the trigger mechanisms.

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DATA AVAILABILITY STATEMENT

The data from this study will be made available on Dryad once published.

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TABLES

TABLE 1. The average proportion of years that trees flowered or fruited in each of the five diameter classes, five crown position classes and four liana score classes*. Superscripts with different letters were significantly different in binomial GLMM with species as a random factor, those with no letters were not significantly different.

		Categories				
Measure	**Phenophase**	**1**	**2**	**3**	**4**	**5**
Tree Diameter	Flower	0.128[a]	0.173[b]	0.150[b]	0.260[c]	0.334[d]
	Ripe Fruit	0.024[a]	0.037[a]	0.053[b]	0.101[c]	0.154[c]
Crown Position	Flower	0.133[a]	0.130[a]	0.182[b]	0.244[c]	0.334[d]
	Ripe Fruit	0.040[a]	0.046[a]	0.082[a]	0.126[b]	0.178[c]
Liana Score	Flower	0.139[a]	0.157	0.107	0.105[b]	
	Ripe Fruit	0.049	0.059	0.040	0.036	

*Diameter classes: 1 = Smallest; 2 = small; 3 = medium; 4 = large; 5 = largest

Crown Position: 1 = no overhead light; 2 = side light; 3 = overhead light; 4 = at crown level; 5 = emergent

Liana score: 1 = no lianas; 2 = lianas on stem; 3 = lianas in branches but not all of crown; 4 = lianas covering crown

TABLE 2. The ten most abundant species in BFR with the number of trees monitored (N), the percentage of trees fruiting per year (top line) and the average number of fruits on a tree (second line in parentheses) for each of the five DBH classes. In some years the numbers of fruits per tree were not recorded and where there were no values the cell is left blank. These ten species form 71% of tree stems in the forest and 54% of the basal area of trees in the forest.

		DBH Class				
Species	**N**	**1**	**2**	**3**	**4**	**5**
Celtis mildbraedii	450	0.43	1.50	2.50	3.20	5.97
		(5)	(74)		(136)	(317)
Lasiodiscus mildbraedii	369	1.76	1.78	1.53	1.43	2.98
		(70)		(100)		
Funtumia elastica	281	6.46	8.52	10.75	14.50	27.87
		(5)	(5)	(7)	(8)	(9)
Rinorea angustifolia	164	3.48	3.36	8.04	6.04	9.05
		(186)	(35)	(229)	(595)	(450)
Trichilia rubescens	130	0.96	2.69	1.24	2.68	2.62
		(21)	(111)	(28)	(330)	
Cynometra alexandri	96	0.55	1.13	7.88	16.03	21.79
			(203)	(47)	(85)	(180)
Celtis zenkeri	95	1.72	3.57	9.46	13.35	17.22
		(30)	(111)	(201)	(673)	(433)
Celtis gomphophylla	82	18.62	13.69	18.63	32.47	31.83
		(150)	(199)	(168)	(336)	(243)
Belonophora coffeoides	34	3.09	3.57	2.04	3.57	
		(43)		(231)	(24)	
Tapura fischeri	32	0.00	3.06	16.33	6.35	
				(2)	(237)	

TABLE 3. Comparison of binomial GLMM results: GLMM 1 assessing the effects of Dispersal type, crown position (CP), tree size (DBH.GROUP), rate of growth of the trees (GROWTH), lianas score (LIANA) and GUILD on the proportion of years in which a tree flowered or fruited. Species were entered as a random factor in the GLMM.

	Flowering models				***Fruiting models***			
Model selected:	*Growth+ DBH2 + CP + LIANA +(1|Species)*				*Growth+ DBH2 + CP +(1|Species)*			
Coefficients of final model	**Coefficient**	**Standard Error**	**Z-value**	***P***	**Coefficient**	**Standard Error**	**Z-value**	***P***
Intercept	-2.29	0.20	-11.47	**<0.001**	-3.89	0.29	-13.32	**<0.001**
GROWTH	0.15	0.09	1.60	0.11	0.31	0.13	2.38	**0.019**
DBH.GROUP 2	0.15	0.07	1.99	**0.04**	0.25	0.14	1.86	0.062
DBH.GROUP 3	0.20	0.09	2.22	**0.03**	0.65	0.15	4.65	**<0.001**
DBH.GROUP 4	0.59	0.09	6.49	**<0.001**	1.00	0.14	7.06	**<0.001**
DBH.GROUP 5	0.91	0.11	8.02	**<0.001**	1.12	0.17	6.51	**<0.001**
CP score 2	0.03	0.07	0.39	0.695	0.20	0.13	1.51	0.13
CP score 3	0.13	0.08	1.58	0.11	0.22	0.15	1.47	0.14
CP score 4	0.37	0.12	3.19	**0.001**	0.56	0.18	3.09	**0.002**
CP score 5	0.52	0.24	2.18	**0.029**	0.66	0.36	1.84	0.07
LIANA score 2	0.06	0.08	0.85	0.39				
LIANA score 3	0.08	0.12	0.69	0.48				
LIANA score 4	-1.58	0.53	-2.99	**0.002**				

TABLE 4. Correlations between number of individuals and number of species flowering and various measures of climate. Only trees with DBH scores 4 or 5 were included in the analysis. No significant correlations were found where there are no data.

Climate variable	**Number Individuals**			**Number of Species**		
	r value	**Prob**	**Lag (month)**	**r value**	**Prob**	**Lag (month)**
Pioneer Trees						
IOD SST				-0.212	0.023	4
Maximum Temperature	0.183	0.021	0	0.186	0.018	0
Minimum Temperature	-0.173	0.029	0			
Daily Temp. difference	0.211	0.008	0	0.188	0.018	0
Non-pioneer Light Demander						
IOD SST	0.244	0.018	5			
Rainfall				0.205	0.007	7
Maximum Temperature	0.326	<0.001	0	0.230	0.003	0
Minimum Temperature	0.187	0.017	6	0.250	0.001	7
Daily Temp difference	0.248	0.002	0	0.161	0.041	2
Shade-bearer						
IOD SST				0.209	0.028	0
Rainfall	0.180	0.018	4	0.158	0.039	4
Maximum Temperature				-0.353	<0.001	0
Minimum Temperature				-0.194	0.013	4
Daily Temp difference				-0.327	<0.001	0
Auto dispersal (fall from tree)						
ENSO NINO4 SST	0.179	0.029	2	0.201	0.009	2
Ballistic Dispersal						
ENSO NINO4 SST	-0.193	0.019	6			
IOD SST	0.268	0.011	0	0.196	0.039	0
Rainfall	0.204	0.008	0			
Large Fleshy fruit						
Rainfall	0.177	0.021	2	0.247	0.001	2
Maximum Temperature	-0.295	<0.001	0	-0.422	<0.001	0
Minimum Temperature				0.159	0.046	0
Daily Temp difference	-0.290	<0.001	0	-0.391	<0.001	0
Small Fleshy Fruit						
ENSO NINO4 SST	-0.202	0.014	4	-0.229	0.003	2
Maximum Temperature	-0.209	0.008	3	-0.242	0.002	2
Daily Temp difference	-0.241	0.001	7	-0.212	0.002	0
Wind dispersed						
ENSO NINO4 SST	0.173	0.034	0			
IOD SST	0.236	0.022	4	0.184	0.049	4

Rainfall	0.194	0.011	5	0.169	0.027	5
Maximum Temperature	0.283	<0.001	0			
Minimum Temperature	0.238	0.002	5			
Daily Temp difference	0.245	0.011	0			
Capsules dispersed by birds						
Rainfall	0.249	0.011	4			
Minimum Temperature				-0.174	0.027	3
Daily Temp difference				0.207	0.008	3

FIGURES

FIGURE1. The number of trees flowering (A) and fruiting (B) per hectare in each month of the year averaged between 1993-2016. Trees are plotted by their seed dispersal methods. Note the y-axis scale is different between the plots. Rainfall (C) and maximum and minimum temperature (D) values for each day, weekly running mean and monthly average are plotted showing the seasons of the year in BFR and inter- and intra-month variation in climate that occurs consistently between years.

FIGURE 2. Violin plots of the density of flowering (A) and fruiting (B) frequency of all individual trees in each dispersal type category.

