IMPACTS OF GLOBAL CLIMATE CHANGE ON THE PHENOLOGY OF AFRICAN TROPICAL ECOSYSTEMS

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Abstract

The climate has been changing at an unprecedented rate, affecting natural systems around the globe. Its impact has been mostly reflected through changes in species' phenology, which has received extensive attention in the current global-change research, mainly in temperate regions. However, little is known about phenology in African tropical forests. Africa is known to be vulnerable to climate change and filling the gaps is an urgent matter. In this study we assess plant phenology at the individual, site and continental level. We first compare flowering and fruiting events of species shared between multiple sites, accounting for three quantitative indicators, such as frequency, fidelity for conserving a certain frequency and seasonal phase. We complement this analysis by assessing interannual trends of flowering and fruiting frequency and fidelity to their dominant frequency at 11 sites. We complete the bigger picture by analysing flowering and fruiting frequency of African tropical trees at the site and community level. Next, we correlate three climatic indices (ENSO, IOD and NAO) with flowering and fruiting events at the canopy level, at 16 sites. Our results suggest that 30 % of the studied species show plasticity or adaptability to different environments and will most likely be resilient to moderate future climate change. At both site and continental level, we found that annual flowering cycles are dominant, indicating strong seasonality in the case of more than 50% of African tropical species under investigation. We also found that individuals flower and fruit less frequently over time, most probably due to senescence or a possible climate change impact. Moreover, results indicate that flowering and fruiting events of around 30% of species are correlated with one or more climatic phenomenon. However, their response to drier or wetter conditions is variable, highlighting the wide varieties of mechanisms African tropical trees adopt in relation to stress conditions. Altogether, this study fills important gaps and highlights the uniqueness of African tropical forests not reported before.

Table of Contents

List of Figures

List of Tables

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Author’s Declaration

I, Gabriela S. Adamescu, confirm that all material presented in this thesis is my own, except for the following. Fourier analysis code was developed by Ms. Emma Bush (University of Stirling, UK) and my two main maps were created by Dr. Philip Platts (University of York, UK). This work has not been submitted for any other academic award at this, or any other institution. Information derived from other sources is appropriately referenced.

Chapter 1

General Introduction

1. Climate change

Climate has constantly shaped the environment, governed living systems and affected human wellbeing (Hudson & Keatley, 2009). The world is currently experiencing a period of rapid global warming, primarily driven by anthropogenic change, which has no historical precedent in either its rate of change nor its absolute scale (Malhi & Wright, 2004). Greenhouse gases emitted by anthropogenic emissions have increased since the industrial revolution (Sanderson, Hemming, & Betts, 2011). The most common greenhouse gasses include carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), which are either retained in the atmosphere or deposited in plants, soils or oceans. The main contributor to global warming is CO_2, which accounts for 70% of the present greenhouse effect (Houghton, 2009). Measurements from ice cores indicate that before the beginning of industrialisation, CO_2 was relatively stable at a mean value of 280 ppm for many thousand years (Hughes, 2000). Average CO_2 levels have increased dramatically since the Industrial Revolution, reaching 370 ppm in 2000 and continue to increase at a rate of approximately 1.5 ppm per year (Hughes, 2000). Additionally, global temperatures also increased by 0.6 °C in the last 100 years (Walther et al., 2002) and are expected to continue raising by 0.1 °C per decade until 2040 (IPCC, 2014). Besides temperature, precipitation patterns are also changing, however they are inconsistent with regard to both space and time (IPCC, 2014). Such changes in temperature and precipitation are expected to impact natural systems in various ways across continents, with each species responding to it individualistically (Butt et al., 2015). In addition, changes in climate brought by extreme weather events, including hurricanes, windstorms, floods, severe droughts and heavy precipitation, are mainly encountered in the tropics and subtropics, with no uniform pattern across different places (Houghton, 2009). How climate change will affect the Earth ecosystems, wildlife, primary production systems and how these systems will in turn respond to it, are some of the most important questions in the climate change context. Already visible changes have been documented for many terrestrial and marine species globally (Parmesan, 2006; Parmesan & Yohe, 2003; Walther et al., 2002).

2. Impacts of climate change

Noticeable effects of climate change on natural systems are frequently reported as altered interspecific interactions, shifts in distribution and changes in phenology of animals and plants. With climate changing and altering weather conditions, species have crossed boundaries, to search for new suitable habitats. Such examples were reported in the Mediterranean Sea, where new warm-water species emerged and in the sub-Arctic islands, where increased plant diversity and insects were observed (Walther et al., 2002). Additionally, new species have started to inhabit sea anemones in Monterey Bay (Sagarin, Barry, Gilman, & Baxter, 1999). Changes were seen in the shift of isotherms by approximately 300-400 km and 500 m in latitude and elevation, respectively stimulating species to advance towards the poles (Hughes, 2000). Range shifts were reported most often in the case of birds, butterflies and alpine animals, which moved an average of 6.1 km per decade northward (Parmesan & Yohe, 2003).

Earlier onset in spring events, including the arrival of migratory birds, butterflies, shooting and flowering of plants have been previously reported (Visser & Both, 2005; Walther et al., 2002). For example, during a 32-year study in Europe, nine flycatcher (*Ficedula hypoleuca*) populations showed significant laying date advances at the most rapidly warming sites (Both et al., 2004). Moreover, several arctic species have reduced in their range size as a consequence of losing their suitable environmental conditions (Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002). In addition, extreme weather events, such as hurricanes have also affected bird populations, even leading to extinctions as is the case of *Loxigilla portoricensis grandis* subspecies in subtropical forests of Puerto Rico (Butt et al., 2015).

Moreover, it has been suggested that climate change is also influencing the composition, structure and biogeography of forests around the world (Allen et al., 2010). Forests play an important role for natural systems and humankind (Anderson-Teixeira et al., 2015). They are a source of food for animals, regulate hydrological cycles, protect soil resources and influence climate via energy, water and carbon dioxide exchange with the atmosphere (Bonan, 2008). In relation to global warming, forests play a crucial role: they sequester high quantities of carbon annually and store approximately 45% of the terrestrial carbon (Bonan, 2008). Hence, a drier climate could lead to a decreased evaporative cooling, CO_2 loss and initiation of forest dieback (Allen et al., 2010).

Controlled studies have shown that flowering time will most likely change with global warming (Galloway and Burgess, 2012) and forests dynamics are predicted to undergo long-term alterations (Anderson-Teixeira et al., 2015). The easiest way to track changes in the ecology of species is through phenology (Walther et al., 2002), as phenological events of tree species are often synchronised with environmental conditions and change according to variation in weather events (Bertin, 2008). Consequently, phenology has been used as a tool to study climate change impact on natural systems and detect species' response to it.

3. Plant phenology and climate change

Global warming consequences have been monitored through changes in the ecology of species, as previously described (Parmesan, 2006; Parmesan & Yohe, 2003; Walther et al., 2002). Plant phenology refers to the timing of cyclical biological events such as seed germination, leaf development, flowering and fruiting (Fenner, 1998; Kozlowski & Pallardy, 1997; Rathcke & Lacey, 1985). To maximise fitness, phenology of plant species has often evolved to match certain environmental conditions (Stenseth & Mysterud, 2002). Hence, plant phenology can be triggered by abiotic factors (temperature, precipitation), but also by biotic ones (pollinators, seed dispersers, interspecific and intraspecific competition) (S. Sakai, 2001).

Phenological triggers can be divided into proximate and ultimate factors. Proximate factors are the immediate ones, known as environmental initiators, such as certain temperatures or moisture levels that actually trigger an event (Stevenson, Castellanos, Cortés, & Link, 2008). For example, temperate woody species and few perennial herbs were seen in flower when temperature overlapped a certain threshold value (van Schaik, Terborgh, & Wright, 1993). On the other hand, reduced water stress caused by rain or leaf loss trigger flowering events of tropical trees in Central America (Borchert, 1983). Hence, phenological events of plants are synchronised with climatic conditions and any change in weather patterns will lead to cascading effects affecting plant phenology and the entire ecosystem (Menzel et al., 2006; Rosenzweig et al., 2008). In addition to proximate factors, phenological triggers also include ultimate factors, which represent the evolutionary pressures behind the underlying endogenous cycles, which lead to individual idiosyncratic phenology (Fenner, 1998). Biological events such as leafing, flowering, fruiting and germination happen at different times within a year, however they are dependent on each other (e.g. fruiting cannot precede flowering, germination cannot happen before fruiting). Consequently, the timing of the switch between one phase and another is very important for the plant to maintain its fitness (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007). Fruiting events always follow flowering ones, however flowering does not necessarily follow fruiting (Piñero, Sarukhán, & Alberdi, 1982). This may happen when environmental conditions have deteriorated and fruiting process must be aborted. Trees often fruit when environmental conditions for seed dispersal are optimal, as fruiting is a very costly process (Howe & Smallwood, 1982).

In tight connection with the phenology of plants are the animals and insects that complete the ecosystem and rely on young leaves, flowers and fruits to grow and reproduce (Parmesan & Yohe, 2003). However, phenology of one species may differ from others with which it may be tightly connected (Visser & Both, 2005). For example, insects and plants are often temperature and rainfall sensitive, while vertebrates typically rely on photoperiod as cues to reproduce (Visser & Both, 2005). Thus, any phenological change in a lower trophic level could lead to a mismatch in phenology at higher trophic levels.

Phenological changes are widely studied in temperate regions, where individual plants reproduce in a synchronous manner once a year (Shoko Sakai et al., 1999). There, most phenological shifts were documented for bud burst time and migratory patterns of birds (Walther et al., 2002). On the other hand, little is known about potential shifts in tropical phenology where temperature is unlikely to be a limiting factor and where ecosystems are highly complex (Morellato et al., 2016).

4. Tropical phenology

Tropical forests are highly dynamic and diverse and host wide variety of indigenous species (Mark, 2013). In tropical forests, climate is not as restrictive for plant growth as in temperate areas and it is characterised by small differences in temperature and precipitation events (van Schaik et al., 1993). Seasonality in the tropics is dominated by the intertropical convergence zone (ITCZ), a band of warm, moist air that carries precipitation north and south over the equator as the movement of the earth brings different areas closer to the sun (Osborne, 2000). The seasonal movement of the ITCZ creates two seasons, respectively dry and wet, which can be seen once or twice a year depending on the region (Osborne, 2000). Around the equator, additional cycling of warm moist air from evapotranspiration boosts rainfall and reduces seasonality, resulting in high moisture levels found in tropical forests throughout the year (Osborne, 2000).

Tropical forests are characterised by exceptionally high diversity of tree species, which can flower / fruit at any time of the year, often very different from other related or unrelated species (Bawa, Kang, & Grayum, 2003; Zhou et al., 2014). They represent the food source for frugivores, regulate the forest structure (including pollinators and herbivores) and respond very well to changes in climate (Butt et al., 2015). Flowering and fruiting events vary from complete intraspecific synchrony to extreme asynchrony and from constant activity to recurring momentary bursts (van Schaik et al., 1993). Depending on the type of habitat, phenological patterns are seen at different times and vary in their frequencies and duration (Shoko Sakai et al., 1999). In order to flower, a tree must reach an adult phase and accumulate sufficient metabolizable nutrients (Opler, Frankie, & Baker, 1976). However, it is also dependent on the physical conditions of the sites or the neighbouring vegetation and environmental conditions (Bullock & Solis-Magallanes, 1990). Plant species that share common pollinators may separate flowering season to minimize the competition for pollinators or synchronise flowering to attract local pollinators through increase of resource density (S. Sakai, 2001).

Fruiting processes occur when conditions become optimal (Rathcke & Lacey, 1985) and are not the necessary consequence of flowering, as trees may abort small fruits (Stephenson, 1981). In the seasonal neotropics, wind-dispersed species often fruit during dry season as trade winds are very strong (Rathcke & Lacey, 1985). On the other hand, the wet season is preferred by tropical trees that produce fleshly and succulent fruit (Fenner, 1998). The fruiting process requires the highest input of energy and nutrients and only when a certain threshold is reached can the process start (Rathcke & Lacey, 1985). Consequently, for both flowering and fruiting processes, environmental conditions play a critical role in determining the timing, frequency and duration of their patterns (Kozlowski & Pallardy, 1997).

Current knowledge about tropical phenology mainly originates from asian and south american studies. Plant phenology has not received much attention in Africa (Adole, Dash, & Atkinson, 2016), even though the continent is believed to be one of the most susceptible to climate change. Changes initiated by climate are reported to affect distribution and dynamics of forests in Africa, with vegetation expected to contract (IPCC, 2014). Consequently, these changes will also affect seed predators, pollinators, insects and animals that complete the ecosystem and rely on plant phenology to grow and reproduce (Visser & Both, 2005). With trees being at threat from climate change, understanding phenology in Africa has become a fundamental issue in ecology and current gaps must urgently be filled.

5. African continent and future projections in the climate change context

Africa hosts a wide variety of animals and plants and many different types of tropical forests (Sayer, 1992). Current projections suggest that future climate change will affect the intensity of temperature and precipitation and will bring extreme weather events (Connolly-Boutin & Smit, 2016). Mean temperatures are projected to increase in sub-Saharan Africa, reaching between 27.6 - 29.8 °C by the end of the 21st century (Platts, Omeny, & Marchant, 2015). Extended seasonal aridity is expected in the Mediterranean Basin, South East Africa, Eastern Madagascar and the Ethiopian Highlands, while shorter periods are anticipated in the Horn of Africa, Gabon and coastal Angola (Platts et al., 2015).

On the other hand, precipitation projections are more uncertain than temperature and may exhibit higher spatial and seasonal dependence (IPCC, 2014). With regard to the last 3 decades, rainfall patterns have varied in different locations (IPCC, 2014). Increased frequency of extreme weather events are brought by coupled ocean-atmosphere interactions, which have an important role in shaping global and regional climate on interannual (1–4 years) and decadal (5–7 years) time scales (IPCC, 2014). These can trigger severe droughts and increased precipitation events that have been previously documented to affect plant phenology in various different ways (Butt et al., 2015). Overall, there is no common story of how African tropical forests will be affected in the near future, with some places being projected to get drier and others wetter (Zhou et al., 2014). Consequently, Africa may be one of the most interesting continents to study, with trees being threatened by climate, and how phenology is affected by extreme weather events is unknown, hence filling the current gaps is an urgent matter.

To address this issue, coupled ocean atmospheric phenomena are useful to consider in the phenology – climate change context. Well known climatic phenomena affecting weather in Africa are the El Niño–Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD) and the North Atlantic Oscillation (NAO) (C. J. Brown et al., 2016). They have been shown to affect phenological events on other continents from South East Asia (Shoko Sakai et al., 1999) to Central America (Maza-Villalobos, Poorter, & Martínez-Ramos, 2013) studies, but not systematically across Africa (Adole et al., 2016).

6. Extreme weather events and their impact on ecosystems

6.1 El Nino Southern Oscillations (ENSO)

ENSO is a 2-7 year oscillation of sea-surface temperature and atmospheric pressure patterns in the equatorial Pacific (Williams & Hanan, 2011). The positive phase, known as El Niño, is characterised by warm sea surface temperatures (SSTs) in the Eastern Tropical Pacific tropical (Williams & Hanan, 2011). At the opposite pole, La Niña phase brings cool SSTs in the Eastern tropical Pacific (Fig. 3). ENSO is known as one of the most influential phenomena with regard to interannual climatic variability, affecting several tropical rainforest regions. Its intensity can disturb tropical rainforests more than a long-term trend in climate (Malhi & Wright, 2004). In Africa, El Niño brings increased rainfall in East Africa and severe droughts in West Africa (Fig. 1), while La Niña brings the opposite effects in the same regions.

Recently, ENSO has been given a lot of attention and has been associated with the two best known warm periods of 1982/83 and 1997/98, which generated widespread negative ecological, social and economic effects (Tudhope et al., 2001). In South East Asia, El Niño is a causative factor of higher flower and fruit production events (general flowering, GF, events) which have been shown to last for several months (S. Sakai, 2001), whereas La Niña results in lower reproduction, famine and a decline in frugivore population densities (S. Sakai, 2001). Moreover, droughts associated with ENSO also lead to tree mortality as seen in the open *Austrocedrus* woodlands of Patagonia (Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001).

The visible climate shift in the tropical Pacific started around 1976, when an unfamiliar intensity and frequency in ENSO events was seen for the first time (Malhi & Wright, 2004). Since then, ENSO has begun to manifest with a higher intensity and frequency (Butt et al., 2015). With climate change continuing to advance and threaten natural systems, it is crucial to understand what type of consequences it might bring over African tropical forests.

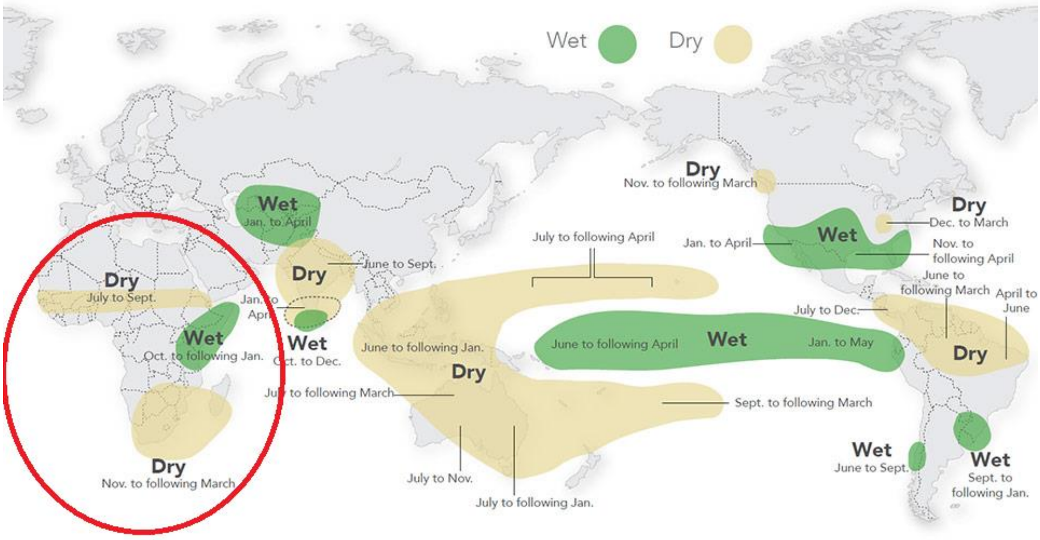

Figure 1. The effects of El Niño phase across the globe. The main focus of this graph is Africa, circled in red, which receives wet weather conditions (shown in green) on the East coast and severe droughts on the West part. The La Niña phase brings the opposite weather conditions in the same areas. Source: (FAO, 2016)

6.2 Indian Ocean Dipole (IOD)

The IOD is also known as a major year to year driver of climate variability that influences Eastern Africa the most (Luo et al., 2010). The IOD is an ocean coupled phenomenon that comprises two phases: warm SSTs in the Eastern Indian Ocean and cool SSTs over the Western Indian Ocean (Williams & Hanan, 2011). The IOD is known to bring rainfall in Africa (Nicholson & Kim, 1997) and has influence on Eastern, Central and Western African vegetation (Williams & Hanan, 2011). The positive phase brings increased rainfall in East Africa and transfers heat in the West (Fig. 2), whereas the negative Dipole Mode brings droughts to East Africa (Marchant, Mumbi, Behera, & Yamagata, 2007). Extreme IOD events interfere with ENSO events and vice versa (Luo et al., 2010) and it is therefore important to consider IOD alongside ENSO when studying phenology in Africa. There is evidence of the past negative impact of extreme IOD events, such as increased precipitations seen in Kenya and neighbouring countries (Marchant et al., 2007). Moreover, these extreme events are predicted to increase in their intensity (Butt et al., 2015), hence understanding and predicting their influence is an important issue.

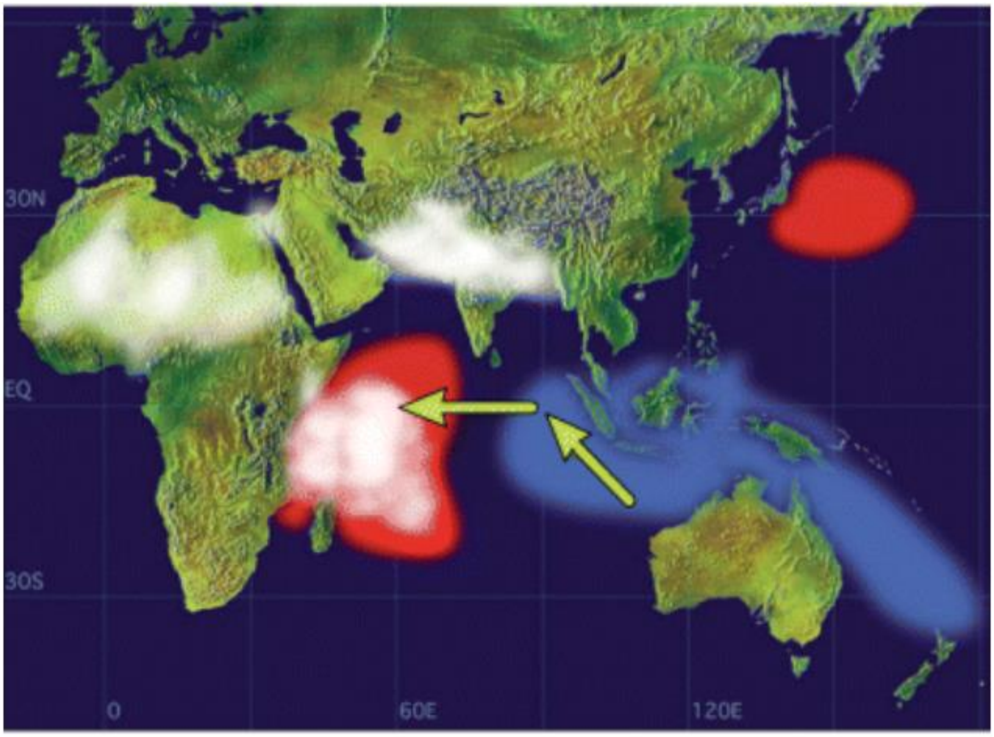

Figure 2. Sea surface anomaly of the Positive Dipole Mode of the Indian Ocean Dipole (IOD). White covers indicate connective activity while arrows indicate the direction of the wind. Source: (Marchant et al., 2007)

6.3 North Atlantic oscillation (NAO)

The North Atlantic Oscillation (NAO) is known as an influential phenomenon of the global climate (Hurrell, 2005). NAO is characterised by differences in the atmospheric pressure between the Arctic and the subtropical Atlantic (Hurrell, 2005). Similar to ENSO and IOD, the NAO also consists of a positive and negative phase. A positive index indicates an increased difference in pressure between the two regions, while a negative index represents a decreased difference than normal (M. E. Brown, de Beurs, & Vrieling, 2010). For both indices, the effects of NAO have been shown to vary with winter and summer seasons, bringing different weather conditions in Africa and other parts of the globe (MetOffice, 2016) (Fig. 3 & 4). During winter, when pressure differences are above normal (positive NAO), temperatures decrease in North Africa, while the opposite is seen when values are below normal (Fig. 3) (MetOffice, 2016). During summer, positive NAO is associated with warmer temperatures in the West and decreased precipitation in the Sahel region (Fig. 4), while negative phases result in cooler temperatures in West Africa (MetOffice, 2016). NAO impact has been mostly reported in Europe and North Africa, but never in the East, Central and West of Africa (Jones, Jonsson, & Wheeler, 1997). As in the case of IOD, ENSO also interferes with NAO effects (Mokhov & Smirnov, 2006). Consequently, it is necessary to investigate its potential impact on the phenology of African tropical trees.

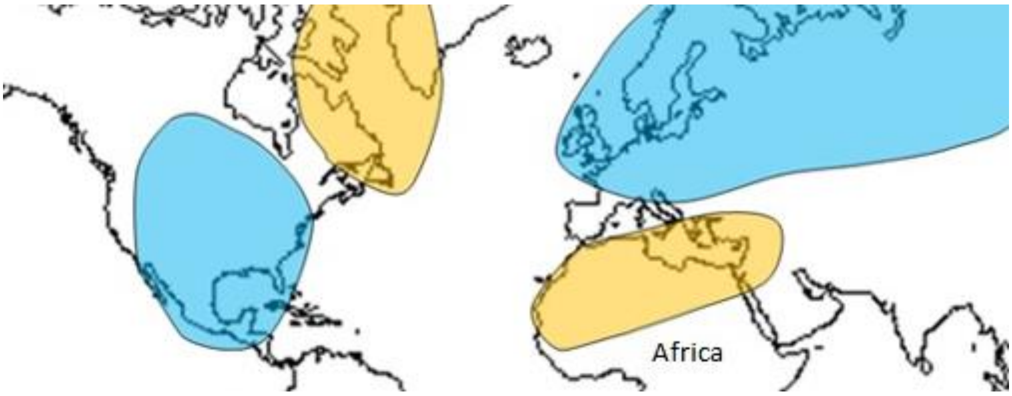

Figure 3. Winter NAO index below 0. Yellow cover indicates warmer temperatures, while blue colder temperature. Source: (MetOffice, 2016)

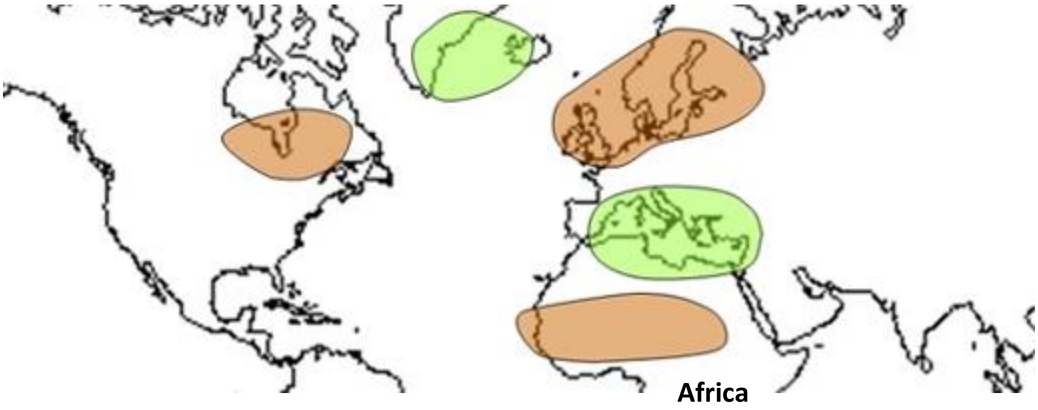

Figure 4. Summer NAO index above 0. Brown cover indicates drier conditions, while green indicates wetter conditions. Source: (MetOffice, 2016)

8. Phenological studies in Africa

Most phenological studies in Africa have focused on animal behaviour as well as seasonal resource availability based on community-level patterns of leafing, flowering and fruiting (Janmaat et al., 2016; Yamagiwa, Basabose, Kaleme, & Yumoto, 2008). Other studies have focused on short-term time points or on single sites (Colin A. Chapman, Chapman, Zanne, Poulsen, & Clark, 2005; Do et al., 2005; Polansky & Boesch, 2013). Studies have usually noted that annual patterns predominate at most sites with various flowering and fruiting times depending on species (C. A. Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Polansky & Boesch, 2013). Site level comparisons at the community-level have been undertaken between just two or three sites (C. A. Chapman et al., 1999; Esler & Rundel, 1999), showing the wide varieties of phenological patterns found in Africa. Canopy level analyses are, however, limited. They cannot inform us about either evolutionary pressures which operate at the individual level or about the accurate phenological patterns governing ecosystems. Consequently, for studies on selective forces of phenology under current scenarios of global climate change, analyses at the individual level are essential. Additionally, to our knowledge, no studies have considered the influence of large climatic phenomena on African tropical forest that will help to adapt to and mitigate future climate change consequences.

Understanding phenological patterns of African tropical tree species is important for several reasons. The timing of flowering and fruiting patterns cannot determine successful recruitment of forest trees (McDade, Bawa, & Hespenheide, 1994), but it is tightly linked to frugivore breeding success, including iconic species such as gorillas and chimpanzees. Phenological research is also important in understanding forest dynamics and structure, including pollinators, seed dispersals and predators. Moreover it is also important to understand interspecific competition between trees and primary production such as timber harvesting, as well as different species interactions but also the economic costs associated with ecotourism (C. A. Chapman et al., 1999; Morellato et al., 2016). In addition, local frugivore abundance often coincides with fruiting timing, hence knowing the spatial and temporal distribution of fruiting may help local communities to develop better forest management strategies (C. A. Chapman et al., 1999). This study will only focus on wet tropical forests.

9. Aims

The second chapter of this thesis will aim to identify phenological patterns of species shared between multiple sites, as well as the interannual change of flowering and fruiting patterns of species found at 12 and 11 sites, respectively. In this chapter we will use three indicators of phenology for flowering and fruiting events: frequency, fidelity to a consistent frequency and seasonal phase. Using these three indicators, we set out to test two hypotheses. Our first hypothesis states that flowering and fruiting events of species shared between several tropical forests will differ in their frequency, fidelity to a consistent frequency and seasonal phase. The second hypothesis we will test states that, for all species recorded across 11 sites, there will be a change in the frequency and fidelity to a consistent frequency of flowering and fruiting events. This chapter is based on individual tree analysis and aims to give insight about the adaptability and plasticity of species as well as a warning about the future of African tropical trees in the current climate change context.

The third chapter of this thesis will aim to study phenology at the canopy level and its relationship with large-scale climatic phenomena such as ENSO, IOD and NAO. Our first hypothesis states that annual cycles dominate African tropical forests. Our second hypothesis states that flowering and fruiting phenology will correlate with large climatic phenomena, including ENSO, IOD and NAO. This chapter aims to inform about the possible changes of phenological patterns in response to future extreme events brought by one of the three climatic phenomena investigated.

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Chapter 2

Identifying site differences and temporal trends in the phenology of African tropical forests

Abstract

Climate change has been affecting natural systems at an unprecedented rate with various ecological impacts. Changes in plant phenology have been widely studied in temperate regions. However, little is known about potential shifts in tropical phenology, where plant growth, flowering and fruiting can occur year round. Current knowledge mostly comes from Asian and South American studies, where phenology has been described in terms of frequency, timing and synchronicity of flowering and fruiting events. However, little is known about African forests. In this study, we analysed flowering events of 5446 trees from 196 species and fruiting ones for 4595 trees from 191 species. All species were monitored across 12 sites, for the flowering analysis and 11 sites for the fruiting analysis, between 6 and 28 years, depending on the site. We used Fourier analysis to assess phenological patterns (dominant frequency, fidelity to a consistent frequency, seasonal phase) across species shared between multiple sites. We further studied temporal trends of flowering and fruiting events for all species. Results showed that the majority of species occurring at multiple sites show different flowering and fruiting frequencies, vary in their fidelity for a particular frequency and show diverse seasonal phases at different sites. These species suggest phenotypic plasticity or a high degree of adaptability to the local environmental conditions irrespective of the genetic inheritance. Interannual trends analysis showed that 75 species are decreasing their flowering and fruiting frequencies, a trend that was consistent across all sites. This may indicate a response to climate change but is perhaps more likely a consequence of increasing age. Temporal change in flowering and fruiting fidelity to a particular frequency was variable between species. This difference may be an indicator of the diversity of strategies tropical trees adopt in order to increase their reproductive success or adapt to climate change.

Introduction

Over recent decades the climate has been warming at an unprecedented rate, significantly impacting natural systems (Deutsch et al., 2008; Sala et al., 2000; Walther et al., 2002). Increases in average global temperature and in the intensity of extreme weather events such as prolonged drought and rainfall are commonly reported (Wu et al., 2015). The impact of such changes on natural systems are noticeable, including shifts in the distribution of species and earlier onset of spring events, such as the arrival of migratory birds and butterflies, shooting and flowering of plants (Visser & Both, 2005; Walther et al., 2002). Phenological complementarity between plants and animals is crucial for ecosystem organisation, processes and survival (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007). Changes in phenology have occurred differently for several species and led to already visible phenological mismatches between species and plant communities (Brown et al., 2016). In turn, these can trigger harmful cascading effects on nectarivores, frugivores and the services they provide to the habitat (Butt et al., 2015). Consequently, without understanding how climate change will impact the lowest trophic levels we cannot mitigate and adapt to future consequences at the level of an entire ecosystem.

Plant phenology refers to the timing of cyclical biological events such as leaf flushing, bud formation, flowering, fruiting and seed germination (Shoko Sakai et al., 1999). Phenology is the foundation of the food chain, which regulates the nature of various inter-specific interactions, directly impacting animal and insect communities that rely on plants to grow and reproduce (Fenner, 1998; Newstrom, Frankie, & Baker, 1994). Many plants synchronise the timing of life history events such as flowering and fruiting with local environmental conditions (Mark, 2013). Consequently, climate is an important factor regulating phenological events in plants, and has become a core focus in ecology (Hudson & Keatley, 2009). Moreover, phenological records are considered a marker of seasonal variations and were one of the first indicators of climate change (Adole, Dash, & Atkinson, 2016; Parmesan, 2006; Parmesan & Yohe, 2003). It was seen that short-term fluctuations in precipitation disrupted phenological patterns of trees in Africa (Anderson, Nordhelm, Moermond, Gone Bi, & Boesch, 2005). With rainfall and drought events increasing in their frequency, we expect changes in phenology to become more visible in the near future.

Phenological changes are widely studied in temperate regions, where individual plants reproduce in synchrony once a year and temperature is the dominant trigger (Fenner, 1998). On the other hand, little is known about potential shifts in tropical phenology, where the vast majority of terrestrial biodiversity resides (Morellato et al., 2016). In the tropics, temperature is often not a limiting factor and phenological events can happen at any time (S. Sakai, 2001). A similar annual pattern seen in the temperate regions has been reported from tropical Asian forests, although the onset and amount of flowering and fruiting varies greatly year on year as a function of rainfall (Mark, 2013). These trends are mostly documented at the individual, population and community level in deciduous species of woody plants, present at the marginal and monsoon tropics (Corlett & Lafrankie, 1998). By contrast, tree species within South American tropical forests show considerable variation in flowering frequency. For example, during a 12 year study in the tropical rainforest of La Selva in Costa Rica, most species were found to have sub-annual cycles and only nine supra-annual flowering cycles (Shoko Sakai et al., 1999). A wider variety of frequencies were seen during a four-year study at Tinigua National Park, MeColombia, where most trees displayed annual patterns of flower production, followed by episodic, continuous, and supra-annual patterns (Stevenson, Castellanos, Cortés, & Link, 2008). Depending on the type of forest and location, phenological events peaked during either, dry (in lowland evergreen forests), wet (in evergreen Atlantic rainforest) or in the transition between dry and wet season (in semi-deciduous forests) (Mark, 2013).

The African continent is the one that is most lacking in research at a continental and individual tree scale and requires attention in order to complete the whole tropical forest phenology picture. African tropical forests are the second-largest on Earth, playing a crucial role in the global carbon cycle and have been neglected due to the paucity of long-term phenological records (Adole et al., 2016; Zhou et al., 2014). Climate change impacts on Africa are predicted to vary regionally, causing some regions to get drier and others wetter (Collier, Conway, & Venables, 2008). Over the last 50-100 years, most of the continental surface temperatures have increased by 0.5 °C and are projected to rise faster than the global average by the end of the 21st century bringing further extreme weather events (IPCC, 2014). Such climate change is highly likely to disrupt phenology across the region (Collier et al., 2008; Malhi, Adu-Bredu, Asare, Lewis, & Mayaux, 2013) . The little we know about African tropical phenology comes from six sites in Central / Eastern Africa, suggesting a pattern of variable flowering more similar to the South American system. At these sites, phenology in Africa has been mostly described at the level of community and region and only very few studies compared phenological patterns between more than three sites (Colin A. Chapman, Chapman, Zanne, Poulsen, & Clark, 2005; C. A. Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Janmaat et al., 2016; Sun et al., 1996). For example, at two African sites, species were found to have different flowering/fruiting patterns such as six, nine, 12 and 24 month, with species shared between sites, showing different patterns (Chapman et al., 1999). However, these studies focus on the canopy level phenology, not individuals. Hence, it is therefore difficult to tell if, a six month canopy level flowering cycle is composed of all individuals flowering twice per year, or two sets of trees flowering on a twelve monthly cycle offset by six months. Plant phenology has been mostly described in terms of timing (date), frequency (e.g. annual, biennial), synchronicity (all individuals together, such as *Hevea brasiliensis* species (Yeang, 2007), or throughout the year such as figs (Harrison, 2005)) and duration at the community and population level (Frankie, Baker, & Opler, 1974; Newstrom et al., 1994; Opler, Frankie, & Baker, 1976; Carel P. van Schaik, Terborgh, & Wright, 1993). On the other hand, in a study that considered temporal variation in phenology, warmer temperatures increased flowering events at two forests in South America (Pau et al., 2013). In the current context of climate change, we need to understand phenology across Africa better, as well as its progress over time. This will indicate how species differ from one location to another, their degree of plasticity and cues they use to reproduce that will add up to the future climate change mitigation strategies.

Our aim here is to assess phenology at the individual tree level for different species shared between different tropical forests across the African continent. Chapman et al., (1999) showed that species shared between two African sites differ in their flowering and fruiting phenologies. Hence, our first hypothesis is that species shared between multiple sites will show different flowering and fruiting frequencies, vary in their fidelity for a consistent frequency and differ in their seasonal phase (time of the year where species flower / fruit). Secondly, our second hypothesis is that interannual flowering and fruiting patterns are changing over time with regard to frequency and fidelity to a consistent frequency. However, to our knowledge, this is the first study in an African forest system, specifically addressing the phenological differences between individual tree species located at different locations across Africa, as well as the interannual phenological patterns of individual trees located at various sites. Furthermore, this is the first study to closely assess fidelity to a consistent frequency in terms of flowering and fruiting events at multiple African sites and over time. This aspect is important because it is directly linked to pollinator reliability and specialization, and hence with individual reproductive success (Bawa, Kang, & Grayum, 2003).

Methods

Study sites and data collection

We were provided with data from researchers in charge of each site. In this study we considered data from 11 long-term research sites across East, Central and West Africa (Fig. 5). The sites cover the majority of the African forest types, including montane, submontane, semi-deciduous, evergreen and swamp forests (Table 1). Site elevation and area vary between 80 to 3000 m and from 200 km^2 to approximately 5000 km^2, respectively. There are two distinguished seasons, dry and wet, encountered once or twice a year depending on the geographical position of the site. Average mean temperature ranges between 15 and 31 °C, and mean annual rainfall ranges between 1000 and 2000 mm. Sites are located within national parks/ protected reserves, gazetted to protect high biological diversity and support many endemic species. The phenology data collection at each site was based on monthly data collection accomplished by trained field assistants. Each tree was monitored for flower and fruit presence based on crown observations, using binoculars. Species in this study may not be representative of the community at each site. Species that were recorded are significant food sources for frugivores. Depending on the site, data were collected for between 6 and 28 years.

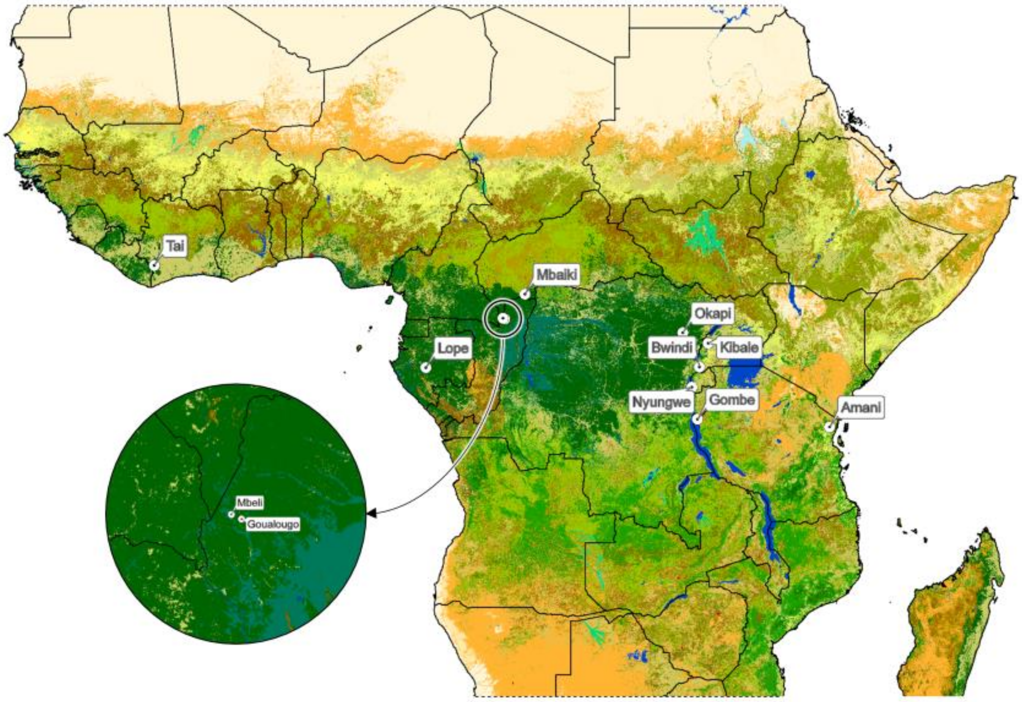


Figure 5. Geographical position of the 11 studied sites. Land cover data, downloaded from ESA at 5° x 5° resolution (Arino, Ramos, Kalogirou, Defourny, & Achard, 2009).

Table 1. Study sites (11), coordinates, country of origin and monitoring period for flowering and fruiting phenology organised from West to East. Latitude and longitude are expressed in decimal degrees. T: total number of trees present at a site; S: total number of species present at a site.

No	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	Flowering	Fruiting
1	Taï National Park	Côte d'Ivoire	5.846389	-7.31222	15 1997 - 2011	Diverse moist evergreen and semi-evergreen forest	80	T: 127 S: 44	T: 127 S: 49
2	Lopé National Park	Gabon	-1.097	11.165	29 1986 - 2014	Semi-evergreen, tropical lowland rainforest	300	T: 47 S:48	T: 44 S: 48
3	Mbeli Bai Forest	Republic of Congo	2.258611	16.41222	12 2004 - 2015	Semi-deciduous rain forest	300	T:12 S:12	T: 11 S: 9
4	Goualougo Triangle	Republic of Congo	2.211617	16.51875	11 2002 – 2012	Semi-deciduous rain forest	300	T:16 S:3	T: 16 S: 6
5	Mbaiki forest	Democratic Republic of the Congo	3.9	17.9	21 1991 - 2011	Humid - tropical forest	560	T:51 S:6	T: 41 S: 6
6	Gombe Stream National Park	Tanzania	-4.611	29.638	13 1997 - 2009	Tropical forests	1000	T:30 S:11	T: 29 S: 10
7	Nyungwe Forest National Park	Rwanda	-2.431	29.263	13 1996 - 2008	Tropical forest	2260	T:43 S:45	T: 50 S: 49

Table 1 continued

No	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	Flowering	Fruiting
8	Bwindi Impenetrable National Park	Uganda	-1.04611	29.77222	9 2008 - 2012	Montane forests	2240	T:15 S:8	T: 13 S: 7
9	Okapi Wildlife Reserve Lenda & Edoro sites	Democratic Republic of the Congo	1.267	28.641	20 1993 - 2012	Humid mixed evergreen forest	750	Okapi Edoro T:50 S:30	missing
								Okapi Lenda T:47 S:27	Okapi Lenda T: 46 S: 20
10	Kibale Forest National Park	Uganda	0.559726	30.35798	11 2005 - 2015	Subtropical moist forest	1500	T:11 S:10	T: 11 S: 7
11	Amani Nature Reserve	Tanzania	-5.13	38.615	7 2006 - 2012	Moist submontane forest	950	T:122 S:14	T: 110 S: 11

Source: **Amani Nature Reserve**, Tanzania – Henry Ndangalasi and Norbert Cordeiro; **Gombe Stream National Park** , Tanzania – Ian Gilby and Anne Pusey; **Nyungwe National Park**, Rwanda – Felix Mulindahabi; **Bwindi Impenetrable National Park**, Uganda – Badru Mugerwa, Frederick Ssali, Dougla Sheil and Martha Robbins**; Kibale National Park**, Uganda – Colin Chapman, **Okapi Wildlife Reserve**; Democratic Republic of Congo – Flory Bujo, Corneille Ewango and Terese Hart; **Lope Reserve**, Gabon – Kate Abernethy and Kath Jeffrey, **Mbeli Bai**; Nouabale Ndoki Park, Congo Republic – Mireille Hockemba and Thomas Breuer; **Mbaiki**, Central African Republic – Adeline Fayolle, **Tai National Park**; Ivory Coast – Christophe Boesch, Leo Polansky; **Goualuogo**, Nouabale Ndoki Park, Congo Republic – Sydney Ndolo, Dave Morgan, and Crickette Sanz.

Individual tree analysis

We carried out statistical analysis using R v 3.3.1 (R Foundation for Statistical Computing, Austria). We analysed flowering and fruiting patterns of individual trees, focusing on the presence / absence of flowering or fruiting. To analyse the phenological patterns, we calculated three quantitative indicators: (1) flowering / fruiting frequency (number of flowering cycles for a given year), (2) fidelity for a particular flowering / fruiting frequency and (3) seasonal phase (time of the year when flowering / fruiting are happening). For a robust estimation of the aforementioned indicators, we used Fourier analysis (following Chapman et al. 1999). We interpolated data for gaps less than 3 months, while for longer gaps, we split the time series into multiple series, which we treated separately. We included all species with at least 10 individual trees for which data were available for at least 60 consecutive months. Trees that died were recorded until death and trees that never flowered or fruited were excluded. Following Fourier analysis, we further removed trees with no detectable frequency peak and species with less than five remaining trees. We analysed 5446 (196 species) and 4596 (190 species) individual trees for the flowering and fruiting, respectively (species name and the number of recorded trees for all sites are located in Appendix 2A and B).

