Phenological and altitudinal changes in plants responding to drying Neotropical Cloud Forests

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ABSTRACT

Precipitation is a main abiotic cue for flowering and fruiting in tropical plants. Global warming is likely to alter abiotic cues in tropical montane cloud forests such as the Monteverde Cloud Forest in Costa Rica. The plants within the Monteverde Cloud Forest rely on cloud cover to provide precipitation through mist during the dry season. With rising sea surface temperatures caused by increased concentrations of atmospheric carbon dioxide, cloud bases are likely to move up in elevation. This has the potential to increase the number of days without mist during the dry season. It is also possible that plant species have changed their altitude ranges in response to warming. Here, I repeat a 1979-81 census of flowering and fruiting plants in the Monteverde Cloud Forest Reserve for a two-week period in mid-July. Sixty-four plant species were noted for flowering or fruiting, and sixteen showed evidence of phenological change. Eight plant species were also found that were previously reported only from lower elevations. Although a small number of plants had atypical patterns, the majority were flowering or fruiting on time. Still, phenology changes of even a few species could impact food webs. Novel communities are likely to form as plants move up in altitude in search of historical mist and seasonal conditions.

Keywords: Costa Rica, phenology, cloud forest, climate change, altitude, novel communities

INTRODUCTION

Phenology

Phenology, the timing of flowering, fruiting, and leaf production of plants, is sensitive to abiotic cues such as temperature and precipitation (Chapman *et al.*, 1999; Gilman *et al.*, 2010; Lenoir *et al.*, 2008; Nadkarni and Wheelwright, 2000; Sherry *et al.*, 2007). Although other biotic factors have an influence on phenology, plants that are able to respond to seasonal variability are better able to maximize the success of their offspring (Chapman *et al.*, 1999; Hamann, 2004). While many temperate regions have plants that rely heavily on seasonal temperature and day length cues, tropical regions do not vary widely in their temperature ranges or day length throughout the year. Instead, these regions contain plants that are more responsive to variation in precipitation (Cleland *et al.*, 2007). This is especially true in regions with one distinct annual wet and dry season, such as tropical regions located north or south of the equator (Cleland *et al.*, 2007). In the tropics, flowers are mostly produced in the late dry season and early wet season when dry pollen is more mobile and less likely to encounter moisture (Hamann, 2004; Koptur *et al.*, 1988). Fruiting is less seasonal, but many fruits appear during the wet season (Hamann, 2004; Koptur *et al.*, 1988). By producing offspring before a rainy period, the seedling of the parent plant will be more likely to be successful in rooting before the next dry season arrives.

In ecological communities, species interactions are driven in part by the timing of plant reproduction (Gilman *et al.*, 2010). Primary consumers that expect resources such as nectar, pollen, seeds, and fruits from plants to arrive at certain times of the year must depend on the timing of phenology. Other organisms may then feed on those primary consumers. All trophic levels within a food web are dependent, in some way, to the timing of plant phenology. Frugivores, which eat primarily fruits, have even been found to be the most dominant group of vertebrates in a majority of tropical forests and thus it is important for these organisms that flowering and fruiting of plants occur at anticipated times (Chapman *et al.*, 1999).

Climate Change

Phenology. In recent years, global climate change has threatened environments with increasing global temperatures and rising concentrations of carbon dioxide stemming from anthropogenic burning of fossil fuels (Gilman *et al.*, 2010; IPCC, 2013). These changes have the potential to affect species interactions throughout trophic levels (Walther, 2010). Plants in the tropics tend to mechanistically respond to seasonal changes in precipitation between dry and wet seasons. Increased atmospheric carbon dioxide directly affects sea surface temperatures which have increased globally since the beginning of the 20th century (IPCC, 2013). Increased sea surface temperatures have an effect on tropical montane cloud forests where plant species rely on cloud cover for moisture through mist during the dry season (Foster, 2001; Goldsmith *et al.*, 2013; Lawton *et al.*, 2001; Pounds *et al.*, 1999; Still *et al.*, 1999) (discussed in further detail in 'Cloud Forest' section below).

In the tropics, each organism varies in its response to changing climatic patterns and as this occurs, interactions among species have the potential to fall out of synchronization (Walther, 2010). Tropical plant species can respond to climatic changes by gradually altering the timing of reproductive activities to coordinate with precipitation patterns (Lenoir *et al.*, 2008). This change has been documented in many studies as evidence of the impact of global climate change on ecosystems, although a considerable amount of studies focus on temperate as opposed to tropical environments (Cleland *et al.*, 2007; Sherry *et al.*, 2007). Monitoring changes in the phenology of plants in tropical ecosystems can provide insight as to which plant species are responding to altered climate patterns and is an important indicator as to whether an ecosystem is experiencing a shift.

Altitude Range. Another effect that climate change has been shown to have on plant species is the adjustment of altitude ranges (Gilman *et al.*, 2010). Some plant species may gradually migrate toward cooler temperatures at higher elevations, while the ranges of other species may expand to include higher elevations. Research conducted by using pollen data from lake sediment cores illustrates this process as plant species of the time moved downslope away from cold temperatures during the Last Glacial Maximum (Colwell *et al.*, 2008). Now, as temperatures are exceeding any maximum experienced during the current Holocene period, we would expect this trend to reverse (Colwell *et al.*, 2008). While some plant species are able to adapt, others are more vulnerable to changing climate (Gilman *et al.*, 2010). This includes those that have specialized resource requirements and that are limited in their ability to migrate to suitable conditions (Gilman *et al.*, 2010). This process has been well documented in temperate regions, but studies of the same process in the tropics are scarce (Colwell *et al.*, 2008; Lenoir *et al.*, 2008). It is difficult to monitor changes in altitude ranges of plant species in the tropics due to generally dense vegetation as well as a lack of baseline information.

Models of elevation range shifts by plant species in the tropics have shown ecotones moving upslope (Foster, 2001). As plant species shift upward in altitude, populations decrease, and elevation ranges tend to be smaller than those for temperate species (Colwell *et al.*, 2008). Other anthropogenic activities such as deforestation and fragmentation can inhibit the movement of plant species, at which time it is difficult to predict their future (Colwell *et al.*, 2008). Available baseline data for tropical plant species’ altitude ranges can be used to observe if the altitude ranges of any species have changed. This has implications for the entire ecosystem as the decrease in diversity or abundance of plant species could possibly affect adjacent trophic levels. Observing both altitude range shifts and changing phenology of plant species in the tropics can be an important indication of whether increased atmospheric carbon dioxide concentrations are having, and will continue to have an impact on the community as a whole.