FIGURE 3. Anomaly scores comparing the monthly number of individuals (left) and species (right) flowering with the average monthly number across the 24 years. The dotted horizontal line gives the mean across all months. A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

FIGURE 4. Anomaly scores comparing the monthly number of individuals (left) and species (right) fruiting with the average monthly number across the 24 years. The dotted horizontal line gives the mean across all months. A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

FIGURE 5. Differences in A) rainfall, B) maximum temperature and C) minimum temperature between 1993-1998 and 2011-2016. The black areas of the chart show where average rainfall between 1993-1998 was higher than the average rainfall between 2011-2016 and grey areas show where the average rainfall was greater between 2011-2016. A 15-day running mean was used to smooth some of the variation but provide more detail than monthly averages.

FIGURE 1.

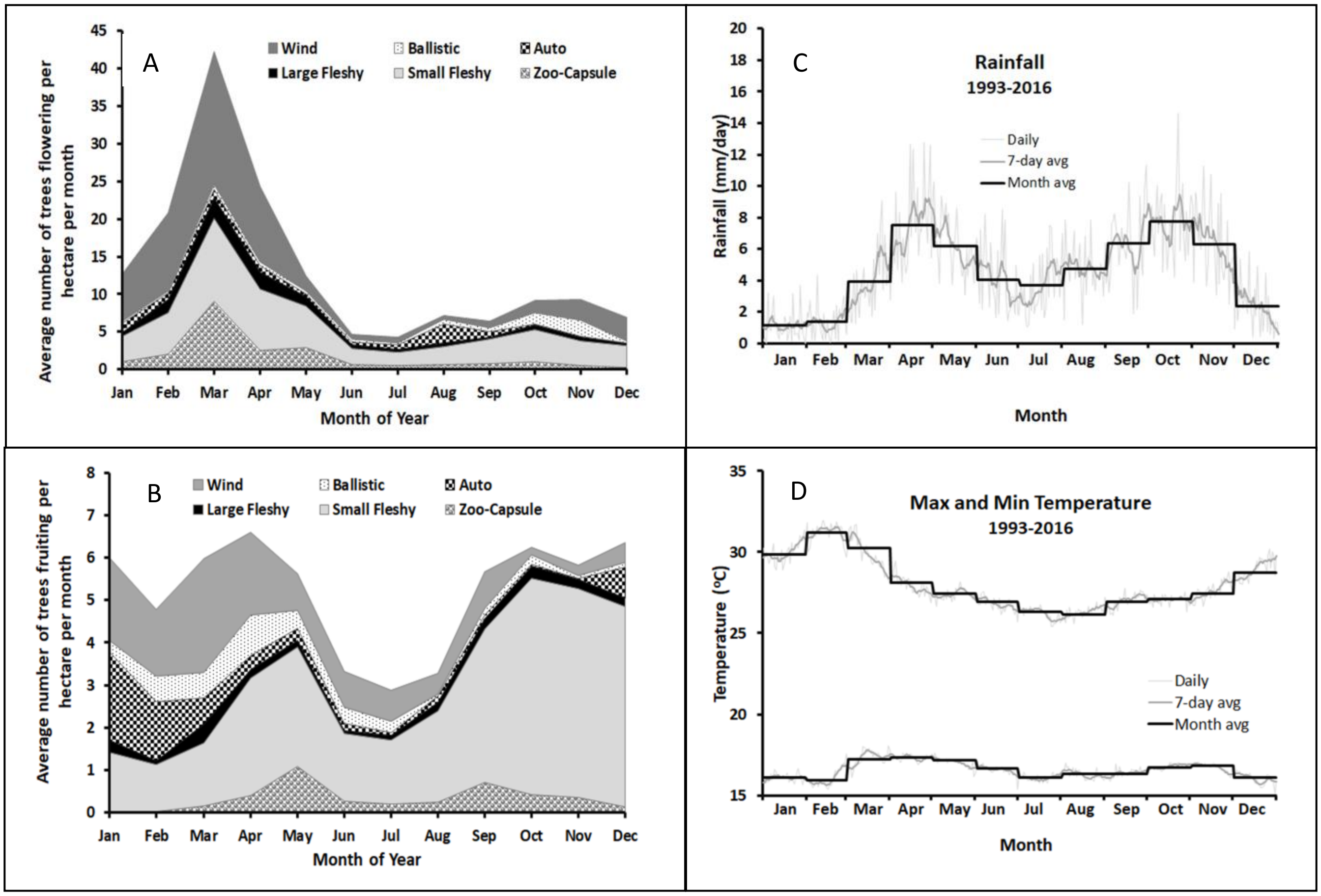

A
Wind
Ballistic
Auto
Large Fleshy
Small Fleshy
Zoo-Capsule
Average number of trees flowering per hectare per month
Month of Year
B
Average number of trees fruiting per hectare per month
C
Rainfall
1993-2016
Daily
7-day avg
Month avg
Rainfall (mm/day)
Month
D
Max and Min Temperature
1993-2016
Temperature (°C)
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

FIGURE 2.

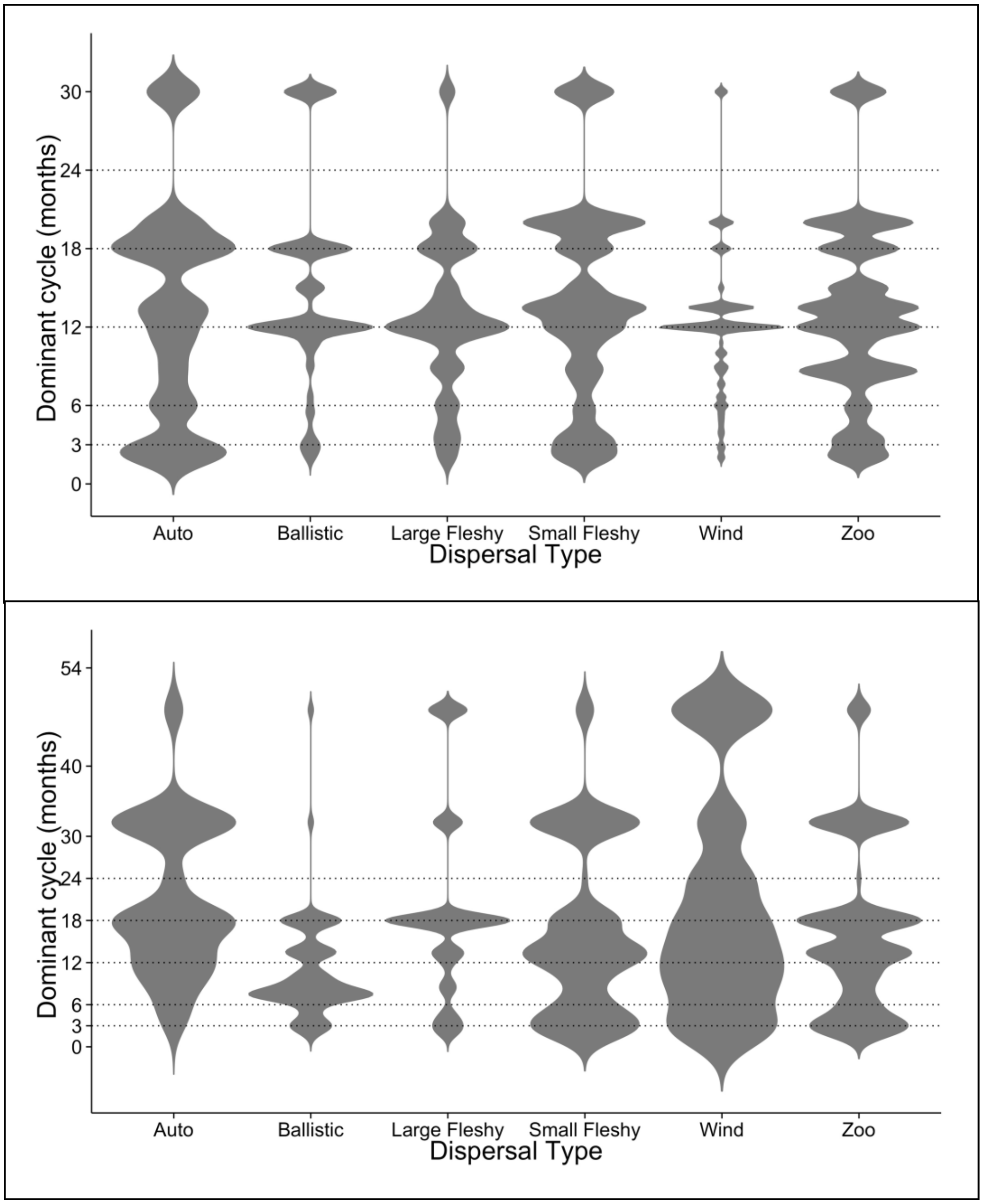
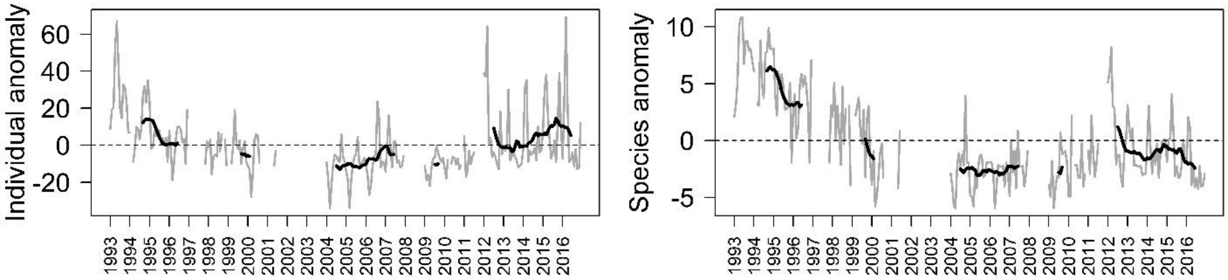
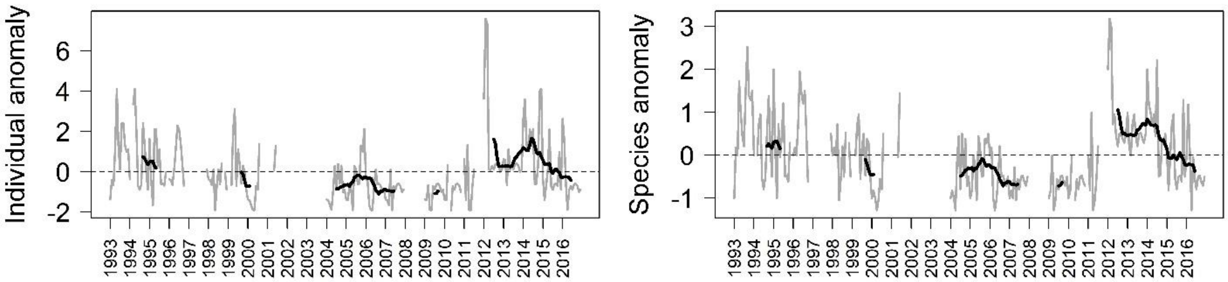