Fourier analysis

In order to assess the major cyclic patterns for flowering and fruiting across the sites, we used Fourier analysis to identify dominant cycles per individual tree. Fourier is a spectral analytical method used to decompose a time series into a sum of sine and cosine functions of different frequencies and is a robust analysis in determining plants' dominant cycles (Platt & Denman 1975). Bush et al. (2016) showed how it could be used to assess phenology activity in tropical trees at the individual-level, allowing for the diversity of cycles and level of synchrony present in the phenology of tropical plant species. We calculated the Fourier spectrum for each individual tree using the R function spectrum from the R base package 'stats' (R Core Team 2015). Following the guidelines in Bush et al. (2016) we smoothed the raw spectrum using a Daniell kernel (a moving average smoother) with varying spans depending on the time series length to give a bandwidth of 0.1. This gives sufficient resolution in the spectral estimate to assess dominant cycles while suppressing irrelevant fine-scale structure. We assessed the smoothed spectral estimate for each individual tree and extracted the cycle frequency with the highest power, representing the strongest cycle in the data. Bush et al. (2016) warn that time series with little cyclic activity can sometimes produce Fourier transforms with high power in non-relevant low frequencies (e.g. the full length of the time series). To account for this we screened out individuals where the dominant cycle identified from the spectrum was greater than half the length of the time series (resulting in exclusion of 9% of trees for flowering and 13% of trees for fruiting). These further data exclusions following Fourier analysis resulted in samples of 5,446 individuals (196 species) for the flowering analysis and 4,595 individuals (191 species) for the fruiting analysis. Prior applying the minimum 60 months threshold numbers were 11211 individuals (469 species) for the flowering analysis and 10517 individuals (453 species), respectively (See Table 2). Individual time series ranged from 60 to 339 months long (mean = 123 months) with site differences in data length.

Fourier analysis displays the results as a periodogram, in which the position of the highest peak on the X axis represents the dominant flowering frequency of each individual tree, while on the Y axis the fidelity score of each tree for that particular frequency that was normalised for species comparison by dividing each score by the total number of species. Hence, as the score increases the fidelity to a particular frequency becomes stronger. This means that trees stick to a particular cycle. The height of the periodogram on the Y axis indicates how tightly each tree keeps its dominant frequency over the studied period. To ensure comparability between sites we normalised each wavelength height by dividing each point in the spectral estimate by the total area under the peridogram for each individual tree. In order to ease interpretation we calculated seasonal phase only for trees that had dominant cycle lengths of 6 and 12 months. We calculated the seasonal phase by simulating a cosine curve, starting at the beginning of January with the empirical time series dominant frequency. The difference between the two peaks in radians represents the seasonal phase. This was then converted to time by the following equations,

$$if\ \Phi_{radians} > 0, \qquad \Phi_{months} = \frac{\Phi_{radians}}{(2\pi/\lambda)}$$

$$if\ \Phi_{radians} < 0, \qquad \Phi_{months} = \frac{\Phi_{radians} + 2\pi}{(2\pi/\lambda)}$$

(1)

where Φ is the phase in radians and λ is frequency in months.

Assessing phenology of species found at multiple sites

To test whether there are significant differences in phenology of the species found at multiple sites across Africa, we fitted two generalized linear models (GLMs) predicting each of the three response variables (frequency, fidelity for a conserved frequency and seasonal phase). In the first model, we estimated parameters for species, site and the interaction between species and site, which we then compared with a model excluding the interaction term. We compared models using ANOVA (Hudson & Keatley, 2009). Where the interaction was significant, we determined the species driving the change, by applying a post hoc test to compare the error bars overlap between the estimated frequencies, fidelity for a particular frequency and seasonal phases between sites. If error bars did not overlap, species were considered to differ significantly between sites. In the frequency and fidelity analysis, 45 species were found at multiple sites. In the seasonal phase comparison, only 28 species were present at multiple sites, having six and 12 months flowering / fruiting frequencies. The results will be displayed as violin plots that show the density of individual trees having a particular frequency, predictability and seasonal phase (y-axis). Frequency will be displayed in months, while predictability is expressed as numbers from 0 to the maximum length of each tree. Predictability of a tree flowering or fruiting increases with numbers. Seasonal phase is displayed from January to December.

Assessing phenology interannual trends

To test for trends over time, we adopted the same Fourier analysis on a 5-year moving window for each individual tree, and calculated frequency and fidelity for a constant frequency for each overlapping five year period. Due to the paucity of trees with six and 12 months frequencies, we did not calculate the temporal trends for the seasonal phase phenology. For each tree we regressed both frequency and fidelity scores over time and estimated the rate of change for both indicators. To test whether there are species that significantly differ in the rate of change between sites, we fitted two generalized linear models (GLMs) for each indicator (frequency and fidelity to a particular frequency). In the first model, we estimated parameters for species, site and the interaction between species and site, which we then compared with a model excluding the interaction term, using ANOVA. The species, showing statistically significant rates of change were extracted by comparing them with the 0 baseline of the first model. We also assessed weather species’ phenology patterns are specific to the location where they were present.

Results

Site comparison - Flowering frequency

We found a significant interaction between species and sites ($\chi^2 = 1.21$, df = 49, $p<0.001$), driven by 13 species (Table 2). The majority of species, showed conserved flowering frequencies between sites (e.g. *Anonidium mannii* generally showed annual flowering patterns: Fig 6a), but 13 (of the total of 45) differed between sites, sometimes substantially (e.g. *Irvingia excelsa* showed a dominant flowering frequency of three months at Mbeli Bai but at Okapi Edoro site, most trees flowered every 18 months (Fig 6b)). Apart from these, at both sites trees also scored other dominant flowering frequencies such as 12 and 20 months at Mbeli Bai and 13, 24 and 30 months at the Okapi Edoro site (Fig 6a,6b). Several different species present at two close sites, Okapi Lenda and Okapi Edoro, also showed significantly different flowering frequencies.

Table 2. GLM model summary for flowering frequency. Flowering frequencies for 13 significant species ($p<0.001$) shared between multiple sites. Estimate (β) represents versus frequency in months.

No	Species	Site	β	SE
1	*Anthonotha macrophylla*	Okapi Edoro	0.1806	0.0304
	Anthonotha macrophylla	Okapi Lenda	0.0723	0.0304
2	*Croton haumanianus*	Okapi Edoro	0.1577	0.0221
	Croton haumanianus	Okapi Lenda	0.0908	0.0277
3	*Grewia oligoneura*	Mbeli	0.1458	0.0304
	Grewia oligoneura	Okapi Edoro	0.2203	0.0340
	Grewia oligoneura	Okapi Lenda	0.0845	0.0277
4	*Irvingia excelsa*	Mbeli	0.2608	0.0321
	Irvingia excelsa	Okapi Edoro	0.0500	0.0267
5	*Margaritaria discoidea*	Okapi Edoro	0.1086	0.0304
	Margaritaria discoidea	Okapi Lenda	0.1908	0.0248
6	*Myrianthus holstii*	Amani	0.2195	0.0165
	Myrianthus holstii	Nyungwe	0.0950	0.0215
7	*Panda oleosa*	Lope	0.2244	0.0321
	Panda oleosa	Tai	0.0727	0.0233
8	*Pentadesma butyracea*	Lope	0.0908	0.0267
	Pentadesma butyracea	Tai	0.1312	0.0148
9	*Pseudospondias microcarpa*	Gombe	0.0741	0.0233
	Pseudospondias microcarpa	Lope	0.2561	0.0278
10	*Sacoglottis gabonensis*	Lope	0.0822	0.0221
	Sacoglottis gabonensis	Tai	0.1209	0.0099
11	*Sarcocephalus pobeguinii*	Okapi Edoro	0.1264	0.0248
	Sarcocephalus pobeguinii	Okapi Lenda	0.1837	0.0290
12	*Strombosia pustulata*	Okapi Edoro	0.0890	0.0227
	Strombosia pustulata	Tai	0.1235	0.0116
13	*Strombosiopsis tetrandra*	Okapi Edoro	0.1713	0.0304
	Strombosiopsis tetrandra	Okapi Lenda	0.0953	0.0340

β: parameter estimate; SE: standard error

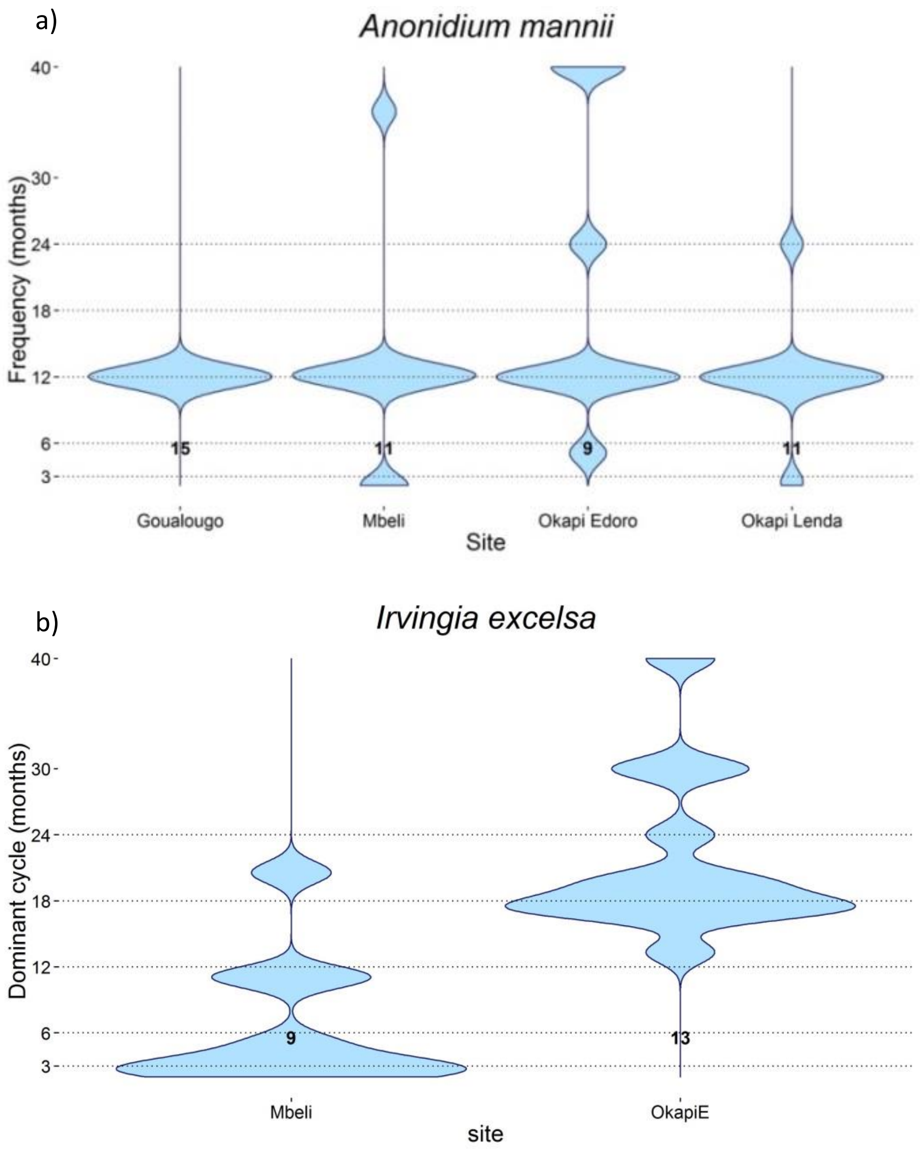


Figure 6. Violin plots showing density of individual flowering frequencies for species, present at multiple sites. The numbers present on the graphs represent the total number of trees found at each site. The two contrasting species show the dominant flowering frequency between several sites. *Anonidium mannii* species (a) shows an annual flowering frequency across four sites: Goualougo, Mbeli, Okapi Edoro, Okapi Lenda. *Irvingia excelsa* (b) shows significantly different flowering frequencies between Mbeli and Okapi Edoro sites. Full plots for all significantly different flowering frequencies are available in Appendix 2C. Full plots for species that have similar flowering frequencies across multiple sites are held in Appendix 2D.

Site comparison - Predictability of flowering frequency

We found again a significant interaction between species and site (χ^2 = 2056.9, df = 49, p<0.001), driven by 28 species, indicating that species vary in their fidelity for a particular frequency across different sites (Table 3). Less than half of species showed conserved fidelity scores for a certain frequency between sites (e.g. *Uapacaa guineensis* species fidelity scores ranged between four and seven across four sites (Fig 7a), but 28 species (of the total of 45) substantially differed across sites (e.g. *Sarcocephalus pobeguinii* showed lower fidelity scores, ranging from one to four at Okapi Lenda and from four to nine at Okapi Edoro (Fig 7b). Seven species (*Croton haumanianus, Cynometra alexandri*, *Erythrophleum suaveolens*, *Julbernardia seretii, Macaranga schweinfurthii, Margaritaria discoidea, Sarcocephalus pobeguinii*) again showed statistically significant fidelity scores between Okapi Lenda and Okapi Edoro sites (Table 3).

Table 3. GLM model summary for fidelity to a particular flowering frequency. Predictability scores of flowering frequencies for 28 significant (p<0.001) species present at multiple sites.

No	Species	Site	β	SE
1	*Albizia gummifera*	Nyungwe	9.2982	0.4735
	Albizia gummifera	Okapi Lenda	6.7369	0.5959
2	*Canarium schweinfurthii*	Lope	6.5276	0.6880
	Canarium schweinfurthii	Okapi Lenda	10.0977	0.5959
3	*Croton haumanianus*	Okapi Edoro	5.3358	0.4735
	Croton haumanianus	Okapi Lenda	7.1450	0.5959
4	*Cynometra alexandri*	Okapi Edoro	4.9410	0.3043
	Cynometra alexandri	Okapi Lenda	6.8006	0.6527
5	*Detarium macrocarpum*	Lope	4.6793	0.5330
	Detarium macrocarpum	Mbeli	3.0963	0.6527
6	*Duboscia macrocarpa*	Tai	6.1444	0.4615
	Duboscia macrocarpa	Lope	11.8324	0.6224
	Duboscia macrocarpa	Mbeli	7.7488	0.6527
7	*Erythrophleum suaveolens*	Okapi Edoro	7.4305	0.6224
	Erythrophleum suaveolens	Okapi Lenda	4.4963	0.6527

Table 3 continued

No	Species	Site	β	SE
8	*Gilbertiodendron dewevrei*	Mbeli	7.3024	0.5959
	Gilbertiodendron dewevrei	Okapi Lenda	8.9520	0.3043
9	*Irvingia excelsa*	Mbeli	3.8220	0.6880
	Irvingia excelsa	Okapi Edoro	9.1416	0.5725
10	*Julbernardia seretii*	Okapi Edoro	4.6612	0.2949
	Julbernardia seretii	Okapi Lenda	11.0606	0.6224
11	*Macaranga schweinfurthii*	Okapi Edoro	*5.3269*	*0.5517*
	Macaranga schweinfurthii	Okapi Lenda	*7.1690*	*0.4504*
12	*Magnistipula butayei*	Tai	*4.4427*	*0.6224*
	Magnistipula butayei	Nyungwe	*5.9974*	*0.5517*
13	*Margaritaria discoidea*	Okapi Edoro	5.4808	0.6527
	Margaritaria discoidea	Okapi Lenda	4.0854	0.5330
14	*Myrianthus holstii*	Amani	3.2262	0.3540
	Myrianthus holstii	Nyungwe	5.2162	0.4615
15	*Nauclea diderrichii*	Lope	3.5642	0.4865
	Nauclea diderrichii	Okapi Edoro	5.3826	0.5517
	Nauclea diderrichii	Tai	4.3841	0.3185
16	*Neoboutonia macrocalyx*	Bwindi	7.6215	0.6880
	Neoboutonia macrocalyx	Nyungwe	6.2485	0.5959
17	*Olea capensis*	Bwindi	11.5646	0.6527
	Olea capensis	Nyungwe	7.9664	0.4615
18	*Parkia bicolor*	Lope	9.8726	0.6527
	Parkia bicolor	Tai	8.6183	0.3112
19	*Pentadesma butyracea*	Lope	11.9013	0.5725
	Pentadesma butyracea	Tai	6.4875	0.3185
20	*Podocarpus latifolius*	Bwindi	5.6897	0.5330
	Podocarpus latifolius	Nyungwe	3.7490	0.3649
21	*Prunus africana*	Bwindi	6.6162	0.6527
	Prunus africana	Nyungwe	4.9208	0.5330
22	*Pseudospondias microcarpa*	Gombe	6.3418	0.5006
	Pseudospondias microcarpa	Lope	4.4352	0.5959
23	*Pycnanthus angolensis*	Lope	15.1751	0.5330
	Pycnanthus angolensis	Tai	8.6108	0.2467

Table 3 continued

No	Species	Site	β	SE
24	*Sacoglottis gabonensis*	Lope	8.8083	0.4735
	Sacoglottis gabonensis	Tai	5.9158	0.2118
25	*Sarcocephalus pobeguinii*	Okapi Edoro	5.1345	0.5330
	Sarcocephalus pobeguinii	Okapi Lenda	3.0614	0.6224
26	*Strombosia pustulata*	Okapi Edoro	7.3431	0.4865
	Strombosia pustulata	Tai	5.6680	0.2485
27	*Trichoscypha acuminata*	Lope	4.5184	0.5725
	Trichoscypha acuminata	Mbeli	6.9660	0.7298
28	*Vitex doniana*	Lope	8.5437	0.3833
	Vitex doniana	Mbeli	5.4954	0.6527

β: parameter estimate; SE: standard error

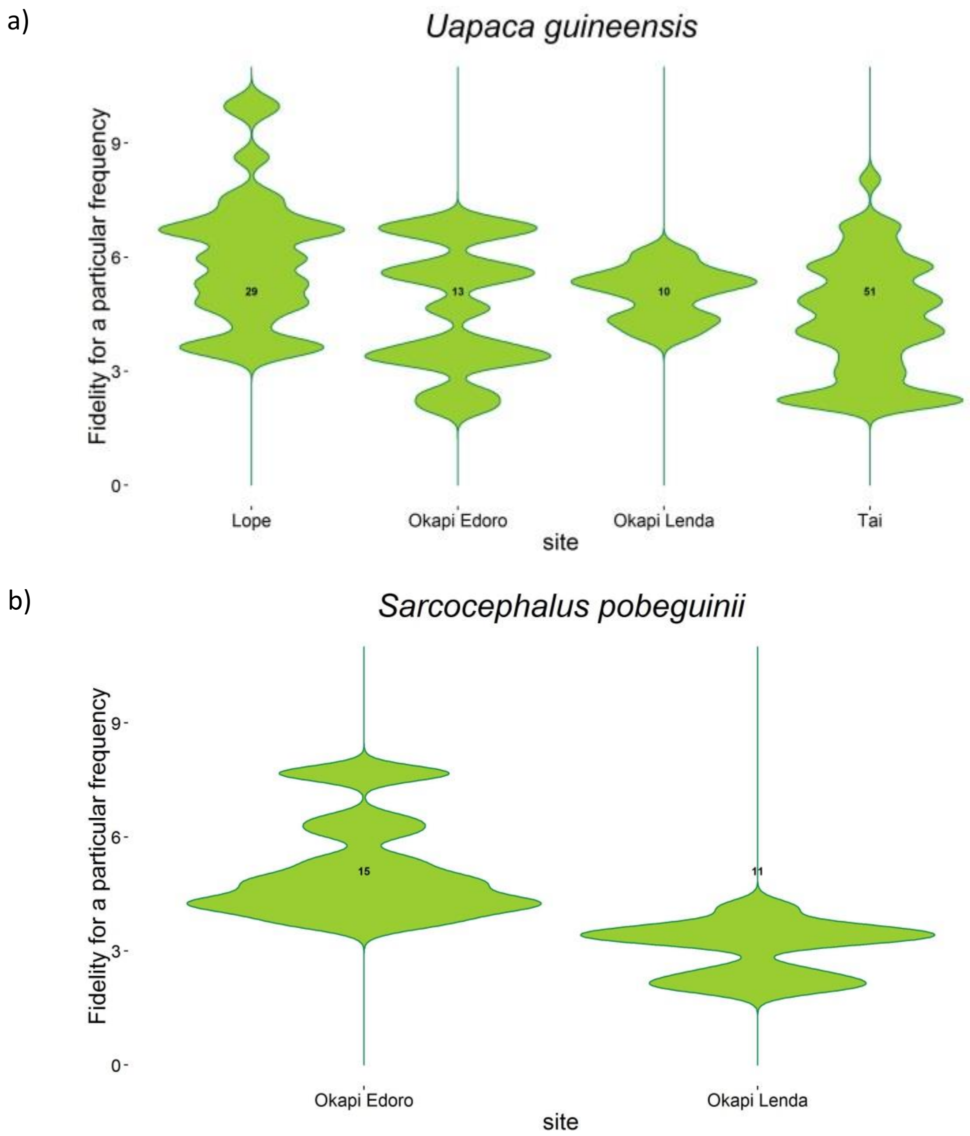


Figure 7. Violin plots showing density of fidelity scores for each individual tree and species, present at multiple sites. The numbers present on the graphs represent the total number of trees found at each site. The fidelity of a tree for a particular cycle increases with the numbers on the Y axis. The two contrasting species show the dominant fidelity scores between several sites. *Upaca guineensis* species (a) shows same range of fidelity scores across four sites: Lope, Okapi Edoro, Okapi Lenda and Tai. *Sarcocephalus pobeguinii* (b) shows significant different ranges between Okapi Edoro and Okapi Lenda sites. Full plots for all species that vary in their fidelity for a particular frequency across different sites are available in Appendix 2E. Full plots for species that do not vary in their fidelity for a particular frequency are held in Appendix 2F.

Site comparison - Seasonal phase

3003 individual trees (188 species) exhibited six or 12 month flowering frequencies, allowing calculation of flowering seasonality. Of these, 28 species were present at multiple sites. We again found a significant interaction between species and site (χ^2 = 365.87, df = 28, p<0.001), driven by 18 species which showed significantly different seasonality of flowering between sites (Table 4). More than half of species, showed conserved seasonality of flowering between sites (e.g. *Gilbertiodendron dewevrei* species generally flowered mostly throughout March across two different sites (Fig 8a), but 18 (of the total of 28) differed between sites (e.g. *Irvingia grandifolia* species flowered in October at Lope, in February at Mbeli and between April and November at Tai (Fig 8b). We found again six species (*Croton haumanianus, Cynometra alexandri*, *Dialium corbisieri*, *Hallea stipulosa, Julbernardia seretii, Macaranga schweinfurthii*), present at Okapi Edoro and Okapi Lenda sites, to have significantly different flowering times (Table 4).

Table 4. GLM model summary for flowering seasonal phase. Flowering seasonal phase for 18 significant (p<0.001) tree species present at multiple sites.

No	Species	Site	β	SE
1	*Albizia gummifera*	Nyungwe	-0.18543	0.2333
	Albizia gummifera	Okapi Lenda	1.71293	0.2632
2	*Canarium schweinfurthii*	Lope	2.40444	0.2909
	Canarium schweinfurthii	Okapi Lenda	1.69135	0.2632
3	*Croton haumanianus*	Okapi Edoro	-0.01697	0.2421
	Croton haumanianus	Okapi Lenda	2.5383	0.2520
4	*Cynometra alexandri*	Okapi Edoro	0.46503	0.2117
	Cynometra alexandri	Okapi Lenda	1.74683	0.2760
5	*Dialium corbisieri*	Okapi Edoro	-2.45382	0.3563
	Dialium corbisieri	Okapi Lenda	2.39114	0.3563
6	*Hallea stipulosa*	Okapi Edoro	1.40471	0.2760
	Hallea stipulosa	Okapi Lenda	0.64812	0.3903
7	*Irvingia grandifolia*	Lope	-1.41419	0.2254
	Irvingia grandifolia	Mbeli	1.15574	0.3903
	Irvingia grandifolia	Tai	-0.34723	0.3086
8	*Julbernardia seretii*	Okapi Edoro	-2.07733	0.2254
	Julbernardia seretii	Okapi Lenda	2.85296	0.2632

Table 4 continued

No	Species	Site	β	SE
9	*Macaranga schweinfurthii*	Okapi Edoro	-2.7974	0.3299
	Macaranga schweinfurthii	Okapi Lenda	1.5255	0.2182
10	*Margaritaria discoidea*	Okapi Edoro	-2.0139	0.3563
	Margaritaria discoidea	Okapi Lenda	2.0380	0.2760
11	*Neoboutonia macrocalyx*	Bwindi	-0.2398	0.3903
	Neoboutonia macrocalyx	Nyungwe	1.9508	0.3299
12	*Parinari excelsa*	Nyungwe	-1.0780	0.3903
	Parinari excelsa	Okapi Lenda	2.3311	0.2909
	Parinari excelsa	Tai	-0.4825	0.1331
13	*Parkia bicolor*	Lope	0.3864	0.2760
	Parkia bicolor	Tai	0.3383	0.1331
14	*Pentadesma butyracea*	Lope	2.2698	0.2520
	Pentadesma butyracea	Tai	1.6070	0.2760
15	*Strombosia pustulata*	Okapi Edoro	-1.4221	0.2909
	Strombosia pustulata	Tai	-1.8585	0.1347
16	*Strombosiopsis tetrandra*	Okapi Edoro	-1.6071	0.3903
	Strombosiopsis tetrandra	Okapi Lenda	1.4406	0.3086
17	*Tetrapleura tetraptera*	Goualougo	1.8256	0.2420
	Tetrapleura tetraptera	Lope	1.3152	0.2117
18	*Uapaca guineensis*	Lope	1.1821	0.1820
	Uapaca guineensis	Okapi Lenda	-0.3306	0.2909
	Uapaca guineensis	Tai	0.6349	0.2117

β: parameter estimate; SE: standard error

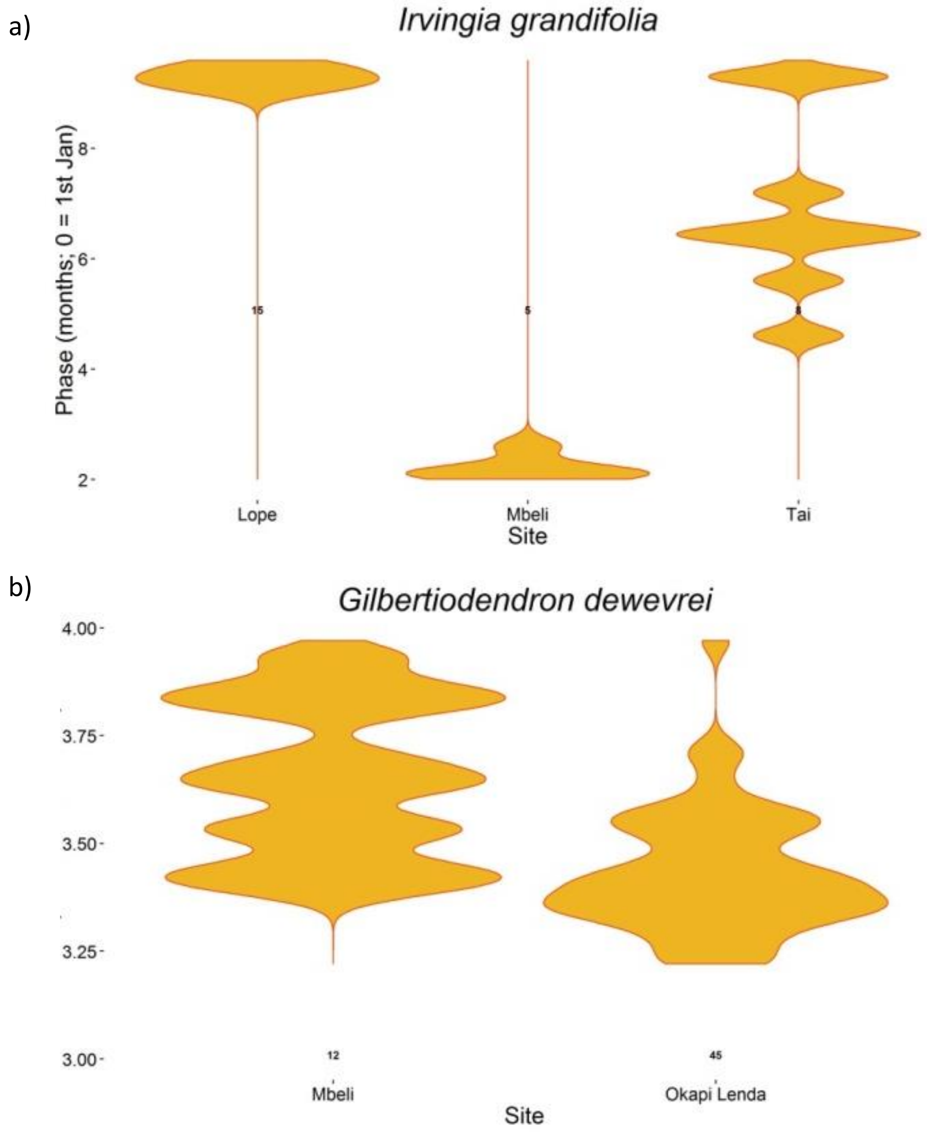


Figure 8. Violin plots showing density of individual trees and species' flowering seasonality. Months are expressed in numbers (0 - January, 1 – February, 2 – March, 3 – April, 4 – May, 5 – June, 6 – July, 7 – August, 8 – September, 9 – October, 10 – November, 11 – December). The two contrasting species show the dominant flowering time between several sites. *Gilbertiodendron dewevrei* species (a) flowers between March and April at two sites: Mbeli and Okapi Lenda. *Irvingia grandifolia* species (b) shows significant different flowering times between Lope, Mbeli and Tai. Full plots for all species that have significantly different seasonal phases across different sites are available in Appendix 2G. Species that do not have different seasonal phases are held in Appendix 2H.

Site comparison - Fruiting phenology

As for flowering we found significant differences in frequency, fidelity for a particular fruiting frequency and fruiting seasonality for species shared between different sites. Results were qualitatively similar to those for flowering and full results are displayed in Appendix 2I-2M. Only where substantive differences were found we do comment on fruiting below.

Temporal trends

We found strong evidence that flowering frequency declined over time for all species, except two, in most sites. However, the two species were not statistically significant. Across species that showed evidence of a decline in flowering frequency over time, 75 species (54%) were statistically significant (Fig. 9). This result shows that trees slightly increase the interval of their flowering cycle from, for example, 6 months to 7 months and so on across several years. If this trend continues at this speed, in time, flowering events may decline significantly. Moreover, shifts in flowering frequency over time are species and site specific ($\chi^2 = 0.21$, df = 20, $p<0.001$) such that the greatest change was found at Tai, Okapi Lenda and Amani.

On the other hand, we found less consistent evidence in relation to fidelity for a particular flowering frequency, with only 16% (22) of species explaining a significant interaction between site and species ($\chi^2 = 80.374$., df =20, $p<0.001$), with half increasing its fidelity for a particular flowering frequency and the other half decreasing it (Fig. 10). This result shows that some trees might be predictable in their flowering frequency, while other might not. Significant species were mostly found at Tai, which is one of the sites with a long and complete dataset.

As with flowering, fruiting frequency is also decreasing over time ($\chi^2 = 76.511$., df =9, $p<0.05$), with 60% of species showing statistically significant slopes (Appendix 2N). Temporal changes in fidelity for a particular fruiting frequency are also significant, changing for 16% of species, though the proportion of species showing a significant decline in fidelity for a particular frequency was similar to those showing increases ($\chi^2 = -0.069$., df =9, $p<0.001$) (Appendix 2O). Individual trees and species recorded for fruiting analysis are not identical to the ones recorded for flowering analysis; however most of the species are shared between both groups.

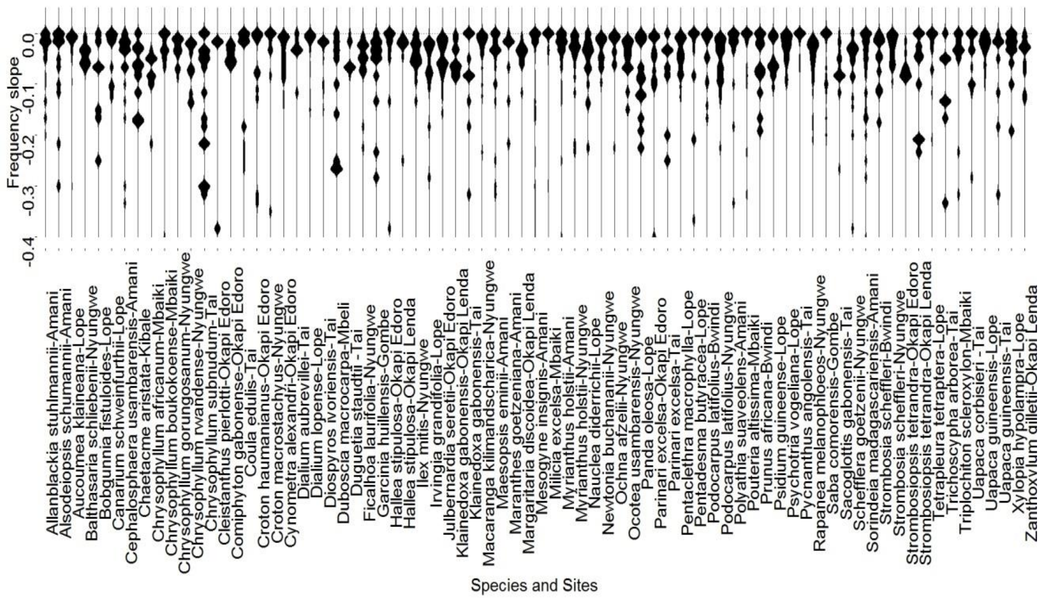


Figure 9. Violin plots showing change in frequency of flowering events over time for 75 statistically significant species. Each tree has a specific slope that shows the direction of flowering frequency, which is displayed in the violin plot. The majority of individuals showed either zero or a negative change in frequency, indicating that species flowered less frequently over time. Comparison was done with the 0 baseline.

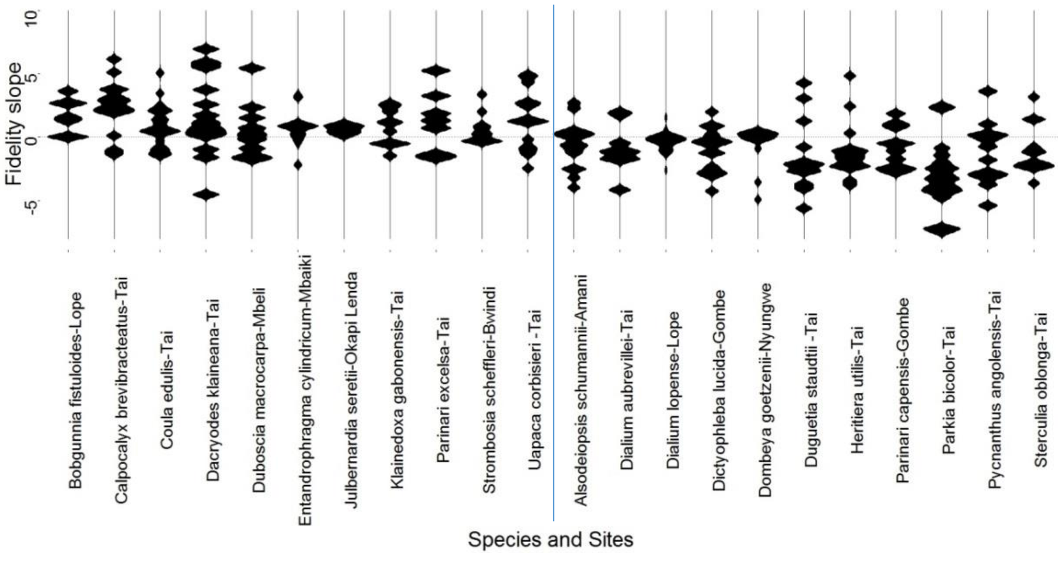


Figure 10. Change in fidelity for a particular flowering frequency over time for 22 statistically significant species. Blue line separates positive slopes (left) from negative slopes (right). Comparison was done with the 0 baseline. The figure is a violin plot, showing the density of slopes with a certain value). Each tree has a specific slope that shows the direction of flowering predictability, which is displayed in the violin plot. Half

of individuals showed either a negative or a positive change in their fidelity to keep a particular frequency, indicating that species flowered less frequently over time.

Discussion

Using a novel Fourier based analysis, we successfully estimated flowering patterns for 5446 individual trees, of 196 species and fruiting patterns for 4595 trees of 191 species across 11 sites with a long and complete dataset. Our results supported both hypotheses and revealed novel trends not reported before. Overall, we found many significant differences between the phenology of tree species between sites and identified consistent patterns of temporal change in flowering of African tropical forest tree species.

Flowering frequency of species shared between multiple sites

As expected from earlier work (Borchert, 1980; C. A. Chapman et al., 1999), we found good support for our first hypothesis, which states that there are significant differences in terms of phenology of species shared between multiple sites. We found that 29% of species showed different dominant flowering frequencies at different sites. However, over 70% of species did not show differences in flowering frequency between sites, suggesting that for them frequency is a conserved trait. These species did not have fewer data than the ones in the 30% group. Our results support the much smaller geographical scale work of (Newstrom et al., 1994), who also found most tropical species to have matching flowering frequencies across multiple sites, though he also reported a few species that show different frequencies across various sites, perhaps in response to different hydrological regimes.

For example, (Newstrom et al., 1994) reported that *Ceiba pentandra* species, which grows in wet forests flower supra-annually and annually in dry forests, whilst *Hamelia patens* flowers continuously in lowland forests and annually in tropical dry forests. These differences highlight the plasticity of some tropical trees species and their adaptiveness to the local environment conditions. We also found species in very close proximity to show different flowering frequencies. For some trees of the same species, growing at Okapi Edoro and Okapi Lenda, only about 35 km apart and connected by continuous forest, flowering frequencies appeared significantly different. Both forests differ in forest community such that Okapi Edoro a diverse mixed forest, while Okapi Lenda is comprised of monodominant forest of

Gilbertiodendron dewevrei species (Condit et al., 2005; Makana et al., 2011). No substantial difference has been reported between the two forest types in terms of climate, soil and history (Gubista, 1999). Consequently, there is something more important such as probably pollinators that play an important role in setting the flowering frequencies. Or this perhaps indicates that for those species that do show differences between sites, phenotypic plasticity rather than local adaptation interferes with the site level variation. Similar local variation in flowering frequency (over just 10km) has been reported before in a study by (Chapman et al. 1999), which focused on community wide patterns of flowering and fruiting phenology for 67 species. In this study, several species shared between sites exhibited different flowering and fruiting frequencies and differed in the density of trees in flower between the two sites. There is no precise explanation for the difference in phenological patterns observed between the Okapi Edoro and Okapi Lenda sites in our study andwe call for further investigation of phenological patterns and better characterisation of the African sites at the level of microclimate, community composition and local weather conditions.

Fidelity for a particular flowering frequency of species shared between multiple sites

Because of the rapid changing climate (Anderson-Teixeira et al., 2015; O’Gorman, 2012) and reports from Central America (McDade, Bawa, & Hespenheide, 1994) and South East Asia (Maza-Villalobos, Poorter, & Martínez-Ramos, 2013; Pei et al., 2015) that found unpredictable flowering frequencies due to variation in precipitation or temperature, we expected the fidelity for a particular flowering frequency to be different for species shared between multiple sites. This pattern was exhibited by approximately 60% of the species, where individual species varied greatly in their fidelity to their dominant flowering frequency. This stands in total contrast to the situation in the temperate zone where trees are highly predictable (Shoko Sakai et al., 1999), presumably reflecting the weaker constraints posed by the less seasonal variation in weather across tropical sites. This indicates that individual trees are able not only to modify how much energy they invest in reproduction each season, but also exactly when they do this. However, exactly what the implications of such flexibility in flowering frequencies in tropical trees still lack a robust explanation. Since flowering frequency is relatively conserved, but fidelity for a particular one is variable, it seems plausible that an endogenous rhythm modulates the propensity to flower, but exact timing may be triggered by an environmental cue that is itself more variable in timing in the tropics than in the temperate zone (Borchert, 1980, 1983). Such plasticity would have clear advantages to ensure optimal match to environmental conditions and is well established over relatively small time scales in temperate regions (Shoko Sakai et al., 1999). Variation of a particular flowering frequency has been previously reported in angiosperms (Kindlmann & Balounová, 1999). It was proposed that in angiosperms unpredictability of flowering frequency is a result of the investment in sexual reproduction that affects the probability of flowering. It could be likely that high energy investment in fruiting events at times may interfere with the frequency of flowering, since all the phenophases are interconnected with each other (Bawa et al., 2003). In the tropics parasites survive all year, hence it may pay a tree to be less predictable with regard to its flowering and fruiting events in order to avoid parasites' virulence (Anders, 1998).

Seasonal phase of species shared between multiple sites

Because our different sites have very different seasonal patterns of temperature and rainfall, we expected flowering seasonal phases to be different for species shared between multiple sites, and approximately 64% of them did show this pattern. It has been previously reported that flowering time is related to the most favourable time for pollen transfer, with wind pollinated species flowering during the dry season, when the intensity of trade winds reach their peak (Gentry, 1974). Otherwise, flowering times differ within species growing at different strata (Kozlowski & Pallardy, 1997). Although differences between sites on opposite sides of the continent could easily be explained in terms of timing of the rains, solar radiation, minimum temperature, in Okapi Reserve, we again found species that differed significantly in seasonal phase between Edoro and Lenda sites. Such local scale variation is unlikely to be driven by differing seasonality and confirms earlier observations of local scale variation in phenology (Tomlinson & Zimmerman, 2000), that are still lacking a robust explanation. Differences in flowering time can be linked to plasticity of individual species, their genetic inheritance or responses to local environmental conditions (Bawa et al., 2003; Borchert, 1980; Tomlinson & Zimmerman, 2000), but exactly what drives local scale variation is yet to be identified.

To conclude, in contrast with the results found in temperate regions and Asia we found that African tropical trees species have heterogeneous patterns in terms of frequency, fidelity to conserve a particular frequency and seasonal phase, even between species present at adjacent sites. Patterns found here resemble more those found in Central and South American tropical forests. Several factors can impact phenology such as large differences in seasonality, altitude, micro-environmental conditions, local weather circumstances and community composition (Fenner, 1998; Mark, 2013) and it is perhaps unsurprising that we find such differences. However, we call for more intense research in order to be able to mitigate future climate change consequences in Africa.

Interannual trends of flowering frequency

One of our strongest results was that all species flowered less over time. In contrast to flowering time, which is widely noted to be changing at least in temperate zones (Bertin, 2008) flowering frequency has received very little attention and this is the first such general report we know. Frequency changes are only really likely in tropical systems, where plants do not need to maintain strict annual frequencies imposed by day length and temperature limits (S. Sakai, 2001), and there are only a few studies that tackle phenological change in African tropical forests (Adole et al., 2016). There are two likely causes of such a change: a large scale (pan continental) forcing event affecting all species equally (e.g. climate change) (Parmesan, 2006; Parmesan & Yohe, 2003) or an endogenous change affecting all individual trees equally, such as gradual senescence (Marshall, Avritt, Maliakal-Witt, Medeiros, & Shaner, 2010). We know that young forests flower more frequently than mature ones (Van Schaik, 1986) and so it seems plausible that the decrease in flowering frequency we found is simply a function of senescence. Moreover, trees that died were not replaced with new ones; hence the population age was not well-adjusted with new young trees. Alternatively, regional changes in weather conditions could have also affected flowering frequency especially for those species that use environmental cues as their primary trigger. For example, timing of tree fruit production at Kibale National Park, Uganda has been related to shifts in climate, with some trees experiencing fruit abortion due to unfavourable climatic conditions (Colin A. Chapman et al., 2005). The increase in frequency and intensity of extreme weather events are projected to impact tropical forests (Zelazowski, Malhi, Huntingford, Sitch, & Fisher, 2011) and regional changes in weather events initiated by climatic phenomena such as El Niño–Southern Oscillation are well known to affect fruiting production in both the New World (Wright & Calderón, 2006) and Asia (Shoko Sakai, 2002). However, we consider such climate change as a less likely driver of the observed pattern not because the climate has not been changing during the studies, but because the rates of change and the degree of change have been most likely variable across the sites (Butt et al., 2015). Climate change impact in the tropics is driven by extreme weather events, but their implications at the regional scale are uncertain and controversial (Zelazowski et al., 2011). Consequently, concluding that climate is delaying flowering frequency would currently be premature. Delay across flowering patterns may lead to several cascading effects on the ecosystem strata, causing temporal shifts in phenology. If the same phenological pattern found by us stays consistent, it may lead to phenological mismatches between plants and pollinators, hence affecting population survival, species boundaries and ecosystem services (Hart, Salick, Ranjitkar, & Xu, 2014). However, more research is needed to test this hypothesis.

Interannual trends for fidelity to a particular flowering frequency

As climate change is advancing at an unprecedented rate (Walther et al., 2002), we expected the fidelity of a tree for a particular flowering frequency to change over time, and for 16% of species it did significantly. In our findings, species were divided into two groups: for some species fidelity for a particular frequency increased, while for others it decreased. For both categories there are advantages and disadvantages and the strategy adopted is most likely species-specific. For a tree that increases its fidelity for a particular frequency over time, an advantage could consist of the conservation for specific pollinators that rely on certain tree species to grow and reproduce (Fenner, 1998). A disadvantage could represent a phenology mismatch between animals that change their phenology in response to climate change and species that adapt very well to new climatic conditions. This in turn may lead to species extinction (Morellato et al., 2016).

A flower with a low fidelity to a particular frequency can either flower less or more often over time. Bawa et al. (2003) reported that flowering less often is likely to confer a disadvantage because unpredictability of flowering frequency will reduce pollinator fidelity and specialization. Flowering more regularly than usual may increase the population of that particular species, enhance reproductive success or reduce seed predators (Bawa et al., 2003). Unpredictability can also be a mechanism of reducing reproduction failure triggered by inconsistent pollinators (Bawa et al., 2003). However, in our study we found equal number of species with increased / decreased fidelity for a particular flowering frequency, which can suggest that no change is actually encountered and the significant increase / decrease in the fidelity for a particular frequency shown by several species is just by chance. This speculation is supported also by our fruiting results that show equal proportion of species showing different directions in fidelity for a particular frequency over time.