Cloud Forests

Monteverde is located on the Pacific slope of Costa Rica and is home to a tropical montane cloud forest. Cloud forests form as orographic uplift of trade winds creates clouds over tropical montane forests (Lawton *et al.*, 2001). These are known as one of the earth's most endangered and rare ecosystems (Goldsmith *et al.*, 2013). They play a large role in capturing water for the hydrologic cycle and prevent runoff and erosion in watersheds (Nadkarni *et al.*, 2000). Tropical montane cloud forests make up less than two percent of the tropical forests of the world (Goldsmith *et al.*, 2013) and are lost at a higher rate than tropical forests per year through deforestation and timber extraction (Nadkarni *et al.*, 2000).

During the dry season in Monteverde, which typically lasts from February to May, montane cloud forests rely on cloud cover as a main source of moisture through mist (Foster, 2001; Lawton *et al.*, 2001; Pounds *et al.*, 1999). As carbon dioxide concentrations in the atmosphere continue to rise, tropospheric and sea surface temperatures increase (Graham, 1995). Consequently, this affects cloud patterns and forces cloud bases hundreds of meters upslope during the dry season, known as the lifting-cloud-base hypothesis (Goldsmith *et al.*, 2013; Lawton *et al.*, 2001; Pounds *et al.*, 1999; Still *et al.*, 1999). The shifting of cloud bases toward higher elevations has been observed within montane forests of Central America (Benning *et al.*, 2002). Along with decreasing the frequency of mist days during the dry season, increasing carbon dioxide concentrations are projected to increase surface temperatures and decrease precipitation (Karmalkar *et al.*, 2011; Pounds *et al.*, 1999). These trends prevail even when the effects of El Nino are taken into account (Lawton *et al.*, 2001; Pounds *et al.*, 1999). Decreased cloud cover increases water demand for cloud forest plant species and increased temperatures could worsen the effect by increasing evapotranspiration (Goldsmith *et al.*, 2013; Still *et al.*, 1999). Not only are tropical montane cloud forests rare and endangered, they harbor many aesthetic endemic species (Still *et al.*, 1999). Without contact with clouds, it is unknown what will happen to cloud forests and how the plant community will respond.

The goal of this case study is to examine typical and atypical phenology as well as range shifts in the Monteverde Cloud Forest Reserve. I specifically address the following questions: 1) are observed plant species occurring in the same elevation ranges and 2) are observed plant species flowering and fruiting at the same time as observed by Koptur *et al.* (1988). By using baseline data by Koptur *et al.* (1988), on the timing of fruiting and flowering and altitude ranges of understory plants in the Monteverde Cloud Forest Reserve, I attempt to uncover typical and atypical phenology as well as range shifts to determine if these findings are related to increased temperatures and moisture demand in the Monteverde cloud forest. This case study uses observations of flowering and fruiting as well as altitude ranges of plants in the Monteverde Cloud Forest to test the theory that increasing atmospheric carbon dioxide concentrations will alter the phenology and ranges of understory plant species within cloud forests.

METHODS

Study Site

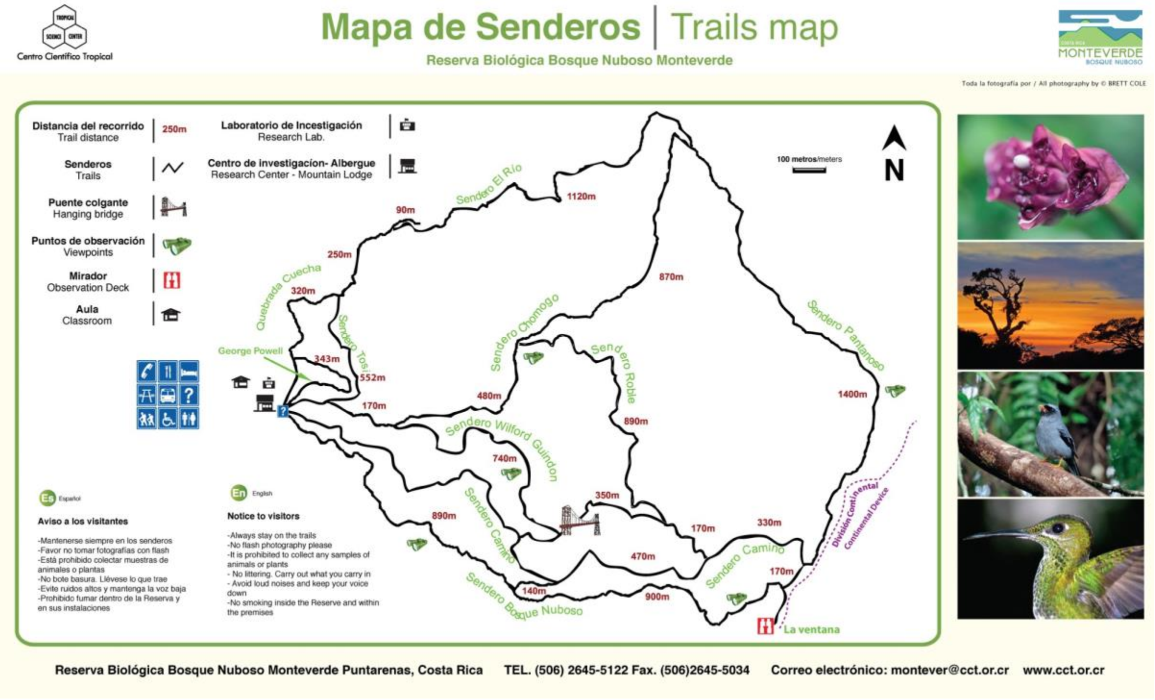
This case study was located on trails within the Monteverde Cloud Forest Reserve on the Pacific side of the continental divide in Costa Rica. Monteverde is in the tenth district of the county Canton in the Province of Puntarenas (Nadkarni *et al.*, 2000). This area is situated between 1550-1650 m asl and is classified as a Lower Montane Rain Forest life zone with a canopy height of 25-35m (Haber *et al.*, 2000). The Monteverde Cloud Forest is found in an altitudinal range that experiences cloud cover during most of the year (Nadkarni *et al.*, 2000). Clouds allow for increased precipitation through interception of water by the canopy and decreased evapotranspiration and solar radiation (Nadkarni *et al.*, 2000).