Dominant cycle (months)
30
24
18
12
6
3
0
Auto
Ballistic
Large Fleshy
Small Fleshy
Wind
Zoo
Dispersal Type
Dominant cycle (months)
54
40
30
24
18
12
6
3
0
Auto
Ballistic
Large Fleshy
Small Fleshy
Wind
Zoo
Dispersal Type

FIGURE 3.

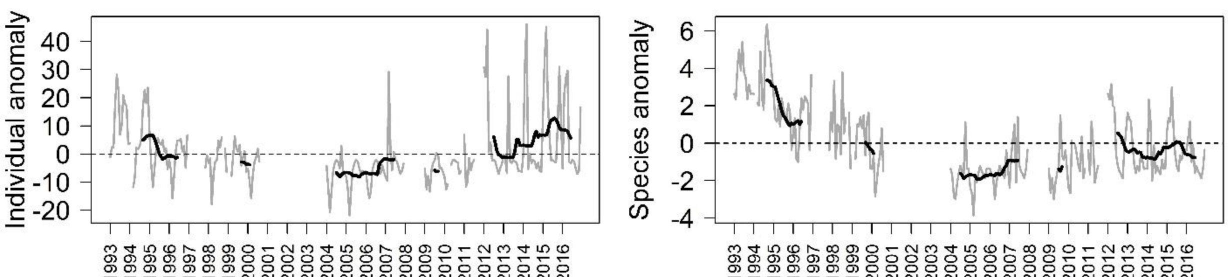
a. All trees



b. Pioneer trees



c. Non-pioneer Light Demander



d. Shade-bearer

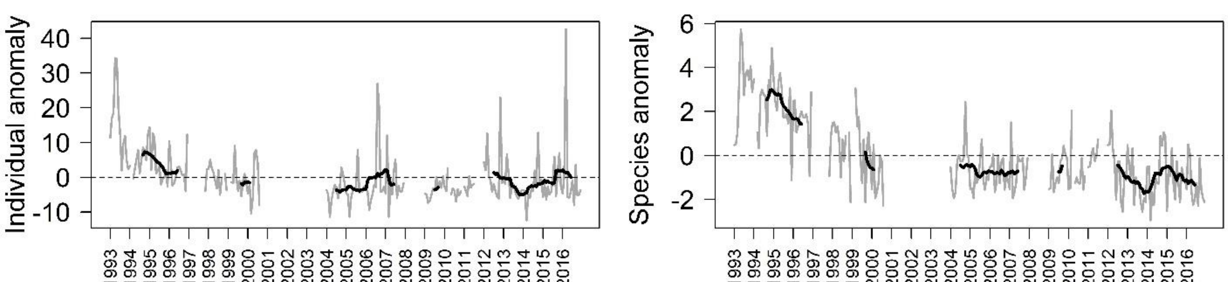
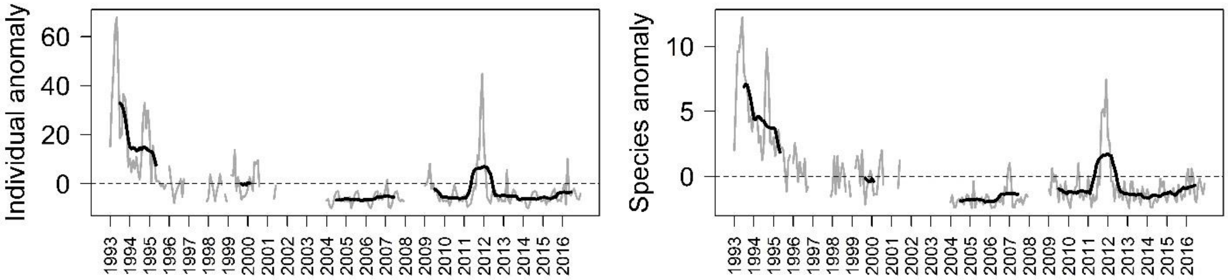
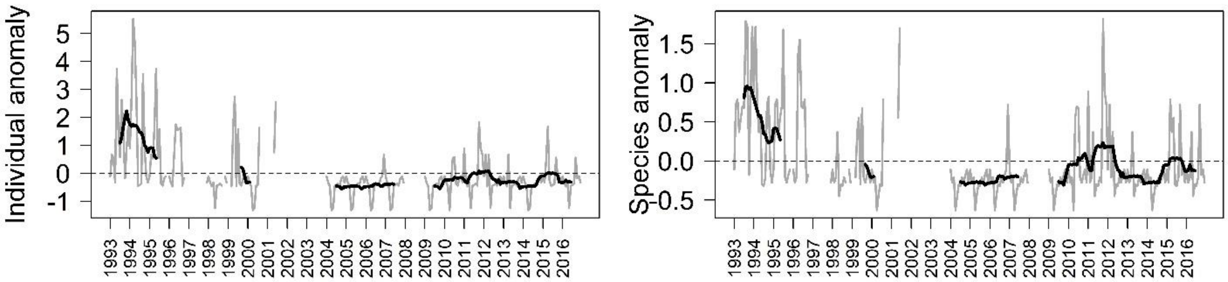


FIGURE 4.