Conclusions

Phenology provides key knowledge on how ecosystems respond to regional and global climate changes. Understanding phenology of African tropical forests is crucial to adapt to and mitigate future climate related impacts. Here we fill several gaps in our knowledge of the phenology of African tropical forests and demonstrate plasticity of several African tropical species for all three quantitative indicators: frequency, fidelity to conserve a particular frequency and seasonal phase. Moreover, we have showed that flowering and fruiting frequency decrease over time, most likely due to senescence and call for further research to prove this theory.

Appendices

Appendix 2A. Species name and number of trees recorded at each site for the flowering analysis.

Species	Site											
	Amani	Bwindi	Gombe	Goualoug	Kibale	Lope	Mbaiki	Mbeli	Nyungwe	Okapi Edoro	Okapi Lenda	Tai
Afzelia bella	0	0	0	0	0	0	0	0	0	0	0	9
Agelaea paradoxa	0	0	0	0	0	0	0	0	0	0	0	16
Alangium chinense	0	0	0	0	0	0	0	0	18	0	0	0
Albizia gummifera	0	0	0	0	0	0	0	0	19	0	12	0
Albizzia grandibracteata	0	0	0	0	8	0	0	0	0	0	0	0
Allanblackia stuhlmannii	57	0	0	0	0	0	0	0	0	0	0	0
Alsodeiopsis schumannii	16	0	0	0	0	0	0	0	0	0	0	0
Alstonia boonei	0	0	0	0	0	0	0	0	0	0	11	0
Anisophyllea obtusifolia	5	0	0	0	0	0	0	0	0	0	0	0
Anonidium mannii	0	0	0	15	0	0	0	11	0	9	11	0
Anthonotha macrophylla	0	0	0	0	0	0	0	0	0	10	10	0
Antidesma vogelianum	0	0	0	0	0	21	0	0	0	0	0	0
Apodytes dimidiata	0	0	0	0	0	0	0	0	0	15	0	0
Aucoumea klaineana	0	0	0	0	0	47	0	0	0	0	0	0
Balthasaria schliebenii	0	0	0	0	0	0	0	0	12	0	0	0
Beilschmiedia rwandensis	0	0	0	0	0	0	0	0	14	0	0	0
Bersama abyssinica	0	0	0	0	0	0	0	0	19	0	0	0
Blighia welwitschii	0	0	0	0	0	0	0	0	0	9	0	0
Bobgunnia fistuloides	0	0	0	0	0	11	0	0	0	0	0	0
Bridelia brideliifolia	0	0	0	0	0	0	0	0	16	0	0	0
Calpocalyx aubrevillei	0	0	0	0	0	0	0	0	0	0	0	70
Calpocalyx brevibracteatus	0	0	0	0	0	0	0	0	0	0	0	83
Canarium schweinfurthii	0	0	0	0	0	9	0	0	0	0	12	0
Carapa grandiflora	0	0	0	0	0	0	0	0	22	0	0	0
Casearia runssorica	0	0	0	0	0	0	0	0	15	0	0	0
Cassia mannii	0	0	0	0	0	0	0	0	0	14	0	0
Cassipourea ruwenzoriensis	0	0	0	0	0	0	0	0	13	0	0	0
Celtis adolfi-fridericii	0	0	0	12	0	0	0	0	0	8	12	0
Celtis africana	3	0	0	0	0	0	0	0	0	0	0	0
Celtis durandii	0	0	0	0	10	0	0	0	0	0	0	0
Celtis mildbraedii	0	0	0	0	0	0	0	0	0	0	8	0
Celtis tessmannii	0	0	0	0	0	10	0	0	0	0	0	0
Cephalosphaera usambarensis	29	0	0	0	0	0	0	0	0	0	0	0
Chaetacme aristata	0	0	0	0	10	0	0	0	0	0	0	0
Chionanthus africanus	0	0	0	0	0	0	0	0	9	0	0	0
Chrysophyllum africanum	0	0	0	0	0	0	14	0	0	0	0	0
Chrysophyllum boukokoense	0	0	0	0	0	0	23	0	0	0	0	0
Chrysophyllum gorungosanum	0	0	0	0	0	0	0	0	17	0	0	0
Chrysophyllum rwandense	0	0	0	0	0	0	0	0	7	0	0	0
Chrysophyllum subnudum	0	0	0	0	0	0	0	0	0	0	0	81
Chrysophyllus africanum	0	0	0	0	0	13	0	0	0	0	0	0
Cissus dinklagei	0	0	0	0	0	10	0	0	0	0	0	0
Cleistanthus pierlotti	0	0	0	0	0	0	0	0	0	10	13	0
Cola lateritia	0	0	0	0	0	0	0	0	0	0	11	0
Cola lizae	0	0	0	0	0	12	0	0	0	0	0	0
Comiphyton gabonense	0	0	0	0	0	0	0	0	0	20	0	0
Coula edulis	0	0	0	0	0	0	0	0	0	0	0	125
Croton haumanianus	0	0	0	0	0	0	0	0	0	19	12	0
Croton macrostachyus	0	9	0	0	0	0	0	0	10	0	0	0
Cynometra alexandri	0	0	0	0	0	0	0	0	0	46	10	0
Dacryodes buettneri	0	0	0	0	0	11	0	0	0	0	0	0
Dacryodes klaineana	0	0	0	0	0	0	0	0	0	0	0	74
Daniellia thurifera	0	0	0	0	0	0	0	0	0	0	0	19
Detarium macrocarpum	0	0	0	0	0	15	0	10	0	0	0	0
Dialium aubrevillei	0	0	0	0	0	0	0	0	0	0	0	97
Dialium corbisieri	0	0	0	0	0	0	0	0	0	16	12	0
Dialium lopense	0	0	0	0	0	36	0	0	0	0	0	0
Dialium pentandrum	0	0	0	0	0	0	0	0	0	10	0	0
Dictyophleba lucida	0	0	18	0	0	0	0	0	0	0	0	0
Diospyros dendo	0	0	0	0	0	27	0	0	0	0	0	0
Diospyros ivoriensis	0	0	0	0	0	0	0	0	0	0	0	92
Diospyros polystemon	0	0	0	0	0	18	0	0	0	0	0	0
Diospyros sanza-minika	0	0	0	0	0	0	0	0	0	0	0	90
Diospyros soubreana	0	0	0	0	0	0	0	0	0	0	0	59
Diospyros zenkeri	0	0	0	0	0	11	0	0	0	0	0	0
Diplorhynchus condylocarpon	0	0	18	0	0	0	0	0	0	0	0	0
Dombeya goetzenii	0	0	0	0	0	0	0	0	13	0	0	0
Dombeya mukou	0	0	0	0	9	0	0	0	0	0	0	0
Drypetes gerrardii	0	7	0	0	0	0	0	0	0	0	0	0
Duboscia macrocarpa	0	0	0	0	0	11	0	10	0	0	0	20
Duguetia staudtii	0	0	0	0	0	0	0	0	0	0	0	41
Elaeis guineensis	0	0	1	0	0	0	0	0	0	0	0	0
Entandrophragma angolense	0	0	0	0	0	0	0	0	0	0	0	25
Entandrophragma cylindricum	0	0	0	0	0	0	51	0	0	0	0	0
Entandrophragma excelsum	0	0	0	0	0	0	0	0	17	0	0	0
Erythrophleum suaveolens	0	0	0	0	0	0	0	0	0	11	10	0
Erythroxylum mannii	0	0	0	0	0	0	0	0	0	0	0	10
Eucalyptus	0	0	0	0	7	0	0	0	0	0	0	0
Ficalhoa laurifolia	0	0	0	0	0	0	0	0	21	0	0	0
Ficus lutea	0	0	0	0	0	0	0	0	0	9	0	0
Ficus oreodryadum	0	0	0	0	0	0	0	0	9	0	0	0
Ficus sansibarica	0	0	0	0	0	0	0	0	0	0	0	13
Funtumia latifolia	0	0	0	0	10	0	0	0	0	0	0	0
Galiniera coffeoides	0	0	0	0	0	0	0	0	14	0	0	0
Ganophyllum giganteum	0	0	0	0	0	10	0	0	0	0	0	0
Garcinia huillensis	0	0	15	0	0	0	0	0	0	0	0	0
Gilbertiodendron dewevrei	0	0	0	0	0	0	0	12	0	0	46	0
Gilbertiodendron splendidum	0	0	0	0	0	0	0	0	0	0	0	25
Greenwayodendron suaveolens	0	0	0	0	0	10	0	0	0	0	0	0
Grewia oligoneura	0	0	0	0	0	0	0	10	0	8	12	0
Hallea stipulosa	0	0	0	0	0	0	0	0	0	12	8	0
Harungana madagascariensis	0	0	17	0	0	0	0	0	0	0	0	0
Harungana montana	0	0	0	0	0	0	0	0	12	0	0	0
Heisteria parvifolia	0	0	0	0	0	11	0	0	0	0	0	0
Heritiera utilis	0	0	0	0	0	0	0	0	0	0	0	62
Ilex mitis	0	0	0	0	0	0	0	0	19	0	0	0
Irvingia excelsa	0	0	0	0	0	0	0	9	0	13	0	0
Irvingia gabonensis	0	0	0	0	0	23	0	0	0	0	0	0
Irvingia grandifolia	0	0	0	0	0	20	0	9	0	0	0	30
Irvingia wombolu	0	0	0	0	0	0	0	0	0	10	0	0
Ixora burundensis	0	0	0	0	0	0	0	0	10	0	0	0
Julbernardia seretii	0	0	0	0	0	0	0	0	0	49	11	0

Appendix 2A continued

Species	Site											
	Amani	Bwindi	Gombe	Goualougo	Kibale	Lope	Mbaiki	Mbeli	Nyungwe	Okapi Edoro	Okapi Lenda	Tai
Klainedoxa gabonensis	0	0	0	0	0	10	0	2	0	12	10	76
Macaranga capensis	12	0	0	0	0	0	0	0	0	0	0	0
Macaranga kilimandscharica	0	0	0	0	0	0	0	0	24	0	0	0
Macaranga schweinfurthii	0	0	0	0	0	0	0	0	0	14	21	0
Maesa lanceolata	0	0	0	0	0	0	0	0	20	0	0	0
Maesopsis eminii	29	0	0	0	0	0	0	0	0	0	0	0
Magnistipula butayei	0	0	0	0	0	0	0	0	14	0	0	11
Manilkara zenkeri	0	0	0	0	0	0	0	0	0	13	0	0
Maranthes goetzeniana	9	0	0	0	0	0	0	0	0	0	0	0
Margaritaria discoidea	0	0	0	0	0	0	0	0	0	10	15	0
Massularia acuminata	0	0	0	0	0	8	0	0	0	0	0	0
Maytenus acuminata	0	0	0	0	0	0	0	0	17	0	0	0
Memecylon lateriflorum	0	0	0	0	0	0	0	0	0	0	0	49
Memecylon polyanthemos	0	0	0	0	0	0	0	0	0	0	0	19
Memecylon walikalense	0	0	0	0	0	0	0	0	18	0	0	0
Mesogyne insignis	15	0	0	0	0	0	0	0	0	0	0	0
Milicia excelsa	0	0	0	0	0	10	26	0	0	9	0	0
Milletia dura	0	0	0	0	10	0	0	0	0	0	0	0
Monanthotaxis congoensis	0	0	0	0	0	10	0	0	0	0	0	0
Monanthotaxis poggei	0	0	20	0	0	0	0	0	0	0	0	0
Musanga cecropioides	0	0	0	0	0	0	0	0	0	0	18	0
Myrianthus arboreus	0	0	0	0	0	11	0	0	0	0	0	0
Myrianthus holstii	34	0	0	0	0	0	0	0	20	0	0	0
Nauclea diderrichii	0	0	0	0	0	18	0	0	0	14	0	42
Nauclea xanthoxylon	0	0	0	0	0	0	0	0	0	0	0	22
Neoboutonia macrocalyx	0	9	0	0	0	0	0	0	12	0	0	0
Newtonia buchananii	0	0	0	0	0	0	0	0	15	0	0	0
Ochna afzelii	0	0	0	0	0	0	0	0	16	0	0	0
Ocotea usambarensis	0	0	0	0	0	0	0	0	13	0	0	0
Odyendea zimmermannii	6	0	0	0	0	0	0	0	0	0	0	0
Olea capensis	0	10	0	0	0	0	0	0	20	0	0	0
Olea welwitschii	0	0	0	0	4	0	0	0	0	0	0	0
Olinia rochetiana	0	0	0	0	0	0	0	0	30	0	0	0
Ongokea gore	0	0	0	0	0	10	0	0	0	0	0	0
Panda oleosa	0	0	0	0	0	9	0	0	0	0	0	17
Parinari capensis	0	0	17	0	0	0	0	0	0	0	0	0
Parinari excelsa	0	0	0	0	0	0	0	0	12	13	11	75
Parkia bicolor	0	0	0	0	0	10	0	0	0	0	0	44
Pentaclethra macrophylla	0	0	0	0	0	26	0	0	0	0	0	0
Pentadesma butyracea	0	0	0	0	0	13	0	0	0	0	0	42
Pentadesma reyndersii	0	0	0	0	0	0	0	0	16	0	0	0
Podocarpus latifolius	0	15	0	0	0	0	0	0	32	0	0	0
Polyathia suaveolens	21	0	0	0	0	0	0	0	0	0	0	0
Polyscias fulva	0	0	0	0	0	0	0	0	17	0	0	0
Porterandia cladantha	0	0	0	0	0	12	0	0	0	0	0	0
Pouteria altissima	0	0	0	0	0	0	13	0	0	0	0	0
Pouteria aningeri	0	0	0	0	0	0	0	0	0	0	0	27
Prunus africana	0	10	0	0	0	0	0	0	15	0	0	0
Prunus africanum	0	0	0	0	9	0	0	0	0	0	0	0
Pseudospondias microcarpa	0	0	17	0	0	12	0	0	0	0	0	0
Psidium guineense	0	0	0	0	0	17	0	0	0	0	0	0
Psychotria mahonii	0	0	0	0	0	0	0	0	33	0	0	0
Psychotria vogeliana	0	0	0	0	0	26	0	0	0	0	0	0
Pterocarpus soyauxii	0	0	0	0	0	10	0	0	0	0	0	0
Pterocarpus tinctorius	0	0	20	0	0	0	0	0	0	0	0	0
Pycnanthus angolensis	0	0	0	0	0	15	0	0	0	0	0	70
Rapanea melanophloeos	0	0	0	0	0	0	0	0	28	0	0	0
Rawsonia lucida	4	0	0	0	0	0	0	0	0	0	0	0
Ricinodendron heudelotii	0	0	0	0	0	0	0	0	0	0	19	0
Rytiginia kigeziensis	0	0	0	0	0	0	0	0	16	0	0	0
Saba comorensis	0	0	29	0	0	0	0	0	0	0	0	0
Sacoglottis gabonensis	0	0	0	0	0	19	0	0	0	0	0	95
Santiria trimera	0	0	0	0	0	10	0	0	0	0	0	0
Sarcocephalus pobeguinii	0	0	0	0	0	0	0	0	0	15	11	0
Schefflera goetzenii	0	0	0	0	0	0	0	0	13	0	0	0
Scottelia klaineana	0	0	0	0	0	0	0	0	0	0	0	53
Scytopetalum tieghemii	0	0	0	0	0	0	0	0	0	0	0	19
Sorindeia madagascariensis	70	0	0	0	0	0	0	0	0	0	0	0
Staudtia kamerunensis	0	0	0	0	0	11	0	0	0	0	0	0
Sterculia oblonga	0	0	0	0	0	0	0	0	0	0	0	40
Strombosia pustulata	0	0	0	0	0	0	0	0	0	18	0	69
Strombosia scheffleri	0	10	0	0	8	0	0	0	29	0	0	0
Strombosiopsis tetrandra	0	0	0	0	0	0	0	0	0	10	8	0
Symphonia globulifera	0	0	0	0	0	0	0	0	17	0	0	0
Synsepalum afzelii	0	0	0	0	0	0	0	0	0	0	0	26
Syzygium cordatum	0	10	0	0	0	0	0	0	0	0	0	0
Syzygium guineense	0	0	0	0	0	0	0	0	41	0	0	0
Tabernaemontana penduliflora	0	0	0	0	0	0	0	11	0	0	0	0
Tetrapleura tetraptera	0	0	0	16	0	20	0	0	0	0	0	0
Thomandersia laurifolia	0	0	0	0	0	0	0	10	0	0	0	0
Trichoscypha acuminata	0	0	0	0	0	13	0	8	0	0	0	0
Trichoscypha arborea	0	0	0	0	0	0	0	0	0	0	0	54
Triplochiton scleroxylon	0	0	0	0	0	0	28	0	0	0	0	0
Uapaca corbisieri	0	0	0	0	0	0	0	0	0	0	0	76
Uapaca guineensis	0	0	0	0	0	29	0	0	0	13	10	51
Uvariastrum pierreanum	0	0	0	0	0	11	0	0	0	0	0	0
Vitex doniana	0	0	0	0	0	29	0	10	0	0	0	0
Vitex fischeri	0	0	20	0	0	0	0	0	0	0	0	0
Xylia evansii	0	0	0	0	0	0	0	0	0	0	0	9
Xylopia aethiopica	0	0	0	0	0	11	0	0	0	0	0	0
Xylopia hypolampra	0	0	0	0	0	6	0	0	0	0	0	0
Xylopia quintasii	0	0	0	0	0	11	0	0	0	0	0	3
Zanha golungensis	0	0	0	0	0	0	0	0	0	0	0	19
Zanthoxylum gilletii	0	0	0	0	0	0	0	0	0	0	10	0

Appendix 2B. Species name and number of trees recorded at each site for the fruiting analysis.

Species	Sites										
	Amani	Bwindi	Gombe	Goualougo	Kibale	Lope	Mbaiki	Mbeli	Nyungwe	Okapi Lenda	Tai
Afrosersalisia rwandensis	0	0	0	0	0	0	0	0	11	0	0
Afzelia bella	0	0	0	0	0	0	0	0	0	0	11
Agelaea paradoxa	0	0	0	0	0	0	0	0	0	0	24
Alangium chinense	0	0	0	0	0	0	0	0	18	0	0
Albizia gummifera	0	0	0	0	0	0	0	0	22	12	0
Allanblackia stuhlmannii	38	0	0	0	0	0	0	0	0	0	0
Allophylus abyssinicusÊ	0	9	0	0	0	0	0	0	0	0	0
Alsodeiopsis schumannii	13	0	0	0	0	0	0	0	0	0	0
Annickia chlorantha	0	0	0	0	0	10	0	0	0	0	0
Anonidium mannii	0	0	0	11	0	0	0	0	0	0	0
Antidesma vogelianum	0	0	0	0	0	19	0	0	0	0	0
Apodytes dimidiata	0	0	0	0	0	0	0	0	11	0	0
Aucoumea klaineana	0	0	0	0	0	43	0	0	0	0	0
Balthasaria schliebenii	0	0	0	0	0	0	0	0	14	0	0
Beilschmiedia rwandensis	0	0	0	0	0	0	0	0	12	0	0
Bersama abyssinica	0	0	0	0	0	0	0	0	18	0	0
Bobgunnia fistuloides	0	0	0	0	0	11	0	0	0	0	0
Bridelia brideliifolia	0	0	0	0	0	0	0	0	14	0	0
Calpocalyx aubrevillei	0	0	0	0	0	0	0	0	0	0	49
Calpocalyx brevibracteatus	0	0	0	0	0	0	0	0	0	0	60
Carapa grandiflora	0	0	0	0	0	0	0	0	25	0	0
Casearia barteri	0	0	0	0	0	0	0	0	11	0	0
Cassipourea ruwensorensis	0	0	0	0	0	0	0	0	12	0	0
Celtis adolfi-fridericii	0	0	0	11	0	0	0	0	0	9	0
Celtis africa	0	0	0	0	10	0	0	0	0	0	0
Celtis africana	0	0	0	0	9	0	0	0	0	0	0
Celtis durandii	0	0	0	0	10	0	0	0	0	0	0
Celtis mildbraedii	0	0	0	7	0	0	0	9	0	12	0
Celtis tessmannii	0	0	0	0	0	10	0	0	0	0	0
Cephalosphaera usambarensis	24	0	0	0	0	0	0	0	0	0	0
Chaetacme aristata	0	0	0	0	11	0	0	0	0	0	0
Chionanthus africanus	0	0	0	0	0	0	0	0	10	0	0
Chrysophyllum africanum	0	0	0	0	0	0	10	0	0	0	0
Chrysophyllum boukokoense	0	0	0	0	0	0	30	0	0	0	0
Chrysophyllum gorungosanum	0	0	0	0	0	0	0	0	19	0	0
Chrysophyllum lacourtianum	0	0	0	13	0	0	0	0	0	0	0
Chrysophyllum subnudum	0	0	0	0	0	0	0	0	0	0	75
Chrysophyllus africanum	0	0	0	0	0	13	0	0	0	0	0
Cissus dinklagei	0	0	0	0	0	9	0	0	0	0	0
Cleistanthus libericus	0	0	0	0	0	0	0	0	7	0	0
Cleistanthus pierlotti	0	0	0	0	0	0	0	0	0	12	0
Cola lizae	0	0	0	0	0	10	0	0	0	0	0
Coula edulis	0	0	0	0	0	0	0	0	0	0	126
Croton haumanianus	0	0	0	0	0	0	0	0	0	12	0
Croton macrostachyus	0	7	0	0	0	0	0	0	0	0	0
Croton megalocarpus	0	0	0	0	0	0	0	0	20	0	0
Cynometra alexandri	0	0	0	0	0	0	0	0	0	10	0
Dacryodes buettneri	0	0	0	0	0	11	0	0	0	0	0
Dacryodes klaineana	0	0	0	0	0	0	0	0	0	0	58
Daniellia thurifera	0	0	0	0	0	0	0	0	0	0	9
Detarium macrocarpum	0	0	0	0	0	13	0	3	0	0	0
Dialium aubrevillei	0	0	0	0	0	0	0	0	0	0	95
Dialium corbisieri	0	0	0	0	0	0	0	0	0	12	0
Dialium lopense	0	0	0	0	0	34	0	0	0	0	0
Dictyophleba lucida	0	0	20	0	0	0	0	0	0	0	0
Diospyros dendo	0	0	0	0	0	27	0	0	0	0	0
Diospyros ivoriensis	0	0	0	0	0	0	0	0	0	0	34
Diospyros polystemon	0	0	0	0	0	18	0	0	0	0	0
Diospyros sanza-minika	0	0	0	0	0	0	0	0	0	0	76
Diospyros soubreana	0	0	0	0	0	0	0	0	0	0	50
Diospyros zenkeri	0	0	0	0	0	11	0	0	0	0	0
Dombeya mukou	0	0	0	0	9	0	0	0	0	0	0
Dombeya torrida	0	0	0	0	0	0	0	0	11	0	0
Duboscia macrocarpa	0	0	0	0	0	9	0	4	0	0	0
Duboscia macrocarpa	0	0	0	0	0	0	0	0	0	0	19
Duguetia staudtii	0	0	0	0	0	0	0	0	0	0	32
Ekebergia capensis	0	0	0	0	0	0	0	0	11	0	0
Elaeis guineensis	0	0	17	0	0	0	0	0	0	0	0
Englerodendron usambarense	6	0	0	0	0	0	0	0	0	0	0
Entandrophragma angolense	0	0	0	0	0	0	0	0	0	0	20
Entandrophragma cylindricum	0	0	0	0	0	0	31	0	0	0	0
Entandrophragma excelsum	0	0	0	0	0	0	0	0	20	0	0
Erythrophleum suaveolens	0	0	0	0	0	0	0	0	0	10	0
Erythroxylum mannii	0	0	0	0	0	0	0	0	0	0	10
Eucalyptus	0	0	0	0	7	0	0	0	0	0	0
Ficalhoa laurifolia	0	0	0	0	0	0	0	0	21	0	0
Ficus elasticoides	0	0	0	0	0	0	0	0	0	0	21
Ficus oreodryadum	0	0	0	0	0	0	0	0	29	0	0
Ficus sansibarica	0	0	0	0	0	0	0	0	0	0	30
Ficus vallis-choudae	0	0	14	0	0	0	0	0	0	0	0
Funtumia latifolia	0	0	0	0	1	0	0	0	0	0	0
Galiniera saxifraga	0	0	0	0	0	0	0	0	11	0	0
Ganophyllum giganteum	0	0	0	0	0	10	0	0	0	0	0
Garcinia huillensis	0	0	13	0	0	0	0	0	0	0	0

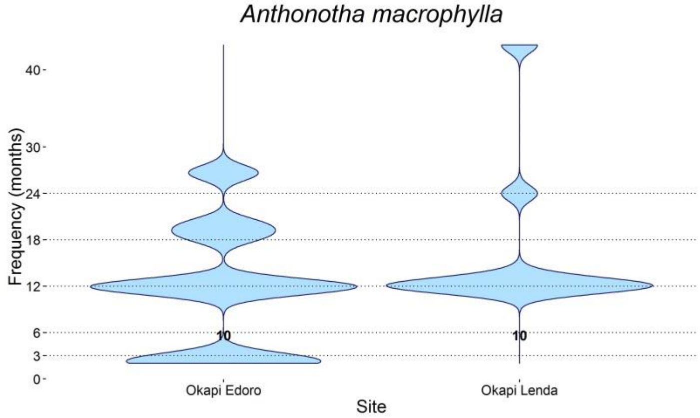
Appendix 2B continued

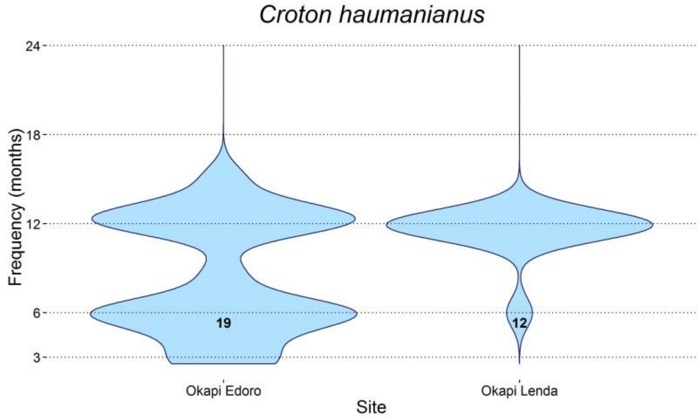
Species	Sites										
	Amani	Bwindi	Gombe	Goualougo	Kibale	Lope	Mbaiki	Mbeli	Nyungwe	Okapi Lenda	Tai
Gilbertiodendron splendidum	0	0	0	0	0	0	0	0	0	0	25
Greenwayodendron suaveolens	0	0	0	0	0	10	0	0	0	0	0
Grewia mildbraedii	0	0	0	0	0	0	0	0	10	0	0
Grewia oligoneura	0	0	0	0	0	0	0	0	0	5	0
Gymnosporia acuminata	0	0	0	0	0	0	0	0	10	0	0
Hallea stipulosa	0	0	0	0	0	0	0	0	0	10	0
Harungana madagascariensis	0	0	15	0	0	0	0	0	0	0	0
Heisteria parvifolia	0	0	0	0	0	11	0	0	0	0	0
Heritiera utilis	0	0	0	0	0	0	0	0	0	0	45
Ilex mitis	0	0	0	0	0	0	0	0	14	0	0
Irvingia excelsa	0	0	0	0	0	0	0	8	0	0	0
Irvingia gabonensis	0	0	0	0	0	22	0	0	0	0	0
Irvingia grandifolia	0	0	0	0	0	20	0	0	0	0	33
Ixora burundiensis	0	0	0	0	0	0	0	0	9	0	0
Julbernardia seretii	0	0	0	0	0	0	0	0	0	11	0
Keayodendron bridelioides	0	0	0	0	0	0	0	0	0	0	8
Klainedoxa gabonensis	0	0	0	0	0	9	0	10	0	10	85
Macaranga capensis	9	0	0	0	0	0	0	0	0	0	0
Macaranga kilimandscharica	0	0	0	0	0	0	0	0	23	0	0
Macaranga schweinfurthii	0	0	0	0	0	0	0	0	0	18	0
Maesa lanceolata	0	0	0	0	0	0	0	0	15	0	0
Maesopsis eminii	33	0	0	0	0	0	0	0	0	0	0
Magnistipula butayei	0	0	0	0	0	0	0	0	14	0	0
Magnistipula butayei	0	0	0	0	0	0	0	0	0	0	14
Manilkara mabokeensis	0	0	0	8	0	0	0	0	0	0	0
Margaritaria discoidea	0	0	0	0	0	0	0	0	0	15	0
Massularia acuminata	0	0	0	0	0	10	0	0	0	0	0
Memecylon lateriflorum	0	0	0	0	0	0	0	0	0	0	37
Memecylon polyanthemos	0	0	0	0	0	0	0	0	0	0	9
Memecylon walikalense	0	0	0	0	0	0	0	0	21	0	0
Mesogyne insignis	98	0	0	0	0	0	0	0	0	0	0
Milicia excelsa	0	0	0	0	0	10	9	0	0	0	0
Monanthotaxis congoensis	0	0	0	0	0	10	0	0	0	0	0
Monanthotaxis poggei	0	0	19	0	0	0	0	0	0	0	0
Musanga cecropioides	0	0	0	0	0	0	0	0	0	13	0
Musanga leo-errerae	0	0	0	0	0	0	0	0	6	0	0
Myrianthus arboreus	0	0	0	0	0	10	0	0	0	0	0
Myrianthus holstii	29	0	0	0	0	0	0	0	9	0	0
Nauclea diderrichii	0	0	0	0	0	18	0	0	0	0	75
Nauclea xanthoxylon	0	0	0	0	0	0	0	0	0	0	63
Newtonia buchananii	0	0	0	0	0	0	0	0	13	0	0
Ochna afzelii	0	0	0	0	0	0	0	0	13	0	0
Odyendea zimmermannii	6	0	0	0	0	0	0	0	0	0	0
Olea capensis	0	5	0	0	0	0	0	0	19	0	0
Olinia rochetiana	0	10	0	0	0	0	0	0	31	0	0
Ongokea gore	0	0	0	0	0	10	0	0	0	0	0
Panda oleosa	0	0	0	0	0	12	0	10	0	0	27
Parinari capensis	0	0	13	0	0	0	0	0	0	0	0
Parinari excelsa	0	0	0	0	0	0	0	0	17	9	74
Parkia bicolor	0	0	0	0	0	10	0	0	0	0	45
Pentaclethra macrophylla	0	0	0	0	0	25	0	0	0	0	0
Pentadesma butyracea	0	0	0	0	0	13	0	0	0	0	45
Pentadesma reyndersii	0	0	0	0	0	0	0	0	19	0	0
Podocarpus latifolius	0	0	0	0	0	0	0	0	28	0	0
Polyathia suaveolens	33	0	0	0	0	0	0	0	0	0	0
Polyscias fulva	0	0	0	0	0	0	0	0	17	0	0
Porterandia cladantha	0	0	0	0	0	12	0	0	0	0	0
Pouteria altissima	0	0	0	0	0	0	14	0	0	0	0
Pouteria aningeri	0	0	0	0	0	0	0	0	0	0	22
Prunus africana	0	9	0	0	0	0	0	0	13	0	0
Pseudospondias microcarpa	0	0	8	0	0	11	0	0	0	0	0
Psidium guineense	0	0	0	0	0	13	0	0	0	0	0
Psychotria mahonii	0	0	0	0	0	0	0	0	27	0	0
Psychotria vogeliana	0	0	0	0	0	23	0	0	0	0	0
Pterocarpus soyauxii	0	0	0	0	0	10	0	8	0	0	0
Pycnanthus angolensis	0	0	0	0	0	15	0	0	0	0	72
Rapanea melanophloeos	0	0	0	0	0	0	0	0	27	0	0
Ricinodendron heudelotii	0	0	0	0	0	0	0	0	0	18	0
Rytigynia kigeziensis	0	0	0	0	0	0	0	0	18	0	0
Saba comorensis	0	0	26	0	0	0	0	0	0	0	0
Sacoglottis gabonensis	0	0	0	0	0	19	0	0	0	0	101
Santiria trimera	0	0	0	0	0	10	0	0	0	0	0
Sapium ellipticum	0	0	0	0	0	0	0	0	8	0	0
Sarcocephalus pobeguinii	0	0	0	0	0	0	0	0	0	10	18
Schefflera goetzenii	0	0	0	0	0	0	0	0	18	0	0
Scottelia klaineana	0	0	0	0	0	0	0	0	0	0	51
Scytopetalum tieghemii	0	0	0	0	0	0	0	0	0	0	20
Sorindeia madagascariensis	32	0	0	0	0	0	0	0	0	0	0
Staudtia kamerunensis var. gabonensi	0	0	0	0	0	11	0	0	0	0	0

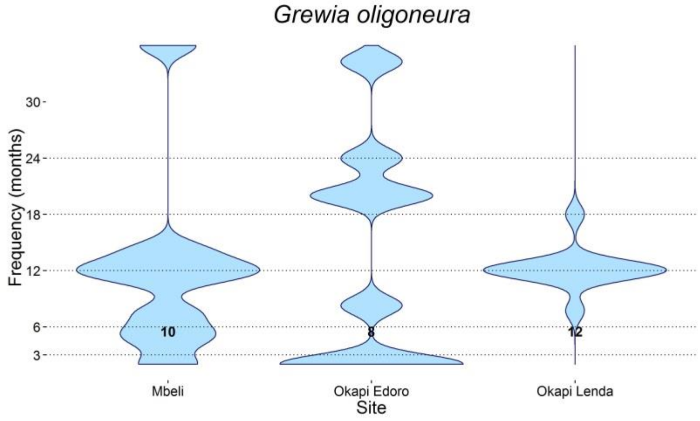
Appendix 2B continued

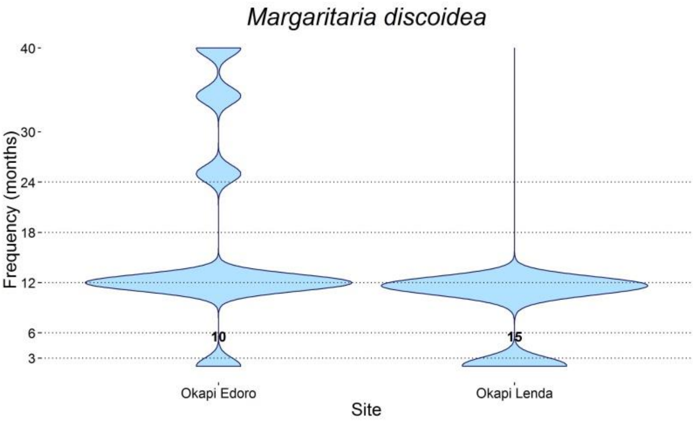
Species	Sites										
	Amani	Bwindi	Gombe	Goualougo	Kibale	Lope	Mbaiki	Mbeli	Nyungwe	Okapi Lenda	Tai
Sterculia oblonga	0	0	0	0	0	0	0	0	0	0	24
Strombosia pustulata	0	0	0	0	0	0	0	0	0	0	19
Strombosia scheffleri	0	8	0	0	0	0	0	0	32	0	0
Strombosiopsis tetrandra	0	0	0	0	0	0	0	0	0	11	0
Symphonia globulifera	0	0	0	0	0	0	0	0	27	0	0
Synsepalum afzelii	0	0	0	0	0	0	0	0	0	0	11
Syzygium cordatum	0	12	0	0	0	0	0	0	0	0	0
Syzygium guineense	0	0	0	0	0	0	0	0	48	0	0
Syzygium owariense	0	0	0	0	0	0	0	0	0	0	7
Tabernaemontana penduliflora	0	0	0	0	0	0	0	7	0	0	0
Tabernaemontana stapfiana	0	0	0	0	0	0	0	0	9	0	0
Tetrapleura tetraptera	0	0	0	14	0	20	0	0	0	0	0
Treculia africana	0	0	0	0	0	0	0	0	0	0	15
Trichoscypha acuminata	0	0	0	0	0	11	0	0	0	0	0
Trichoscypha arborea	0	0	0	0	0	0	0	0	0	0	36
Triplochiton scleroxylon	0	0	0	0	0	0	38	0	0	0	0
Uapaca corbisieri	0	0	0	0	0	0	0	0	0	0	51
Uapaca guineensis	0	0	0	0	0	27	0	0	0	0	48
Uvariastrum pierreanum	0	0	0	0	0	11	0	0	0	0	0
Vitex doniana	0	0	0	0	0	29	0	0	0	0	0
Vitex fischeri	0	0	20	0	0	0	0	0	0	0	0
Xylia evansii	0	0	0	0	0	0	0	0	0	0	12
Xylopia aethiopica	0	0	0	0	0	11	0	0	0	0	0
Xylopia hypolampra	0	0	0	0	0	6	0	0	0	0	0
Xylopia quintasii	0	0	0	0	0	12	0	0	0	0	8
Xylopia spp.	0	0	0	0	0	0	0	7	0	0	0
Zanha golungensis	0	0	0	0	0	0	0	0	0	0	15

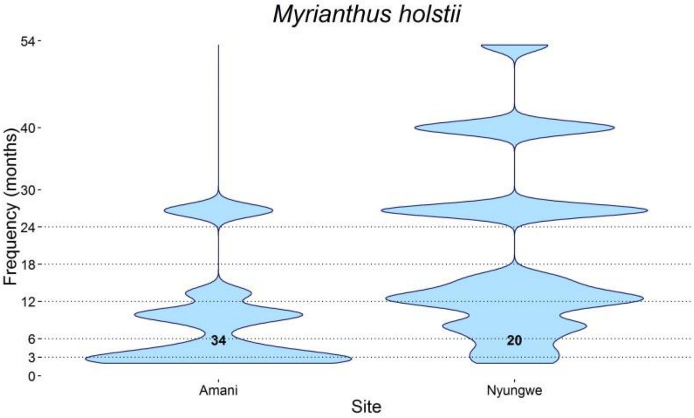
Appendix 2C. Species showing significantly different flowering frequencies across various sites.

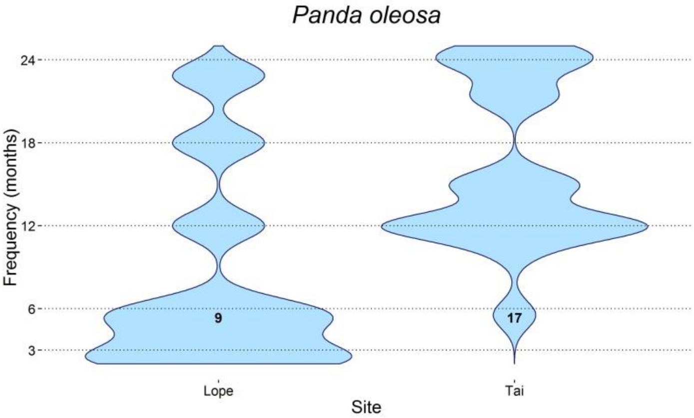


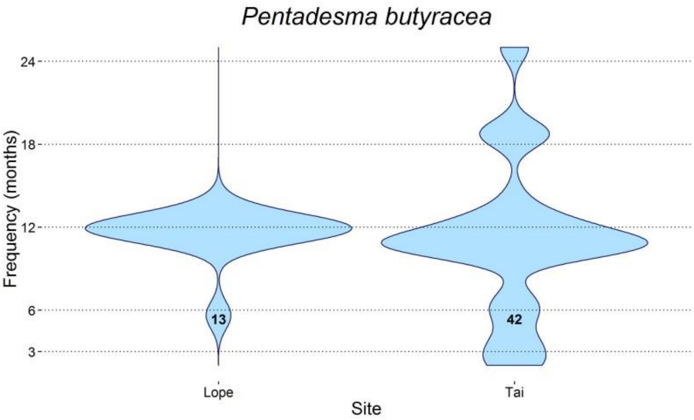


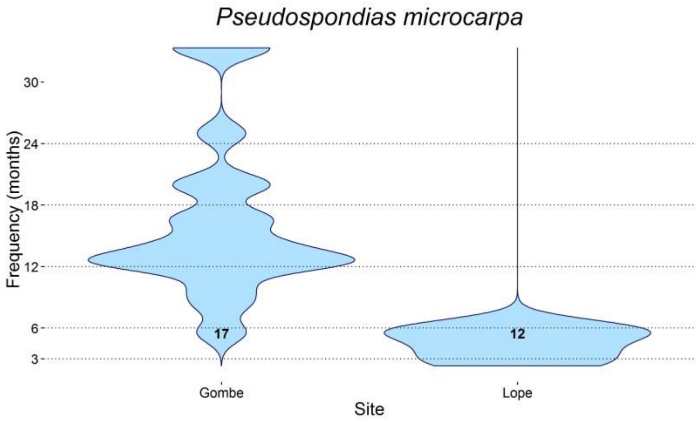


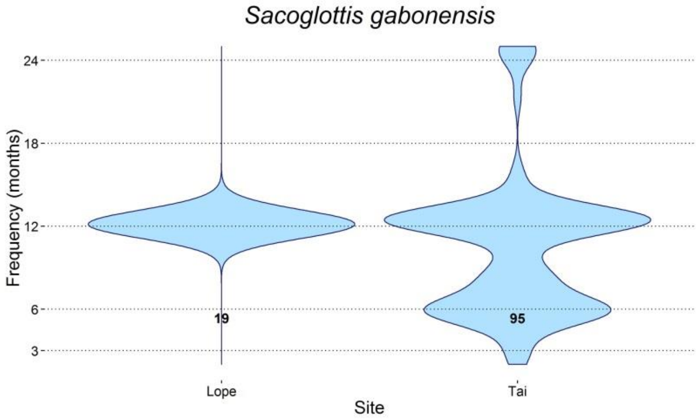

Margaritaria discoidea
Frequency (months)
40
30
24
18
12
6
3
10
15
Okapi Edoro
Okapi Lenda
Site

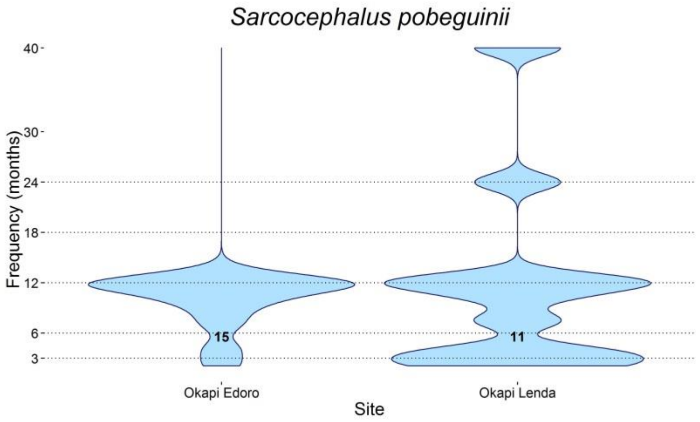

Myrianthus holstii
Frequency (months)
54
40
30
24
18
12
6
3
0
34
20
Amani
Nyungwe
Site

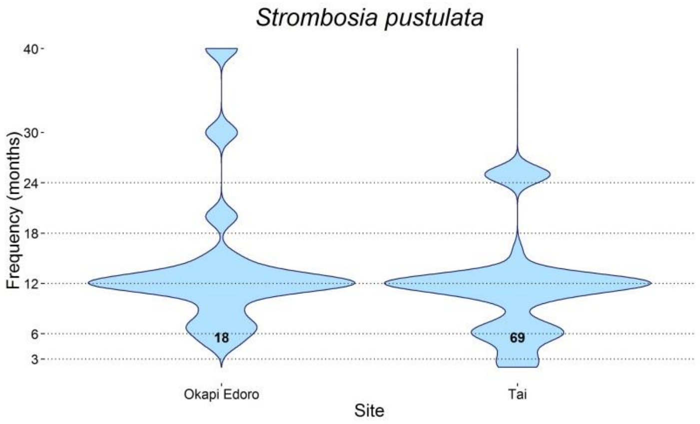

Panda oleosa
Frequency (months)
24
18
12
6
3
9
17
Lope
Tai
Site

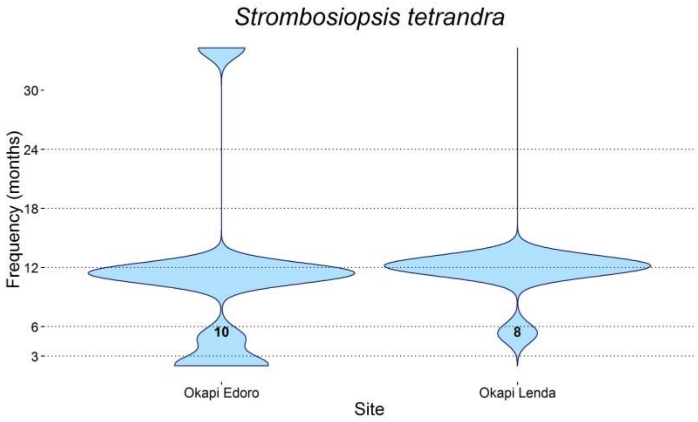

Pentadesma butyracea
Frequency (months)
24
18
12
6
3
13
42
Lope
Tai
Site


Pseudospondias microcarpa
Frequency (months)
30
24
18
12
6
3
17
12
Gombe
Lope
Site

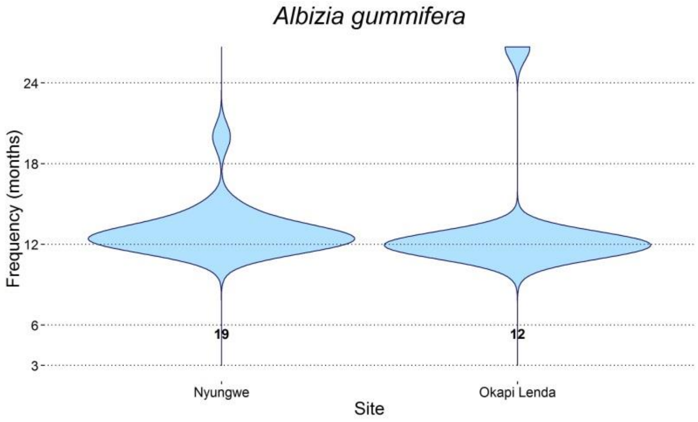

Sacoglottis gabonensis
Frequency (months)
24
18
12
6
3
19
95
Lope
Tai
Site

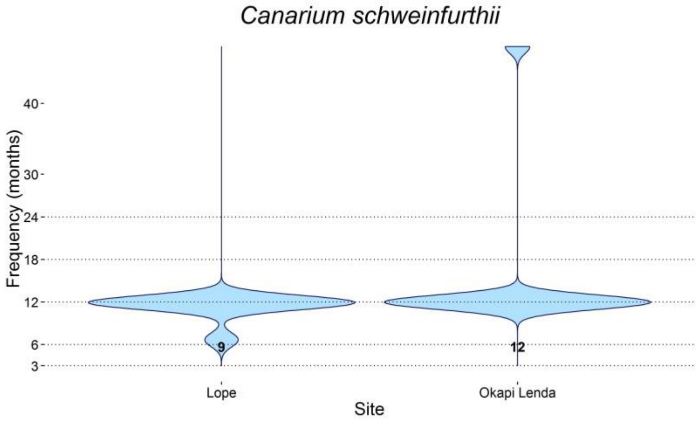

Sarcocephalus pobeguinii
Frequency (months)
40
30
24
18
12
6
3
15
11
Okapi Edoro
Okapi Lenda
Site

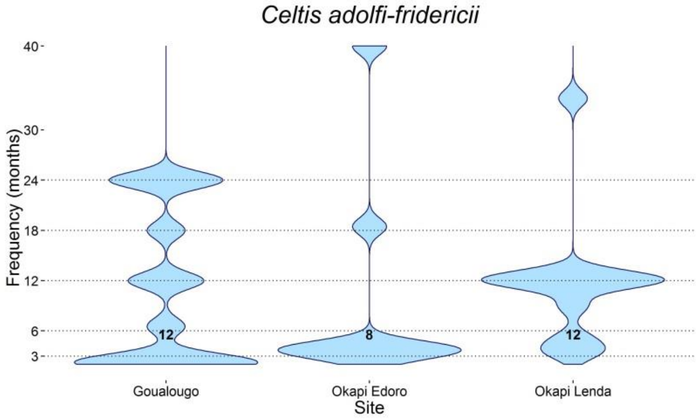

Strombosia pustulata
Frequency (months)
40
30
24
18
12
6
3
18
69
Okapi Edoro
Tai
Site

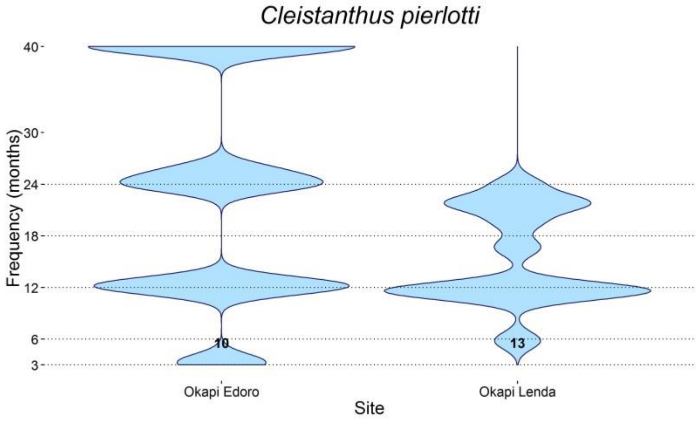

Strombosiopsis tetrandra
Frequency (months)
30
24
18
12
6
3
10
8
Okapi Edoro
Okapi Lenda
Site

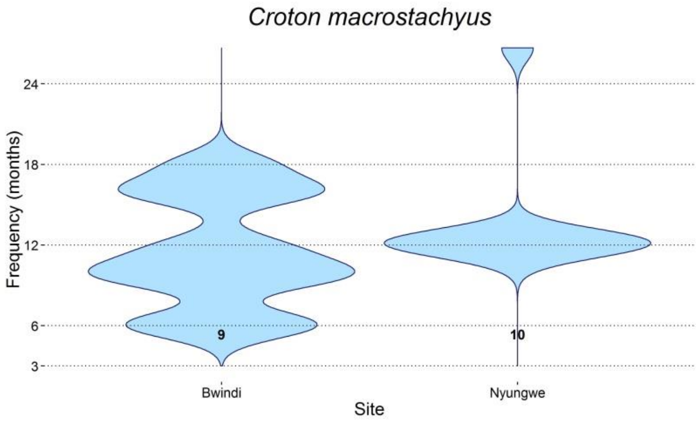
Appendix 2D. Species showing no difference in their flowering frequencies across different sites.