Temperatures in Monteverde range from 9-27 degrees Celsius annually with a mean of 18.5 degrees (Nadkarni *et al.*, 2000). Annual precipitation ranges from 2-3 meters per year (Nadkarni *et al.*, 2000). This tends to be an underestimation because of the inability of rain gauges to measure cloud precipitation and mist accurately (Nadkarni *et al.*, 2000). The Intertropical Convergence Zone gives Monteverde a six month wet season from May to October, a three month transition season from November to January, and a three month dry season from February to April (Nadkarni *et al.*, 2000).

Observation Scheme

All plant species observed to be fruiting and flowering were recorded within 1550-1650 m asl for two weeks in mid-July of 2014. Species were identified using Costa Rican field guides when possible (Gargiullo et al, 2008; Haber *et al.*, 2000). The remaining species were identified by Costa Rican plant experts William Haber and Willow Zuchowski. The baseline study by Koptur *et al.* (1988) included areas of three different forest types in Monteverde; Lower Montane Wet Forest (1320-1460 m asl), Lower Montane Wet Forest/ Rain Forest Transition (1480-1520 m asl), and Lower Montane Rain Forest (1550-1650 m asl). This case study only examined places described as Lower Montane Rain Forest, by Koptur *et al.* (1988). Observations were conducted on the full length of all of the trails inside the reserve with the exception of Sendero El

Rîo, Sendero Pantanoso, and Sendero Chomogo north of where it meets Sendero Roble because these were closed due to the number of trees that had fallen (Fig 1) (Monteverde Cloud Forest Biological Reserve, n.d.). This study represents a non-random, spot sampling method in order to abide by the rules set forth by the Cloud Forest Reserve to reduce disturbance by remaining on the trails. Plant species located off of the trails, which were easily identifiable from a distance, were included. This sampling method may introduce bias towards the similar environments that are represented by the presence of trails.



Aviso a los visitantes

-Mantenerse siempre en los senderos
-Favor no tomar fotografías con flash
-Está prohibido colectar muestras de animales o plantas
-No bote basura. Llévese lo que trae
-Evite ruidos altos y mantenga la voz baja
-Prohibido fumar dentro de la Reserva y en sus instalaciones

Notice to visitors

-Always stay on the trails
-No flash photography please
-It is prohibited to collect any samples of animals or plants
- No littering. Carry out what you carry in
- Avoid loud noises and keep your voice down
-No smoking inside the Reserve and within the premises

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Figure 1. A map of trails located within the Monteverde Cloud Forest Reserve that were used to observe flowering and fruiting in understory plants. The same location was used by Koptur *et al.* (1988) allowing a uniform comparison of phenology of plants from 1978-81 to 2014. (Monteverde Cloud Forest Reserve, n.d.).

Study Organisms

Along the trails of the Monteverde Cloud Forest Reserve, trees and shrubs in the understory bearing flowers and fruits were observed and recorded. Epiphytes and climbing plants were purposefully excluded to repeat methodology conducted by Koptur *et al.* (1988) who only observed trees, subshrubs, shrubs, and herbs. Plants were located close to trails for ease of identification with minimal damage to surrounding understory. Height of plants observed were typically below 3 m due to inability to identify plants of taller stature. A few species were recorded from the height of a suspension bridge located within the reserve to include a few taller tree species. The species that were recorded by Koptur *et al.* (1988) spanned a larger range and individuals were tagged and recorded over a two-year period. This case study differs because it only represents plants from similar environments near trails in one elevation zone over a two-week period.

Phenological Census

During two weeks, beginning mid-July of 2014, flowers and fruits were observed along the trails in the Monteverde Cloud Forest Reserve. Plants were identified to the species level. The number of individuals of each species flowering, fruiting or both was also noted. Methodology remained consistent with Koptur *et al.* (1988) with the exception of time spent observing individual plants as well as a transect method. I also only looked for fruiting and flowering phenology and did not take leaf dropping and other phenology behaviors into consideration.

Data were then compared to phenology patterns of Koptur *et al.* (1988) to determine whether the flowering and fruiting patterns were typical or atypical. Koptur *et al.* (1988) provided a list of the months each species were seen flowering or fruiting from 1978-81 and this was used as a baseline. Plants found both flowering and fruiting were considered atypical if timing of either fruiting, flowering or both were outside the range defined by Koptur *et al.* (1988). If both flowering and fruiting were observed in a species and the timing of either flowering or fruiting was outside the range provided by Koptur *et al.* (1988) it was also considered atypical.

Next, I noted whether the timing was early or late. If the months of flowering and fruiting provided by Koptur *et al.* (1988) indicated that phenology observed was one or two months prior to or after those I observed, then those were considered to be flowering or fruiting either late or early accordingly. If there were more than two months between phenological observations by Koptur *et al.* (1988) and those I recorded, then those species were considered ‘greater than three months’ as opposed to defining them as early or late.

Altitude Range Census

When comparing observed species to the study by Koptur *et al.* (1988), elevation zone where the species was found was also taken into consideration. Koptur *et al.* (1988) provided a description of three life zones over different altitudinal gradients that were repeatedly observed over the span of two years. Koptur *et al.* (1988) noted the life zone where each individual species were found. Because I only observed plants in the highest of the three forest types described by Koptur *et al.* (1550-1650 m asl), plants observed previously by Koptur *et al.* (1988) in only one of the two lower forest types were considered to have possibly migrated to higher elevations or expanded their altitude range.

RESULTS

Phenology

In the two years of study completed by Koptur *et al.* (1988) 81 species of plants in flowering or fruiting stages were recorded from 1550-1650 m asl in the Monteverde Cloud Forest Preserve. In the two weeks I conducted this study, 64 species of understory trees and shrubs were recorded flowering or fruiting during mid-July of 2014 (Appendix A). Of these 64 species, 27 species appeared in the study conducted by Koptur *et al.* (1988) and the other 37 did not appear in Kopter *et al.* (1988).

In comparison with phenology recorded by Koptur *et al.* (1988) ten species expressed typical flowering and fruiting patterns while sixteen were found to be atypical (Fig 2). One species, *Solanum pertenue* (Solanaceae) was unknown to show typical or atypical phenology because it was only observed fruiting in the current season and Koptur *et al.* (1988) did not provide information about months of fruiting for this species. There were eight species that were observed to be atypically flowering, five species that were observed to be atypically fruiting, and three species that were both flowering and fruiting atypically.