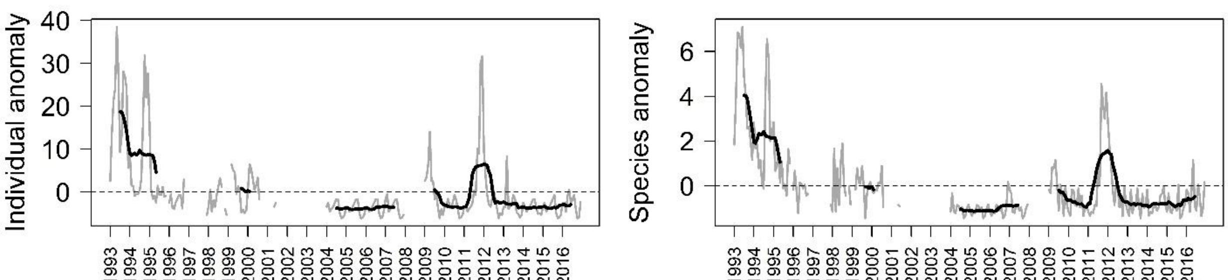
a. All trees



b. Pioneer trees



c. Non-pioneer Light Demander



d. Shade-bearer

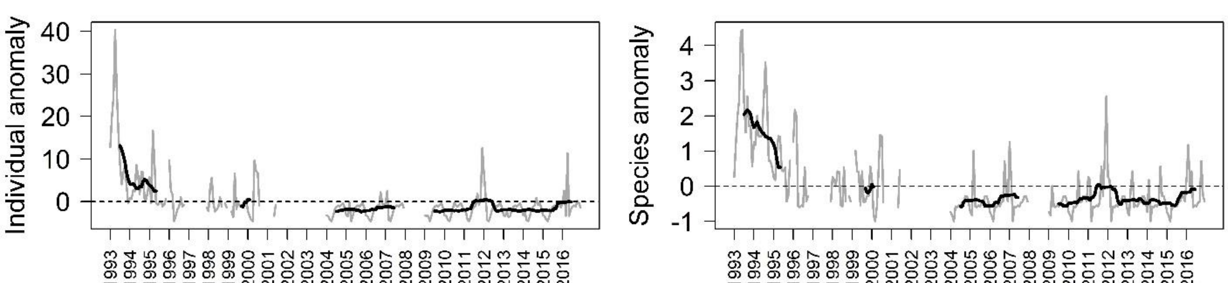
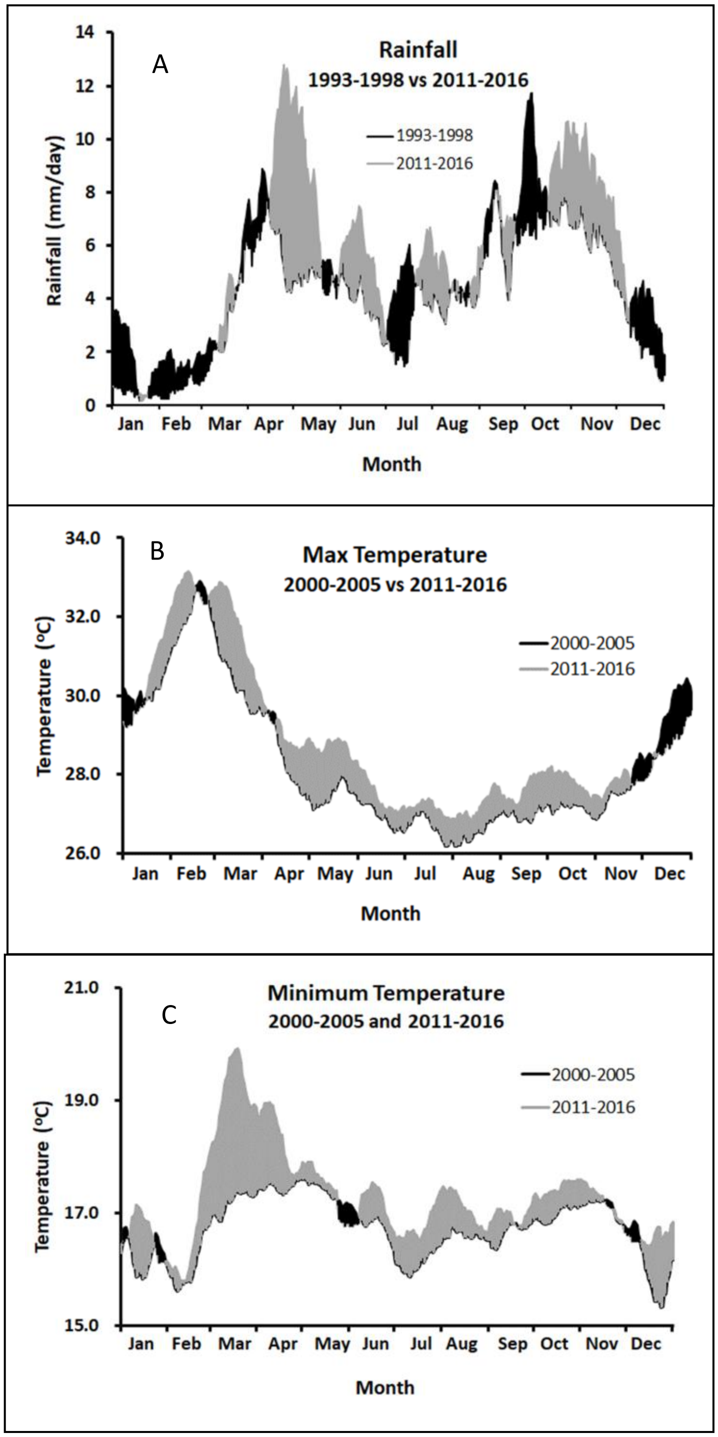


FIGURE 5.


A
Rainfall
1993-1998 vs 2011-2016
1993-1998
2011-2016
Rainfall (mm/day)
0
2
4
6
8
10
12
14
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month
B
Max Temperature
2000-2005 vs 2011-2016
2000-2005
2011-2016
Temperature (ºC)
26.0
28.0
30.0
32.0
34.0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month
C
Minimum Temperature
2000-2005 and 2011-2016
2000-2005
2011-2016
Temperature (ºC)
15.0
17.0
19.0
21.0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

SUPPLEMENTARY MATERIAL

FIGURE S1.

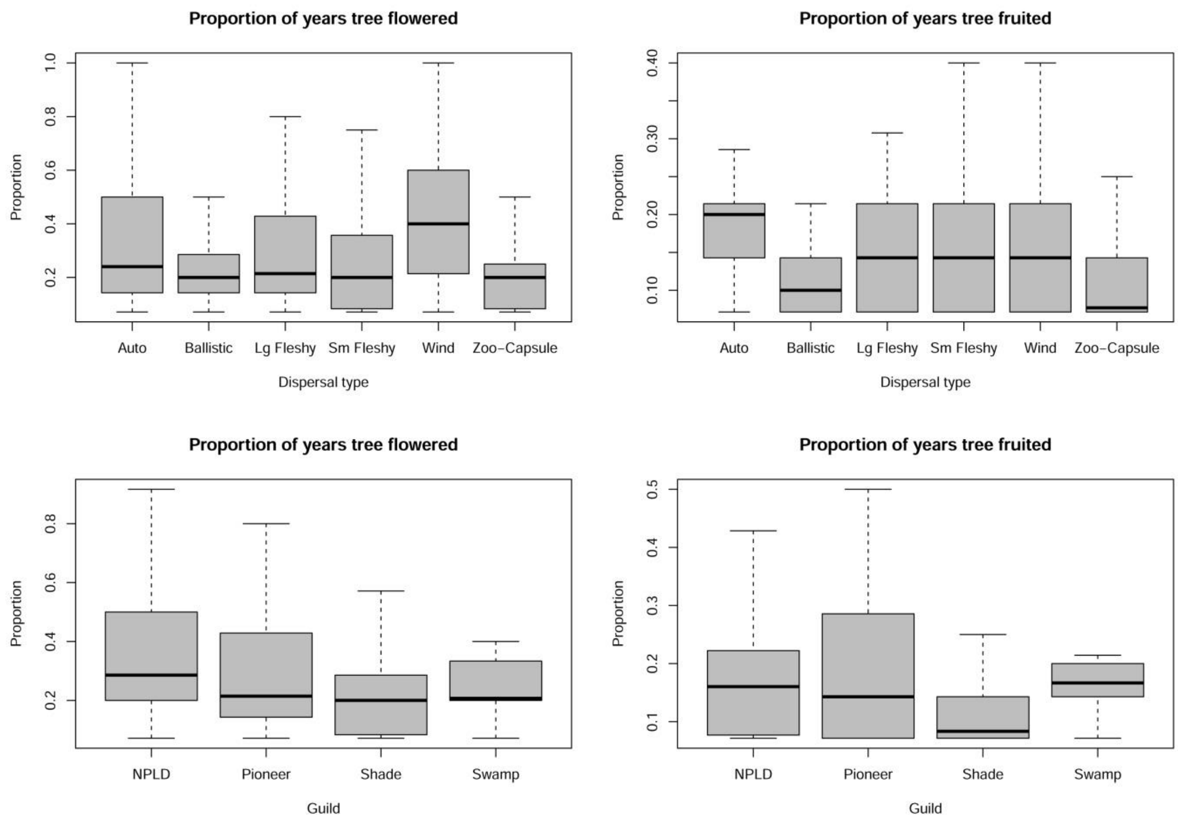


FIGURE S2. Violin plots of the density of flowering (top) and fruiting (bottom) frequency of all individual trees in each guild type.