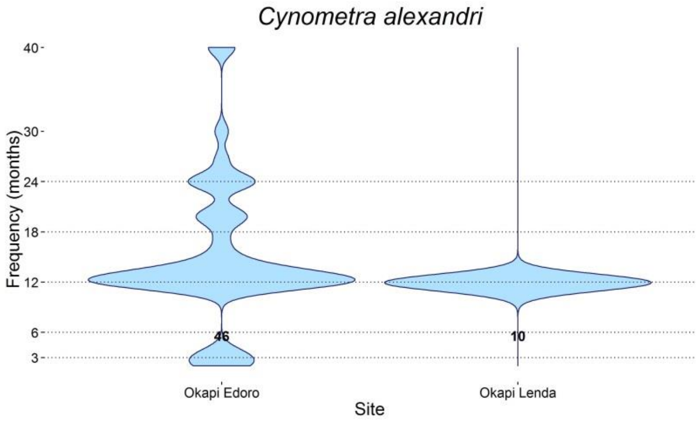




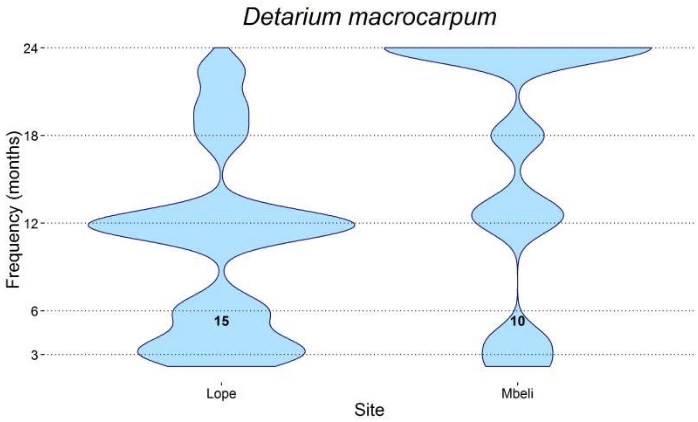




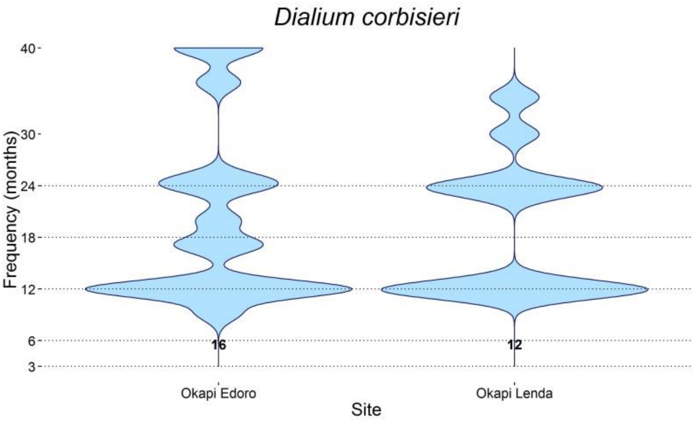
Croton macrostachyus

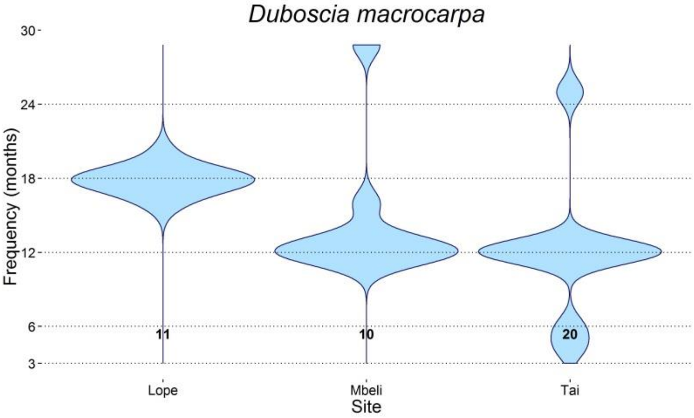


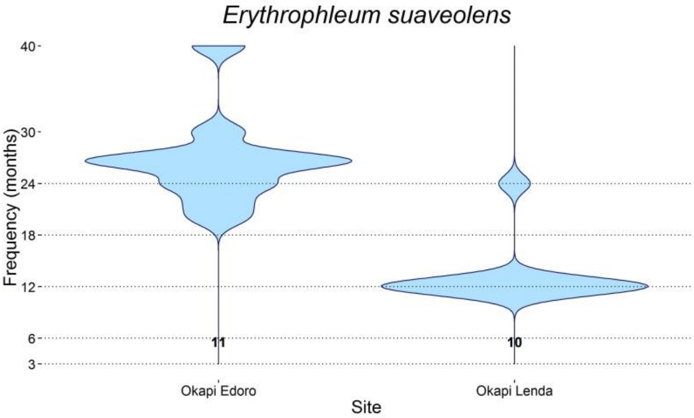
Cynometra alexandri

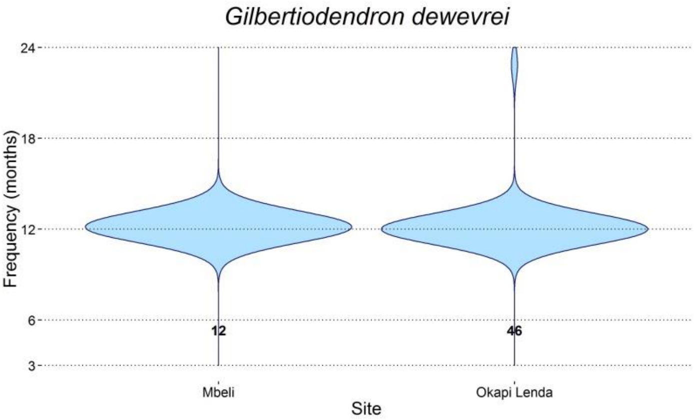


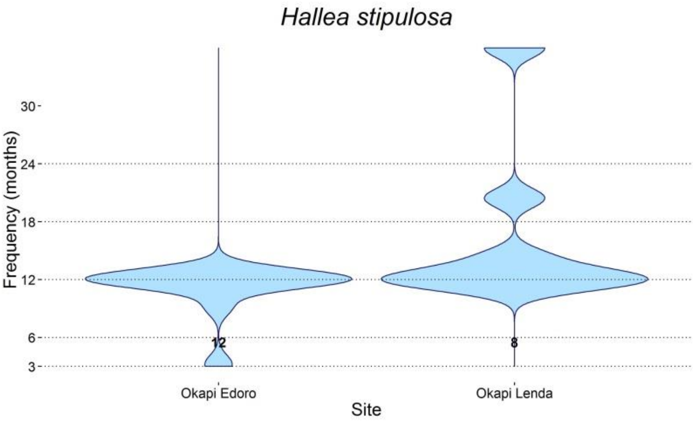
Detarium macrocarpum

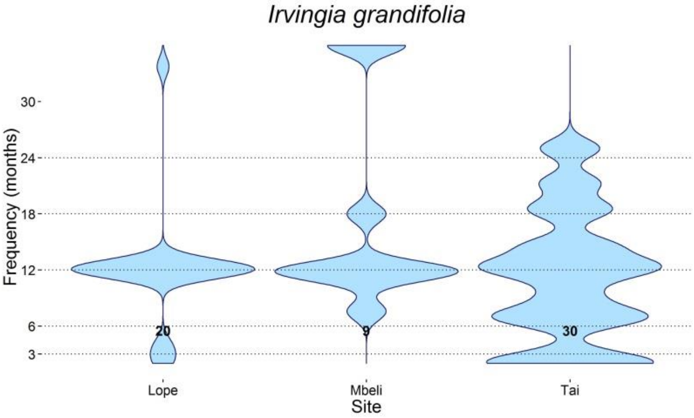

Dialium corbisieri

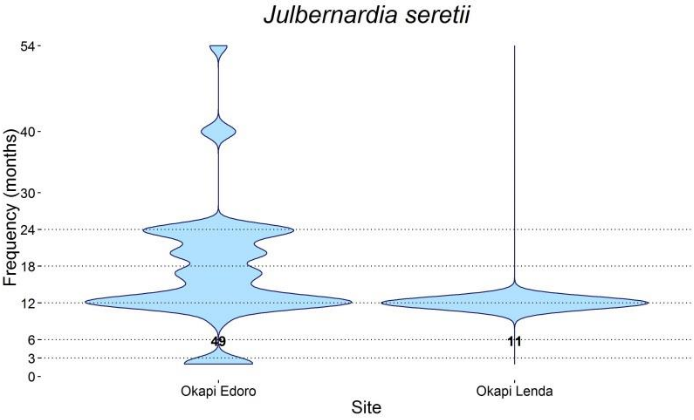

Duboscia macrocarpa

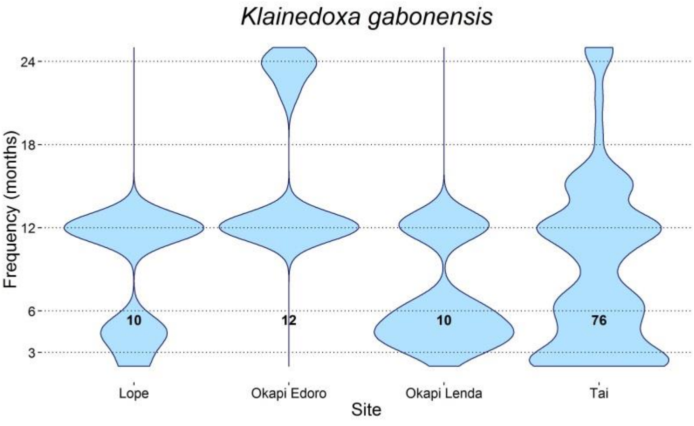

Erythrophleum suaveolens

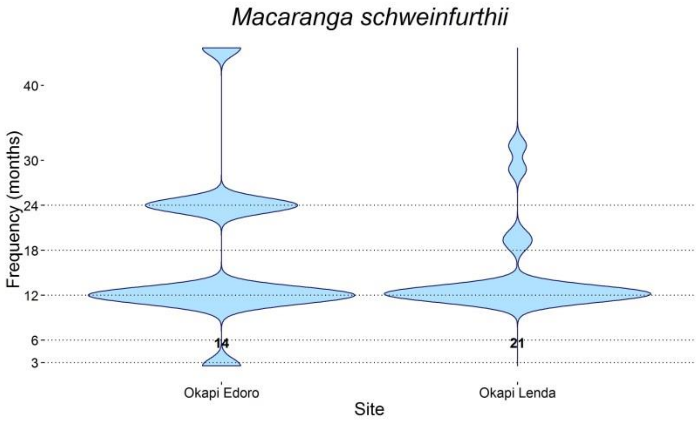

Gilbertiodendron dewevrei

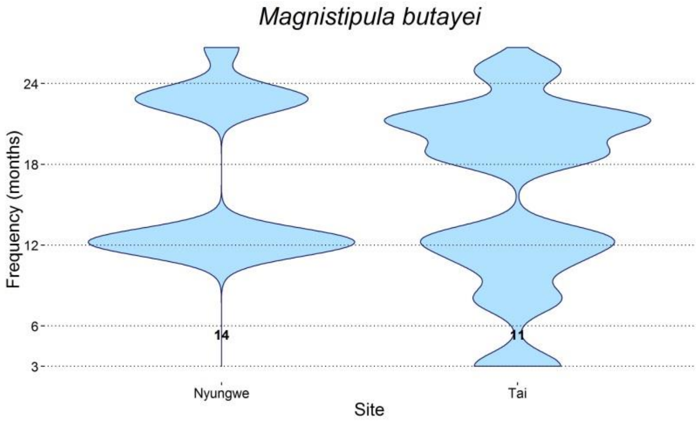

Hallea stipulosa
Frequency (months)
30
24
18
12
6
3
12
8
Okapi Edoro
Okapi Lenda
Site

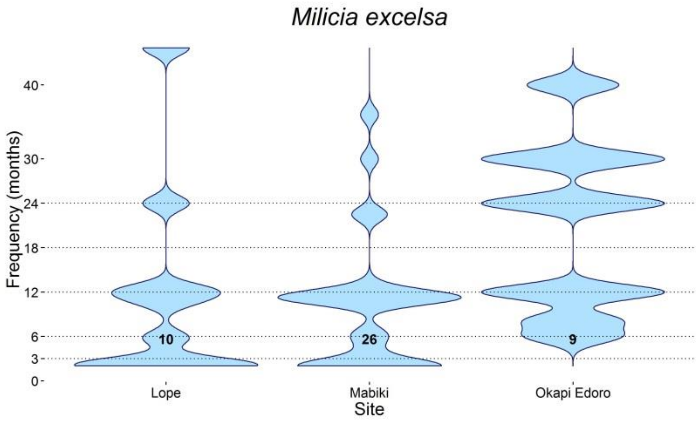

Irvingia grandifolia
Frequency (months)
30
24
18
12
6
3
20
9
30
Lope
Mbeli
Tai
Site

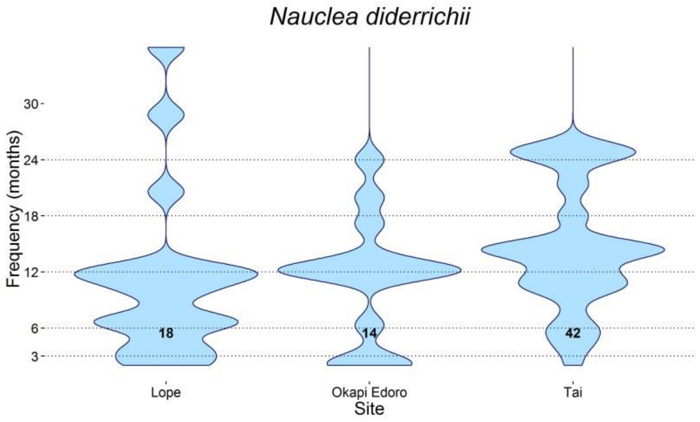

Julbernardia seretii
Frequency (months)
54
40
30
24
18
12
6
3
0
49
11
Okapi Edoro
Okapi Lenda
Site

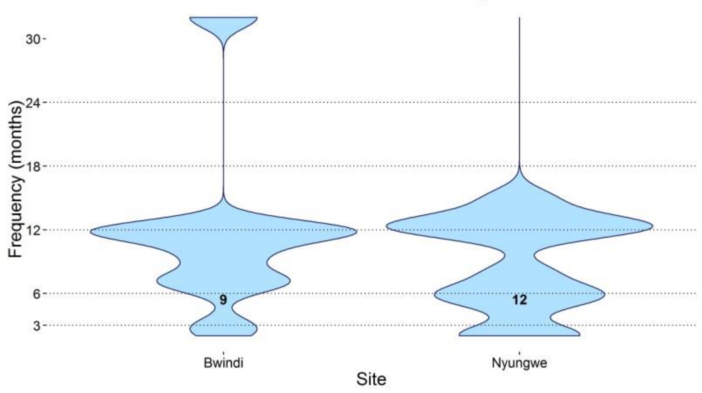

Klainedoxa gabonensis
Frequency (months)
24
18
12
6
3
10
12
10
76
Lope
Okapi Edoro
Okapi Lenda
Tai
Site

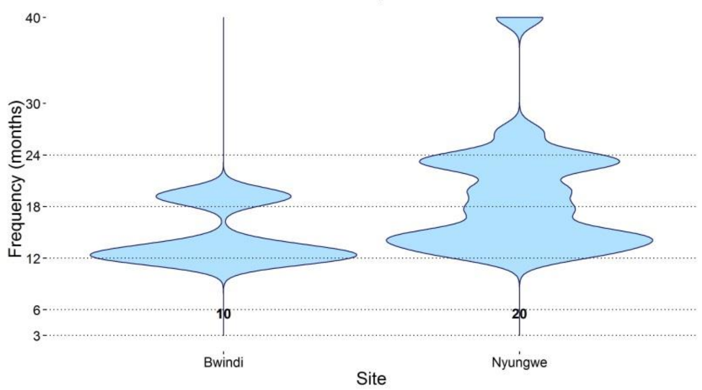

Macaranga schweinfurthii

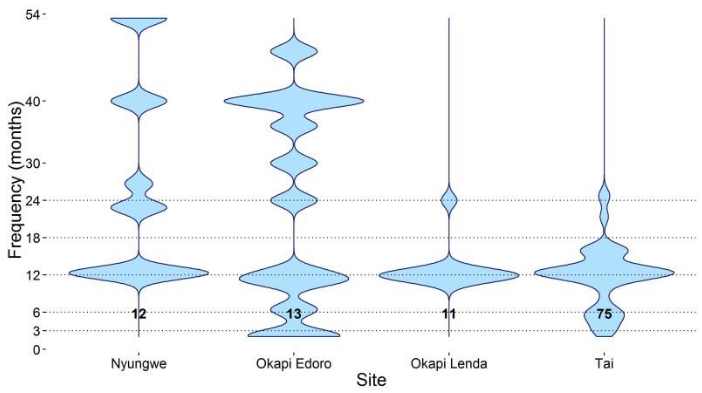

Magnistipula butayei

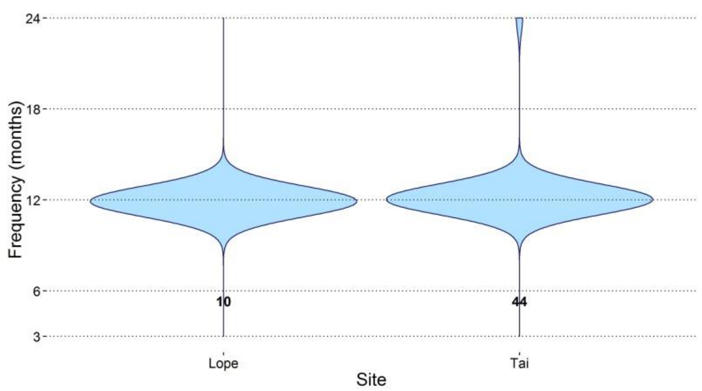

Milicia excelsa

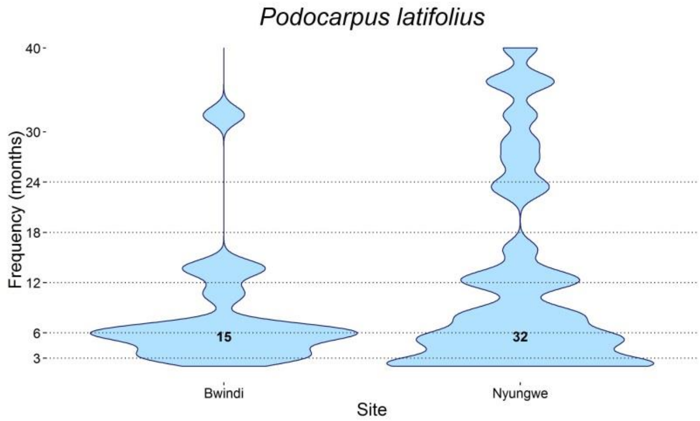

Nauclea diderrichii

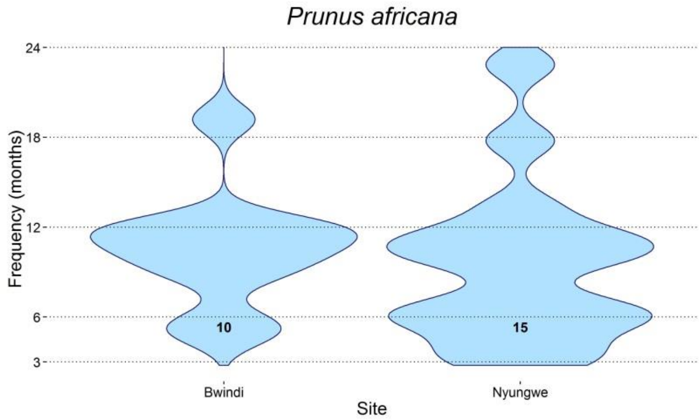

Neoboutonia macrocalyx

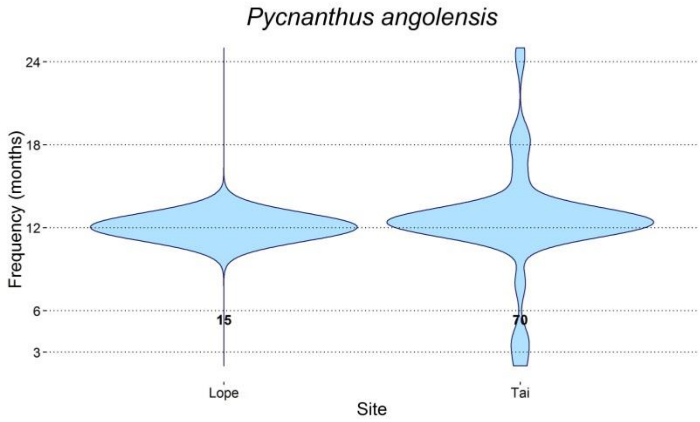

Olea capensis

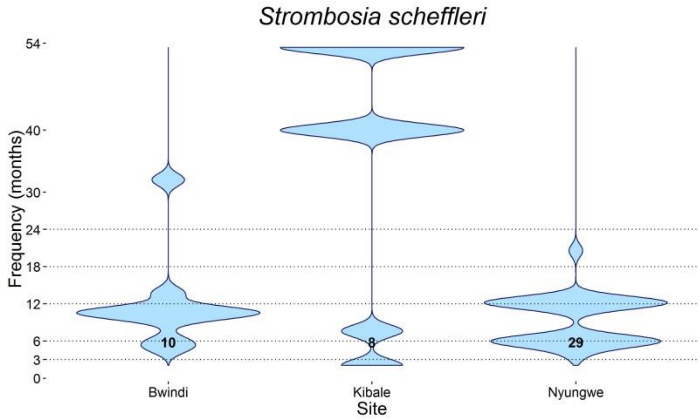

Parinari excelsa

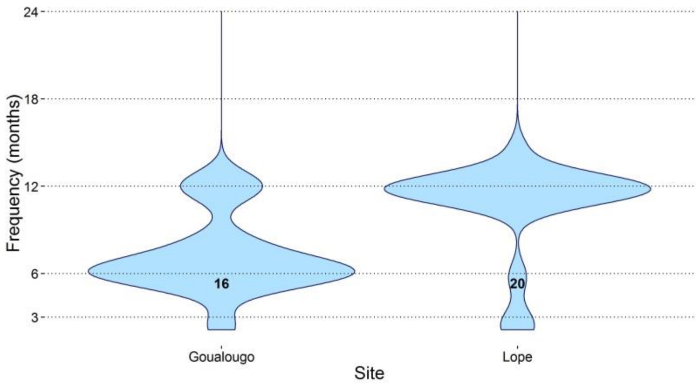

Parkia bicolor


Podocarpus latifolius
Frequency (months)
40
30
24
18
12
6
3
15
32
Bwindi
Nyungwe
Site

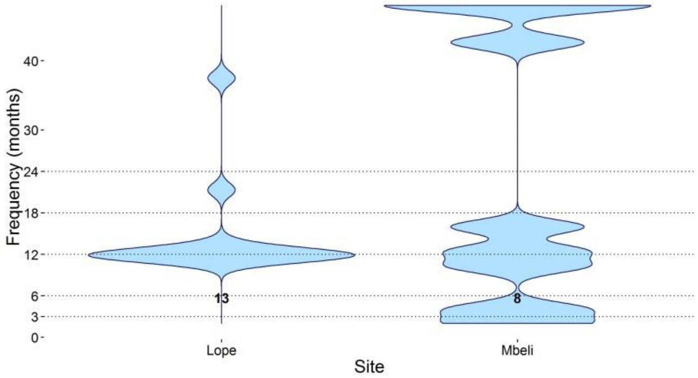

Prunus africana
Frequency (months)
24
18
12
6
3
10
15
Bwindi
Nyungwe
Site


Pycnanthus angolensis
Frequency (months)
24
18
12
6
3
15
70
Lope
Tai
Site

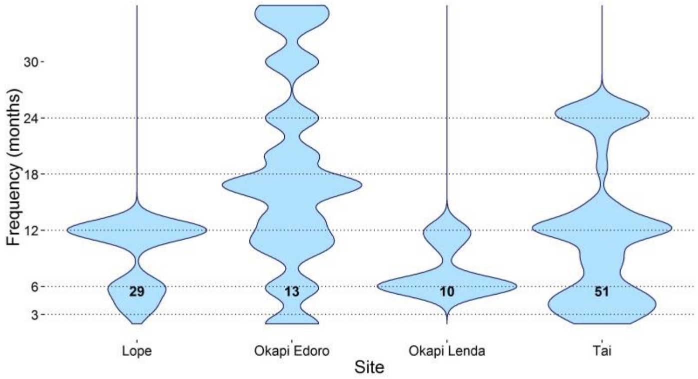

Strombosia scheffleri
Frequency (months)
54
40
30
24
18
12
6
3
0
10
8
29
Bwindi
Kibale
Nyungwe
Site



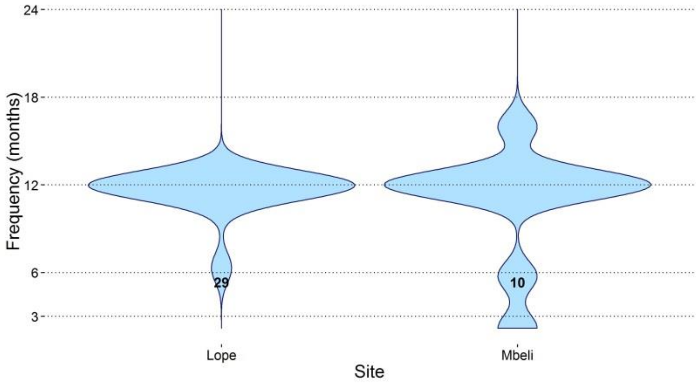
Tetrapleura tetraptera



Trichoscypha acuminata

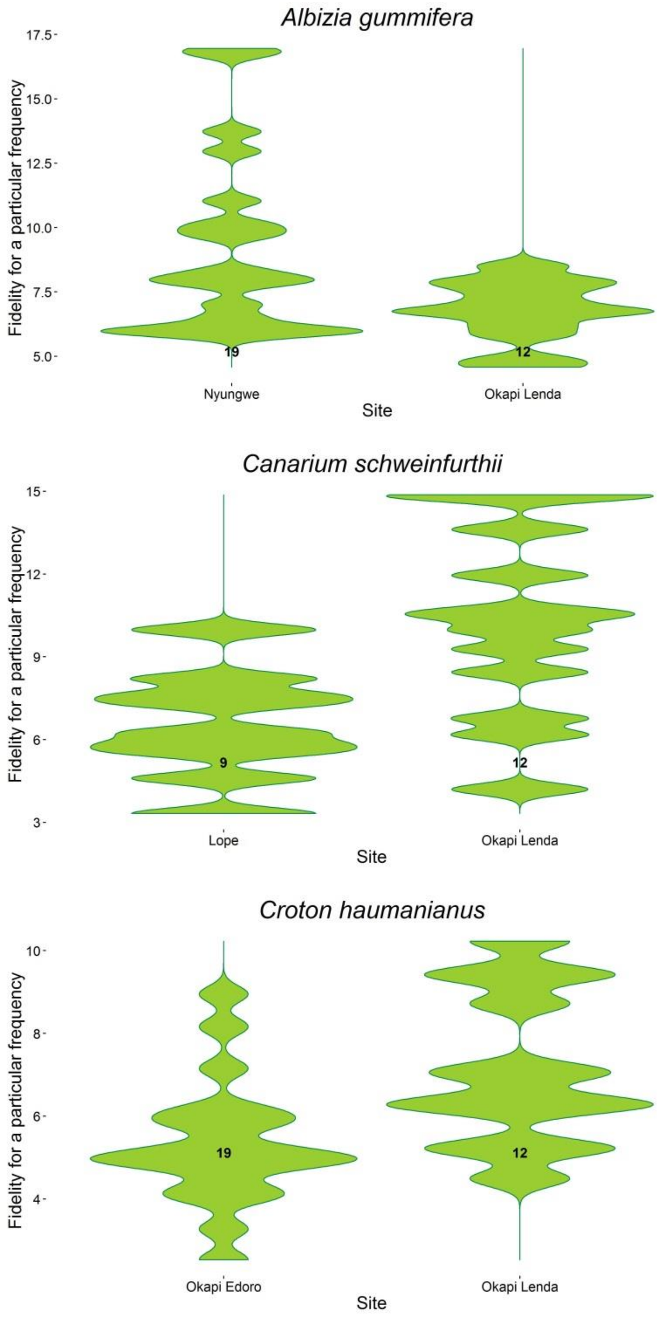


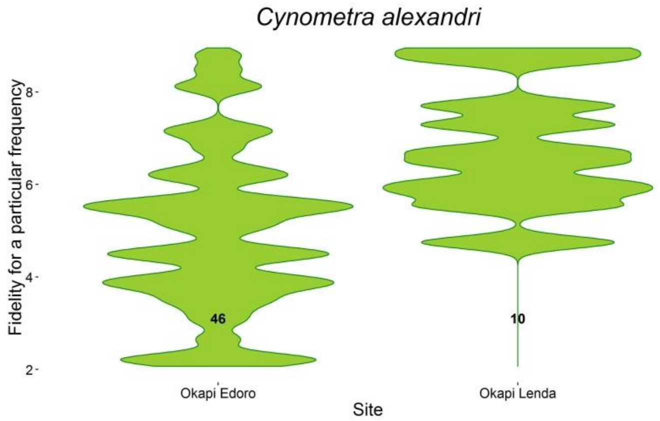
Uapaca guineensis

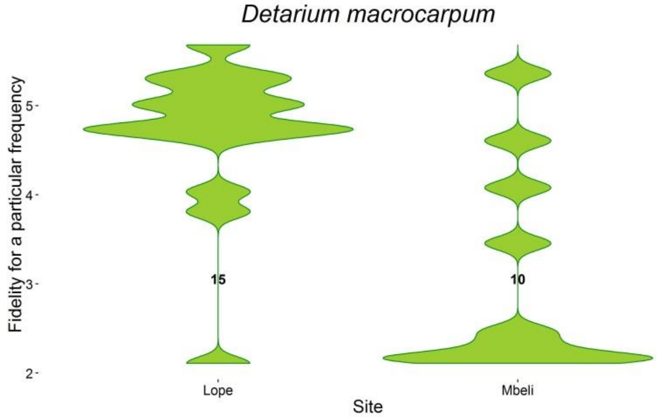


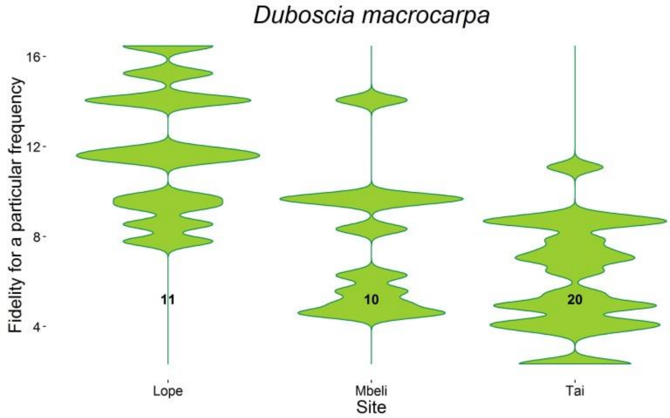
Vitex doniana

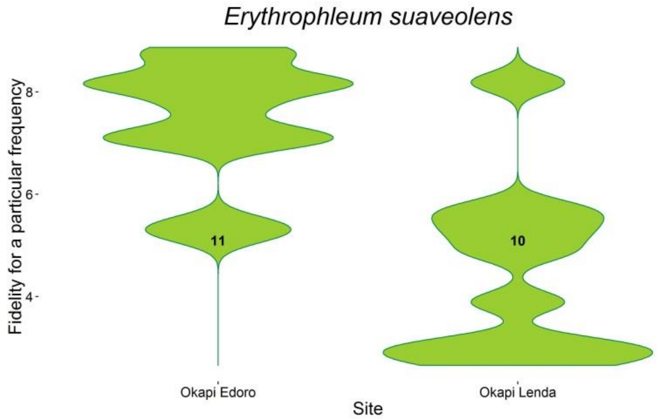
Appendix 2E. **Species that significantly vary in their fidelity for a particular flowering frequency across different sites.**

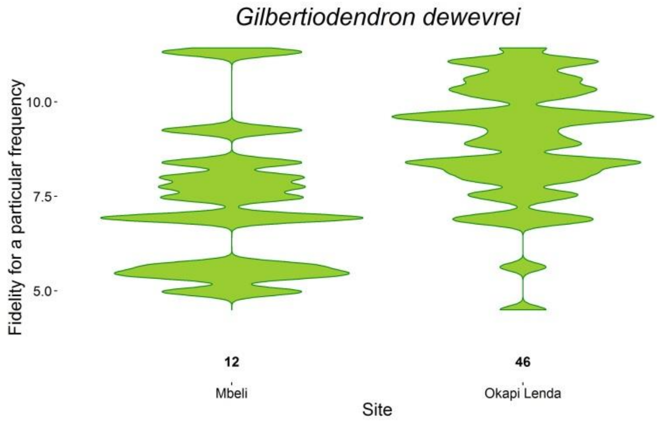


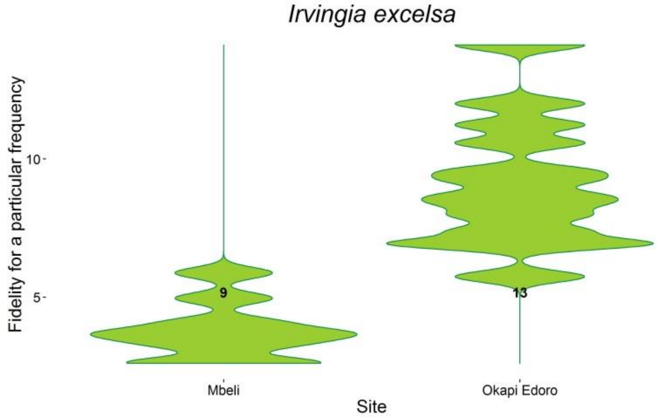

Cynometra alexandri

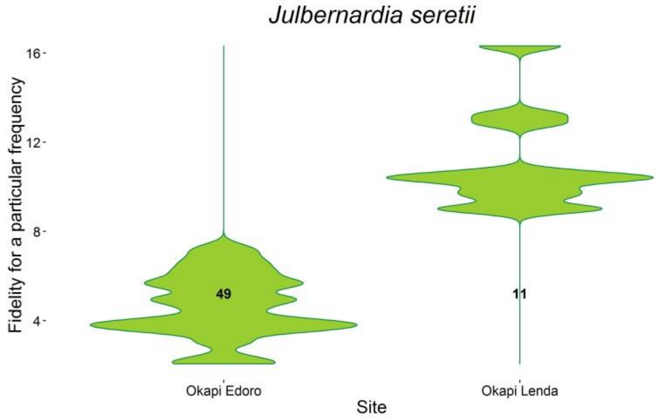

Detarium macrocarpum

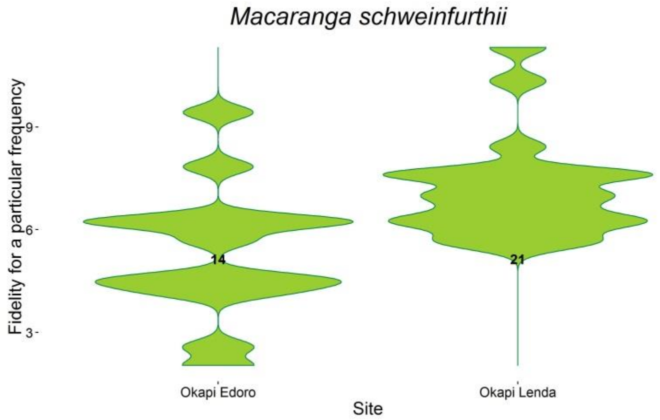

Duboscia macrocarpa

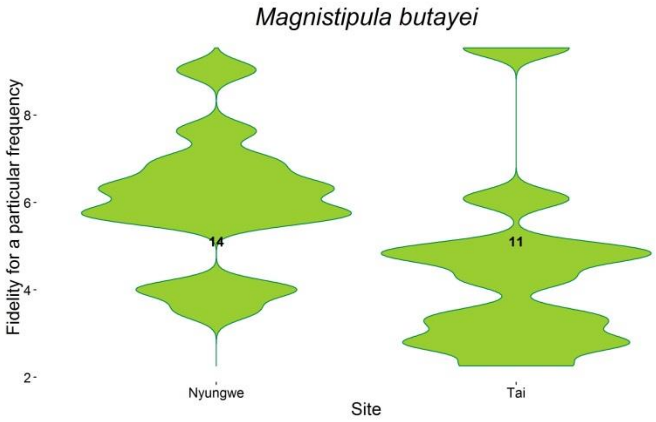

Erythrophleum suaveolens


Gilbertiodendron dewevrei
Fidelity for a particular frequency
10.0
7.5
5.0
12
46
Mbeli
Okapi Lenda
Site

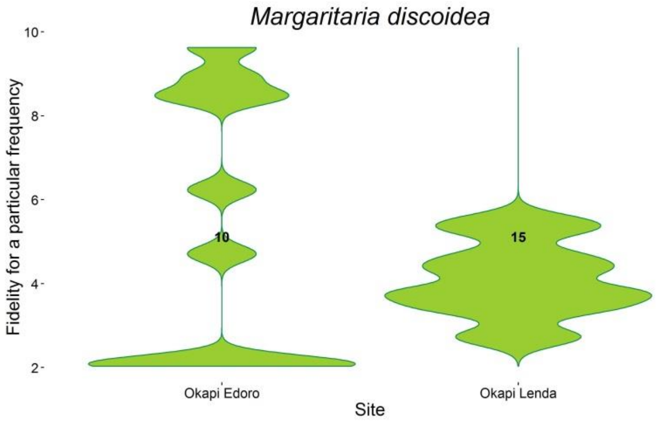

Irvingia excelsa
Fidelity for a particular frequency
10
5
9
13
Mbeli
Okapi Edoro
Site


Julbernardia seretii
Fidelity for a particular frequency
16
12
8
4
49
11
Okapi Edoro
Okapi Lenda
Site

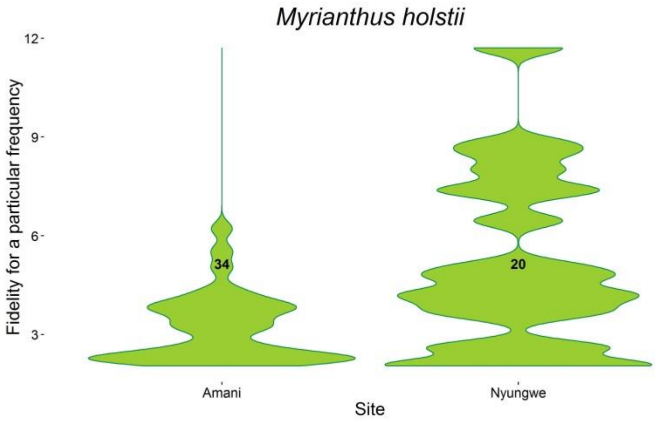

Macaranga schweinfurthii
Fidelity for a particular frequency
9
6
3
14
21
Okapi Edoro
Okapi Lenda
Site