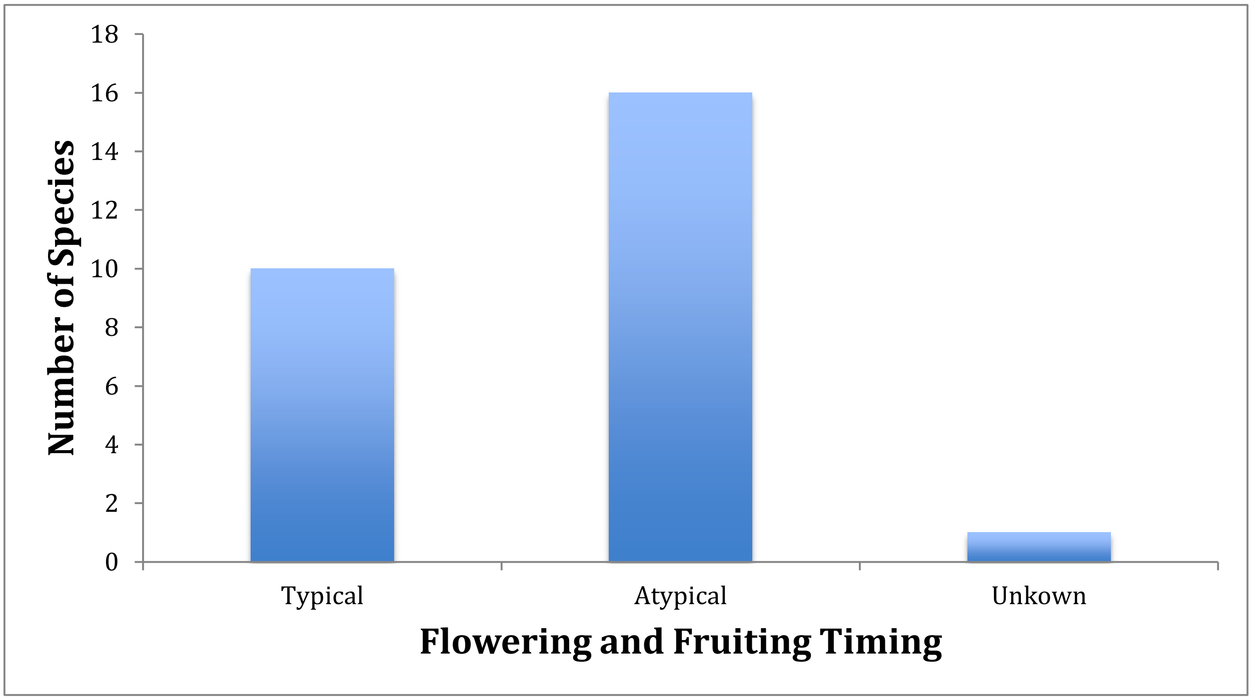

Figure 2. Patterns of flowering and fruiting in plants recorded in the Monteverde Cloud Forest Reserve for two weeks in mid-July. Months of typical flowering and fruiting recorded by Koptur *et al.* (1988) during two years of observation in the same areas were compared with data found of plants that were currently flowering and fruiting. Depending on whether or not plants recorded were flowering, fruiting, or both, timelines provided by Koptur *et al.* (1988) were used as a baseline to determine if the timing of flowering and fruiting were typical or atypical according to timing observed between 1978-81. One species, *Solanum pertenue* (Solanaceae) could not be regarded as typical or atypical because it was only seen fruiting and a timeline for fruiting of this species was not given in the study by Koptur *et al.* (1988).

Koptur *et al.* (1988) provided ranges of months that each species of plant recorded could be flowering or fruiting in based upon observations. When looking at species with atypical phenology in comparison to that found by Koptur *et al.* (1988), this study found the average length of time that flowering or fruiting occurred spanned about 3.5 months. On the other hand, species whose phenology seemed to be occurring at typical times had fruiting and flowering ranges of an average of 5.8 months. Although there is a statistical difference in the two values (W = 39.5, p-value = 0.0496), it is inconclusive whether this is an accurate representation of differences in phenology between the groups of plants that suggest typical and atypical patterns.

Further examination of plant species that exhibited atypical phenology revealed whether early timing, late timing, or timing greater than three months was occurring (Fig 3). Of species with atypical flowering timing, one was found to be early, four were found to be late, and three were greater than three months away from the range defined by Koptur *et al.* (1988). Atypical fruiting patterns were found to be early in two species, late in one species and greater than three months out of their range from 1979-81 in two species. Of those species with atypical flowering and fruiting, late patterns were found in two species and patterns greater than three months away from the baseline was found in one species.