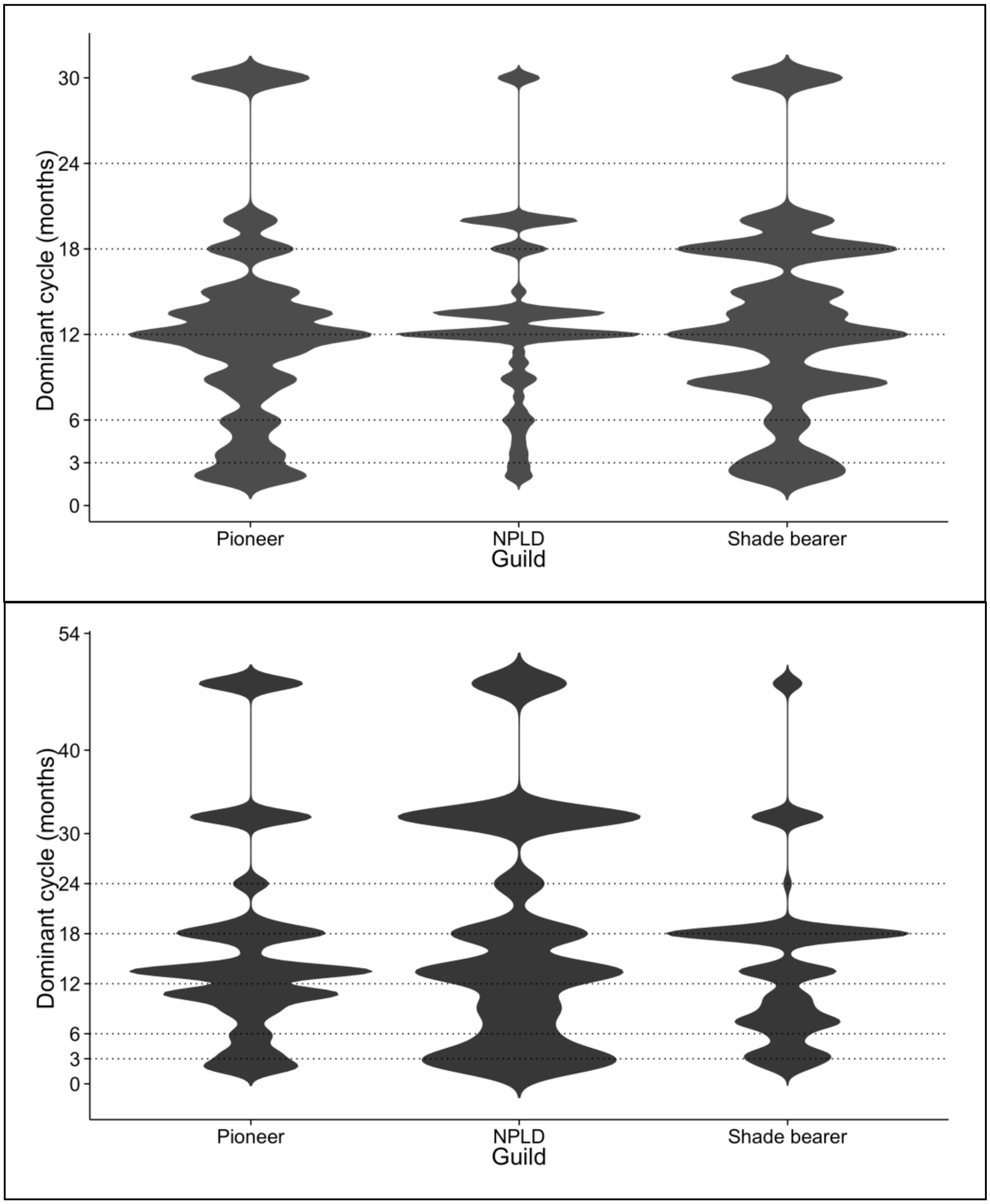


Figure S3. Boxplot of the average number of ripe fruit produced by a fruiting tree plotted by DBH group for all trees that fruited at least once. A quasi-poisson GLM indicated where significant differences occurred between tree size groups and these are flagged with different letters.

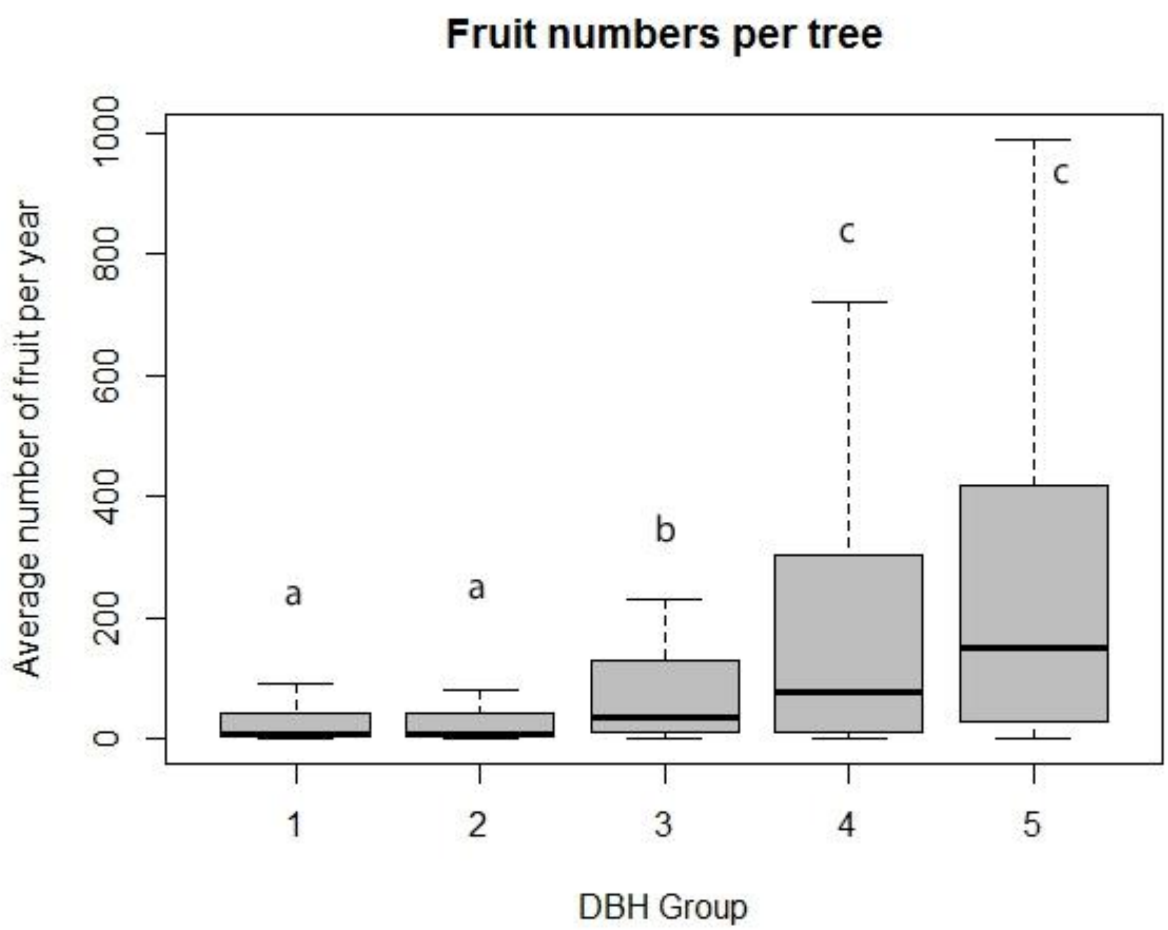


FIGURE S4 Violin plots of the density of flowering (left pair) and fruiting (right pair) frequency of all individual trees in CP.GROUP type (1 = trees below the canopy; 2 = trees at or above the canopy).