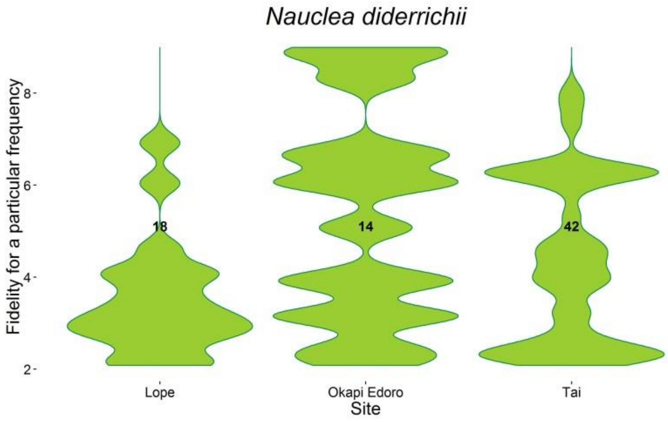
Magnistipula butayei



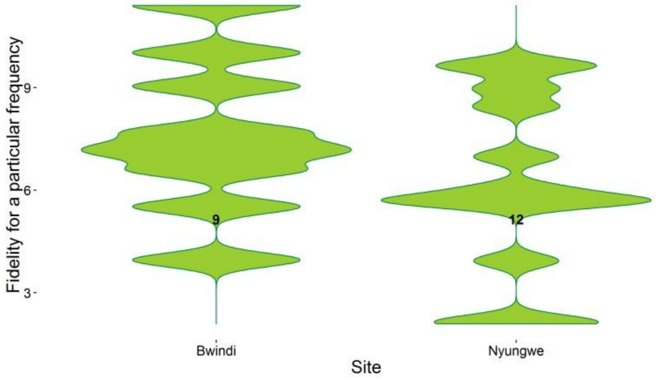
Margaritaria discoidea

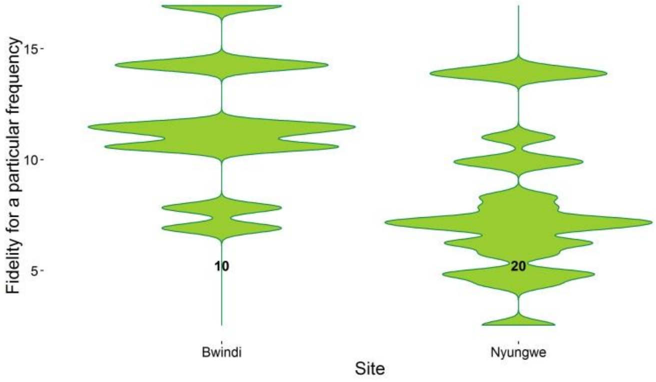


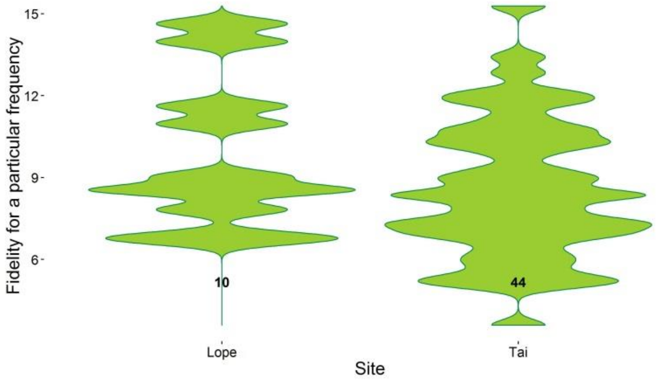
Myrianthus holstii

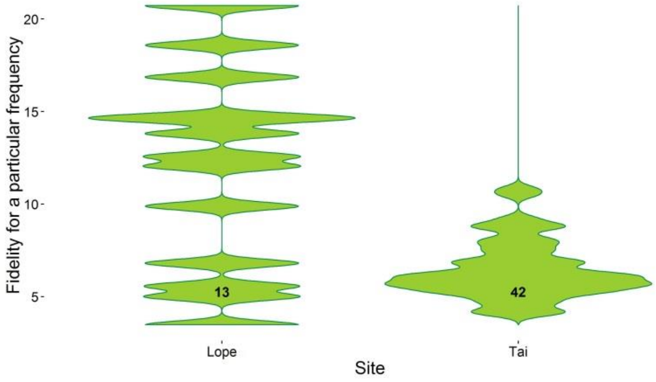


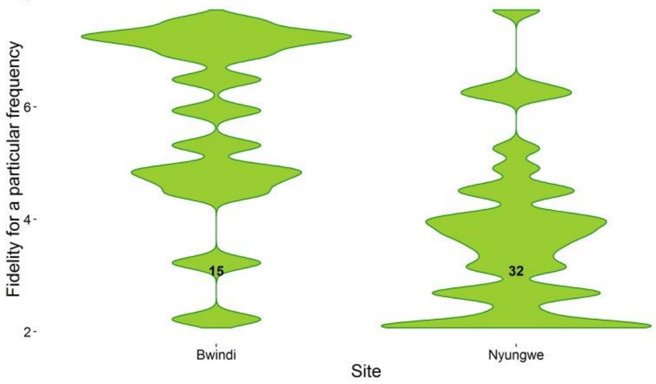
Nauclea diderrichii


Neoboutonia macrocalyx

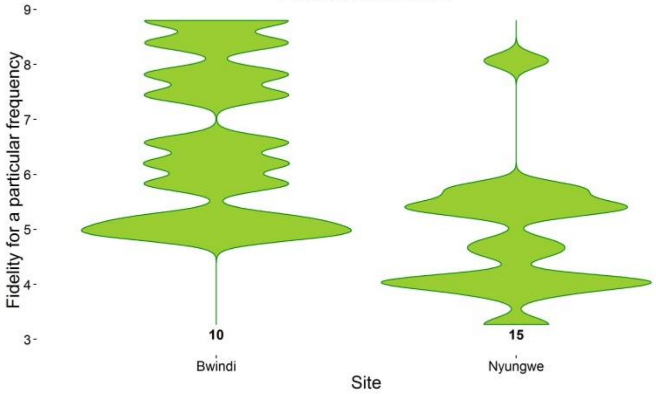

Olea capensis


Parkia bicolor

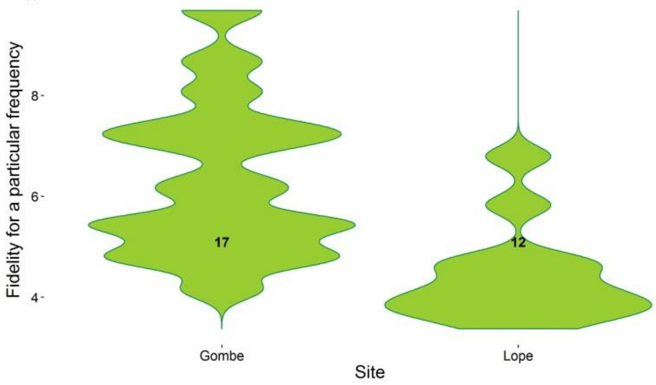

Pentadesma butyracea



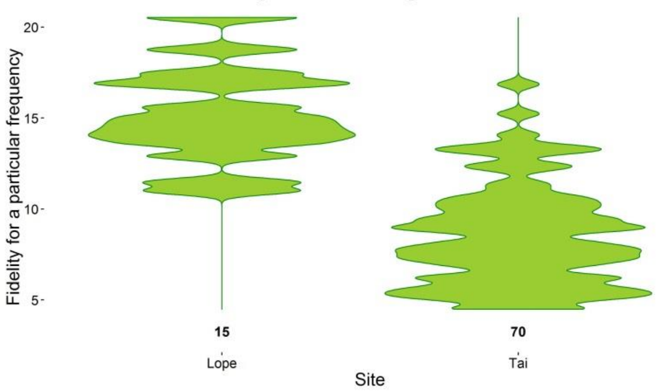
Podocarpus latifolius



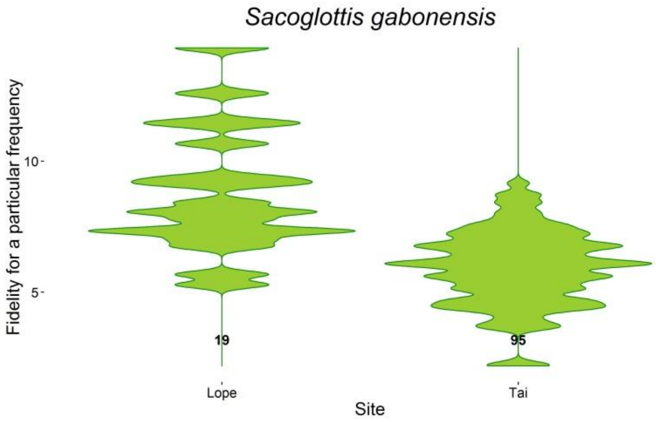
Prunus africana

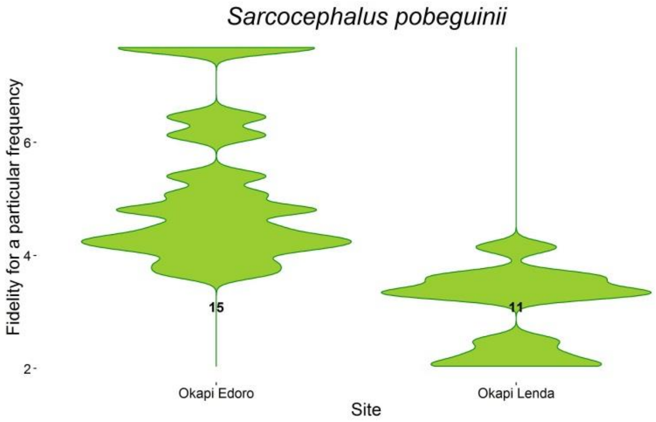


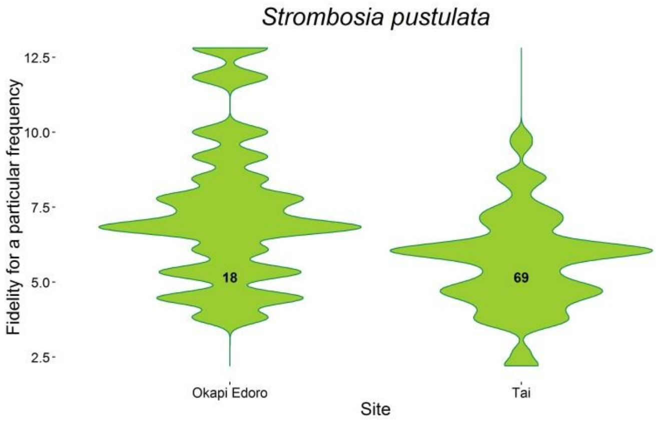
Pseudospondias microcarpa

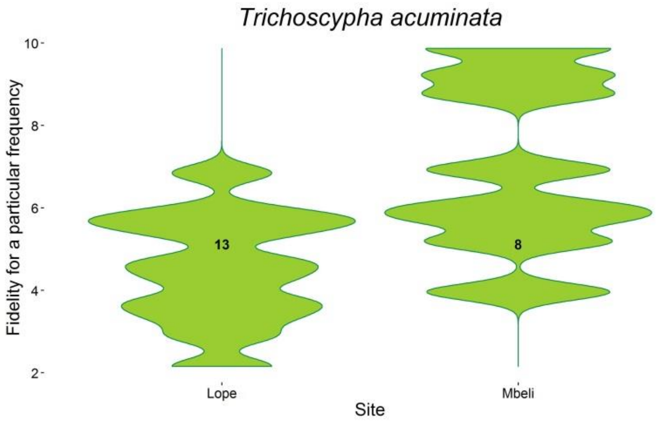


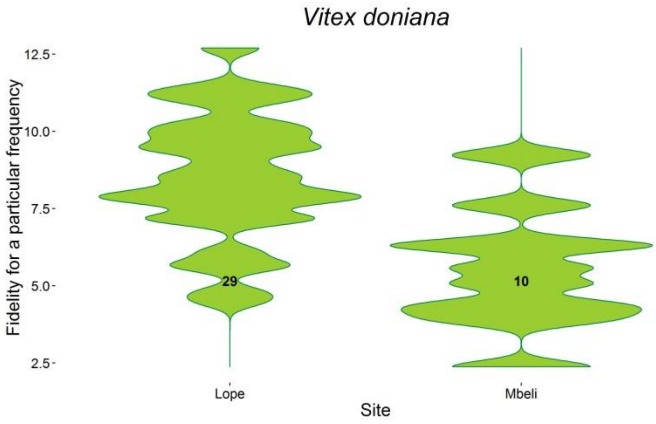
Pycnanthus angolensis


Sacoglottis gabonensis
Fidelity for a particular frequency
10
5
19
95
Lope
Tai
Site

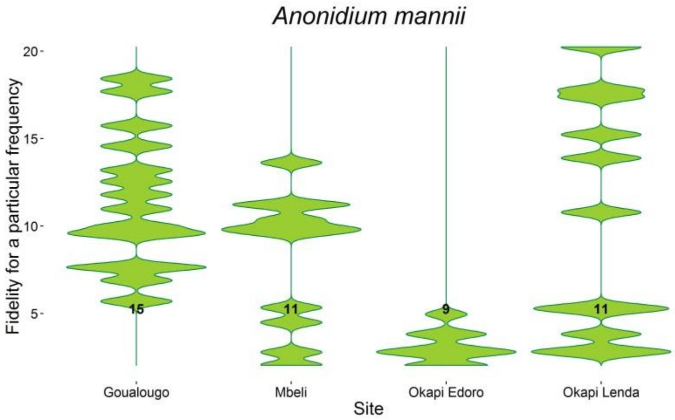

Sarcocephalus pobeguinii
Fidelity for a particular frequency
6
4
2
15
11
Okapi Edoro
Okapi Lenda
Site

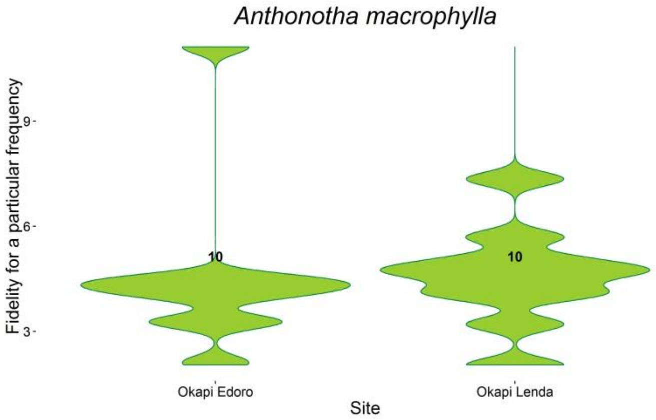

Strombosia pustulata
Fidelity for a particular frequency
12.5
10.0
7.5
5.0
2.5
18
69
Okapi Edoro
Tai
Site

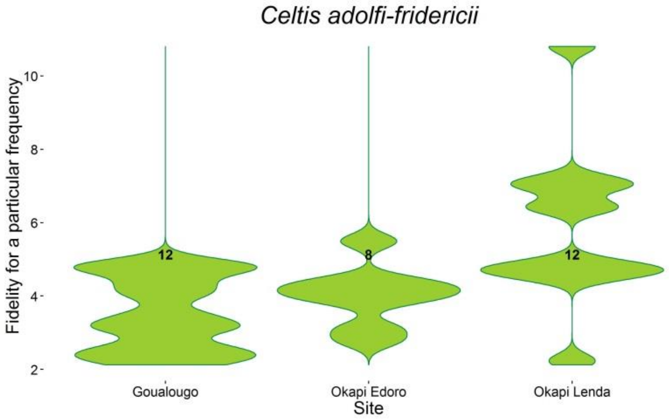

Trichoscypha acuminata
Fidelity for a particular frequency
10
8
6
4
2
13
8
Lope
Mbeli
Site

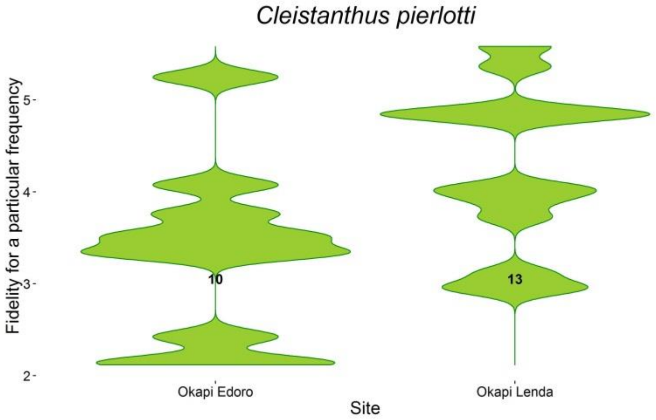

Vitex doniana
Fidelity for a particular frequency
12.5
10.0
7.5
5.0
2.5
29
10
Lope
Mbeli
Site

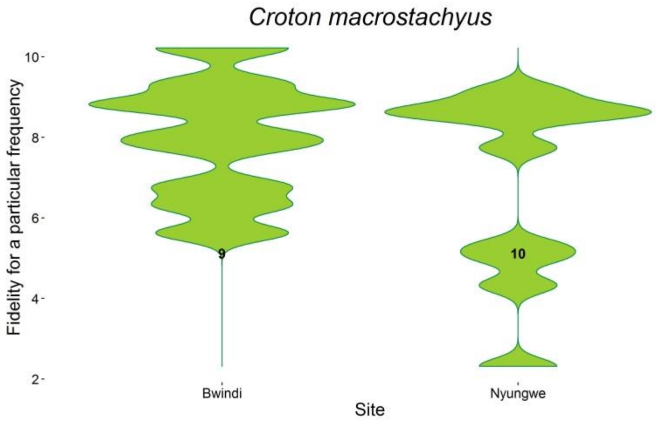
Appendix 2F. Species that do not vary in their fidelity for a particular flowering frequency across different sites.

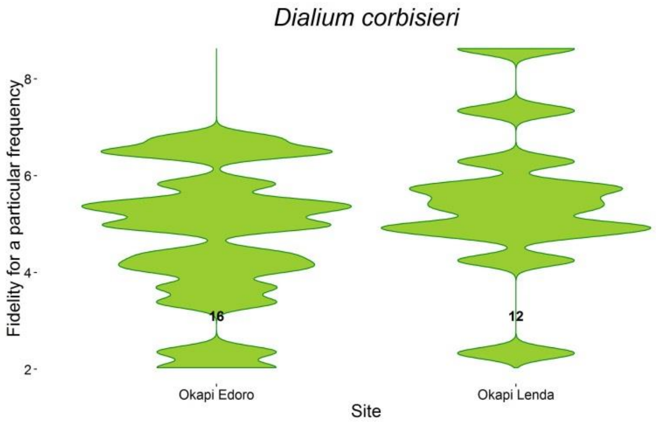


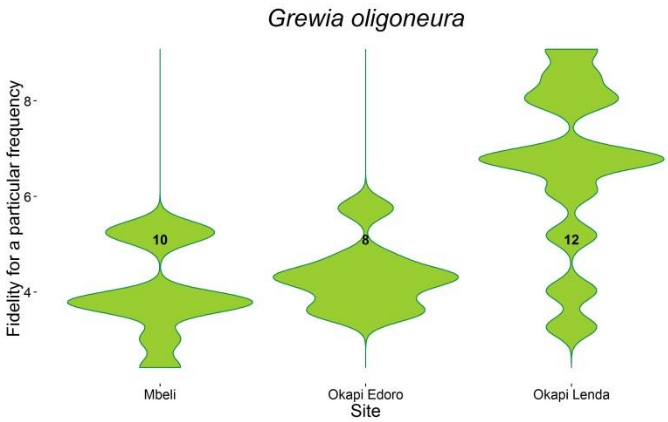


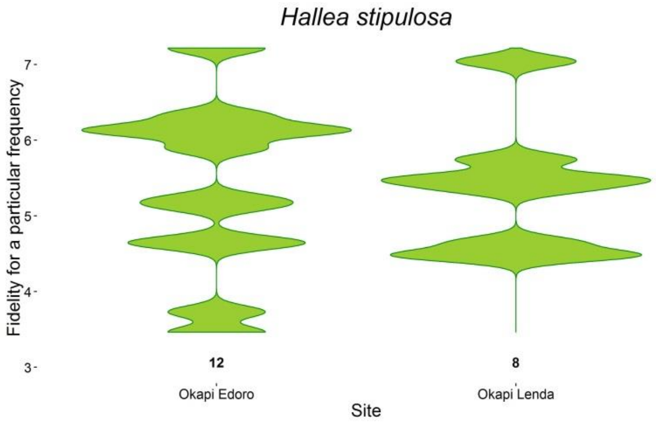


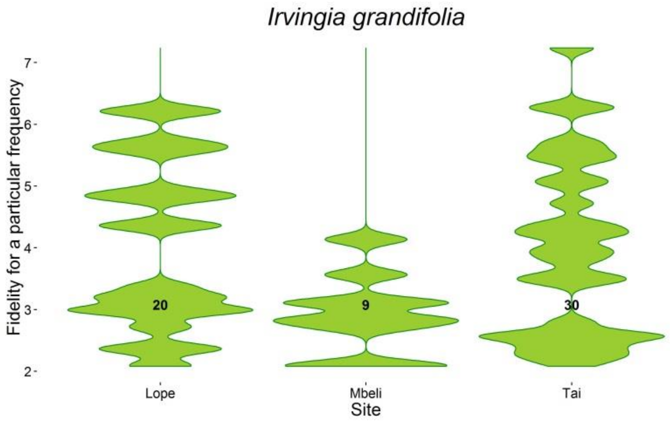


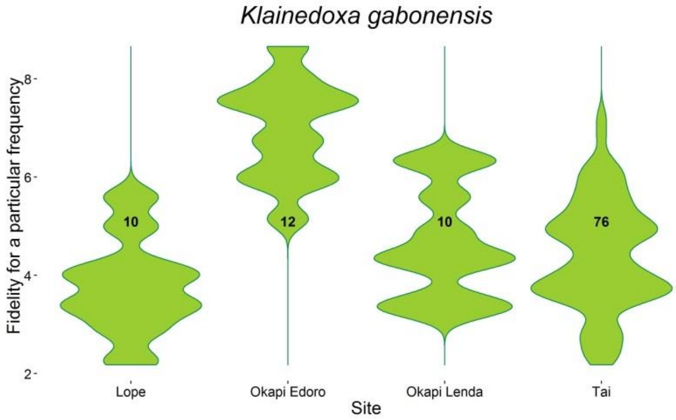

Croton macrostachyus
Fidelity for a particular frequency
10
8
6
4
2
9
10
Bwindi
Nyungwe
Site

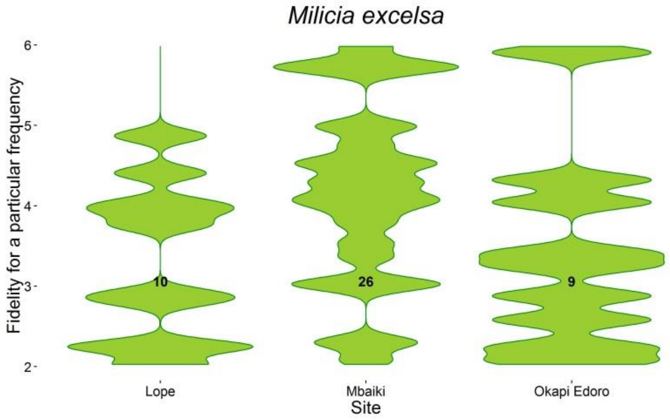

Dialium corbisieri
Fidelity for a particular frequency
8
6
4
2
16
12
Okapi Edoro
Okapi Lenda
Site

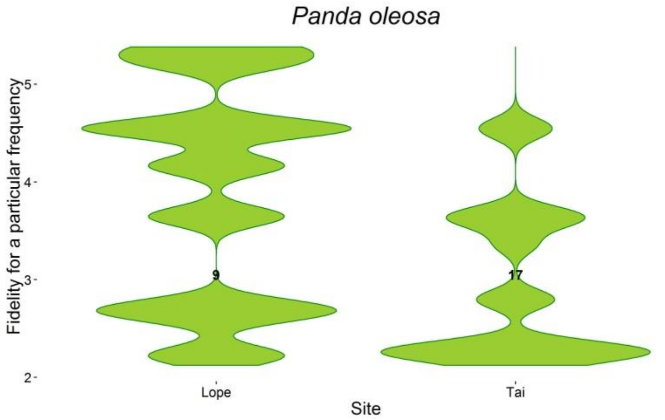

Grewia oligoneura
Fidelity for a particular frequency
8
6
4
10
8
12
Mbeli
Okapi Edoro
Okapi Lenda
Site


Hallea stipulosa
Fidelity for a particular frequency
7
6
5
4
3
12
8
Okapi Edoro
Okapi Lenda
Site

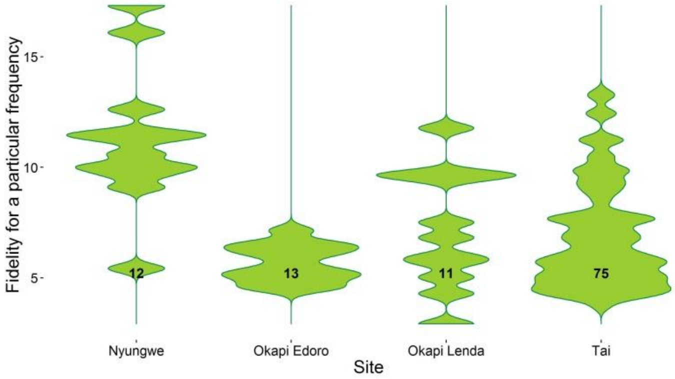

Irvingia grandifolia


Klainedoxa gabonensis

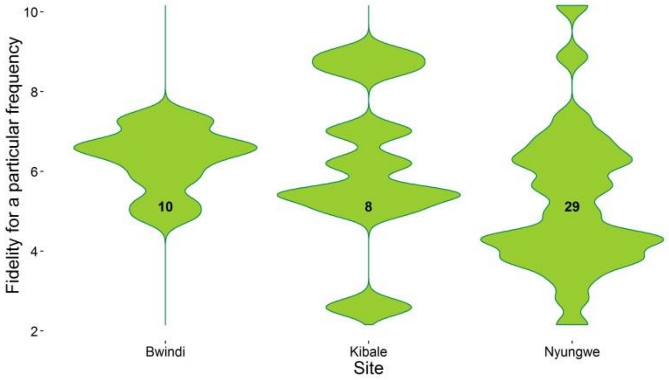

Milicia excelsa


Panda oleosa

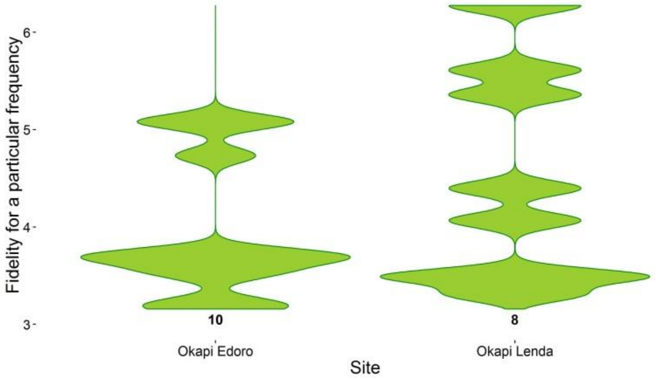
Parinari excelsa



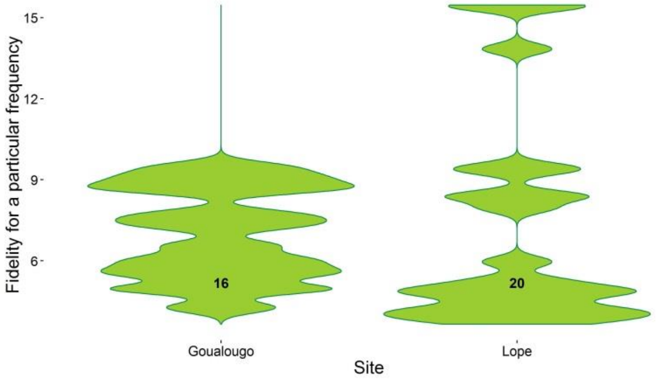
Strombosia scheffleri

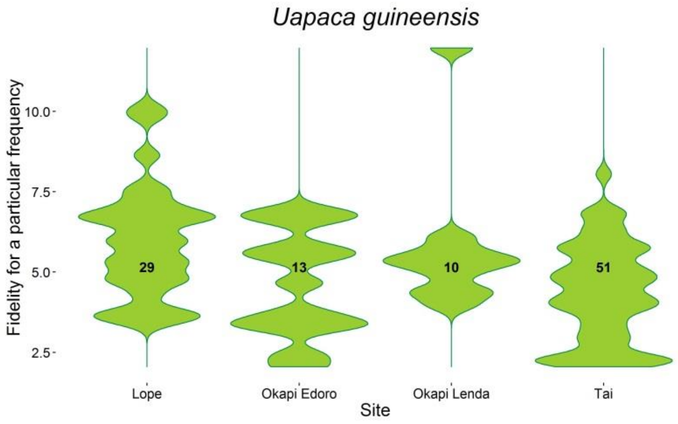


Strombosiopsis tetrandra

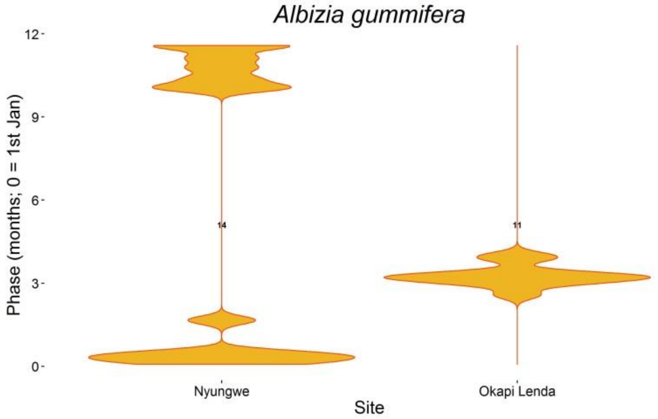


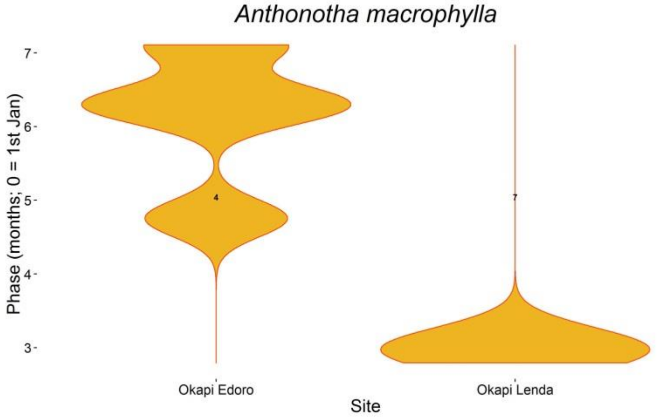
Tetrapleura tetraptera

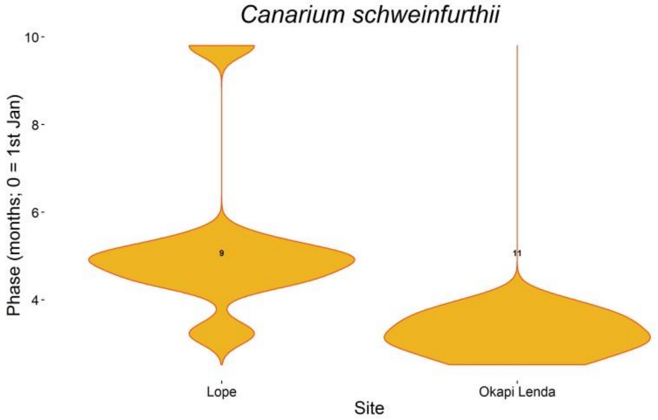


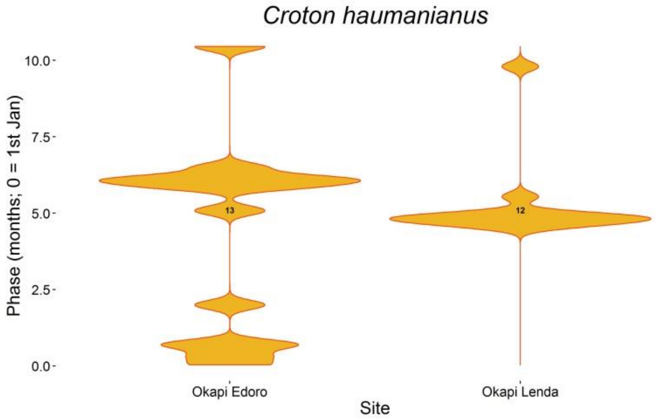

Uapaca guineensis
Fidelity for a particular frequency
10.0
7.5
5.0
2.5
29
13
10
51
Lope
Okapi Edoro
Okapi Lenda
Tai
Site

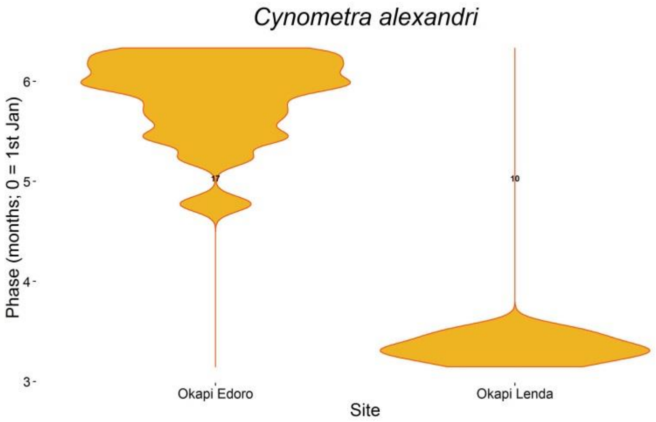
Appendix 2G. Species showing significantly different seasonal phases of flowering across various sites.

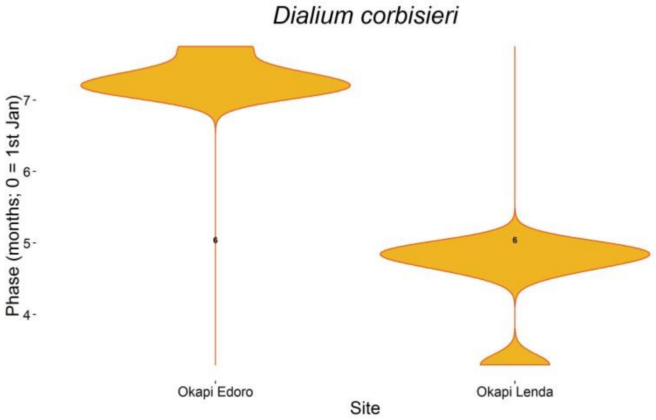

Albizia gummifera

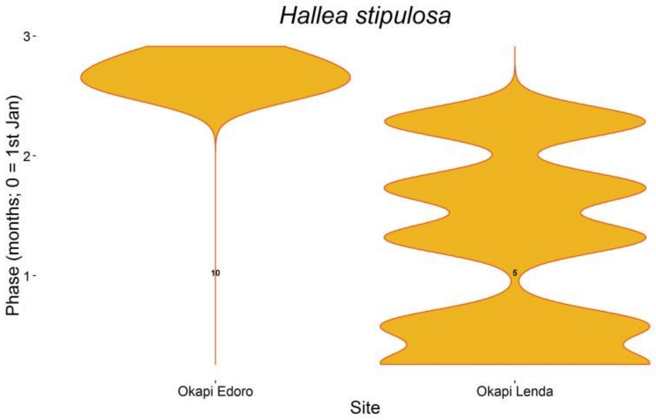

Anthonotha macrophylla

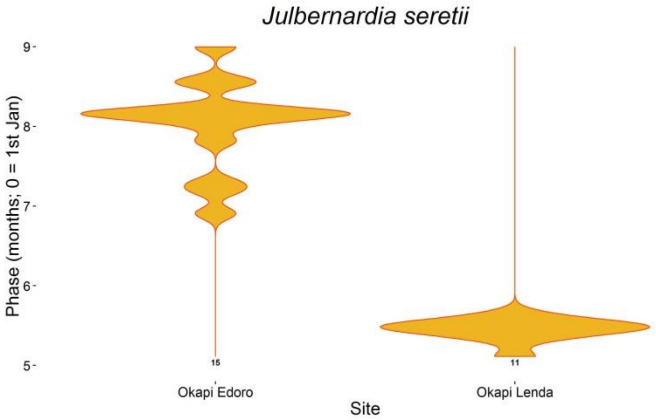

Canarium schweinfurthii

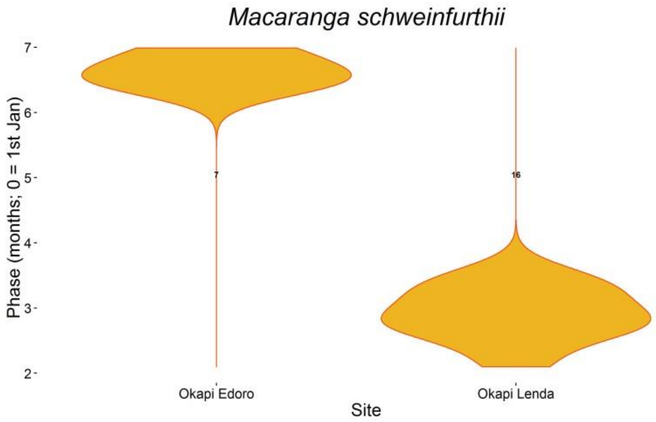

Croton haumanianus

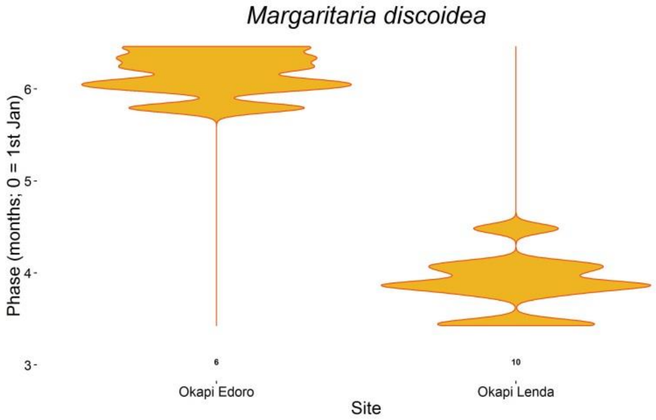

Cynometra alexandri
Phase (months; 0 = 1st Jan)
6
5
4
3
17
10
Okapi Edoro
Okapi Lenda
Site

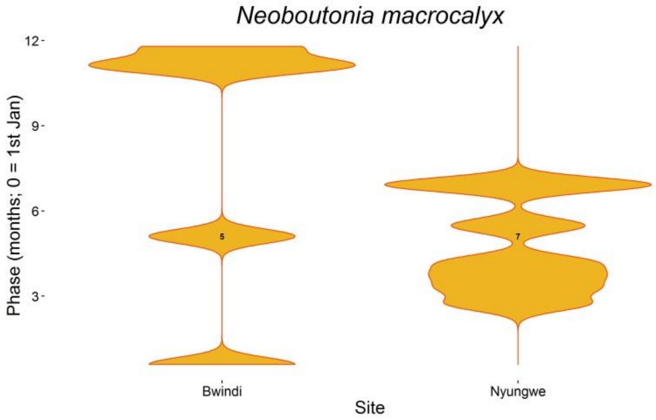

Dialium corbisieri
Phase (months; 0 = 1st Jan)
7
6
5
4
6
6
Okapi Edoro
Okapi Lenda
Site

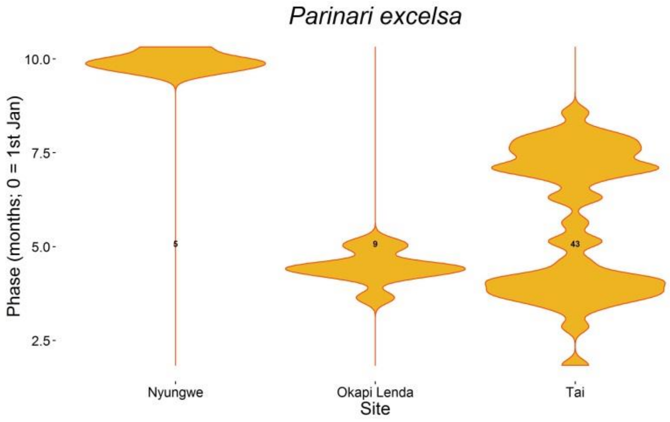

Hallea stipulosa
Phase (months; 0 = 1st Jan)
3
2
1
10
5
Okapi Edoro
Okapi Lenda
Site

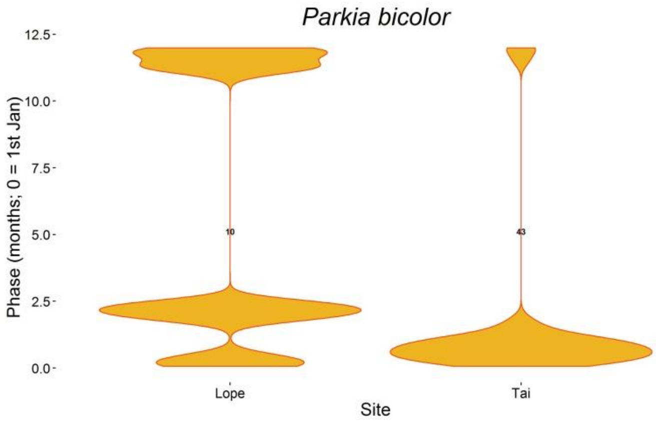

Julbernardia seretii
Phase (months; 0 = 1st Jan)
9
8
7
6
5
15
11
Okapi Edoro
Okapi Lenda
Site


Macaranga schweinfurthii
Phase (months; 0 = 1st Jan)
7
6
5
4
3
2
7
16
Okapi Edoro
Okapi Lenda
Site

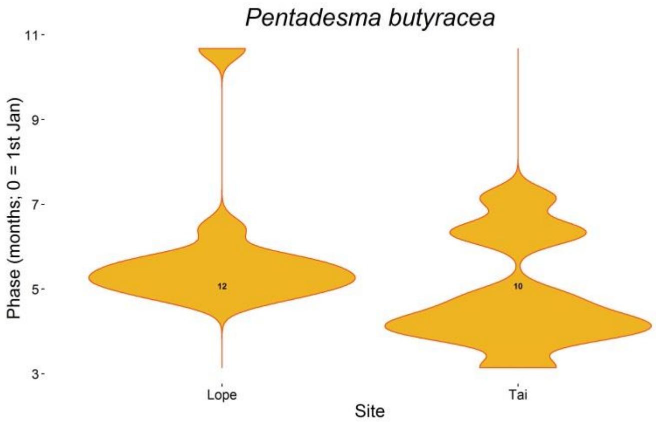

Margaritaria discoidea
Phase (months; 0 = 1st Jan)
6
5
4
3
6
10
Okapi Edoro
Okapi Lenda
Site


Neoboutonia macrocalyx
Phase (months; 0 = 1st Jan)
12
9
6
3
5
7
Bwindi
Nyungwe
Site

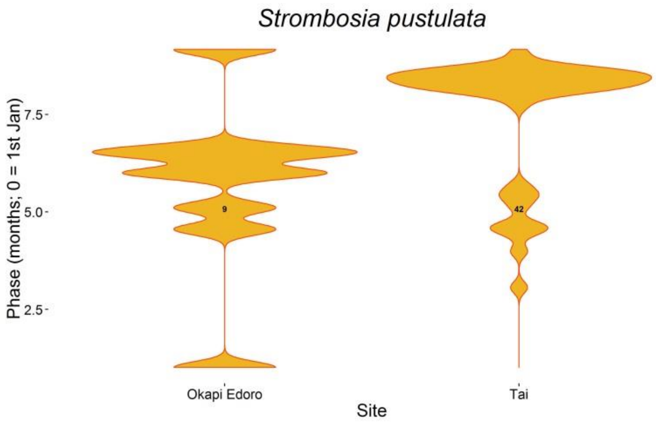

Parinari excelsa
Phase (months; 0 = 1st Jan)
10.0
7.5
5.0
2.5
5
9
43
Nyungwe
Okapi Lenda
Tai
Site



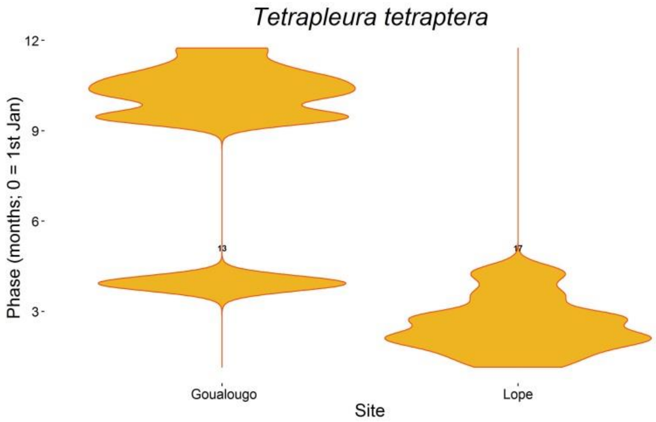
Parkia bicolor



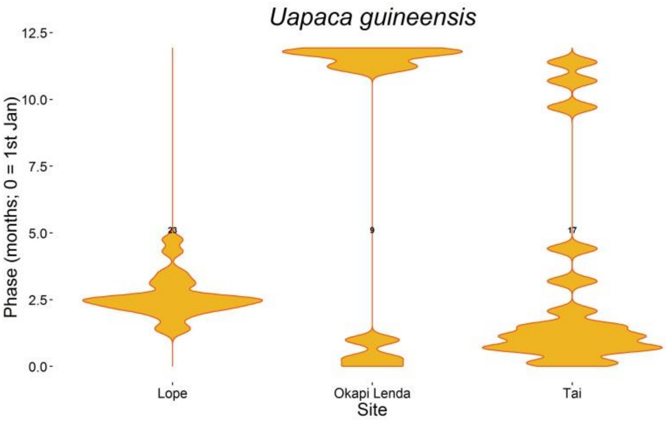
Pentadesma butyracea



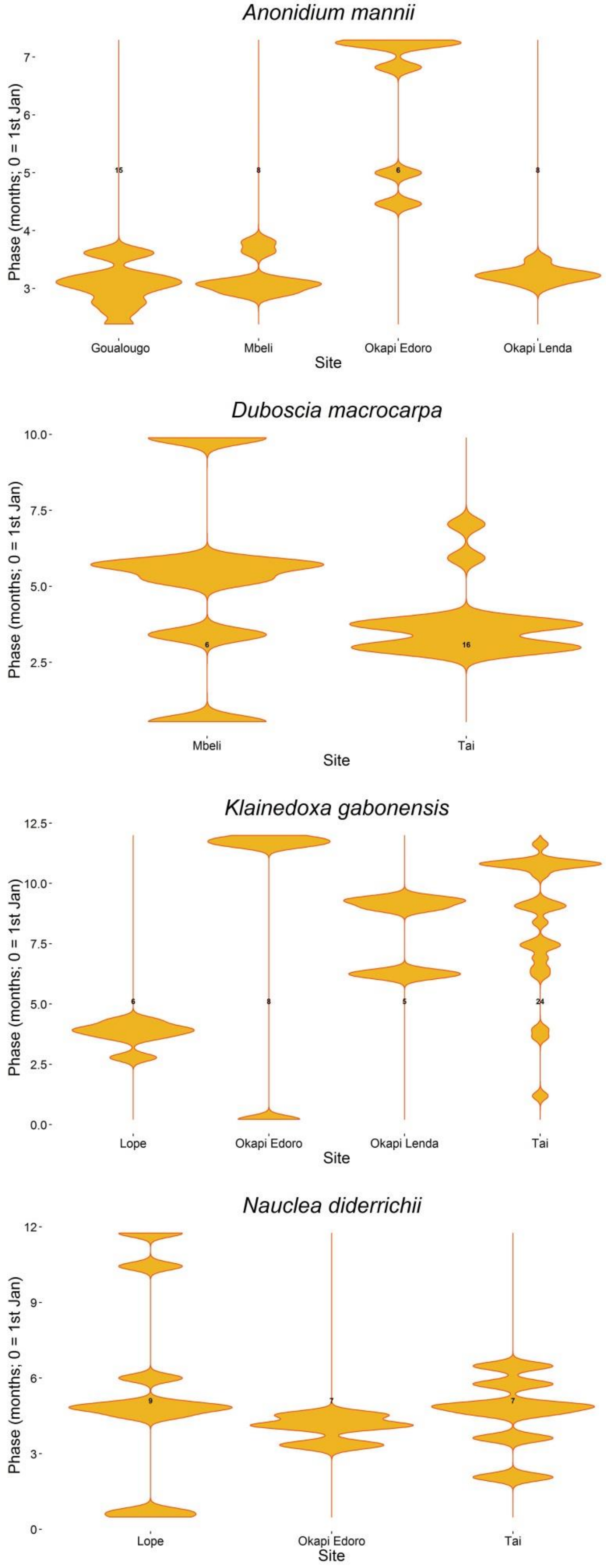
Strombosia pustulata

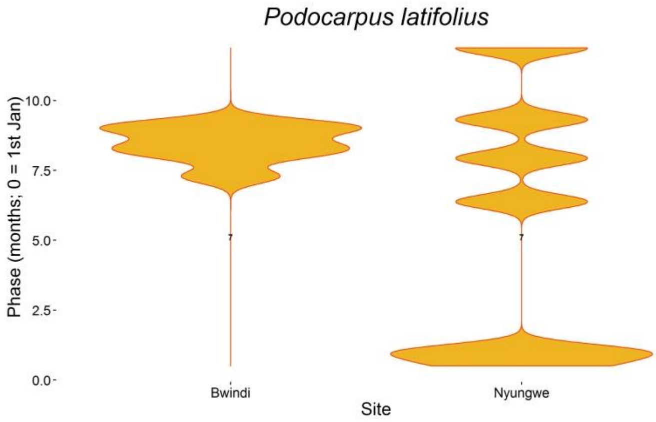


Tetrapleura tetraptera

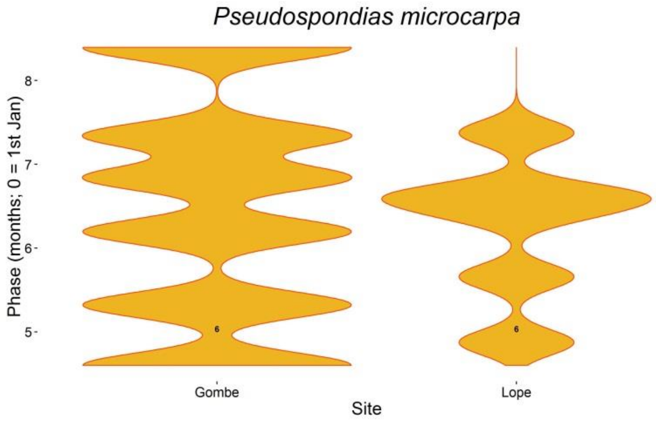

Uapaca guineensis
Phase (months; 0 = 1st Jan)
12.5
10.0
7.5
5.0
2.5
0.0
23
9
17
Lope
Okapi Lenda
Tai
Site

Appendix 2H. Species showing similar seasonal phases of flowering across various sites. each site.