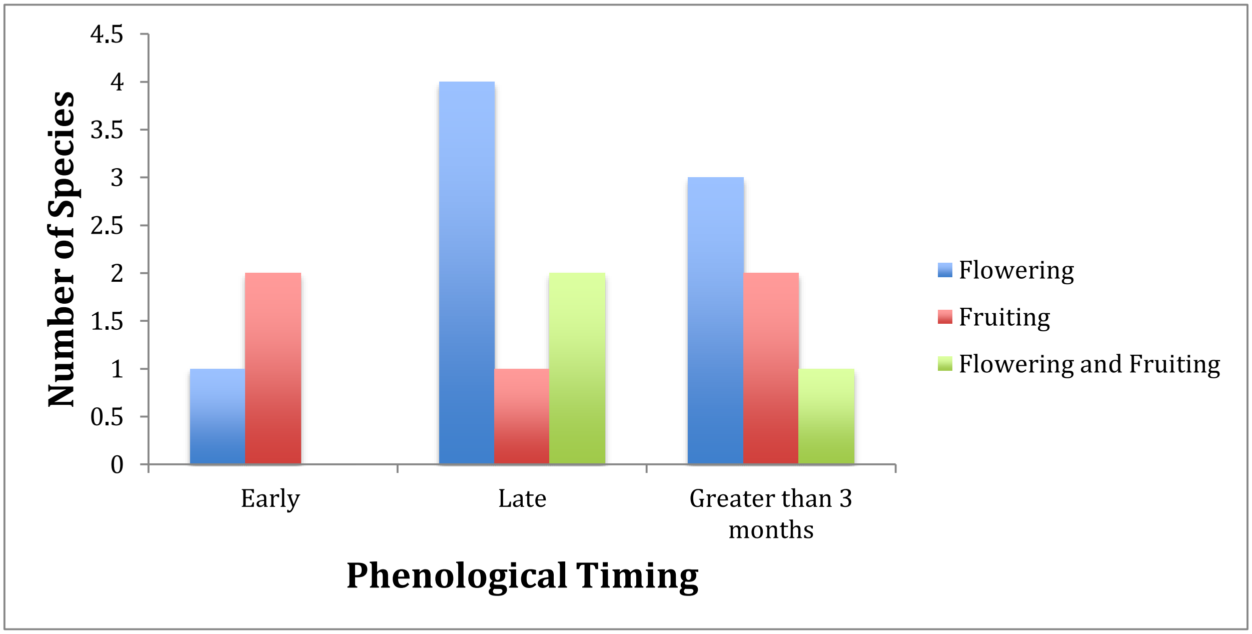

Figure 3. Distribution of plant species found to be flowering, fruiting or both atypically from observations made by Koptur *et al.* (1988) in the Monteverde Cloud Forest Reserve on the Pacific slope in of Costa Rica in Monteverde. Once a species was determined as expressing atypical phenology when compared to Koptur *et al.* (1998) whether that species was exhibiting early or late timing was determined. If a plant species was flowering, fruiting, or both greater than three months away from the time period provided by Koptur *et al.* (1998) than it was considered as being neither early nor late.

Altitude Range Changes

Koptur *et al.* (1988) documented the forest type defined by elevation range where each plant species recorded was found at. Being in the highest forest type according to that study, 19 of the species found had been from a similar altitudinal zone during 1978-81. Seven of the species recorded had previously only been seen at elevations 1480-1520 m and were observed in July of 2014 up into elevations of 1550-1650 m. One plant species, *Besleria solanoides* (Gesneriaceae), had only been seen at elevations 1320-1460 m. This was also a species that exhibited atypical flowering and fruiting greater than three months from the timeline of phenology in comparison with previous studies. In the study conducted by Koptur *et al.* (1988) *B. solanoides* was only found to be fruiting between January and February.

DISCUSSION

Phenology

Out of the 64 species observed flowering and fruiting during mid-July of 2014, only 27 appeared in the study by Koptur *et al.* (1988). The reasons for this are not entirely clear, but could be because Koptur *et al.* used a transect and tagging method while species observed for this study were located near the public trails inside the Monteverde Cloud Forest Reserve in only one of the three elevation ranges Koptur *et al.* (1988) described. While Koptur *et al.* examined the diversity of certain tagged plant species over a wide range of elevations and area beyond public access in the reserve, this study concentrated on a more specific region within the study area of Koptur *et al.* (1988). Incorrect identification of some species is another explanation.

Although recent studies have noticed a trend in flowering of many plant species occurring earlier in the year (Gilman *et al.*, 2010), no pattern was discerned about whether the plant species observed in this study were exhibiting earlier or later timing of phenology. Further investigation into each specific plant species observed to have exhibited atypical phenology during this study gave more information about the unique phenology of some of these species. Although timing of phenology of individual tropical plant species is not well documented, Tropicos.org, sponsored by the Missouri Botanical Garden, supplies phenology charts of some of the plant species in its collection. It is not documented where or when the data for these charts were collected. According to these phenology charts, the timings of flowering in the plant species seems to vary widely throughout the year and are consistent with observations of flowering during this study in all species except for *Pitcairnia brittoniana* (Appendix B). This may indicate that the variability in timing of flowering and fruiting in these plant species extend beyond what was documented by Koptur *et al.* (1988). Within "A Field Guide to Plants of Costa Rica", it is noted that the species *Notopleura uliginosa* and *Hoffmania congesta,* that were observed to be flowering atypically during this study compared with findings of Koptur *et al.*, actually bloom throughout the year (Garguillo *et al.*, 2008). A more detailed baseline study of plant phenology in the Monteverde Cloud Forest may be required to determine whether the plant species in this area have shifting flowering and fruiting patterns.

The impacts of plants flowering and fruiting earlier or later in response to drying conditions induced by global climate change can potentially radiate through intraspecific competition for pollinators and dispersers as well as adjacent trophic levels (Walther 2010). Species in higher trophic levels tend to show a greater reaction to abiotic change than those of lower trophic levels (Gilman *et al.* 2010). Individual plants within a species tend to flower at different times to avoid competition for pollinators. As climate change continues to affect the flowering and fruiting of plants, phenologies are likely to become more homogenous (Reich 1995). This will become a stress for animals as the time range of flowering and fruiting will become shorter and provide limited resources to mutualistic partners that may be active at different times (van Schaik *et al.* 1993).

El Nino

El Nino is an oceanic and climatic process that tends to create warm, dry conditions for tropical areas (Neelin, 2003). El Nino occurs about once every four or five years and is a natural weather occurrence. Studies concerned with whether this phenomenon has an effect on plant phenology have found mixed results (Asner *et al.*, 2000; Hamann, 2004; Wright *et al.*, 1999). A study recording phenology changes in the tropical Philippines in 2004 found that flowering occurred later during an El Nino year, yet concluded that plants are dominated by their “internal seasonal rhythms” and are only minimally altered by El Nino events (Hamann, 2004). While some studies have seen increased productivity during mild El Nino events, others claim that El Nino has been shown to contribute to increased CO_2 levels and leaf drop in tropical areas (Asner *et al.*, 2000; Wright *et al.*, 1999). Although regional variations may result in minute phenology changes of tropical plant species, it has not been concluded that El Nino directly affects long-term patterns of changes in flowering and fruiting patterns of plants (Asner *et al.*, 2000).

The future of El Nino events in association with climate change is also up for debate. Studies tend to agree that precipitation in the tropics will be altered with increased global warming, but different models predict both increases and decreases in precipitation for places like Costa Rica (Neelin, 2003). Climate change has also been projected to increase the frequency and intensity of El Nino events which have the ability to modify large-scale tropical climate patterns due to changes in the thermocline of the Pacific equatorial region (Yeh *et al.*, 2009). The question of whether tropical plant species are capable of adapting to such changes remains unanswered. Differentiating the effects of climate change from El Nino is difficult, although research suggests that long-term fluctuations due to climate change have more of an impact on phenology and altitude ranges of plant species than the short-term presence of El Nino (Asner *et al.*, 2000).