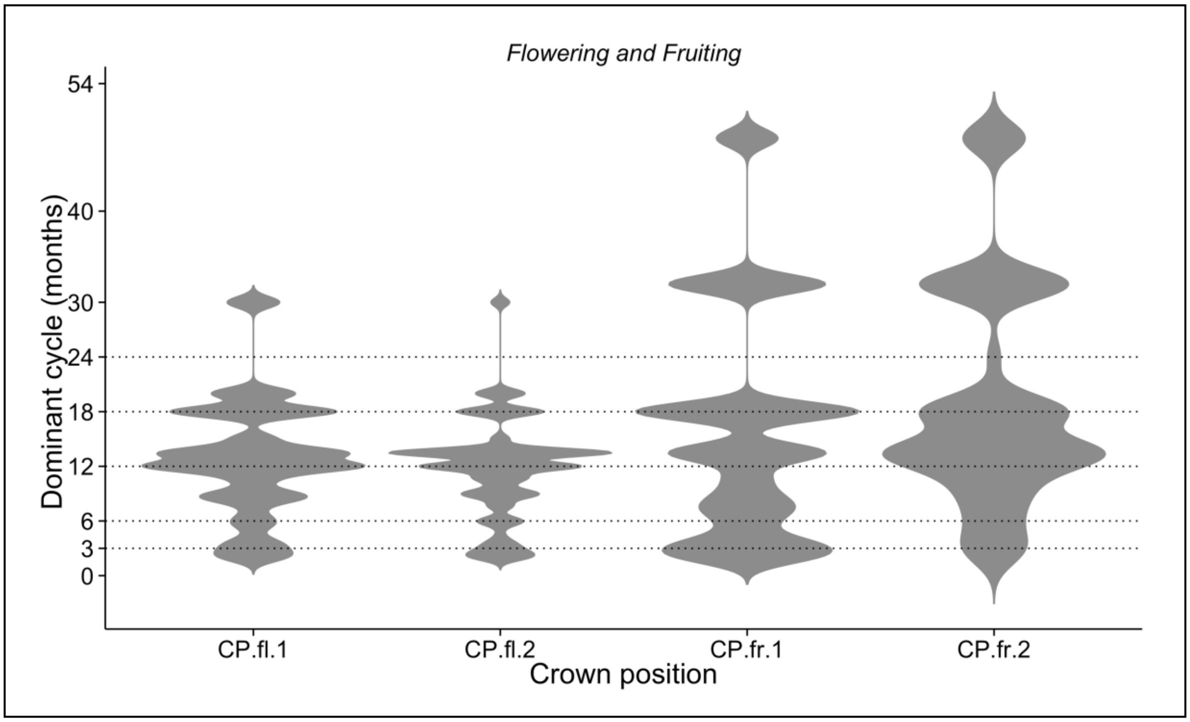
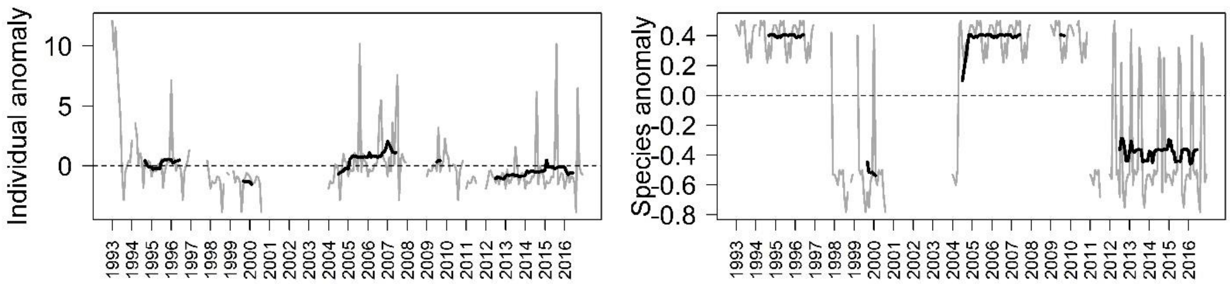
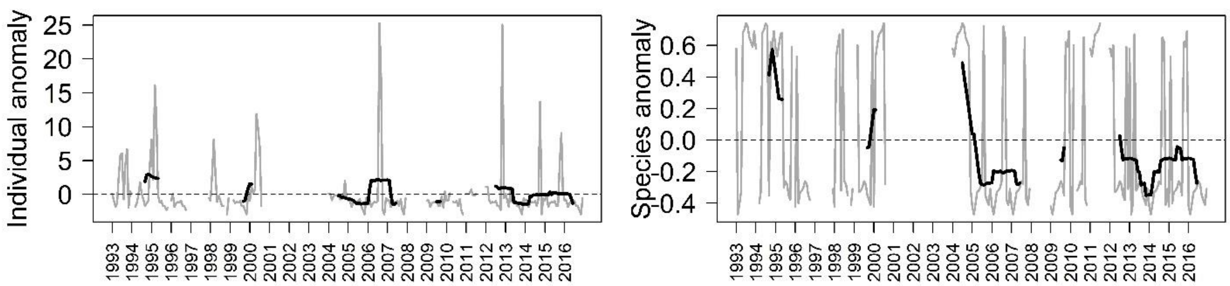


Figure S5 Anomaly scores comparing the monthly number of individuals (left) and species (right) flowering with the average monthly number across the 24 years (dotted horizontal line). A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