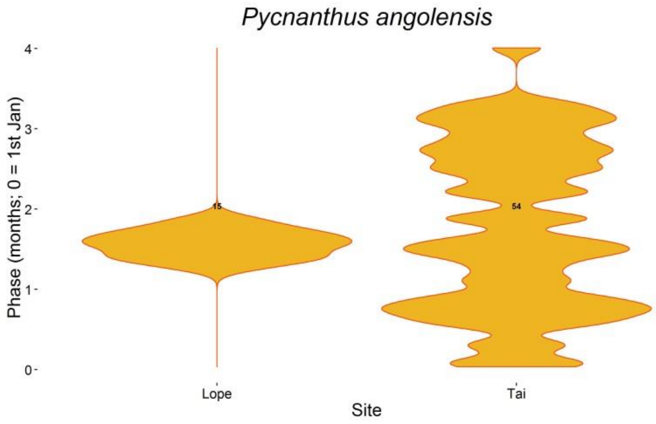




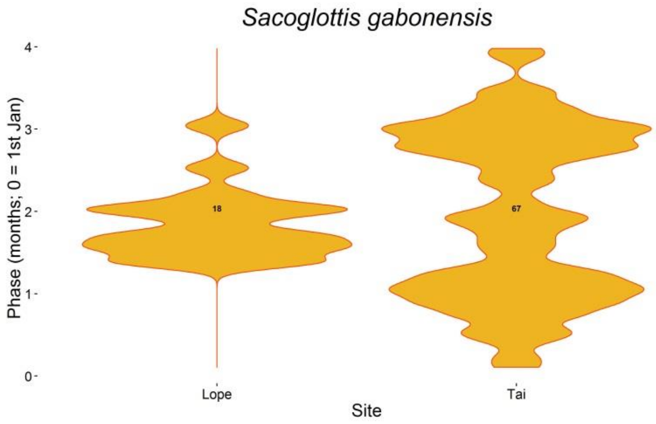
Podocarpus latifolius



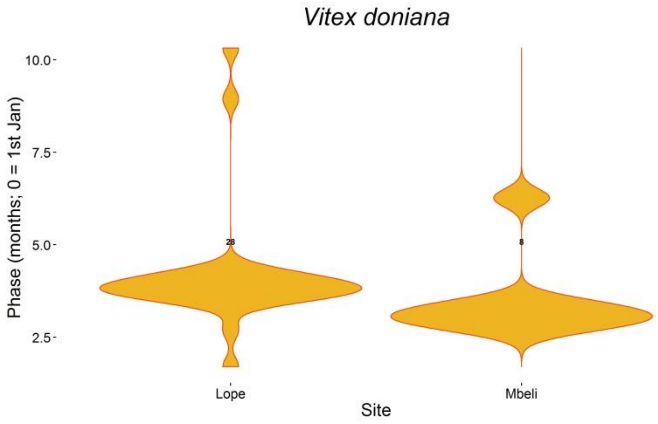
Pseudospondias microcarpa



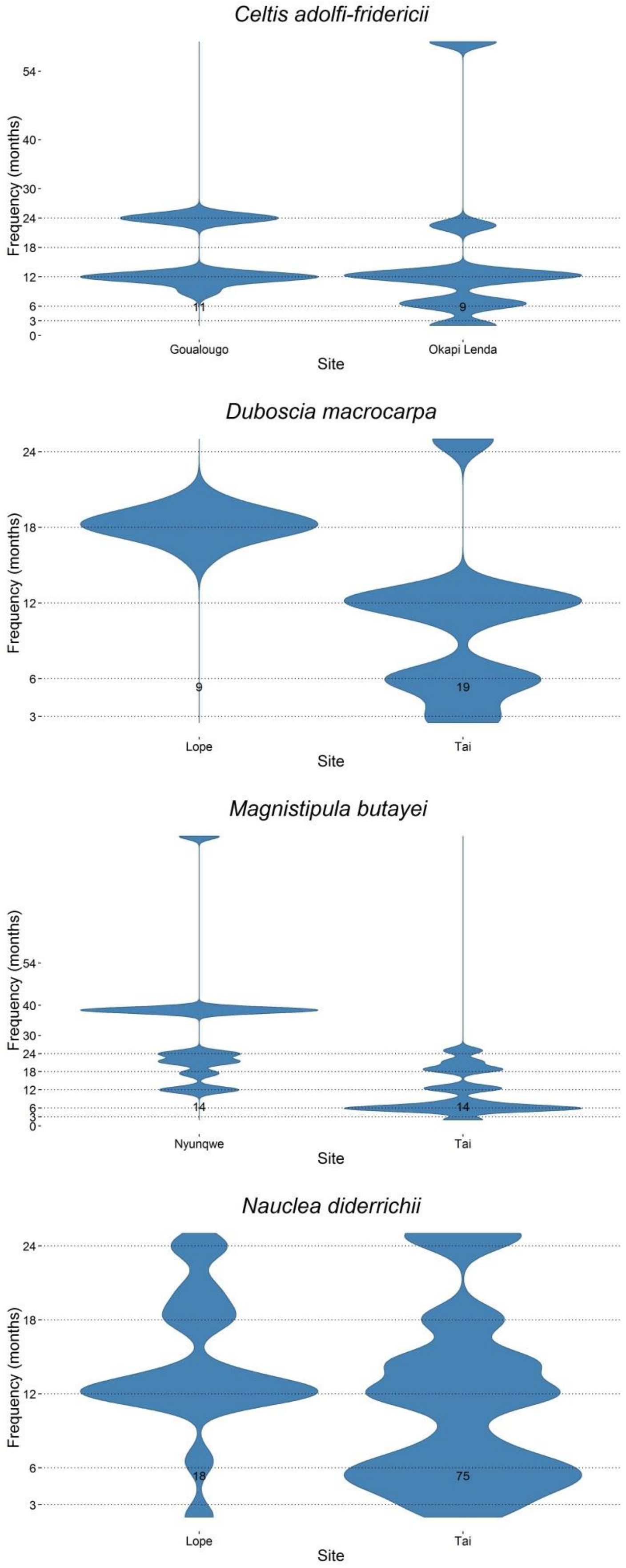
Pycnanthus angolensis

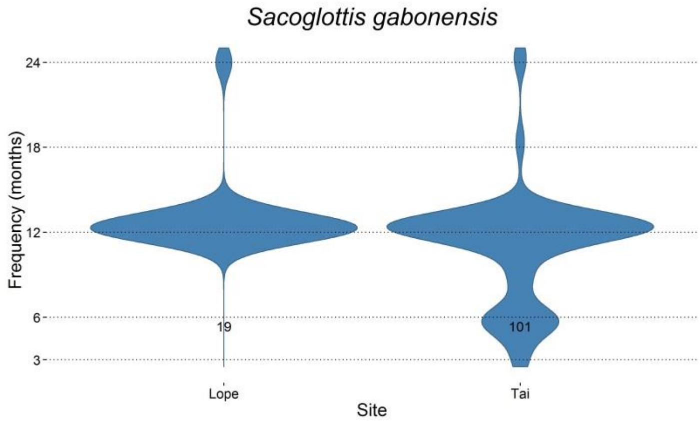


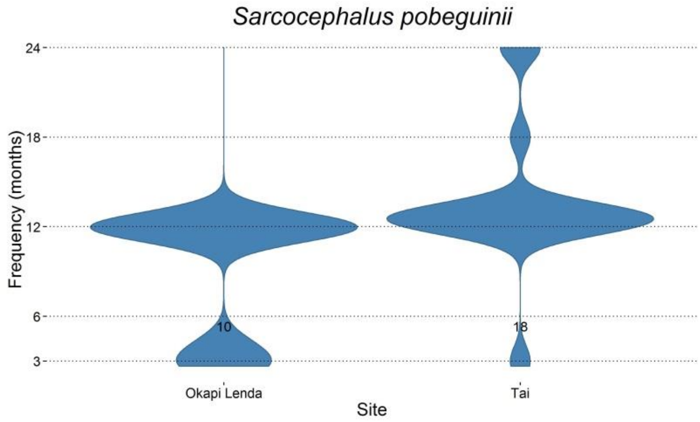
Sacoglottis gabonensis


Vitex doniana
Phase (months; 0 = 1st Jan)
10.0
7.5
5.0
2.5
28
8
Lope
Mbeli
Site

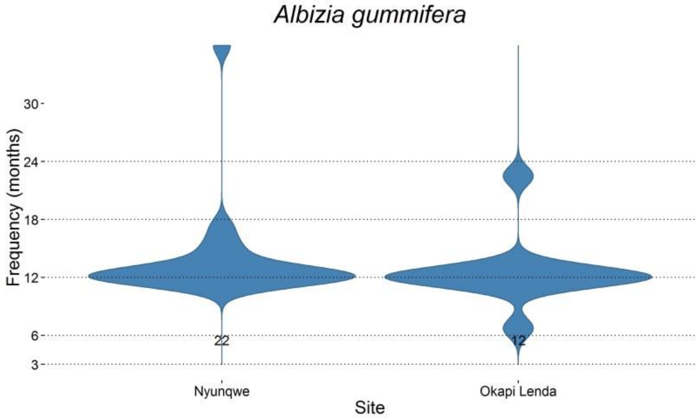
Appendix 2I. Species showing significant differences in their fruiting frequencies across different sites.

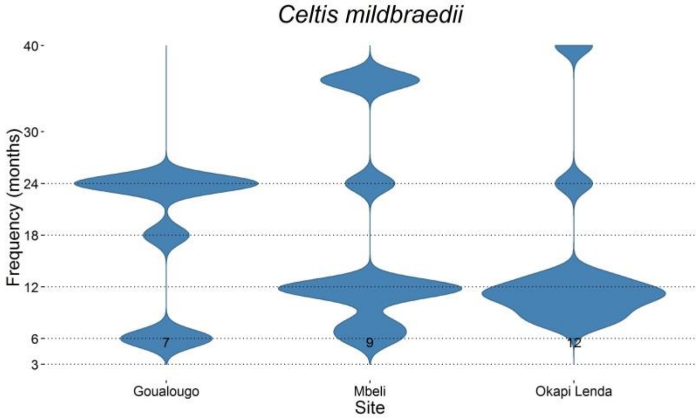


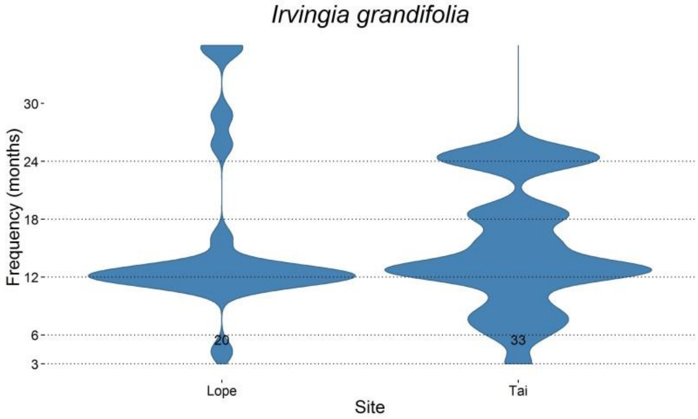

Sacoglottis gabonensis

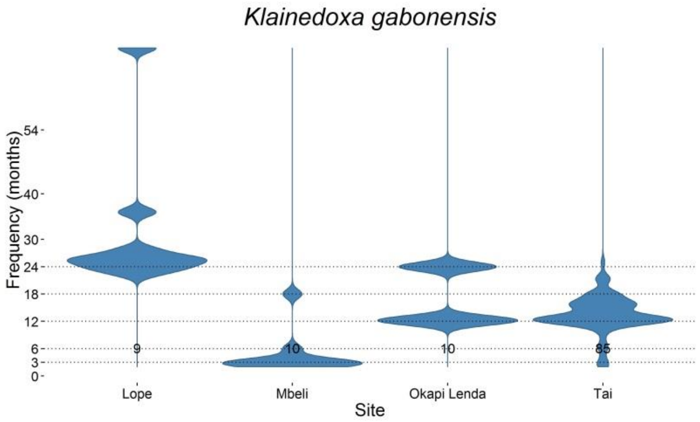

Sarcocephalus pobeguinii

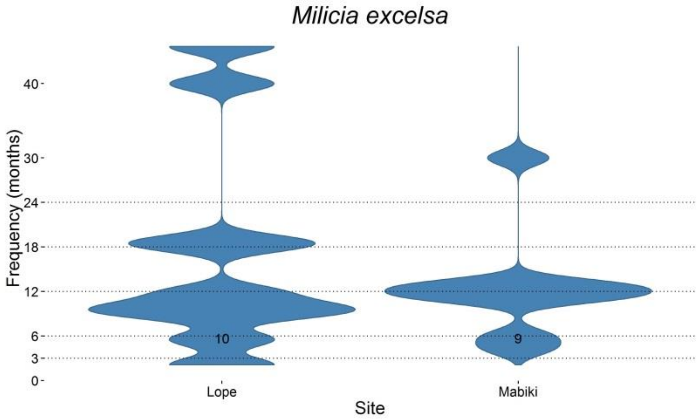
Appendix 2J. Species showing no difference in their fruiting frequencies across different sites.

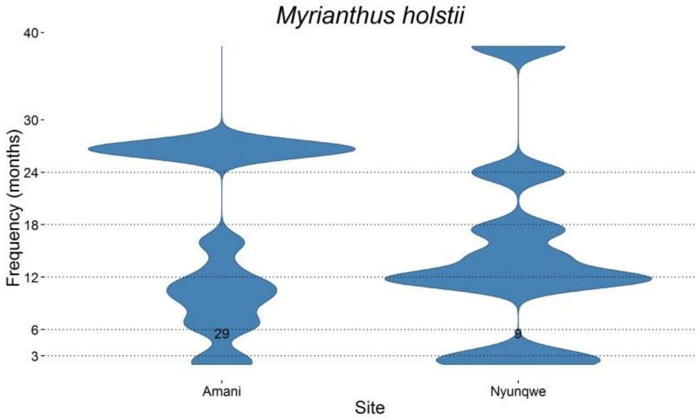


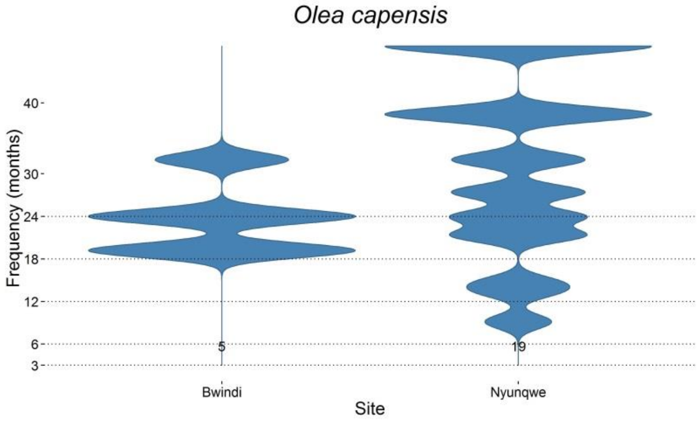


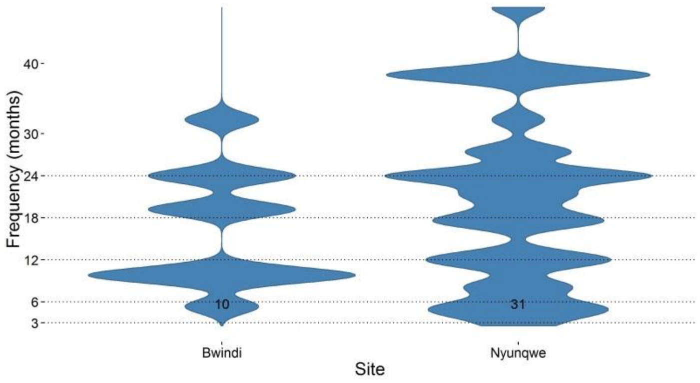


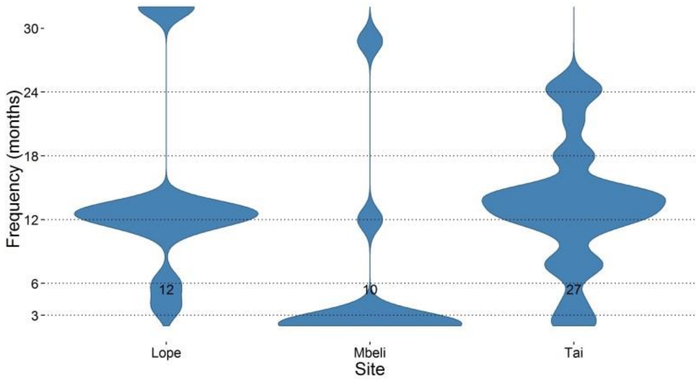

Klainedoxa gabonensis

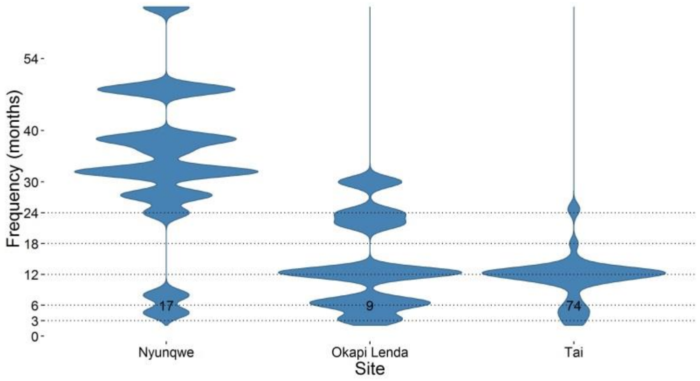

Milicia excelsa

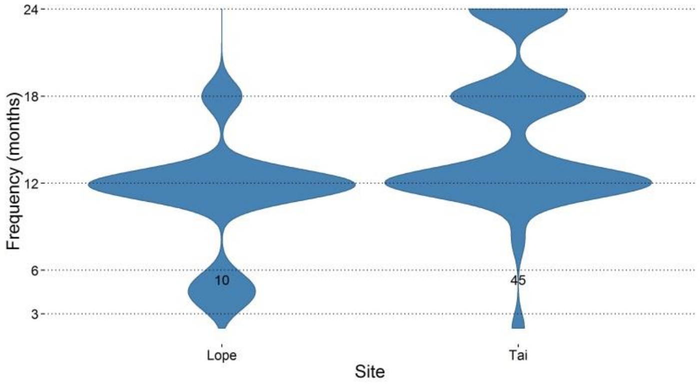

Myrianthus holstii

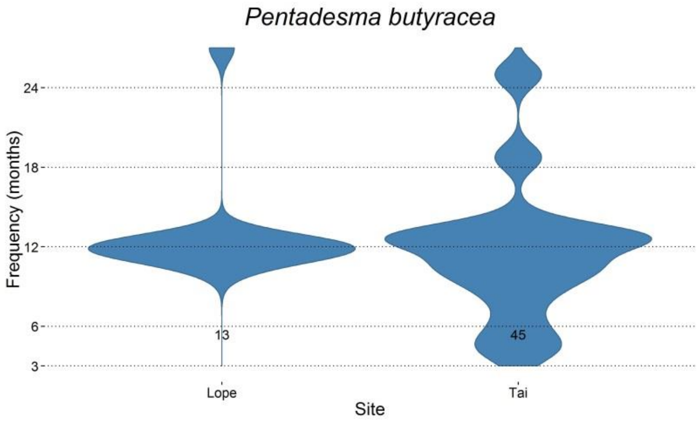

Olea capensis

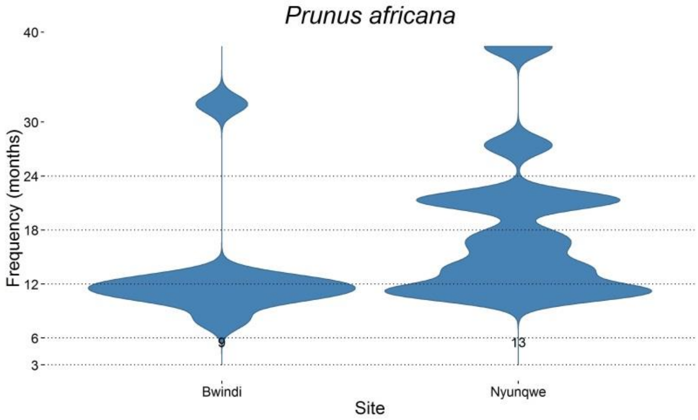

Olinia rochetiana

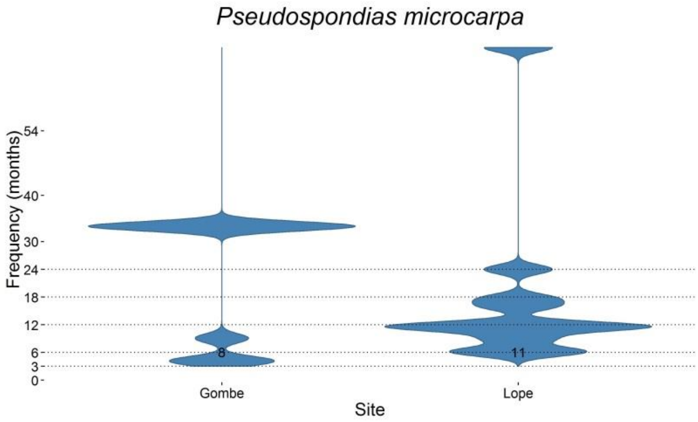

Panda oleosa

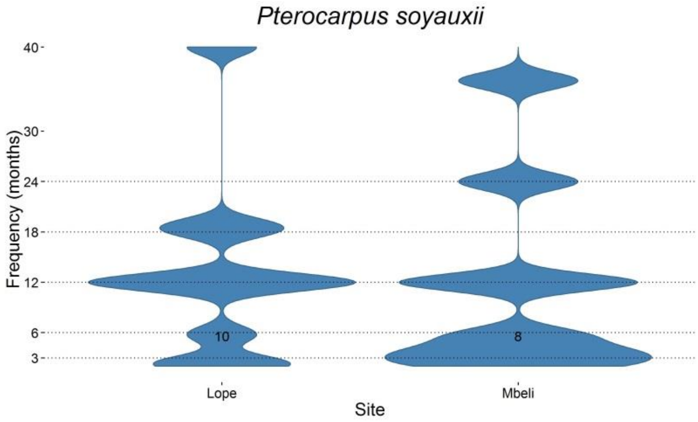

Parinari excelsa

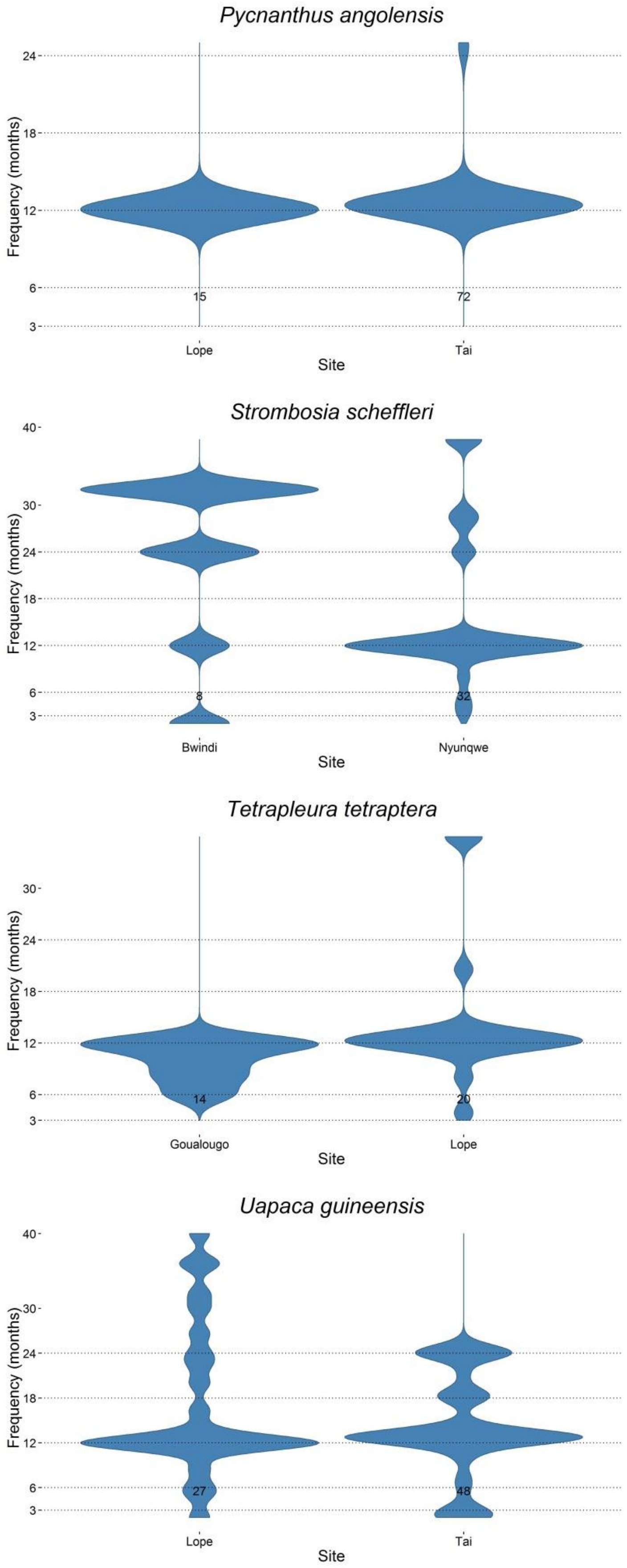

Parkia bicolor

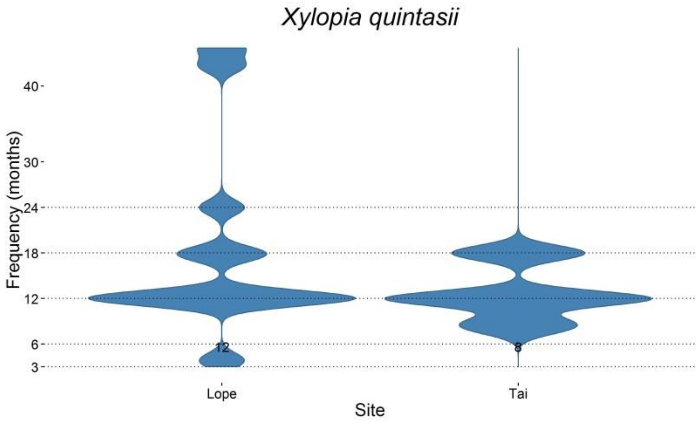

Pentadesma butyracea


Prunus africana

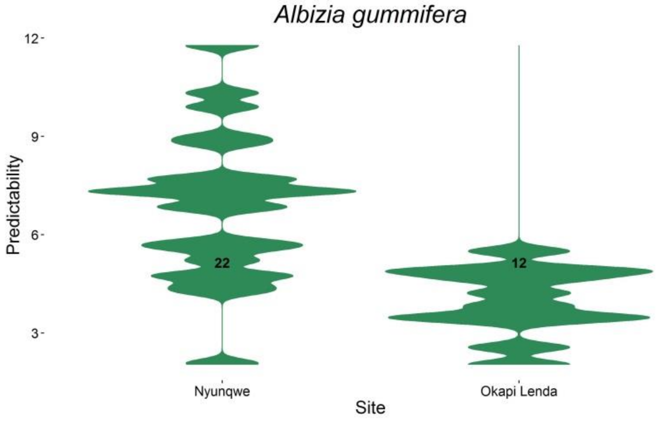

Pseudospondias microcarpa

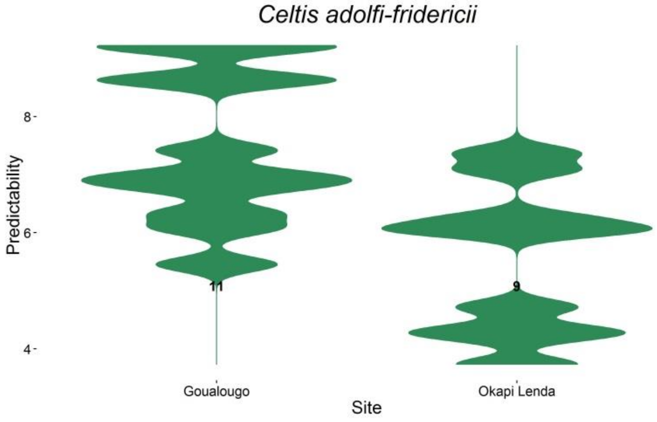

Pterocarpus soyauxii

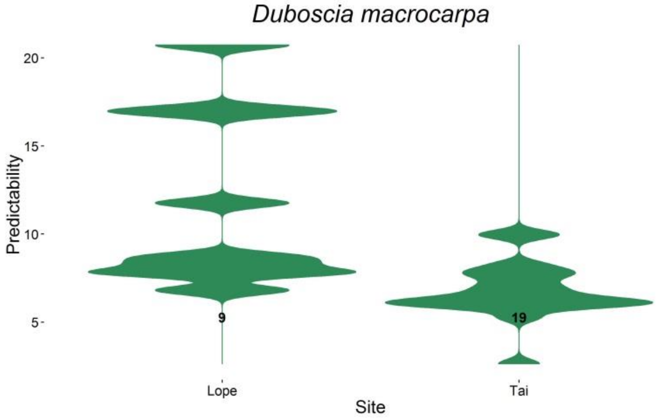

Pycnanthus angolensis
Frequency (months)
24
18
12
6
3
15
72
Lope
Tai
Site
Strombosia scheffleri
Frequency (months)
40
30
24
18
12
6
3
8
32
Bwindi
Nyunqwe
Site
Tetrapleura tetraptera
Frequency (months)
30
24
18
12
6
3
14
20
Goualougo
Lope
Site
Uapaca guineensis
Frequency (months)
40
30
24
18
12
6
3
27
48
Lope
Tai
Site

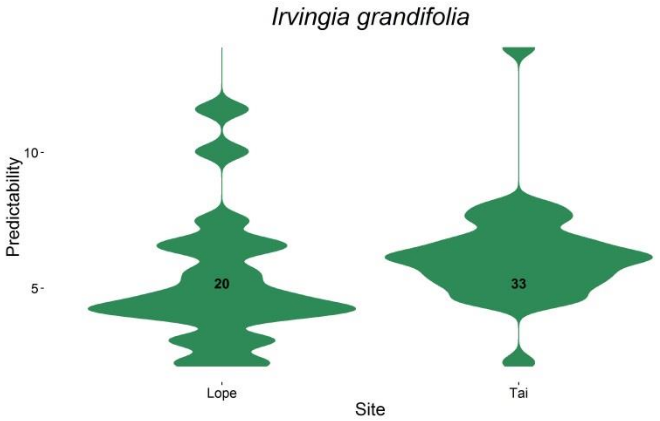

Xylopia quintasii
Frequency (months)
40
30
24
18
12
6
3
12
8
Lope
Tai
Site

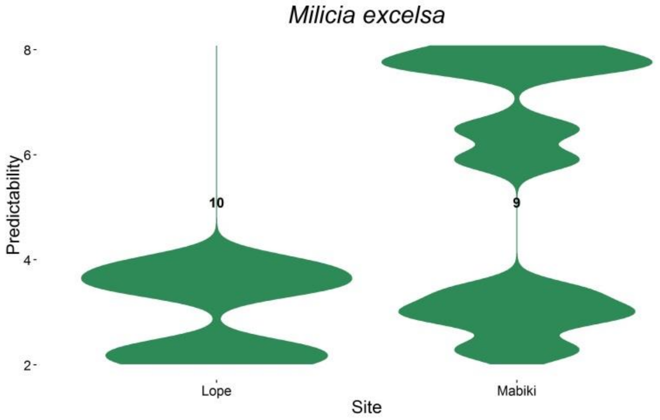
Appendix 2K. Species that significantly vary in their fidelity for a particular fruiting frequency across different sites.

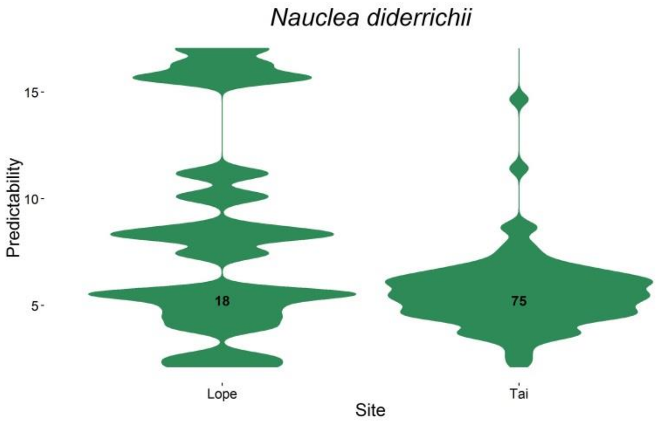


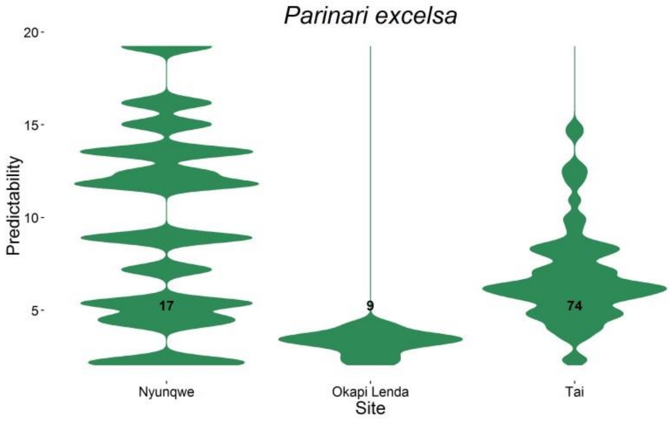


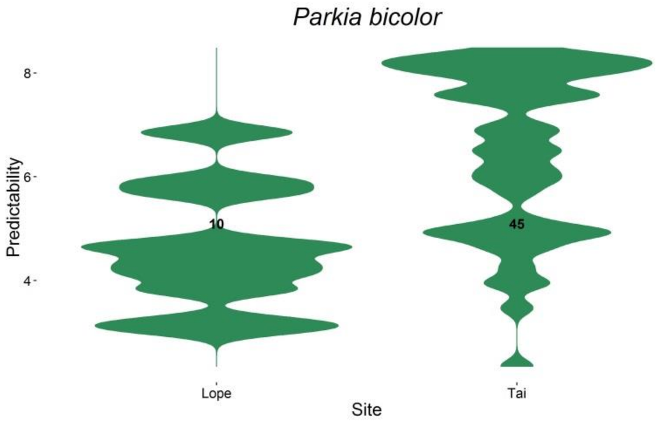


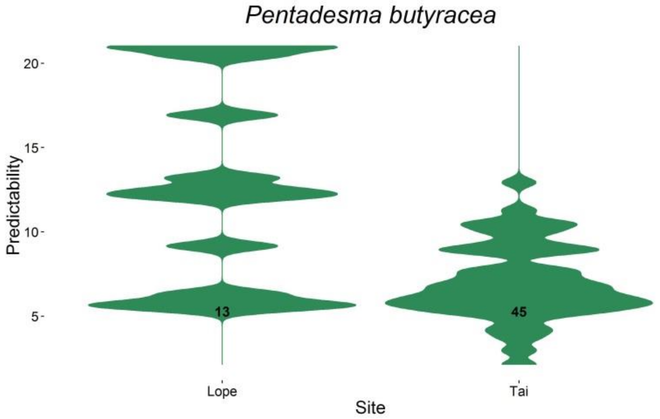

Irvingia grandifolia
Predictability
10
5
20
33
Lope
Tai
Site

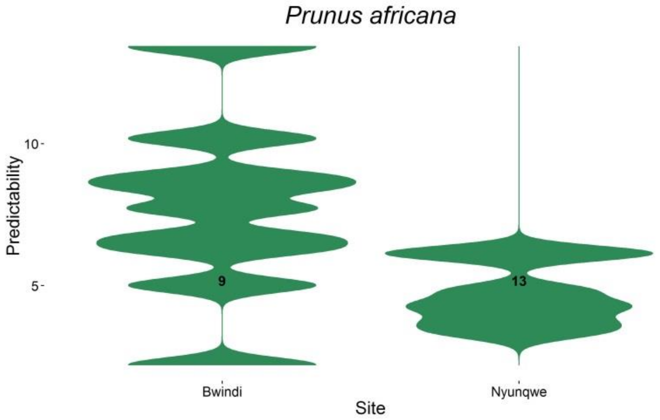

Milicia excelsa
8
6
4
2
Predictability
10
9
Lope
Mabiki
Site

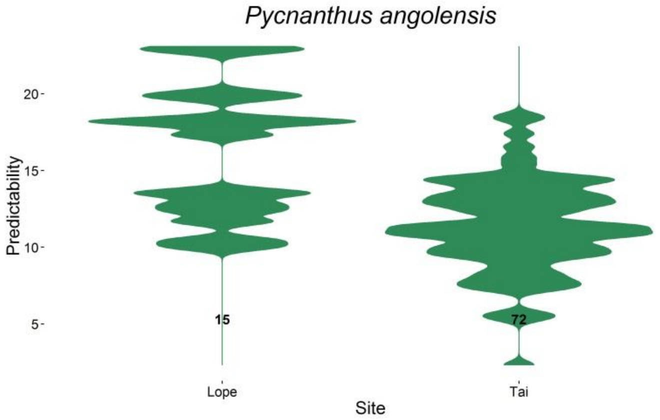

Nauclea diderrichii
15
10
5
Predictability
18
75
Lope
Tai
Site

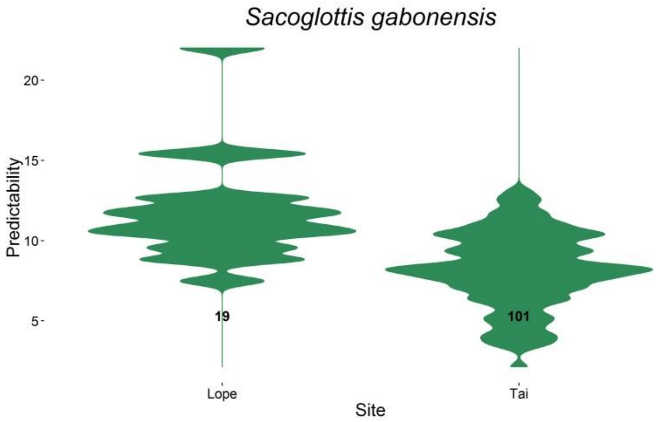

Parinari excelsa
20
15
10
5
Predictability
17
9
74
Nyunqwe
Okapi Lenda
Tai
Site

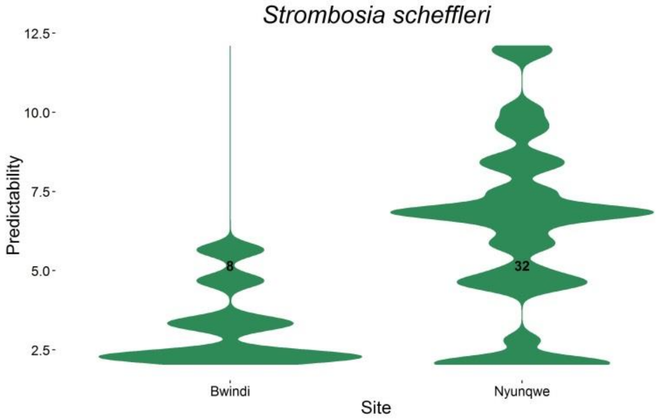

Parkia bicolor
Predictability
8
6
4
10
45
Lope
Tai
Site

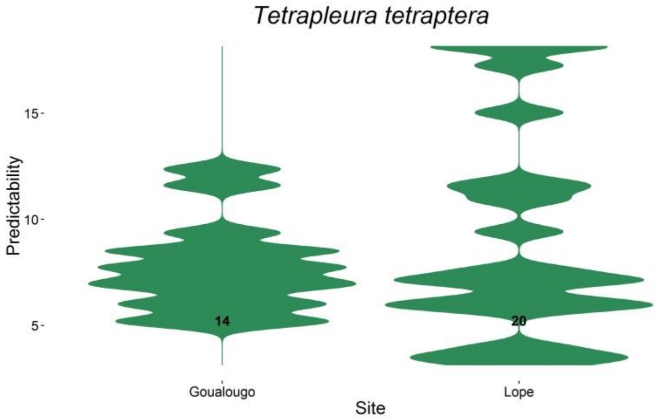

Pentadesma butyracea
Predictability
20
15
10
5
13
45
Lope
Tai
Site

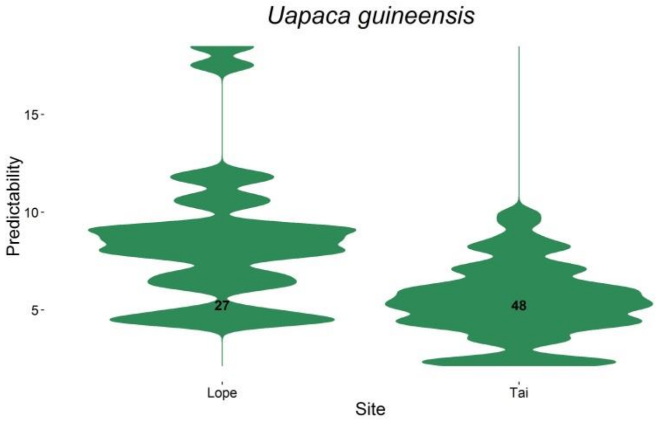

Prunus africana
Predictability
10
5
9
13
Bwindi
Nyunqwe
Site


Pycnanthus angolensis
Predictability
20
15
10
5
15
72
Lope
Tai
Site

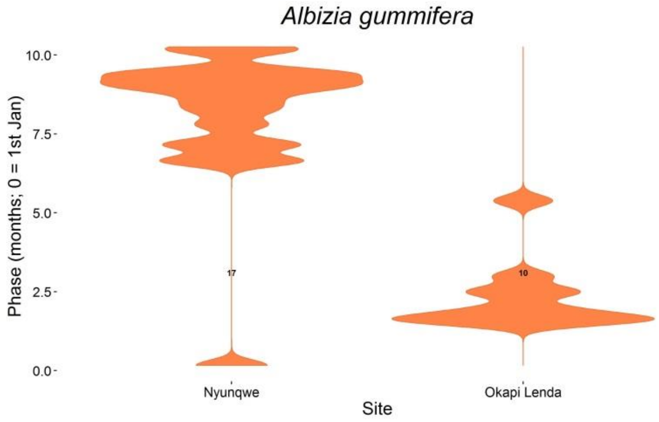

Sacoglottis gabonensis
Predictability
20
15
10
5
19
101
Lope
Tai
Site

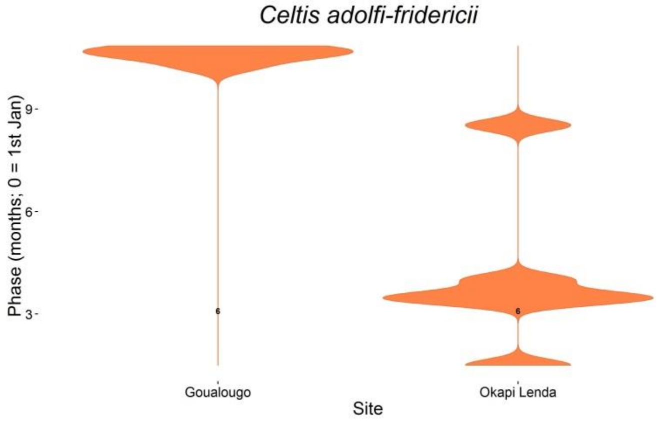

Strombosia scheffleri
Predictability
12.5
10.0
7.5
5.0
2.5
8
32
Bwindi
Nyunqwe
Site

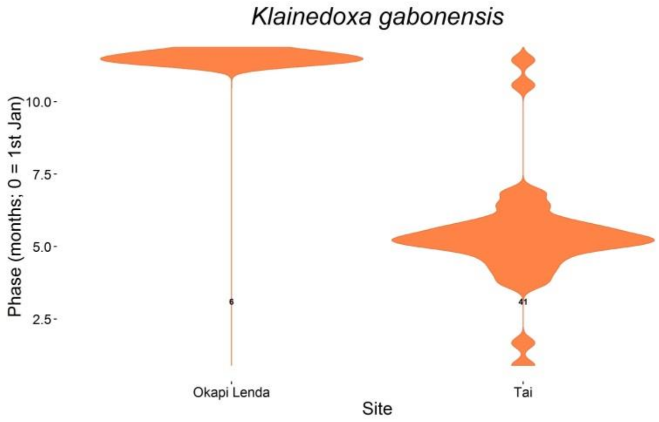

Tetrapleura tetraptera
Predictability
15
10
5
14
20
Goualougo
Lope
Site

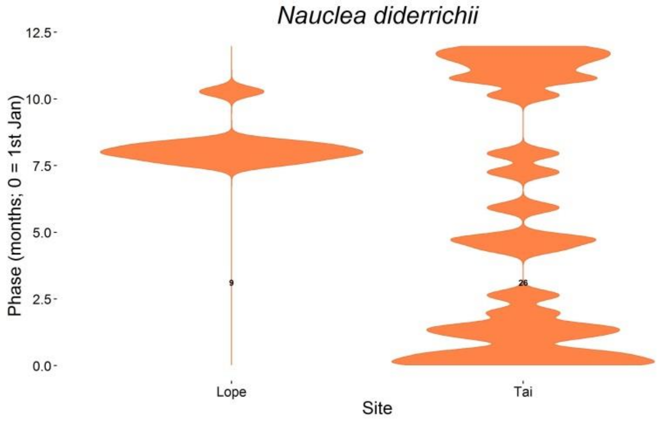

Uapaca guineensis
Predictability
15
10
5
27
48
Lope
Tai
Site

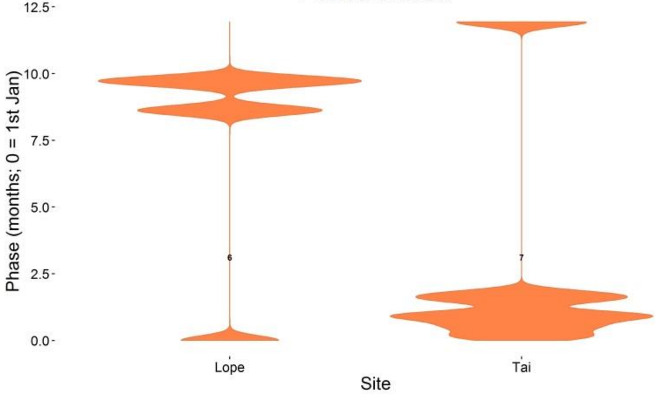
Appendix 2L. Species showing significantly different seasonal phases of fruiting across various sites.