Altitude Range Changes

Just as animals such as birds and reptiles have been documented to be moving up in elevation as the climate in Monteverde warms, understory plants may be starting the same process but at a much slower rate due to their immobility (Pounds *et al.* 1999, Lenoir *et al.* 2008). Plants are a part of closed communities that cannot migrate long distances and either must cope with changing environmental conditions by adapting or go extinct (Gilman *et al.*, 2010). One way species may be found moving up in elevation could be by their mutualistic disperser also inhabiting slightly higher elevations (Pounds *et al.* 1999, Lenoir *et al.* 2008). The one species that was found only between 1320-1460 m asl by Koptur *et al.* and observed between 1550-1650 m asl during this study, *Besleria solanoides*, has fleshy fruits that are dispersed by birds, bats, and a number of other organisms. Bird populations in Monteverde have been found to be migrating up in elevation (Pounds *et al.*, 1999). A study conducted in Costa Rican Lower Montane Forest in 1984 observed birds to be eating the fruits of *Ossaea micrantha, Neea amplifolia*, and *Witheringia solanaceae* (Wheelwright *et al.*, 1984). These three species had also only been found by Koptur *et al.* at elevations lower than 1540 m asl. *Piper phytoloaccifolium*, also only found at elevations lower than 1540 m asl by Koptur *et al.*, is known to be a food for herbivorous bats. While bats have wider elevation ranges and ecological niches than birds, new species of bats have been appearing at higher elevations than previously recorded in the Monteverde Cloud Forest Reserve (LaVal, 2004). Another way plant species could be found at higher than normal elevation ranges may be a result of general mortality of plant species in lower reaches of their elevation ranges. As species continue to move to higher and higher ranges in mountain ecosystems, decreases in population sizes or even extinctions of such species are possible as habitable area decreases as you move up a mountain (Gilman *et al.*, 2010).

Such shifts in elevation ranges are very scarcely documented within the tropical regions, although many such trends have been observed within temperate regions. These temperate region studies describe montane plant species as having the most pronounced shifts in response to changes in abiotic conditions (Colwell *et al.* 2008, Lenoir *et al.* 2008). Elevation ranges tend to be smaller for tropical plants than for temperate plants, but human fragmentation through deforestation in tropical regions increase the potential for inhibited movement (Colwell *et al.*, 2008). Although it is uncertain whether true elevation range shifts were observed in the plant species of this case study because a large-scale evaluation of each species in the regions was not undertaken, the effects of changes in elevation ranges of plant species in tropical montane cloud forests can result in the reorganization of species, leading to novel communities.

Novel Communities

Individuals and species take different approaches to dealing with variation in abiotic conditions and novel communities have the potential to form as a result (Lurgi *et al.* 2012). Variation in sensitivity to new climatic conditions plays a large role in determining the onset of novel communities as each species attempts to satisfy individual needs (Lurgi *et al.* 2012). Even if climate plays a dominant role in determining phenology in an ecosystem, each plant species will not respond in the same way (Walther *et al.*, 2010). The onset of novel communities will contribute to new combinations and organizations of species if the distributions of plant species are changing (Walther *et al.*, 2010). Present interactions between species that had not occurred previously can occur when plants that were spatially separated come to occupy the same area and can also allow new species to become dominant (Lurgi *et al.* 2012; Walther *et al.*, 2010). This has the potential to affect the species evenness of an ecosystem which results in a loss of ecosystem resilience (Elmqvist *et al.*, 2003; Walter *et al.*, 2010). Specialists would be more affected by this than generalists as niche requirements might not be met (Lurgi *et al.* 2012). The lack of evolutionary history shared by new plant species coming into contact with one another has unpredictable consequences, which may not be wholly negative, but are still unpredictable (Gilman *et al.*, 2010).

Future Research

This particular topic could benefit greatly from more long-term and methodical observational research as well as research into true historical range and phenology of these plant species. The Monteverde Cloud Forest spans a far greater distance than the trails allotted for public use. Creating a transect method of study more similar to the original study design by Koptur *et al.* using tags to monitor many individuals of many species of plants over time in this region could uncover more understanding about how the plant community is responding to changing climatic conditions. Looking at population dynamics of specialist mutualistic partners of observed plant species in higher trophic levels could potentially show more significant results as well. More in-depth research and observations concerning cloud cover and mist could accompany this.

CONCLUSION

Observations of phenology changes in understory tree and shrub species in the Tropical Cloud Forest in Monteverde illustrate that many plants exhibit similar reproduction timing compared to almost 40 years ago. A number of species showed the possibility of a new phenology. Possible elevation range changes were also present among eight plant species. If these observations are evidential, this is less likely to be the result of El Nino events because long-term trends from almost 40 years ago indicate that many plants may be shifting their patterns of phenology. These are more likely to be the response to warming sea surface temperatures and shifting precipitation patterns brought on by global climate change than the recurrence of a short-term warming caused by El Nino (Walther, 2010). The data may also indicate that tropical plants that are highly sensitive to changes in precipitation may be adapting to the gradual moisture stress occurring over long periods of time by altering timing of flowering and fruiting or adjusting to new altitudinal ranges.

Although there were observations of plants with new phenology patterns and elevation range changes, many species showed little to no change in either phenology or elevation change. Even though studies have shown that certain species have been disturbed by climatic changes, the effects may not be visible until organisms in higher trophic levels show a difference in behavior (Voigt *et al.* 2003). Population analyses of pollinators or dispersers might be better indicators of whether small-scale changes are occurring in phenology and elevation range changes of plant species that might be too minute to quantify by comparison. Another reason why changes might not be observable in these plant species is because high biodiversity has been found to increase resilience of species within an ecosystem to environmental change (Elmqvist *et al.* 2003). The adaptive capacities of species that inhabit an ecosystem with great species abundance have been shown to have more resilience toward environmental change in both terrestrial and aquatic habitats (Elmqvist *et al.* 2003). Drying of Tropical regions may ultimately lead to environments never before seen and the finite effects of this are largely unexplored.