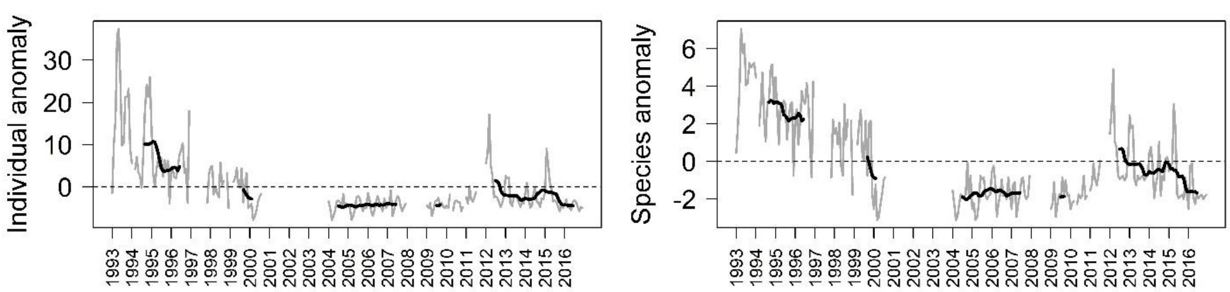
a. Auto dispersal trees



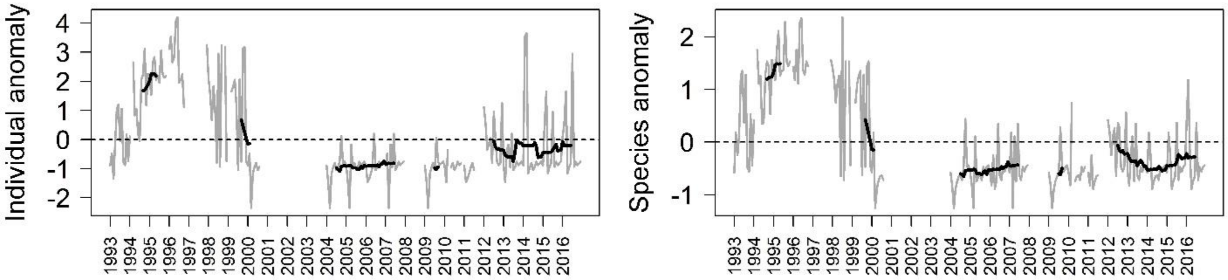
b. Ballistic dispersal



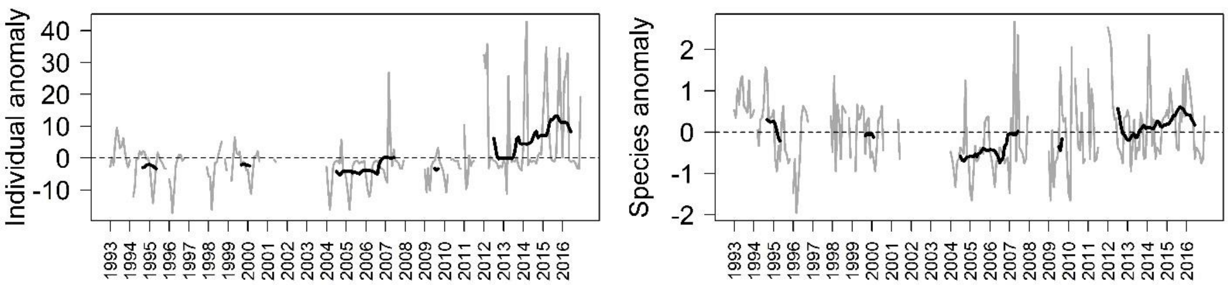
c. Small fleshy fruits



d. Large fleshy fruits



e. Wind dispersal



f. Capsules dispersed by birds

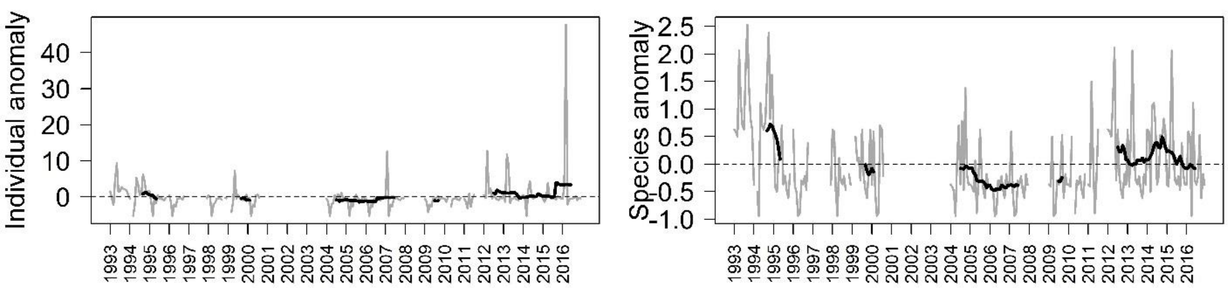
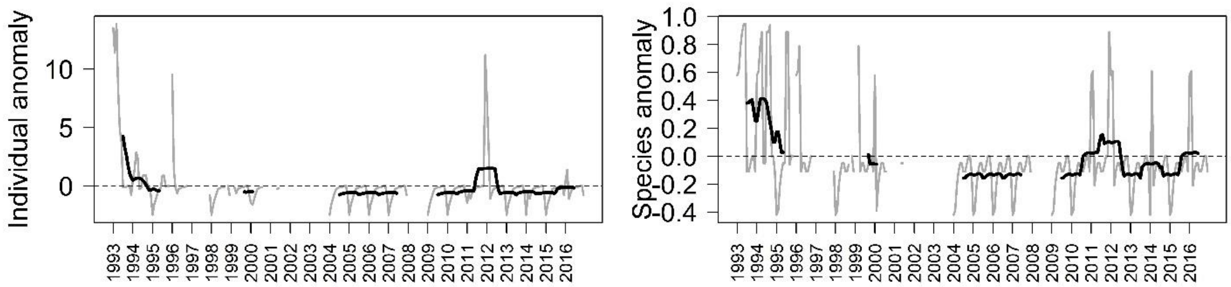
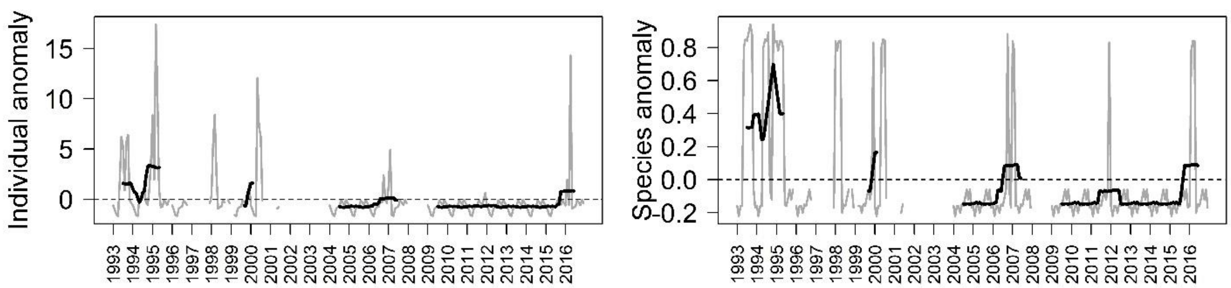


Figure S6 Anomaly scores comparing the monthly number of individuals (left) and species (right) with ripe fruit with the average monthly number across the 24 years (dotted horizontal line). A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