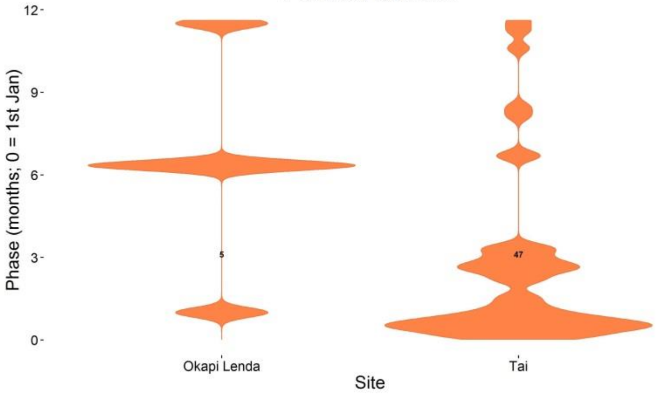




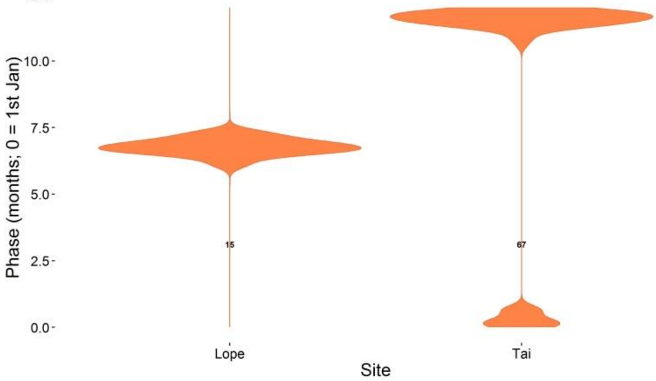




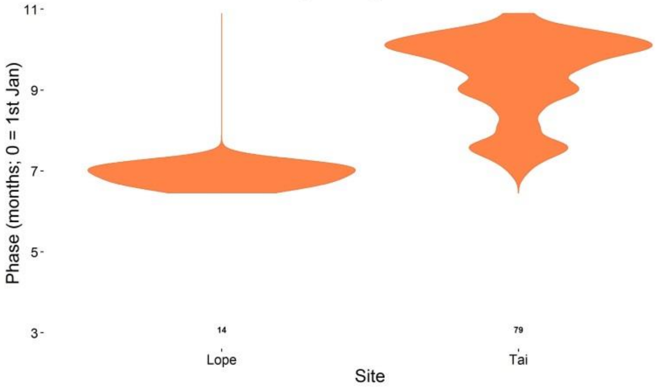
Panda oleosa



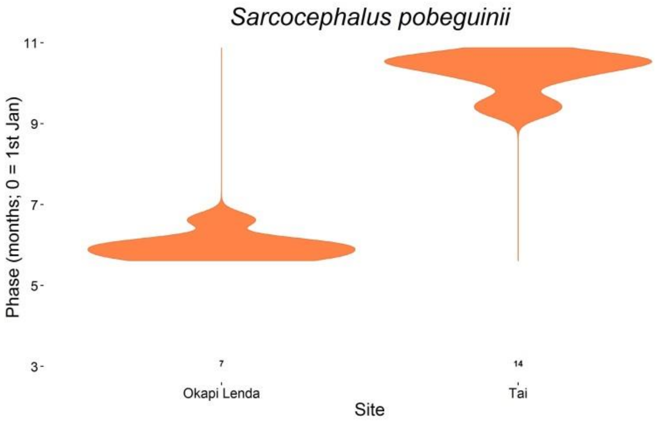
Parinari excelsa



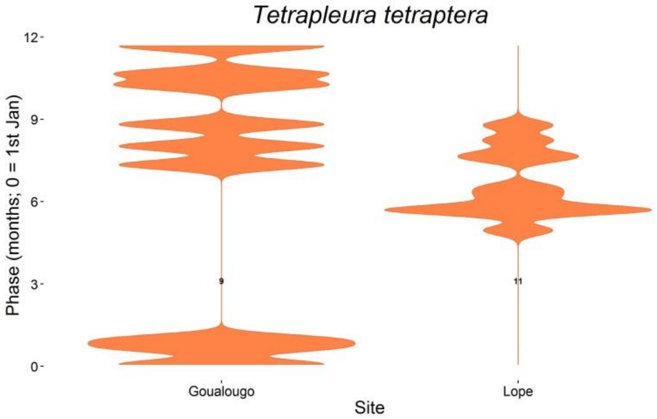
Pycnanthus angolensis



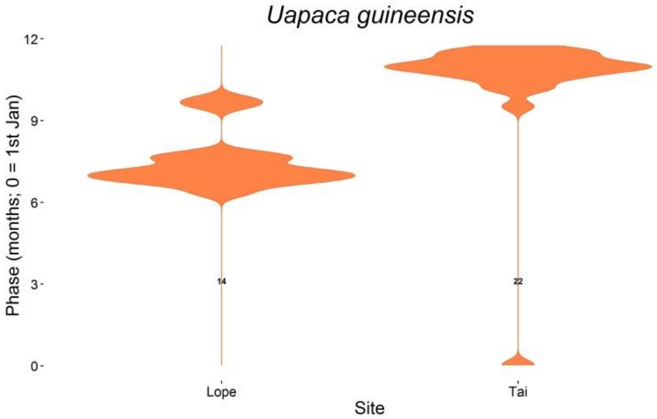
Sacoglottis gabonensis



Sarcocephalus pobeguinii

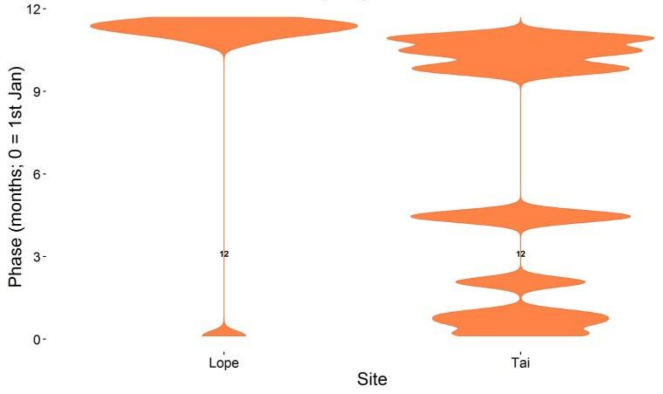


Tetrapleura tetraptera

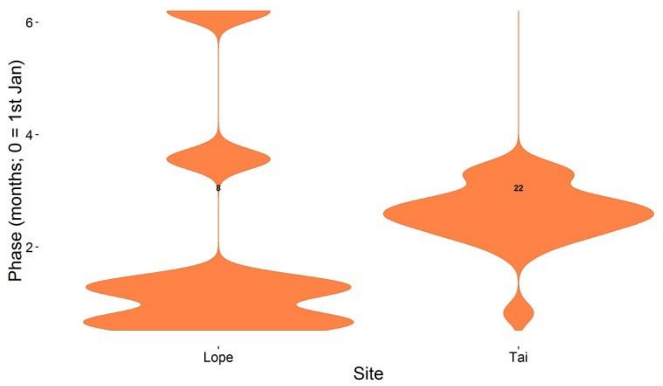


Uapaca guineensis

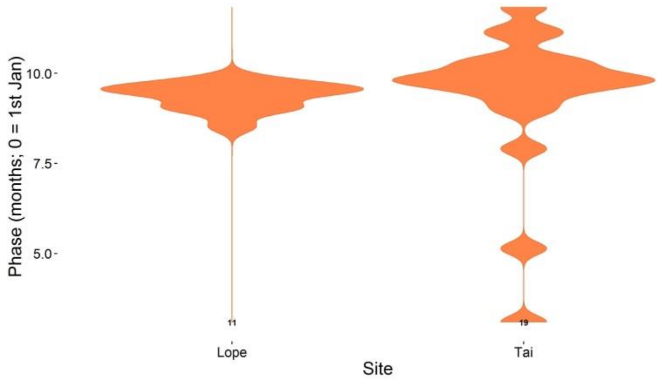
Appendix 2M. Species showing similar seasonal phases of fruiting across various sites.



Irvingia grandifolia

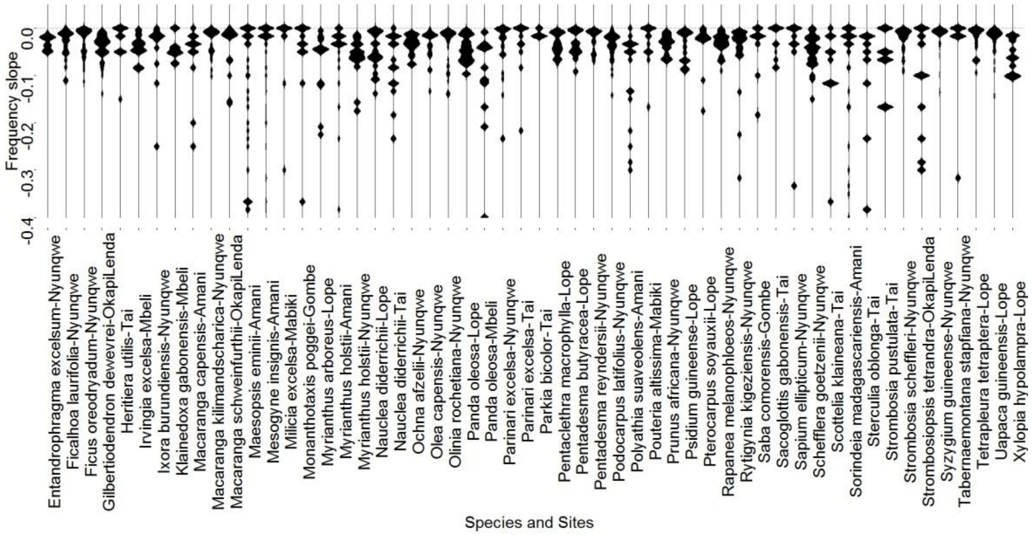


Parkia bicolor

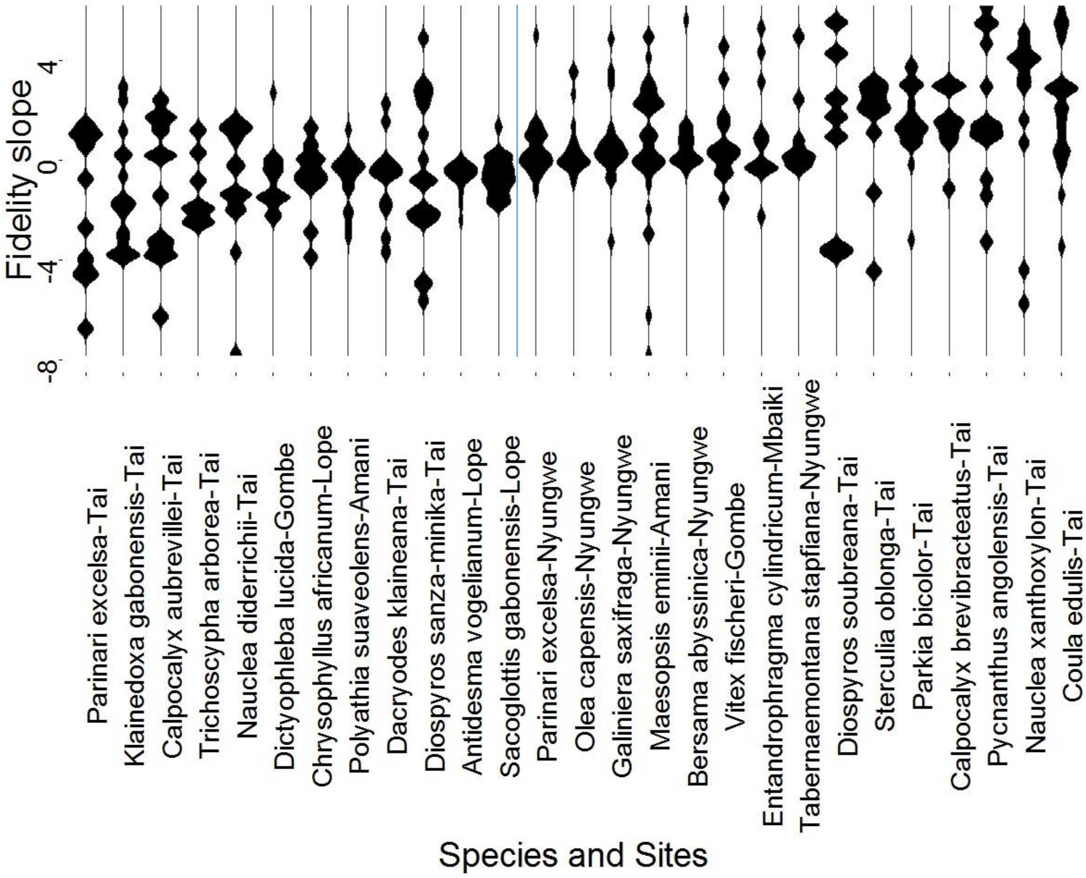


Pentadesma butyracea

Appendix 2N. Change in frequency of fruiting events over time for 54 statistically significant species.



Appendix 2O. Change in fidelity for a particular fruiting frequency over time for 27 statistically significant species.



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Chapter 3

Inconsistent responses of African tropical trees to climatic variation

Abstract

Climate change is advancing at an unprecedented rate affecting many natural systems. These changes are occurring at a global scale, but vary regionally, leading to phenological mismatches between species and plant communities. Changes in plant phenology have been widely studied in temperate regions. However, little is known about potential shifts in tropical phenology, where rainfall is not usually limiting. Current knowledge derives mostly from Asia and South American studies, where annual changes in phenological events have been related to variation in temperature and rainfall associated with large scale climatic phenomena. El Niño–Southern Oscillation (ENSO), Indian Ocean Dipole (IOD) and the North Atlantic Oscillation (NAO) all affect the climate of Africa. Their effects over vegetation phenology have been studied separately, but never in the context of tropical forests in Africa. In this study, we analysed the correlation between flowering (of 658 species) and fruiting patterns (of 595 species) from 16 forest sites across Africa and three climatic phenomena, including El Niño–Southern Oscillation, Indian Ocean Dipole and North Atlantic Oscillation. We also calculated frequency of flowering and fruiting events at the level of site and continent. Across Africa we found that most species showed annual flowering and fruiting frequencies. The same pattern was found at several sites, while at others frequency varied from sub-annual to supra-annual. We found that only 26% and 29% of species showed significant correlations between flowering and fruiting phenology and one or more climatic phenomena. For species that did show a correlation with climate phenomena, we found that, flowering and fruiting events were more often influenced by more than one phenomenon, showing no clear pattern in the direction of change with respect to increased rainfall or drought conditions. This research shows the diversity of responses at the individual level, and the robustness of African tropical forests.

Introduction

The climate has been changing at an unprecedented rate over the last century (IPCC). Climate change impacts have been noted in range shifts globally, the timing of frog breeding, the arrival of migratory bird populations and flowering / fruiting events (Parmesan & Yohe, 2003; Walther et al., 2002). Plant phenology has received intensive attention, as plants synchronise their biological events, such as flowering and fruiting with climate (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007). In the tropics, as in temperate regions, many animal species are directly or indirectly dependent on the availability of resources associated with key phenological events, such as flowering and fruiting that play a major role in the survival and reproduction of insects and animals (Kissling, Sekercioglu, & Jetz, 2012). Importantly, if changes in phenology occur at different rates for different species, it can lead to phenological mismatches between species and plant communities (Brown et al., 2016). Consequently, it is clear that the temporal match between phenological events of plants and animals is crucial for the ecosystem to function (Cleland et al., 2007). Understanding how plant phenology will respond to climate driven changes is therefore essential in order to predict and mitigate future changes in the structure of plant community, animal abundance and ecosystem processes.

Changes in plant phenology have been mostly studied in temperate regions, where most long-term data sets are available (Mark, 2013; Parmesan, 2006; Parmesan & Yohe, 2003). However, little is known about potential shifts in tropical phenology, where temperature is usually not a limiting factor and phenological events could happen at any time of the year (S. Sakai, 2001). Phenology has been challenging to address because tropical forest ecosystems are highly complex and long-term data sets are rare (Hudson & Keatley, 2009). Current knowledge about tropical phenology mainly originates from Asian and South American studies, where phenology has been related to rainfall or a sudden drop in minimum temperature and described in terms of timing, duration and frequency (Mark, 2013). However, African tropical forests phenology has received little attention. African tropical forests are the second largest in the world, host rich biodiversity and play a crucial role in the global carbon cycle (Anderson-Teixeira et al., 2015). It is important to understand African phenology at the continental level in order to complete the global phenology puzzle.

In contrast to the temperate regions, where trees flower regularly once a year, tropical flowering and fruiting events often vary from annual, sub-annual, supra-annual to irregular (Butt et al., 2015; Shoko Sakai et al., 1999). Trees from the Neotropics and Dipterocarp forests of south-east Asia predominantly show supra-annual frequencies (S. Sakai, 2001). In tropical forests of Central America, supra-annual flowering / fruiting frequencies were more often found, however varieties of sub-annual and annual frequencies were also seen (Mark, 2013). Similarly, flowering and fruiting frequencies also vary in the African tropical forests (C. A. Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Janmaat et al., 2016). In South-East Asia and South America phenological events are seen at different times of the year and triggered by different cues, such as a sudden drop in solar radiation, plant moisture availability, heavy rain or increased temperatures (Butt et al., 2015; Corlett & Lafrankie, 1998; Shoko Sakai et al., 1999). At four sites in Africa, trees were reported to flower at the beginning of the dry season and fruit more often during the wet season (Anderson, Nordhelm, Moermond, Gone Bi, & Boesch, 2005; C. A. Chapman et al., 1999; Sun et al., 1996). Seasonality in the tropics is dominated by the intertropical convergence zone (ITCZ), a band of warm air that carries precipitation north and south over the equator (Osborne, 2000). Changes in rainfall distribution can be triggered by extreme weather events, such as intense precipitations and severe droughts (Butt et al., 2015). Both temperature and rainfall are affected by large climatic phenomena, which are a proxy for understanding the impacts of climate change on natural systems (Butt et al., 2015; Cleland et al., 2007). Climatic phenomena are projected to increase in intensity and frequency and hence affect flowering and fruiting events in various different ways (Morellato et al., 2016). African tropical forests are predicted to be mostly affected by changes in the distribution of precipitation rather than temperature (Cleland et al., 2007; Gunarathne & Perera, 2014; O’Gorman, 2012). Well-known climatic phenomena generating inter-annual variability in climate over Africa are El Niño–Southern Oscillation (ENSO), Indian Ocean Dipole (IOD) and North Atlantic Oscillation (NAO) (Brown, de Beurs, & Vrieling, 2010; Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Williams & Hanan, 2011). Depending on their phase and season, climate phenomena bring different weather conditions. Full descriptions of the causes and impacts of each climate phenomenon area are available from (Jones, Jonsson, & Wheeler, 1997; Latif et al., 1998; Marchant, Mumbi, Behera, & Yamagata, 2007). Here we restrict ourselves to a brief overview of each and its impact on rainfall and temperature across Africa.

ENSO is characterised by 3-5 years oscillations of warm (El Niño) and cold (La Niña) phases of the sea surface temperatures in the Pacific (Malhi & Wright, 2004). It is a well-known driver of inter-annual variability, affecting several areas around the world in various different ways (Holmgren et al., 2001). In Africa, El Niño brings increased precipitation in the East and drier conditions in the West and Southern Africa (Holmgren et al., 2001). Studies showed that during the period 1982-2006, woodland, wooded grassland and closed shrubland in Africa showed high vulnerability to El-Niño events (Propastin, Fotso, & Kappas, 2010).The frequency of ENSO events has increased since 1976 and is projected to keep rising in response to climate change (IPCC, 2014). IOD is perhaps less well known and describes the differences in sea surface temperatures (SST) between eastern and western parts of the Indian Ocean (Williams & Hanan, 2011). A positive phase (high SST in the western Indian Ocean) brings severe rainfall in eastern Africa, while the negative phase restricts the precipitation events in the same region (Saji, Goswami, Vinayachandran, & Yamagata, 1999). ENSO and IOD share similar regions of impact in Africa (Williams & Hanan, 2011). Through its impact on precipitation, IOD correlates with NDVI, a remote sensing technique that identifies vegetation change across Congo Basin, Tanzania, parts of the Kalahari and Miombo sites, as well as fragments of coastal West Africa (Williams & Hanan, 2011). The NAO describes the differences between atmospheric pressure over Iceland and the Azores (Brown et al., 2010). During winter, when pressure differences are above normal (positive NAO), temperatures decrease in North Africa, while the opposite is seen when values are below normal (MetOffice, 2016). During summer, positive NAO is associated with warmer temperatures in the West and decreased precipitation in the Sahel region, while negative phases result in cooler temperatures in West Africa (MetOffice, 2016). NAO as well as ENSO correlate with changes in agriculture in South, East and West Africa (Brown et al., 2010).

Several studies have considered looking at the effects of large climatic phenomena and vegetation. ENSO events are well known for triggering mass flowering and fruiting in aseasonal tropical forests in Asia (Corlett, 2009). In tropical semi-deciduous forest in Asia, heavy rain associated with ENSO events ceased flowering and fruiting events (Gunarathne & Perera, 2014). Earlier tree reproduction was reported in tropical forests in both Borneo and Panama during El Niño events (S. Wright & Calderón, 2006), but also by cyclones in Australia (Butt et al., 2015). In North America, angiosperms overall advanced flowering by 3-6 days following a winter with a positive NAO (Szabó, Vincze, & Czúcz, 2016), but at a finer scale in Austria and the Czech Republic just under half of studied species actually showed a significant response (Hubálek, 2016). However, no studies have considered correlations between the three climatic phenomena and flowering and fruiting events of tropical trees across Africa. Although there are examples of all three phenomena correlating with various biological processes across Africa, the overall impacts are not well established for the majority of the African tropical forests but are suspected to be widespread and important (Butt et al., 2015).

Understanding the direction of flowering and fruiting production is crucial in predicting dynamics of rainforest ecosystems in response to environmental changes. In this study we investigate the two hypotheses. The first hypothesis we investigate states that at the continent and site level, annual flowering and fruiting frequencies dominates. The second hypothesis states that flowering and fruiting events of tropical trees species in Africa correlate with one or more of the three climatic phenomena: ENSO, IOD and NAO. To complement this relationship, we also correlated local rainfall at each site with each of the three climatic phenomena indexes, in order to determine which conditions species use to flower / fruit in response to extreme weather events. We assume that sites with strong correlation coefficients between rainfall and climatic phenomenon will also have the highest proportion of tree species responding to that particular phenomenon. We are also interested to investigate which weather conditions will increase / abort flowering and fruiting events, in order to document the direction of species phenology in response to future climate change. We also explore the seasonal phase of flowering and fruiting events. Based on previous work (Anderson et al., 2005; C. A. Chapman et al., 1999), we expect most trees to flower during the dry season, but fruit during the wet season (Anderson et al., 2005; C. A. Chapman et al., 1999).

Methods

Study sites and phenological data collection

We collated data from 17 long-term research sites across East, Central and West Africa (Fig. 1). Sites comprised a great diversity of forests such as montane, sub-montane, semi-deciduous, evergreen and swamps, which stretch from 80 to 3000 m altitude and cover between 200 km^2 and 5000 km^2, respectively (key data summarised in Table 11). There are two distinct seasons, dry and wet, encountered once or twice a year, distinctive to the geographical position of each site. Average mean temperature ranges are between 15 and 31 °C, with annual rainfall between 1000 and 2000 mm. All sites are located within national parks / protected reserves, recognised to protect and host endemic and endangered species. Field assistants recorded monthly presence of flowering and fruiting patterns by examining the crown of over 17, 000 trees of more than 600 species, using binoculars. Depending on the site, data were collected between 6 and 28 years.

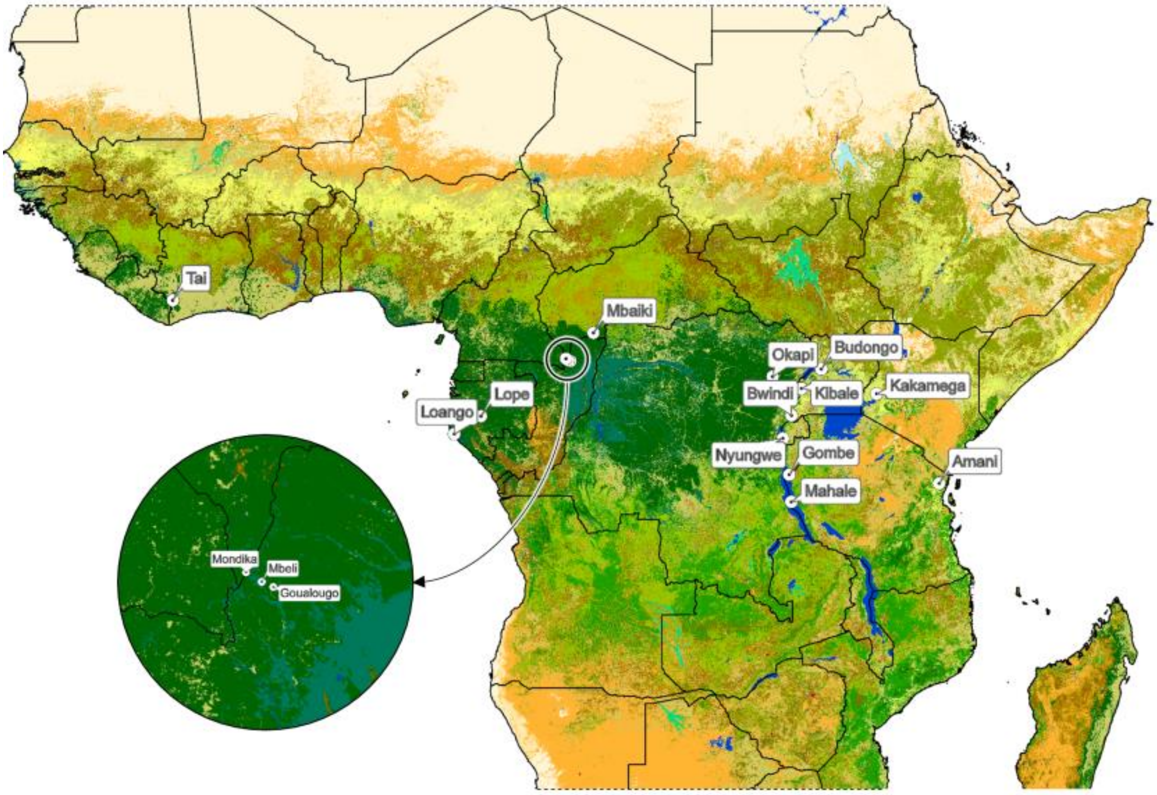

Figure 11. Geographical position of the 16 studied sites. Land cover data, downloaded from ESA at 5° x 5° resolution (Arino, Ramos, Kalogirou, Defourny, & Achard, 2009)

Table 5. Study sites (16), coordinates, country of origin and monitoring period for flowering and fruiting phenology arranged West to East.

Stars indicate p value of Pearson's correlation: *** (p< 0.001), ** (p< 0.01), * (p< 0.05). Latitude and longitude are expressed in decimal degrees.

Site information								Pearson correlation		
No.	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	ENSO – rainfall	NAO – rainfall	IOD – rainfall
1	Taï National Park	Côte d'Ivoire	5.846389	-7.31222	15 1997 - 2011	Diverse moist evergreen and semi-evergreen forest	80	-0.42**	-0.51 ***	-0.004
2	Loango National Park	Gabon	-2.17	9.67	7 2006-2012	Tropical forest	50	-0.39*	0.03	0.29
3	Lopé National Park	Gabon	-1.097	11.165	29 1986 - 2014	Semi-evergreen, tropical lowland rainforest	300	-0.23	0.09	0.17
4	Mondika Forest	Republic of Congo	2.35	16.257	7 1996-2002	Semi-deciduous rain forest	300	-0.13	0.12	-0.06
5	Mbeli Bai Forest	Republic of Congo	2.258611	16.41222	12 2004 - 2015	Semi-deciduous rain forest	300	-0.15	0.04	-0.18
6	Goualougo Triangle, part of Nouabale Ndoki National Parks	Republic of Congo	2.211617	16.51875	11 2002 – 2012	Semi-deciduous rain forest	300	-0.25	0.12	-0.19

Table 5 continued

Site information								Pearson correlation		
No.	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	ENSO – rainfall	NAO – rainfall	IOD – rainfall
7	Mbaiki forest	Democratic Republic of the Congo	3.9	17.9	21 1991 - 2011	Humid - tropical forest	560	-0.18	-0.03	0.07
8	Mahale Mountains National Park	Tanzania	-6.24	29.757	5 2007-2011	Mosaic of vegetation: decidous woodland, semi-deciduous forests	900	0.01	0.05	0.12
9	Gombe Stream National Park	Tanzania	-4.611	29.638	13 1997 - 2009	Tropical forests	1000	0.23	0.21	0.33
10	Nyungwe Forest National Park	Rwanda	-2.431	29.263	13 1996 - 2008	Tropical forest	2260	0.44**	0.12	0.05
11	Bwindi Impenetrable National Park	Uganda	-1.04611	29.77222	9 2008 - 2012	Montane forests	2240	0.10	-0.26	0.33
12	Okapi Wildlife Reserve Lenda & Edoro sites	Democratic Republic of the Congo	1.267	28.641	20 1993 - 2012	Humid mixed evergreen forest	750	-0.25	-0.28	-0.17
13	Kibale Forest National Park	Uganda	0.559726	30.35798	11 2005 - 2015	Subtropical moist forest	1500	-0.34	0.05	-0.10
14	Budongo Forest Reserve	Uganda	1.72	31.556000	21 1993-2013	Moist, semi-deciduous tropical rain forest	1050	0.14	0.15	-0.11

Table 5 continued

Site information								Pearson correlation		
No.	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	ENSO – rainfall	NAO – rainfall	IOD – rainfall
15	Kakamega Forest Reserve	Kenya	0.24	34.865000	11 2005-2015	Tropical forest	1580	-0.36*	-0.30	0.31
16	Amani Nature Reserve	Tanzania	-5.13	38.615	7 2006 - 2012	Moist submontane forest	950	0.52*	0.36*	0.39*

Source: Source: **Amani Nature Reserve**, Tanzania – Henry Ndangalasi and Norbert Cordeiro; **Gombe Stream National Park** , Tanzania – Ian Gilby and Anne Pusey; **Nyungwe National Park**, Rwanda – Felix Mulindahabi; **Bwindi Impenetrable National Park**, Uganda – Badru Mugerwa, Frederick Ssali, Dougla Sheil and Martha Robbins**; Kibale National Park**, Uganda – Colin Chapman, **Okapi Wildlife Reserve**; Democratic Republic of Congo – Flory Bujo, Corneille Ewango and Terese Hart; **Lope Reserve**, Gabon – Kate Abernethy and Kath Jeffrey, **Mbeli Bai**; Nouabale Ndoki Park, Congo Republic – Mireille Hockemba and Thomas Breuer; **Mbaiki**, Central African Republic – Adeline Fayolle, **Tai National Park**; Ivory Coast – Christophe Boesch, Leo Polansky; **Goualuogo**, Nouabale Ndoki Park, Congo Republic – Sydney Ndolo, Dave Morgan, and Crickette Sanz; **Kakamega Forest**, Kenya – Marina Cords; **Mahale Mountains National Park**, Tanzania – Nori Itoh and Kazuhiko Hosaka; **Budongo Forest Reserve**, Uganda – Fred Babweteera and Andrew Plumptre; **Loango National Park**, Gabon – Martha Robbins and Leo Polansky; **Mondika**, Central African Republic – Dian Doran and Natasha Shah.

Climatic data

We collated values of the three climate phenomena impacting African climate from standard sources (ENSO (http://www.esrl.noaa.gov/psd/enso/mei/table.html), IOD (https://crudata.uea.ac.uk/~timo/datapages/naoi.htm) and NAO (https://crudata.uea.ac.uk/cru/data/nao/nao.dat)) between January 1986 and September 2015.

We collected rainfall data from the Chirps dataset that combined ground-based monitoring with satellite derived rainfall data (http://chg.geog.ucsb.edu/data/chirps/) (Funk et al., 2015), starting in 1986 and finishing in 2014, dates consistent with our phenology dataset.

Data analysis

In order to determine the correlations between climatic phenomena and flowering / fruiting events, we focused on the presence / absence of the flowering and fruiting for each individual tree. We assessed canopy level flowering and fruiting status, by calculating the proportion of trees flowering (3480 trees, 658 species) and fruiting (3480 trees, 595 species) for each species within each month and year. We excluded from the analysis all trees that died during the study time as well as those which were recorded for fewer than five years. We used generalised linear models (GLM) to explore the associations between flowering / fruiting events of each species and the three climatic phenomena. We fitted a GLM model with a binomial family, using the logit link function model for each species at each site separately. The dependent variable was the proportion of trees that flowered / fruit in a given month and year. The independent variables used for each species' model were the monthly averages of (1) ENSO, (2) IOD, (3) NAO and (4) a factor indicating the month. It was important to include month to build informative models and account for seasonal variation, which greatly differ between sites. For species that were present at multiple sites, we considered the interaction between each site and the four independent variables mentioned above. We reduced each species model to the minimum adequate model using a backwards selection of non-significant variables. We also calculated which sites were affected or not by chance by each of the three climatic phenomena. To determine this, we used XNomial package in R and looked at the likelihood ratio test p value, which indicates if more species than expected responded to two or more climatic phenomena. The test assessed if the expected number of species responded to two or more climatic phenomena, given the overall probabilities of response to any tested variable. In order to understand the impact of each climate phenomena on the African climate, we first calculated the local correlation between every index and rainfall data, using Pearson’s correlation. We correlated the mean monthly value by averaging data for each month with the corresponding monthly value of each index over a period of 28 years for all sites. Even though our index data was not normally distributed, we used Pearson’s in order to include extreme events in our correlation. Extreme events are important because they are the main drivers of regional climate and would have been missed with a rank correlation such as Spearman’s. Hence, we identified the type of climatic conditions (increased rainfall or draught) at each site associated with each climatic phenomenon. Based on the correlation coefficient, we then interpreted the direction of flowering/ fruiting events with the expected increase versus decrease in rainfall from the correlation test. For example, ENSO has different correlations with local rainfall (from positive to negative).

We also assessed the flowering and fruiting timing at each site by calculating the mean monthly value by averaging data for each month over a period of 28 years for all sites, starting in 1986 and finishing in 2014, dates consistent with our phenology dataset. We defined the dry season as any months where rainfall was less than 100 mm.

Individual tree analysis

We analysed flowering and fruiting patterns at the site and community level using Fourier analysis on individual tree species (see chapter 2 for a full description of our methodology). Among the 16 sites, only 11 sites contained trees meeting all the data quality criteria. Hence, we finally analysed 5446 (196 species) and 4596 (190 species) individual trees for the flowering and fruiting events, respectively. Full details on the considered species are found in Appendix 2A and 2B.

Results

Community and site level analysis of flowering frequency

Across 11 sites and 196 species, 42% of trees showed annual flowering frequencies, followed by 27% sub-annual cycles (typically 6 months (10%)). Supra-annual cycles were seen in 22% of the species, with 24 month frequency being the most common (17% species). The remaining 9% of species did not show any dominant flowering frequency. At the site level, most species flowered annually, a trend that is very well conserved in the West Africa (Fig. 12). In the East and Central Africa, species vary in terms of flowering frequency, with trees at some sites recording wide varieties of frequencies (Fig. 12).

Due to considerable variation between individual species, overall flowering patterns show relatively little seasonal pattern despite considerable differences in seasonality of rainfall between sites (Fig. 13). We found that most Eastern African sites (Nyungwe, Bwindi, Amani, Kakamega and Kibale) had the least seasonal flowering patterns. Regardless of the climatic conditions, at these sites the proportion of trees in flower was approximately the same in each month (Fig 13). We saw that most sites display a seasonal rainfall patterns. Among these, we saw seasonal flowering patterns only at Gombe and Lope sites, with trees flowering during the wet season.

Canopy level analysis - Flowering

At a P-value threshold of 0.05, we found that flowering events of 169 (26%) species out of 659, were significantly correlated with at least one climatic phenomenon. At each site, the highest proportion of species had their flowering patterns affected by two climatic phenomena, followed by one and all three, respectively (Fig. 14). Among all three phenomena, IOD triggered a stronger flowering response (increase or decrease flowering) than ENSO and NAO (Fig. 14).

At the site level, the number of species correlated with each phenomenon differed considerably. ENSO was correlated with flowering for most species at Gombe, Budongo and Lope sites with fewer species affected at Okapi Lenda and Edoro, Mondika, Mbaiki and Amani (Fig. 15). IOD and ENSO correlated with flowering events of species at all sites, with the highest proportion being present in the East Africa at Kibale, Bwindi and Nyungwe sites. Overall, we found that at five sites more species than expected by chance responded to more than one phenomenon and are indicated with a star in Figure 15. Multivariate analysis results for significant and non-significant sites, showing the log-likelihood ratio p value for each site can be found in Appendix 3A.

Model predictions of the flowering slope direction differed from one phenomenon to the other and between sites. At nine sites, more than 50% of species flowered in response to drought conditions triggered by ENSO (Fig. 16). On the other hand, at five sites, most species were triggered by an increase in rainfall. More than 70% of species found at four Eastern sites (Budongo, Gombe, Kakamega and Amani) flowered in response to drought conditions triggered by IOD. At the rest of the sites, a similar percentage of species responded to either drought or increased rainfall conditions initiated by IOD. More species were triggered by an expected increase in rainfall associated with NAO at most sites in Africa (Fig. 16). Exceptions are Mondika, Gombe, Kakamega and Bwindi sites, where species responded more to drought conditions. For species present at Tai, Lope and Okapi Lenda an equal number of species increased / decreased their flowering in response to expected increases in rainfall associated with NAO (Fig. 16).

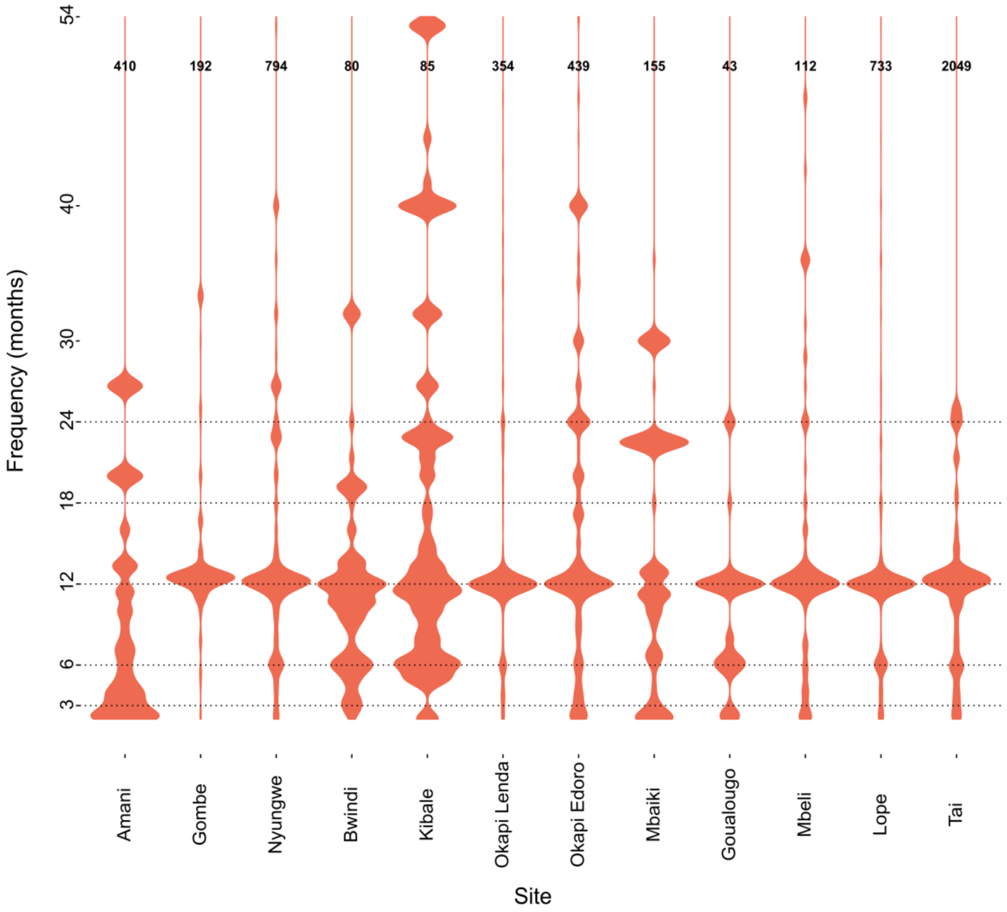

Figure 12. Violin plot showing the density of flowering frequency of all individual trees present at 12 sites. Numbers attached at the high end of the violin plot represent the total number of individual trees considered at each site.

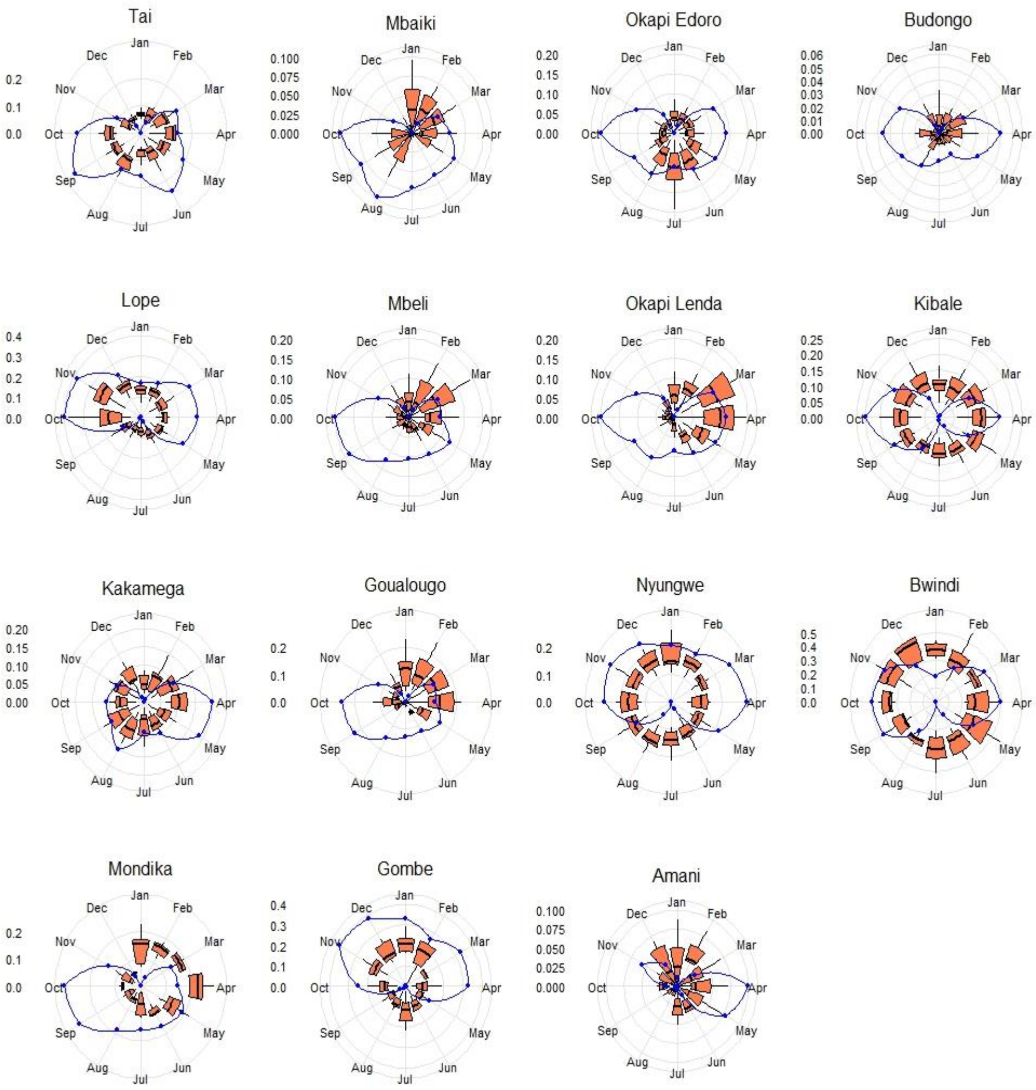

Figure 13. Proportion of individual trees (red boxes) flowering in each month at 15 different sites. Blue graph represents the rainfall for each month normalised to the rainfall of the wettest month. Sites names are represented above.