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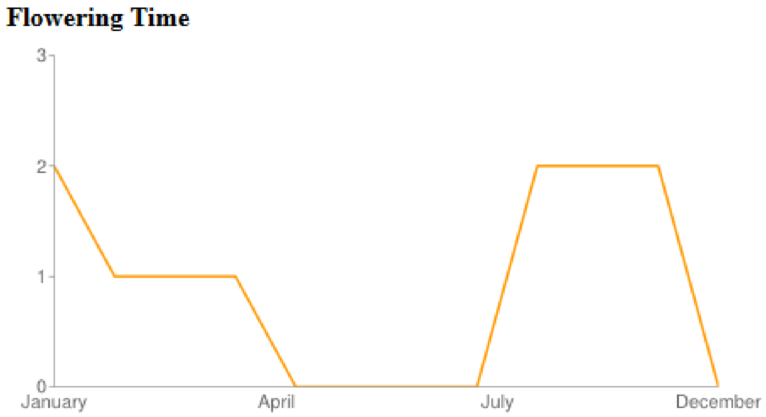
Appendix A

Appendix. List of species recorded and their patterns of flowering and fruiting.
N/A= plants that could not be defined as flowering or fruiting atypically; (fl) = flowering; (fr)= fruiting

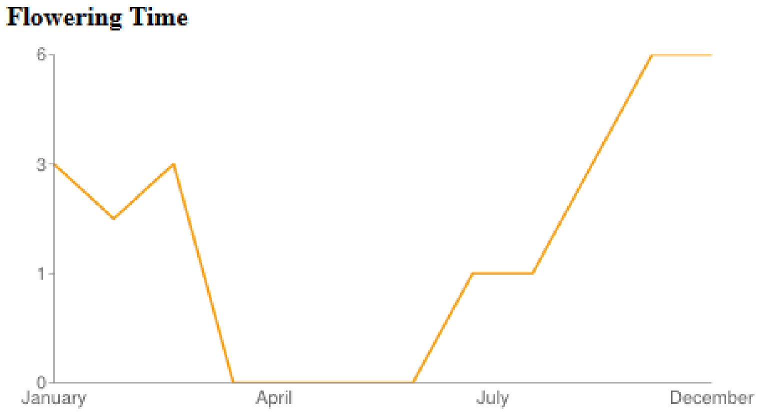
Family	Species	# Flowering	# Fruiting	#Flowering & Fruitin	N/A	In Koptur?	Synomyms	Atypical?	Elevation Difference?
Acanthaceae	Poikilocanthus macranthus	1				Y		X (fl) - late	Y
Acanthaceae	Habracanthus blepharorhacis		3			Y	Hansteinia blepharorhachis	X (fr)- >3m	N
Acanthaceae	Razisea Spicata	1				Y		X (fl) - >3m	N
Actinidiaceae	Sautauria montana			3		N			
Araceae	Spathiphyllum wendlandii	2				N			
Araceae	Anthurium microspadix		7			N			
Araliaceae	Oreopanax xalapensis	1				N			
Arecaceae	Chamaedorea sp	29	109	4		Y			Y
Arecaceae	Calyptrogyne ghiesbreghtia	11	57	3		Y	Calyptrogyne brachystachy	X (fr) - early	N
Arecaceae	Xanthosoma robustum		1			N			
Balsaminaceae	Impatiens walleriana	2				N			
Begoniaceae	Begonia involucrata		1			N			
Begoniaceae	Begonia cooper		2			N			
Bromeliaceae	Pitcairnia brittoniana	9				Y		X (fl)- >3m	N
Campanulaceae	Centropogon solanifolius	1				N			
Campanulaceae	Centropogon costaricae	4				N			
Clusiaceae	Chrysochlamys glauca		1			N			
Commelinaceae	Tradescantia zanonia	11				N			
Compositae	Koanophyllon pittieri			2		N			
Compositae	Clibadium leiocarpum		1			N			
Compositae	Jessea multivenia	2				N			
Conostegia	Conostegia rufescens	5				N			
Cucurbitaceae	Sechium pittieri			1		N			
Cyclanthaceae	Asplundia euryspatha	5				N			
Dilleniaceae	Saurauia veraguensis	1				Y		X (fl)- early	N
Dioscoreaceae	Dioscorea natalia	1				N			
Fabaceae	Mucuna urens		2			N			
Fagaceae	Quercus insignis		1			N			
Gentianaeae	Symbolanthus pulcherrimus	1				Y		X (fl) - late	N
Gesneriaceae	Besleria solanoides			4		Y		X (fl & fr) - >3m	Y
Gesneriaceae	Glossoloma tetragonum	20				N			
Gesneriaceae	Besleria notablis	21				Y			N
Gesneriaceae	Besleria triflora		17			Y			N
Gesneriaceae	Monopyle maxonii	1				N			
Lauraceae	Beilschmiedia costaricensis		1			N			
Melastomatacea	Ossaea micrantha	1		4		Y		X (fl) - >3m	Y
Melastomatacea	Miconia brenesii		1			Y			N
Monmiaceae	Siparuna tonduziana	1		2		Y			N
Myrantaceae	Calcthea marantifolia	3				N			
Ncytaginaceae	Neea psychotrioides		1			Y		X (fr) - >3m	N
Ncytaginaceae	Neea amplifolia	6				Y			Y
Piperaceae	Piper auritum	7				N			
Piperaceae	Piper hispidum		9		25	Y		X (fl & fr) - late	N
Piperaceae	Piper phytoloaccifolium		1			Y			Y
Piperaceae	Piper glabrescens				7	N			
Primulaceae	Parathesis glabra		3			N			
Rubiaceae	Hoffmannia congesta	164	185			Y	Xerococcus congestus Oer	X (fr) - late	N
Rubiaceae	Gonzalagunia rosea		4	9		N			
Rubiaceae	Hoffmannia tonduzii	23				N	Hoffmannia longipetiolata Pol.		
Rubiaceae	Psychotria carthagenensis	40	3			Y		X (fl) - late	N
Rubiaceae	Palicourea lasiorrhachis	2	22	5		Y	Palicourea yw-yw	X (fl)- late	N
Rubiaceae	Psychotria elata	85				Y	Cephaelis elata Sw.		N
Rubiaceae	Notopleura aggregata			19		N			
Rubiaceae	Psychotria chiriquiensis	1				N			
Rubiaceae	Notopleura uliginosa		2			Y	Psychotria uliginosa Sw.	X (fr)- early	Y
Rubiaceae	Psychotria hazenii			1		N			
Rubiaceae	Palicourea albocaerulea	1				Y	Palicourea oblong-blue berry		N
Rubiaceae	Psychotria steyermarkii	1				N			
Solanaceae	Witheringia solanaceae		54	2		Y			Y
Solanaceae	Acnistus arborescens	2				N			
Solanaceae	Cestrum button-berry			2		Y		X (fl & fr) - late	N
Solanaceae	Solanum pertenue		3			Y		Previously Unrecorde	N
Solanaceae	Lycianthes multiflora				1	N			
Urticaceae	Urera elata		43			N			