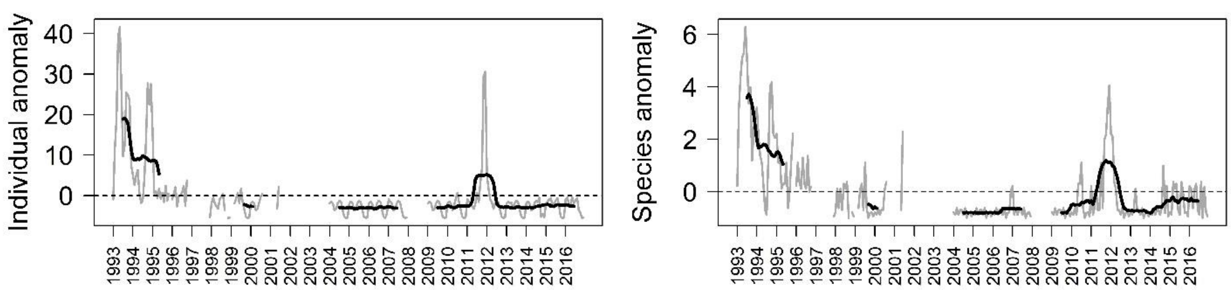
a. Auto dispersal trees



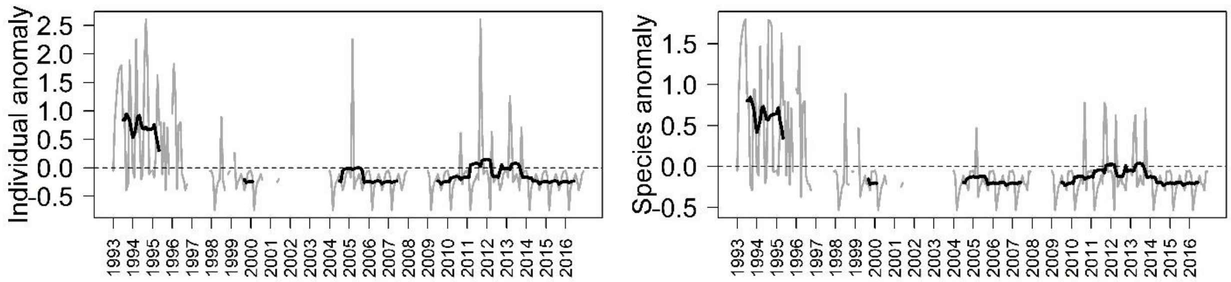
b. Ballistic dispersal



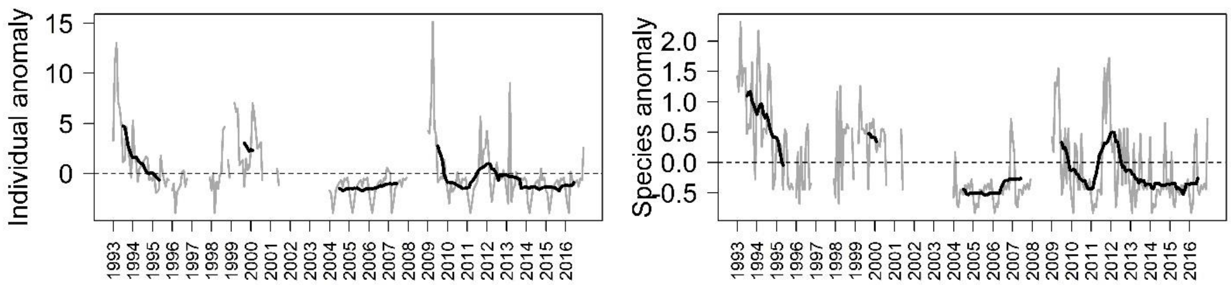
c. Small fleshy fruits



d. Large fleshy fruits



e. Wind dispersal



f. Capsules dispersed by birds

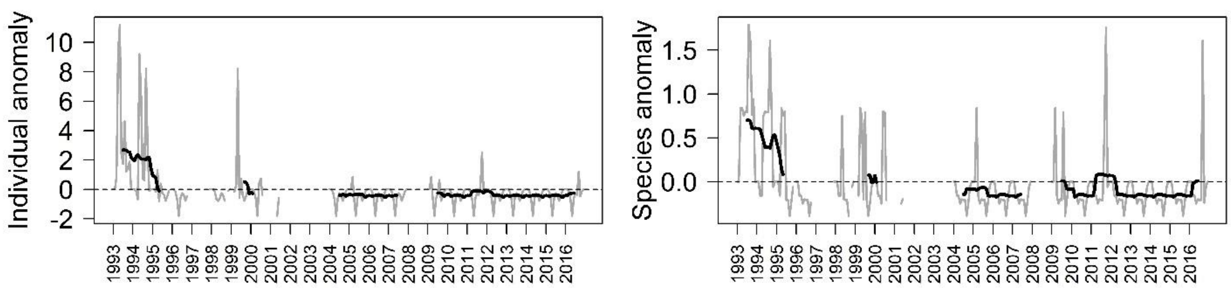
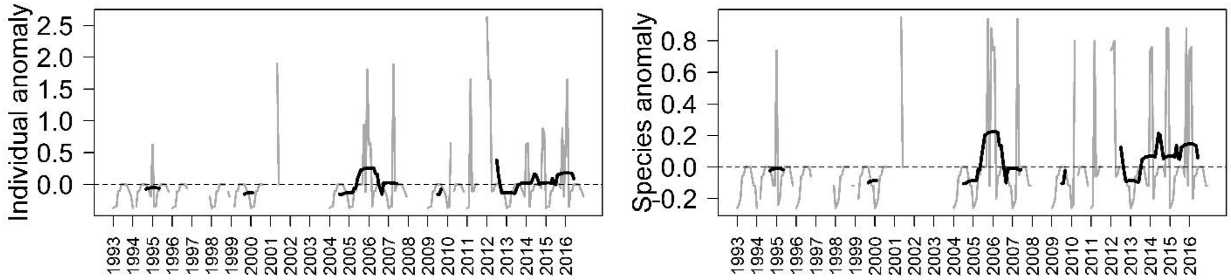
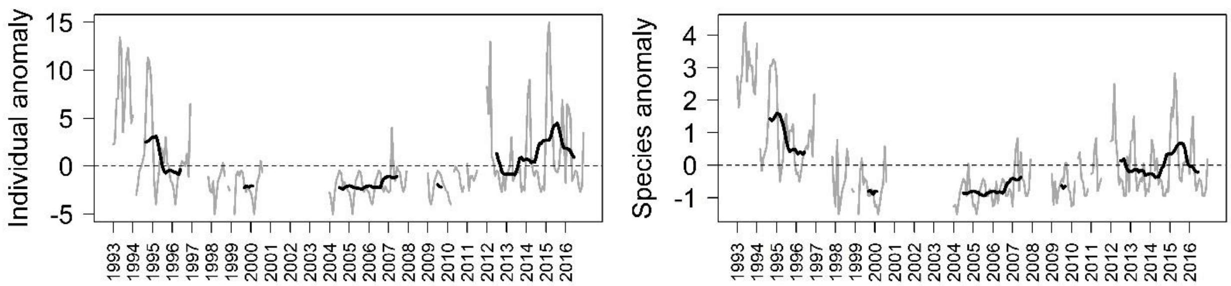


FIGURE S7. Anomaly scores from trees with DBH score 4 or 5 (largest trees), comparing the monthly number of individuals (left) and species (right) with flowers with the average monthly number across the 24 years (dotted horizontal line). A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

a. Pioneer trees



b. Non-pioneer Light Demander



c. Shade-bearer

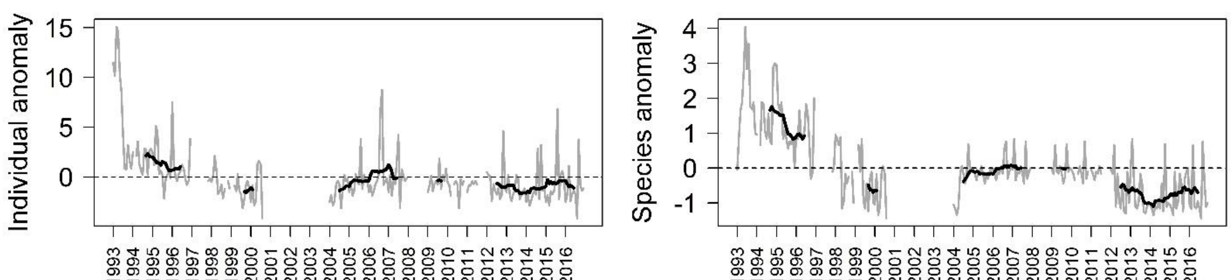
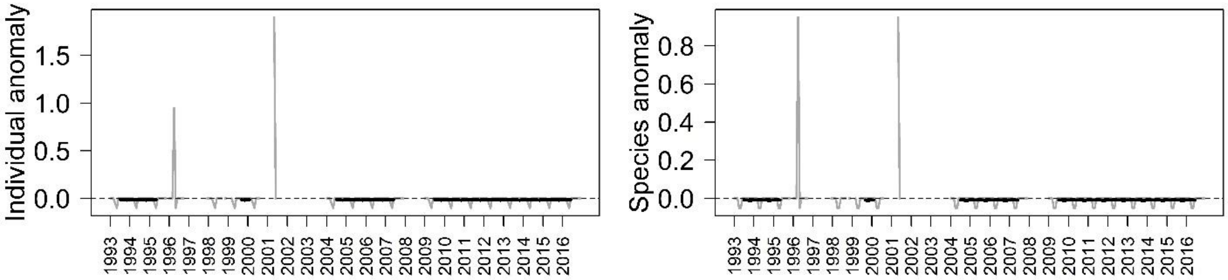
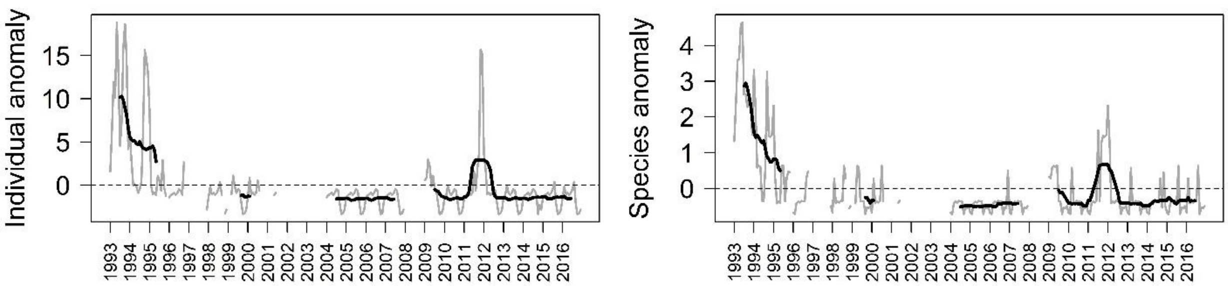


FIGURE S8. Anomaly scores from trees with DBH score 4 or 5 (largest trees), comparing the monthly number of individuals (left) and species (right) with ripe fruit with the average monthly number across the 24 years (dotted horizontal line). A 13-month running mean (black line) is plotted for the average value of the six months prior to and after each specific month.

a. Pioneer trees



b. Non-pioneer Light Demander



c. Shade-bearer