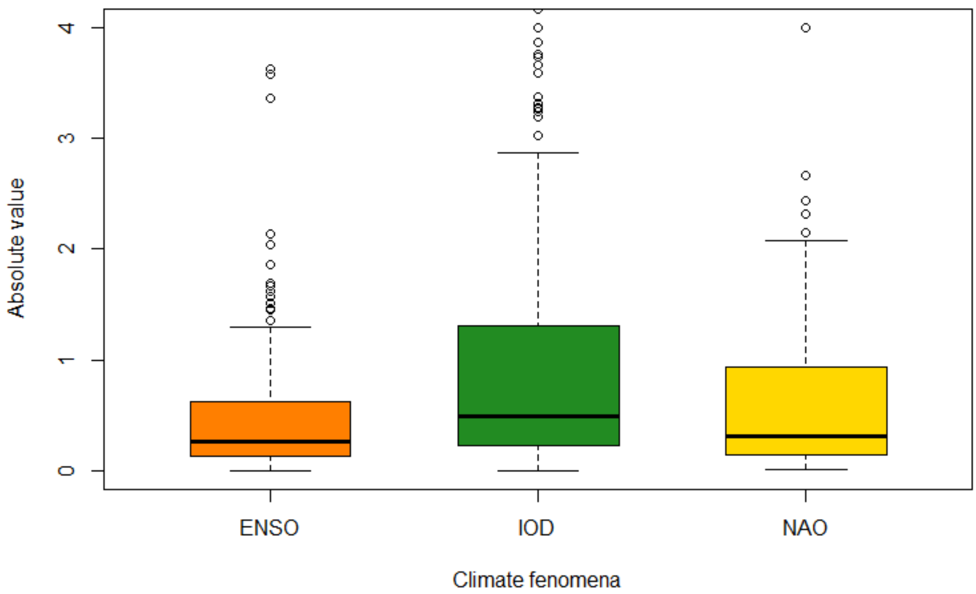

Figure 14. Intensity of ENSO, IOD and NAO on flowering events. Absolute value represents the slope estimate of each species extracted from the GLM model.

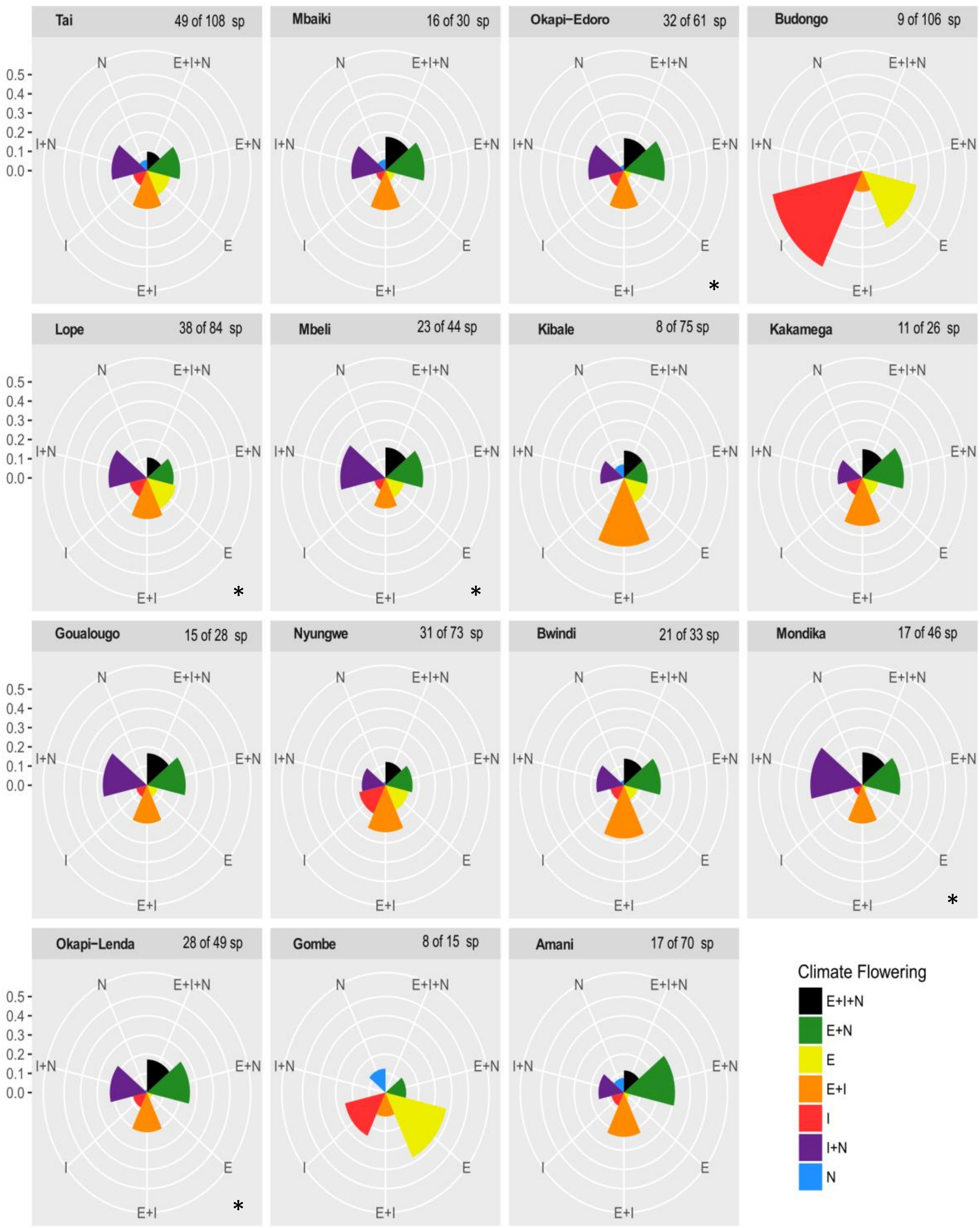

Figure 15. Percentage of species that correlate their flowering patterns with one or more climatic phenomenon at 15 sites. Site names are displayed at the top left of each graph. Stars next to the right, lower corner indicate places where more species were affected by more than one phenomenon than expected by chance ($p < 0.05$). Number of species responding to one or more phenomena and the total number of species present at each site are found at the top right of each graph. Significant species are established via a 0.05 P-value significance threshold. ENSO (indicated by E, in yellow), IOD (indicated by I, in red), NAO (indicated by N, in blue). Circular plot label is displayed on the left side of the group plot.

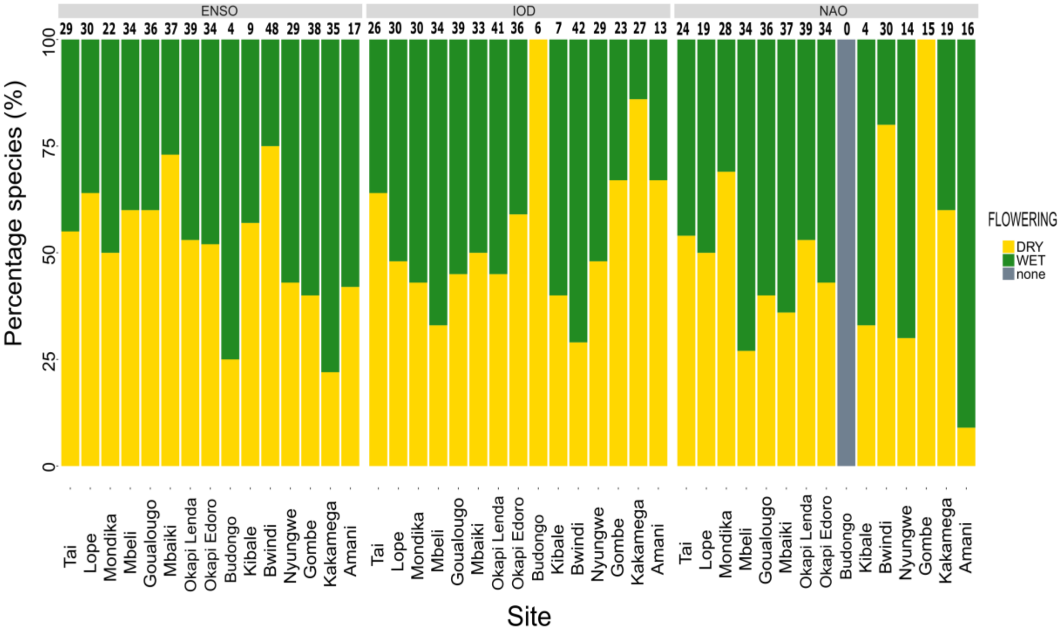

Figure 16. Species' flowering response in relation to increased rainfall or drought conditions brought by the three climatic phenomena. Conditions were established with the aid of the correlations between rainfall and one of the three climatic phenomena. Significant species are established via a 0.05 P-value significance threshold.

Community and site level analysis of fruiting frequency

Across 11 sites and 191 species, 36% showed annual cycles. In contrast to the flowering analysis, supra-annual cycles were nearly as common as annual cycles (31%), with the most frequent frequency again being 24 months (27% species). Sub-annual cycles were encountered only in 20% of species with the dominant one being 6 months (6%). The remaining 12% of species showed no dominant frequency. At the site level, fruiting frequency showed different patterns according to each site. At most sites, we found more than one principal fruiting frequency. We only found one dominant annual pattern at Gombe, Lope and Tai (Fig. 17).

Due to substantial variation between individual species, overall fruiting patterns show relatively little seasonal pattern despite visible differences in seasonality of rainfall between sites (Fig. 18). We found that Lope, Mbeli, Kakamega, Goualougo, Bwindi had the least seasonal flowering patterns. Regardless of the climatic conditions, at these sites the proportion of trees fruiting was similar each month. We saw the most seasonal rainfall patterns at Amani, Bwindi, Gombe, Kibale, Mbaiki, Mahale Loango and Lope sites. Among these, Amani, Gombe, and Mahale sites also had seasonal flowering patterns. We only found trees at Amani fruiting during the dry season and at Gombe and Mahale during the wet season. Overall, at most sites, we found higher proportion of trees fruiting during the wet season (Fig. 18). We found more species to be affected by more than one phenomena than expected by change at six sites.

Canopy level analysis - Fruiting

We found 171 species (29%) out of 595, showing significant correlations with one or more climatic phenomena at a P-value threshold of 0.05. At each site, we found again that the highest proportion of species had their fruiting correlated with two climatic phenomena, followed by one and all three, respectively (Fig. 20). Among all three phenomena, IOD triggered the strongest fruiting response (increase or decrease) than ENSO and NAO (Fig. 19).

At the site level, the number of species correlated with each phenomenon differed significantly. The most visible pattern we found was that ENSO and IOD correlate with fruiting in a high proportion of species at all sites (Fig. 20). We found that NAO alone was the least correlated with fruiting across all sites (Fig. 20). Overall, we found that at six sites more species than expected by chance responded to more than one phenomenon and are indicated with a star in Fig. 20. Multivariate analysis results for significant and non-significant sites, showing the log-likelihood ratio p value for each site can be found in Appendix 3B.

Fruiting slope direction differed from one phenomenon to the other and across sites. At ten sites, more than 50% of species flowered in response to increased rainfall conditions triggered by ENSO. At Gombe site, all species flowered during increased rainfall triggered by ENSO. At Mondika, Mahale and Kibale sites more than 60% of species fruit in response to draught conditions (Fig. 21). At four sites (Lope, Budongo, Nyungwe, Kakamega) fruiting occurred under drought conditions triggered by IOD. On the other hand, at Mondika and Mbeli sites, species fruit in response to drought conditions. More than 50% of fruiting was triggered by an expected increase in rainfall associated with NAO at 11 sites in Africa. Only at Mbeli, Okapi, Bwindi and Kakamega species fruit in response to drought conditions (Fig. 21).

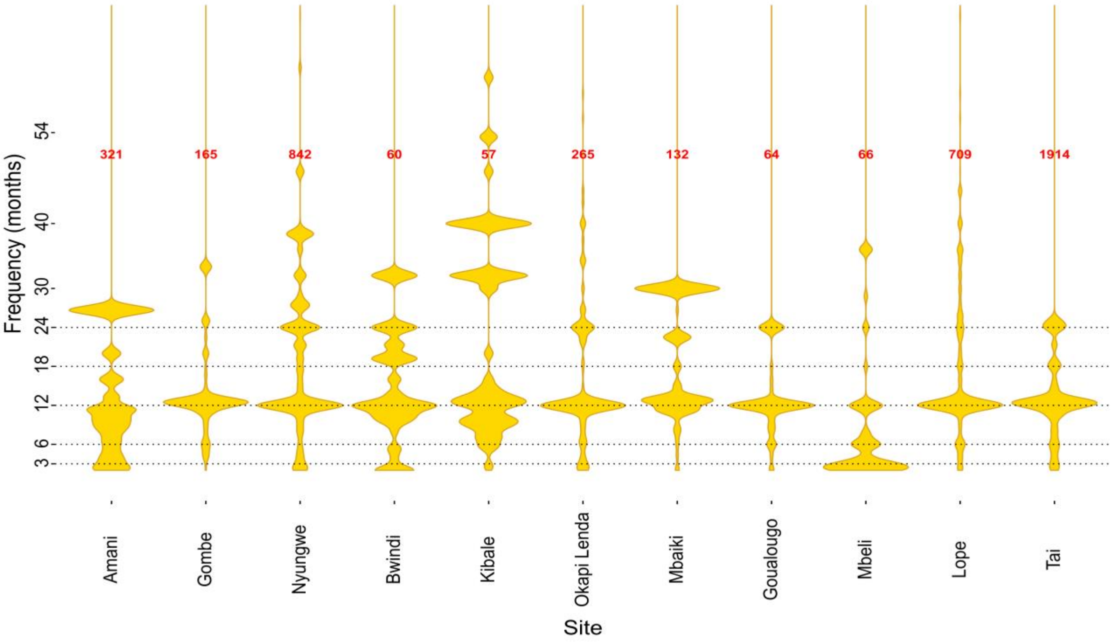

Figure 17. Violin plot showing the density of fruiting frequency of all individual trees present at each site. Numbers in red found on the violin plot represent the total number of individual trees considered in each site.

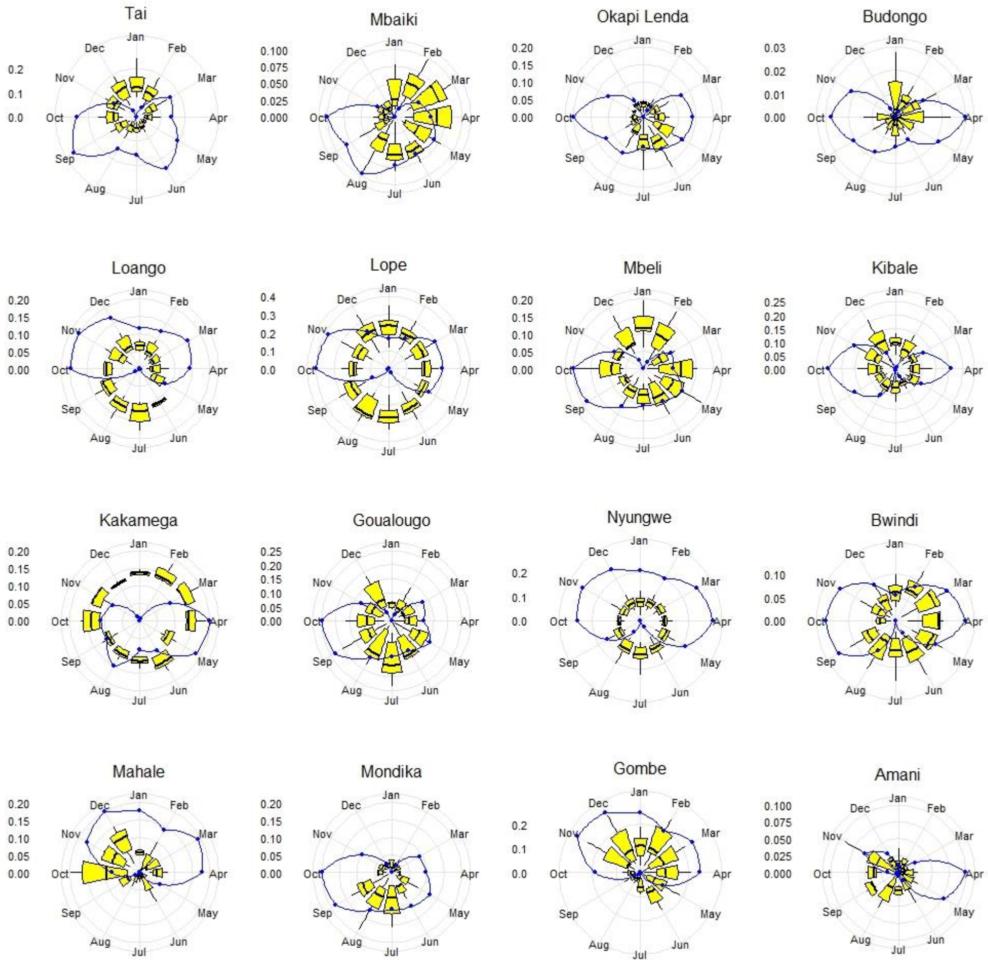

Figure 18. Proportion of individual trees fruiting (yellow boxes) in each month in 16 different sites. Blue graph represents the rainfall for each month normalised to the rainfall of the wettest month. Sites names are represented above each circular plot.

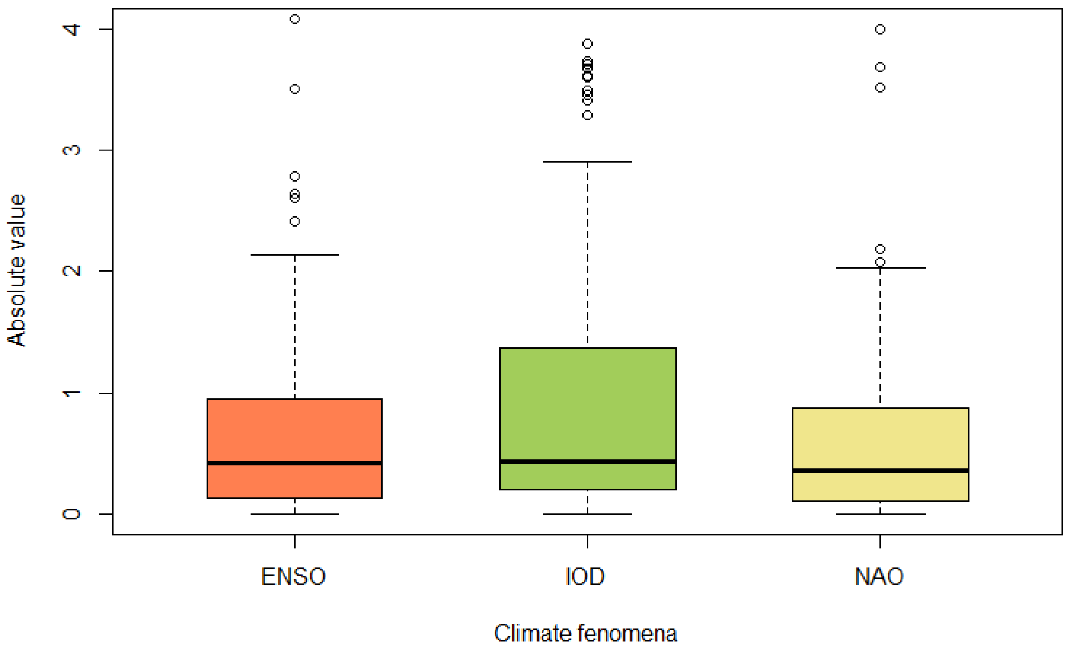

Figure 19. Intensity of ENSO, IOD and NAO on fruiting events. Absolute value represents the slope estimate of each species extracted from the GLM model.

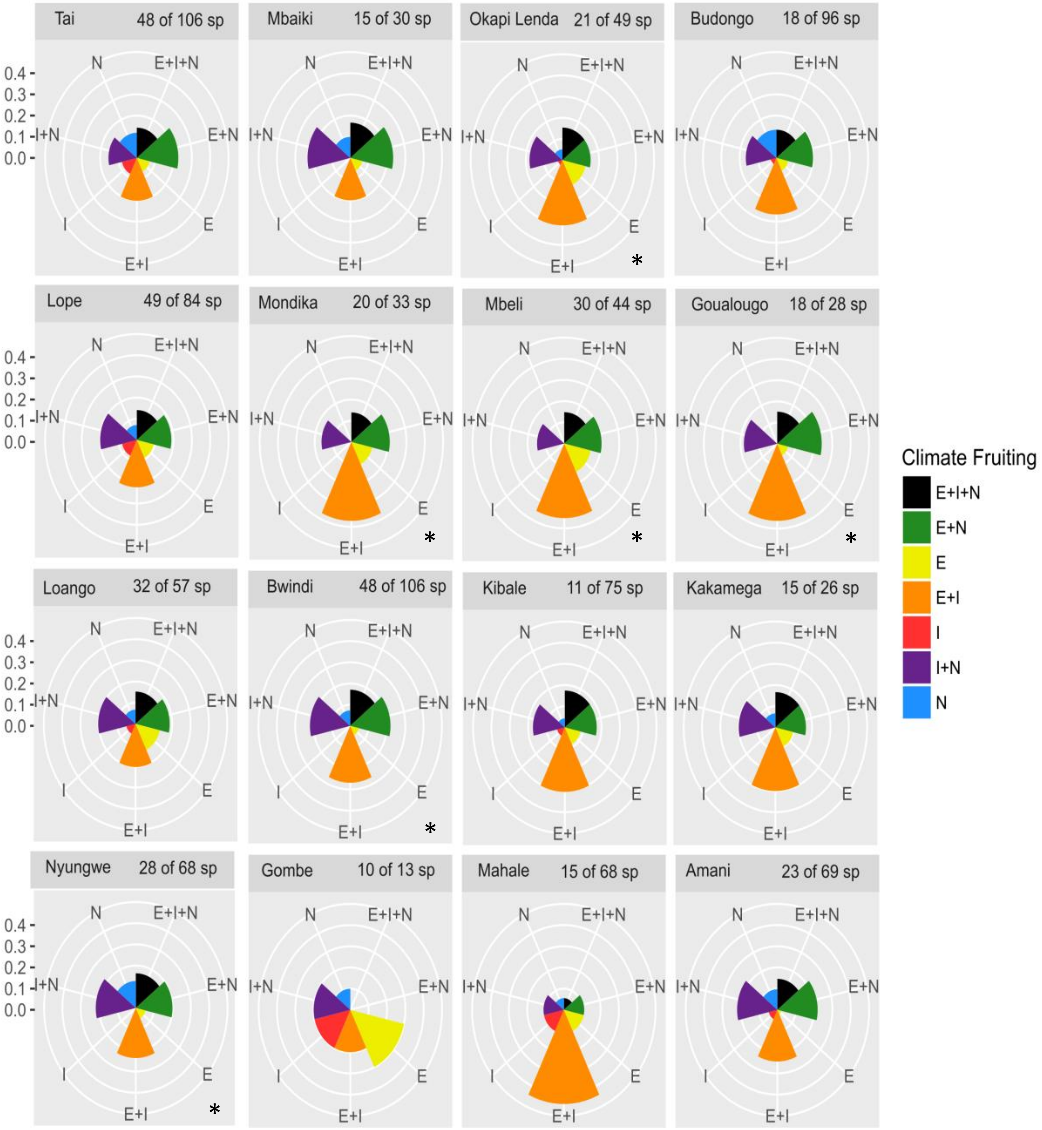

Figure 20. Percentage of species that correlate their fruiting patterns with one or more climatic phenomenon for 16 sites. Site names are displayed at the top left of each graph. Stars in the right, lower corner indicate places where more species were affected by more than one phenomenon than expected by chance ($p < 0.05$). Number of species responding to one or more phenomena and the total number of species present at each site are found at the top right of each graph. Significant species are established via a 0.05 P-value significance threshold. Climatic phenomena are indicated by different colours; ENSO (indicated by E, in yellow), IOD (indicated by I, in red), NAO (indicated by N, in blue). Circular plot label is displayed on the left side of the group plot. Sites are organised from West (left) to East (right).

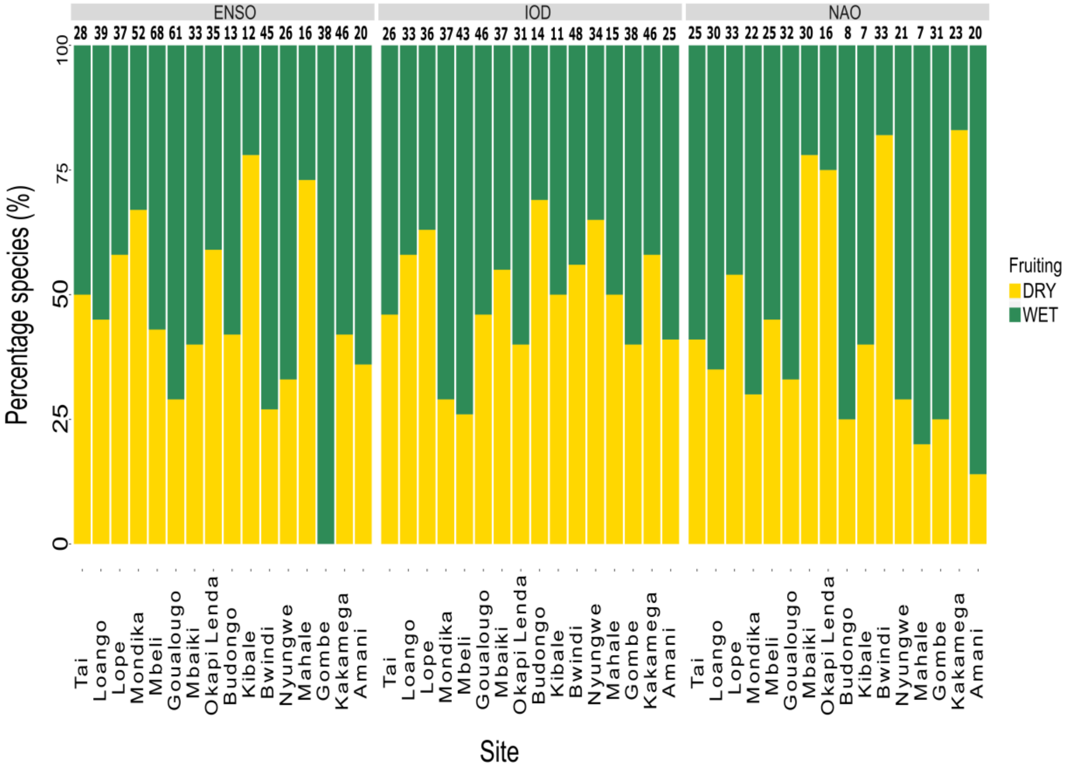

Figure 21. Species' fruiting response in relation to increased rainfall or drought conditions brought by the three climatic phenomena. Conditions were established with the aid of the correlations between rainfall and one of the three climatic phenomena. Significant species are established via a 0.05 P-value significance threshold.

Discussion

Using Fourier based analysis, we effectively estimated flowering patterns for 5446 individual trees, of 196 species and fruiting patterns for 4595 trees of 191 species across 12 and 11 sites, respectively at the site and community level. Moreover, we showed the correlation between climatic phenomena and flowering / fruiting events at 16 sites across Africa and the wide variety of responses showing by trees in response to large-scale climatic phenomena. As expected, we found that across all sites, most species flowered and fruit annually, with a significant minority of species showing sub-annual flowering cycles and supra-annual fruiting patterns. It is worth mentioning that there is a trade-off between flowering and fruiting events, hence fruiting may not necessarily follow flowering. Fruiting takes place only if there are enough resources left after flowering and climatic conditions are favourable (Primack, 1987). As expected, we also found that within most sites, species flowered and fruit annually. However, despite this overall pattern, at some sites there was no clear pattern of a dominant annual flowering / fruiting frequency. Despite individual tree species showing strong seasonality, fruiting and flowering occurred all year round, so that some species flower / fruit during dry or wet season at all sites. We mostly detected heterogeneous flowering and fruiting patterns, with more than three quarters of species being influenced by two or more climatic phenomena at each site. We found remarkable variation from site to site and from species to species in the expected impacts of climatic phenomena on the proportion of trees flowering and fruiting, highlighting the diversity of African tropical forests.

Community and site level flowering and fruiting patterns

In partial agreement with earlier work (Anderson et al., 2005; Chapman et al., 1999; Polansky & Boesch, 2013) we found good evidence that annual flowering and fruiting cycles are the most common among African tropical forest species. Hence, we found that 42% of species showed annual flowering frequencies across 12 sites. Our results are in contrast to the results reported from Central and South America as well as South East Asia tropical forests, where sub-annual and supra-annual frequencies are the most frequent (Mark, 2013; Sakai, 2001). Our results are perhaps more similar to the temperate regions, where annual flowering patterns govern the forests (Sakai, 2001). We also found a predominant annual fruiting pattern, showed by 36% of species, at 11 sites, a result previously reported from other studies in Africa (Chapman et al., 1999; Takenoshita, Ando, & Yamagiwa, 2008). As expected, at the site level annual flowering and fruiting frequency was again the most common. Annual frequency indicates that a regular seasonal cycles, sometimes influenced by additional environmental cues, sets the observed annual pattern. Annual frequencies allow specialization with year-round food supply and were previously reported to be initiated with environmental conditions, such as rainfall and temperature (Borchert, 1980, 1983; Pau et al., 2013; S. Sakai, 2001). However, it is difficult to tell exactly which cues were responsible for triggering phenological events at each site, considering the complexity of these events, which depend on both environmental conditions and endogenous factors, such as carbohydrate stores (Borchert, 1983). Several sites showed various flowering and fruiting patterns, with frequencies varying from sub-annual to supra-annual ones. These results also underline flowering and fruiting complexity and inter-individual variation, previously reported at different sites in Africa (Polansky & Robbins, 2013). Variability in flowering and fruiting patterns between species within the same habitat were also reported and thought to be due to animal-plant relationships (Takenoshita et al., 2008). This is because pollinators and seed dispersals play a crucial role in setting the flowering and fruiting patterns, and hence establishing the diversity in the frequency of phenological patterns in the African tropical forests.

Timing of flowering and fruiting events

In concordance with the study of Chapman et al., 1999) we also found variable timing of both flowering and fruiting events at most sites. As reported elsewhere in Africa (Anderson et al., 2005; Polansky & Boesch, 2013), we found that in the majority of sites, flowering activity peaked at the beginning or during the middle of the wet season. Most fruiting also occurred during the wet season at most sites, as previously reported in Africa (Sun et al., 1996), as well as in South and Central America (Mark, 2013; Smythe, 1970) and Asia (Medway, 1972). However, a minority of species flowered and produced fruit during the dry season, ensuring at each site fruiting and flowering all year round. In our study we report a higher degree of variation than previously quantified, perhaps reflecting the mechanisms African tropical forests employ to maximise their reproduction rate.

Correlation with climatic phenomena

As expected from earlier work (Brown et al., 2010; Chang-Yang, Sun, Tsai, Lu, & Hsieh, 2016; Holmgren et al., 2001; Williams & Hanan, 2011), we found evidence that climatic phenomena such as ENSO, IOD and NAO correlate with flowering and fruiting events in Africa. We found that phenological events are not only affected by one phenomenon, but by a combination of two or more, not previously demonstrated for African tropical forests. Our study supports the suggestion of Chang-Yang et al. (2016), which stated that ecological processes are influenced by several climatic variables driven by different climatic phenomena. However, only 26% and 29% of species correlated their flowering and fruiting patterns, respectively with one or more climatic phenomenon, which is perhaps fewer than expected, based on the results from other continents (Chang-Yang et al., 2016; Shoko Sakai, 2002). One explanation may be the fact that the local temperature and rainfall conditions are correlated to a greater or lesser degree with each of the three phenomena, and the plants only respond to local patterns (Szabó et al., 2016). Poulsen & Clark (2005) suggested that regional changes in temperature and precipitation may be higher than the global average, and hence phenology is more likely to be driven by them. Whilst a similar number of species showed a correlation with ENSO as did with IOD, for those species that showed a correlation with IOD the effect of variation in this parameter was much stronger, resulting in steeper decline or increase in flowering and fruiting patterns. This result, and the unexpectedly high proportion of species that responded to multiple climate phenomena support earlier work that reported high interference of IOD over ENSO effect of Southern African photosynthesis of vegetation greenness (Williams & Hanan, 2011), but contrasts with work on agricultural production across West, South and East Africa, where no IOD effect was reported (Brown et al., 2010). We also found correlations between NAO and flowering and fruiting events, but the proportion of species were lower than in the case of ENSO and IOD, perhaps reflecting the more localised effects of NAO on African climate in areas without representation in our study. In our study, both ENSO and IOD correlated with flowering and fruiting events for some species at all sites, with the highest proportion of species being found in Eastern Africa, as perhaps expected from the stronger climatic impacts in this region. Eastern Africa receives heavy rain when ENSO and IOD indices are positive (Brown et al., 2010), which can drive phenology (Chang-Yang et al., 2016; extended AVHRR & Tucker, 2001). In our study, we showed that higher number of species had their fruiting patterns triggered by both ENSO and IOD, suggesting that fruiting process is more responsive to these two large climatic phenomena than flowering is. Showing that species at five sites in the case of flowering and six sites in the case of fruiting, were affected by two or more phenomena than we would have expected by chance, may imply a high level of complexity in the survival and reproduction mechanism at the level of individual tree. Overall, moving towards a positive index, we found that flowering and fruiting were either increased or decreased, being site and species specific. The wide variety of responses can also depend on the intensity of each phenomenon. Wright and Calderon found that flowering is triggered during moderate El Niño events, and diminished during severe events (2006). However, no evident pattern was seen in the direction of flowering and fruiting patterns in response to unexpected increase in rainfall or drought conditions associated with ENSO, IOD and NAO phenomenon. Moreover, it is worth mentioning that all these phenomena interact with each other, hence the effects we have seen are most probably the result of the interaction between two or more phenomena. It was previously shown that ENSO and IOD impact similar geographic regions, and that their effects interfere with each other, IOD changing the direction vegetation photosynthesis normally has in Africa in response to ENSO (Williams & Hanan, 2011).

There is clear evidence that the three climatic phenomena affect species differently across sites. The strong individualistic responses of tree species in forests across Africa contrasts greatly with tropical forests on other continents (Brearley, Proctor, Nagy, Dalrymple, & Voysey, 2007; Fredriksson & Wich, 2006; Shoko Sakai et al., 1999), where the overall direction of flowering and fruiting events are similar for most species. In most studies, including ours, species usually respond to ENSO effects, but in a tropical forests in Taiwan, Chang-Yang et al. (2016) find no link between ENSO and flowering events (2016). Whereas, with some few exceptions there are strong evidence that rainfall, and climate phenomena that drive rainfall have consistent effects on flowering and fruiting in Asia and South America (Mark, 2013; S. Wright & Calderón, 2006; S. J. Wright, Carrasco, Calderon, & Paton, 1999), in Africa such patterns are far weaker and although individual species may respond strongly, there is such a huge variety of responses that no clear picture is seen. We suggest that the diversity and complexity of African tropical tree species' responses to climate phenomena makes the African continent interesting and slightly more functionally robust than some other regions.

Appendices

Appendix 3A. Multivariate analysis for significant (p<0.05) and non-significant sites with regards to climate phenomena and flowering.

No.	Site	p value
1	Budongo	NA
2	Lope	0.003
3	Tai	0.366
4	Mbaiki	0.228
5	Amani	0.534
6	Bwindi	0.371
7	Nyungwe	0.132
8	Kibale	0.426
9	Okapi-Edoro	0.007
10	Okapi-Lenda	0.003
11	Goualougo	0.076
12	Mbeli	0.011
13	Mondika	0.008
14	Kakamega	0.409
15	Loango	0.001
16	Gombe	0.037

NA: Test not applicable

P value represents the log-likelihood ratio and indicates at which sites more species than we would have expected are affected by two or more phenomena.

Appendix 3B. Multivariate analysis for significant (p<0.05) and non-significant sites with regards to climate phenomena and fruiting.

No.	Site	P value
1	Amani	0.137
2	Bwindi	0.01
3	Gombe	0.19
4	Goualougo	0.002
5	Kakamega	0.054
6	Kibale	0.368
7	Loango	0.068
8	Lope	0.107
9	Mbaiki	0.108
10	Mahale	0.586
11	Mbeli	0
12	Mondika	0
13	Nyungwe	0.003
14	Okapi Lenda	0.049
15	Tai	0.086

P value represents the log-likelihood ratio and indicates at which sites more species than we would have expected are affected by two or more phenomena.

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Chapter 4

Concluding remarks

For the first time, I considered phenology at the individual level across the African continent, using Fourier analysis. In tropical forests in Africa, studies have only addressed phenological patterns at the site level (Chapman et al., 1999, Janmaat et al., 2016, Polansky and Boesch, 2013), or assessed interannual variation in fruiting availability (Chapman et al., 2005). I assessed phenology using three quantitative indicators: frequency, fidelity to a consistent frequency and seasonal timing. This study is the first to closely address fidelity to a consistent frequency in the tropics. Fidelity for a particular flowering / fruiting frequency is an important indicator in evaluating population viability, reproductive success and diversity of climate change responses (Morellato et al., 2016). Hence, using the three phenological indicators, in the first chapter I compared species shared between different types of forests, including montane, sub-montane, semi-deciduous, evergreen and swamps, and demonstrated site and species level variation, interpreting the latter as evidence for plasticity. I showed that for more than 70 % of species shared between different forests, phenology is an evolutionary inherited trait very well conserved, as I found no significant difference with regards to each of the three indicators between sites, despite significant variation in local conditions. Consequently, environmental conditions have allowed these species to stick to their inherited phenological patterns and may be the ones most vulnerable to future climate change effects. On the other hand, regardless of their genetic inheritance, 30% of species present at multiple sites showed different phenological patterns. These species have high phenotypic plasticity and may be the pioneers in climate change resilience, whilst the other 70% of species, may need longer time periods to find evolutionary solutions to climate change. Apart from plasticity, species may have also undergone local adaptation, triggered by selective pressures imposed by different biotic and abiotic pressures.

Next, I assessed interannual trends for all available species, highlighting a significant decrease in flowering and fruiting frequencies of African tropical trees. Interannual trends are important patterns that could demonstrate early indications of climate change impacts. I demonstrated this phenomenon for almost all sites, which makes our results pervasive. The decrease in flowering and fruiting frequency may be a consequence of senescence, impact of climate change or a combination of both and possibly other unknown factors. Because costs of reproduction are age-specific and reproductive effort must increase as trees age (Montesinos et al., 2006), it is plausible that senescence is the biggest contributor to this result. By contrast, I found species to be equally divided between increasing / decreasing fidelity to a particular frequency, or showing no change. It seems most likely that species which showed change in the fidelity for a particular frequency was due to chance variation, as they were divided equally between increasing / decreasing their fidelity to a particular flowering / fruiting frequency and represented only a small number of many species consistent with Type I error rates. Oscillations in the environmental conditions have previously been seen to cause deviation from normal frequencies (Anderson et al., 2005, Chapman et al., 2005), so it seems plausible that many trees can change cycle slightly from year to year in response to different environmental cues, perhaps caused by large-scale climatic phenomena.

Phenological patterns can be significantly influenced by weather extremes driven by natural phenomena (Chang-Yang et al., 2016, Williams and Hanan, 2011, Fredriksson and Wich, 2006). Weather extremes are predicted to increase in their intensity and frequency, threatening to significantly affect tropical forests (IPCC, 2014). However, evidence showing how these phenomena act in concert to drive plant reproduction remains scarce and not previously addressed in the African tropical forests. In our second chapter, for the first time I addressed phenology across a spectrum of 17 tropical forests in relation to ENSO, IOD and NAO (Rajagopalan et al., 1998). The effects of these phenomena can influence phenology in Africa either alone, or in combination with each other (Rajagopalan et al., 1998, Williams and Hanan, 2011). The consequences of ENSO effects in Asia and South America are strong and consistent; however in Africa I found a variety of responses for each tested phenomena (ENSO, IOD, NAO), and species with no clear picture for each site. Moreover, species that responded to climate were more likely to be affected by multiple phenomena at the same time than expected by chance, which may serve to dampen or emphasise their responses. In this study I found that a higher number of species increases their flowering and fruiting events in response to one or more phenomenon. These multiple interactions, plus the large number of species for which no climate phenomena associations were identified, may explain the absence of a consistent pattern and possibly makes African tropical forests functionally more robust than the other tropical forests. This study has confirmed initial patchy evidence, suggesting that Africa is different from other places. I have shown that not only individual species behave differently but also trees within the same species. Why phenology in Africa is so variable and what roles climate and ecology play in this story is the next big question to be addressed. With no single story appropriate for each phenomenon at each site, I have identified the uniqueness of African tropical forests, not previously reported and call for further research in this aspect in order to complete the African tropical forests puzzle.

Strengths of the analysis and caveats for future research of the data analysis

One of the strengths in the current study is the long-term datasets available for several sites, which draw interest for their perspective on interannual trends. They highlighted the fact that shorter term records can give false positive results. The five year moving windows showed that phenological trends occasionally follow periodical patterns. In my analysis I observed that some species have an initial upward trend that is kept for several years, which then switches towards a downwards trend. This observation also informs us that interannual trends analysis requires a minimum years of data, in order to confidently detect the right pattern. Fourier analysis was another asset for our study, as it addressed several challenges, such as sample size and circularity encountered in other popular methods such as bootstrapping, sinusoid-based regression or finite mixture theory and described by (Hudson and Keatley, 2009). Fourier analysis proved robust in calculating the distribution of all frequency cycles in our phenology data and I would recommend it for future analysis.

On the other hand, in our analysis species are not a representative sample of the African tropical forests. At some sites, trees were primarily monitored for research into food availability for primates. Hence, I suggest that future research should account for phenological patterns of more representative trees samples for each site to complete our analysis. Another particularly important component of future studies would be to ensure that new trees are added to the analysis, ensuring the cohort as a whole does not age together, confounding temporal trends and senescence.

Future of Africa

I filled several gaps by documenting flowering / fruiting frequencies across multiple tropical forests, demonstrating the plasticity of several species in response to different environmental conditions, providing the evidence for the decrease of flowering and fruiting frequencies over time (probably due to senescence) and highlighting the robustness of African tropical forests in response to extreme weather events brought by ENSO, IOD and NAO. However, several gaps remain to be filled.

In addition to our three phenological indicators, others should also be considered in order to complete the big phenological picture in Africa. I suggest that indicators such as synchronicity, duration of phenological events and fruit size would prove useful in understanding the adaptiveness of strategies implemented by different species in response to climate change. These indicators are important because together with the ones I have considered they define flowering and fruiting patterns. Completing our analysis with these new parameters will add to our current understanding about the community function and diversity of African tropical forests.

Secondly, in order to understand why species flower and fruit during a particular season I suggest that future work should group species by their functional traits. In most cases, timing of fruit ripening corresponds to the presence of the dispersers (Fenner, 1998). It has been shown that some trees fruit during the dry season, when the intensity of trade winds reaches their peak (Gentry, 1974). On the other hand, species that produce fleshly fruits prefer the wet season, when the best dispersers are found (Fenner, 1998). Grouping species by their functional traits will better indicate how they coordinate their phenological patterns in such diverse ecosystems and what environmental cues are responsible for their phenology.

Thirdly, although I used large-scale climatic phenomena that are a useful proxy for climate change (Brown et al., 2016), the correlations between rainfall and temperature with each of the phenomena can vary markedly from site to site. Trees do not respond directly to large climatic phenomena, but to local conditions (rainfall and temperature) that are triggered by them. I chose to correlate flowering and fruiting events with large climatic phenomena because data on local weather conditions in Africa are very sparse. Weather variables such as temperature and precipitation are available online, but they have been interpolated from different weather stations across Africa and satellite observations lose their accuracy when they are extracted for a specific location. I have seen a low correlation between interpolated data from online sources and local weather records for one site. Accurate rainfall and temperature data at each site should be analysed in parallel with critical thresholds set for each climatic phenomenon (low, medium, high intensity), and integrated with phenological patterns at each site. Hence, how African trees respond on a large-scale to rainfall is still an open question and collection of local temperature and rainfall data should be a priority in order to accurately address it.

The next biological question we need to address is why African tropical forests are so different compared to other tropical forests from Southeast Asia or Central America. In order to answer this question, the next approach would be to compare tropical forest phenology from various different continents in order to search for the particularity of the African tropical forests. Answering this question will allow us to better understand how global climate change will impact forests across Africa and how to better manage changes for the million people that depend on the African forest resources for their futures.

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