Appendix B

Hansteinia blepharorhachis


Flowering Time

Razisea spicata

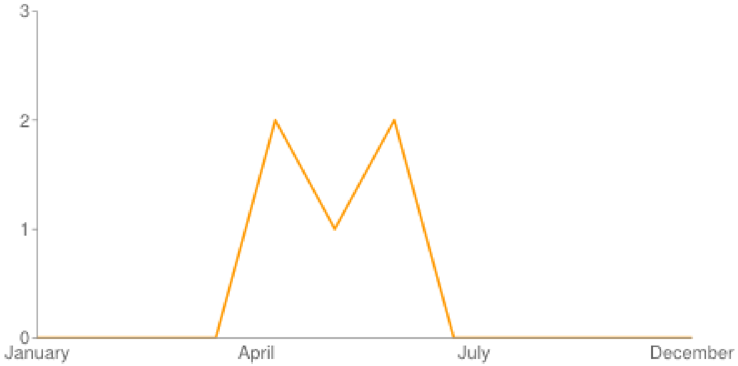

Flowering Time

Calyptrogyne ghiesbreghtiana

Flowering Time

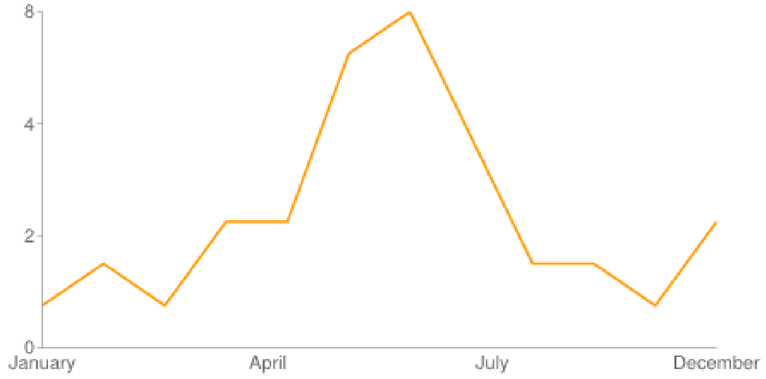
Pitcairnia brittoniana

Flowering Time



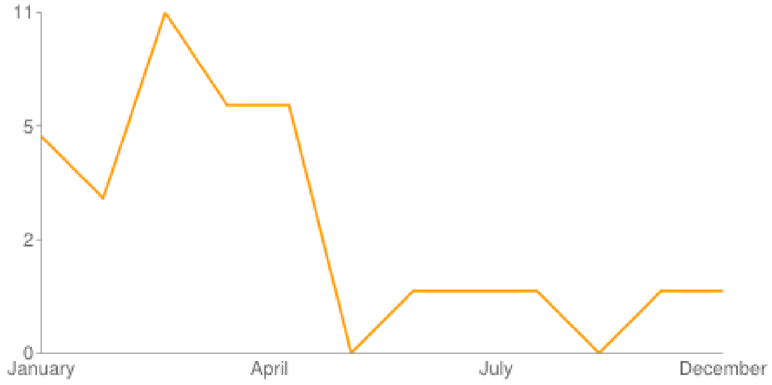
Symbolanthus pulcherrimus

Flowering Time



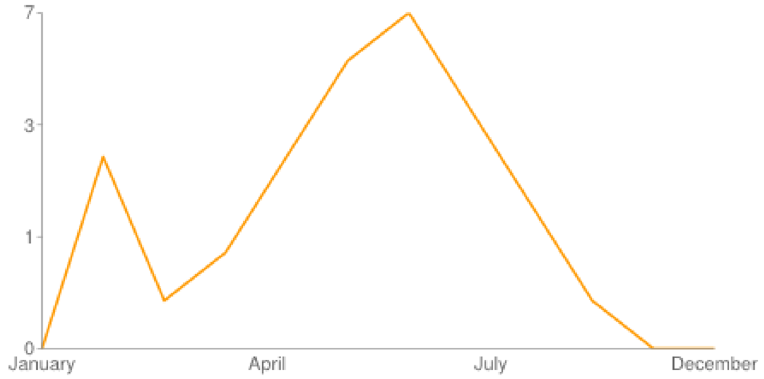
Besleria solanoides

Flowering Time



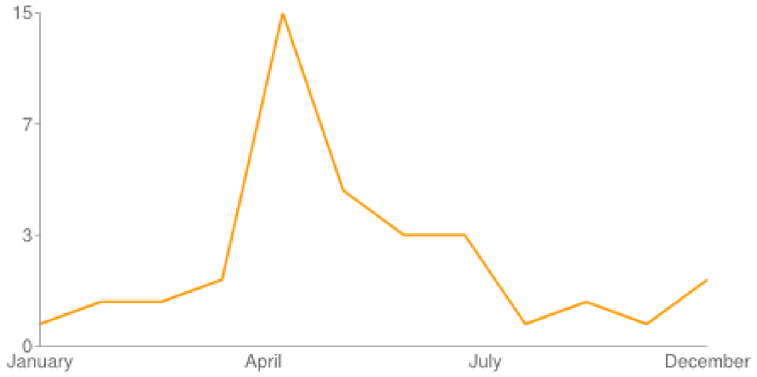
Ossaea micrantha

Flowering Time



Neea psychotrioides

Flowering Time

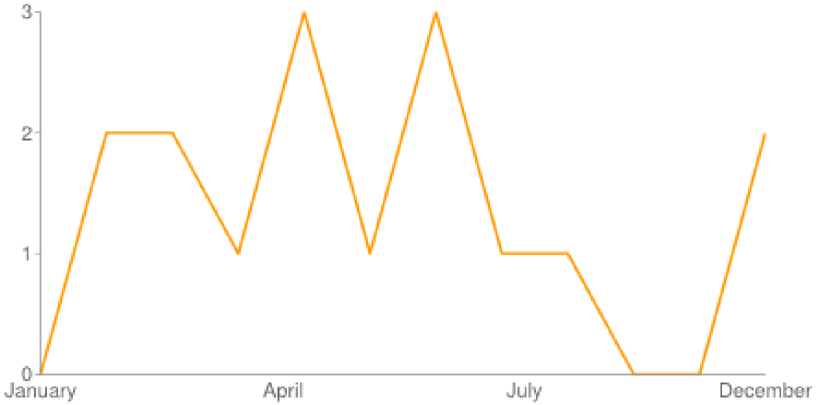


Piper hispidum

Flowering Time

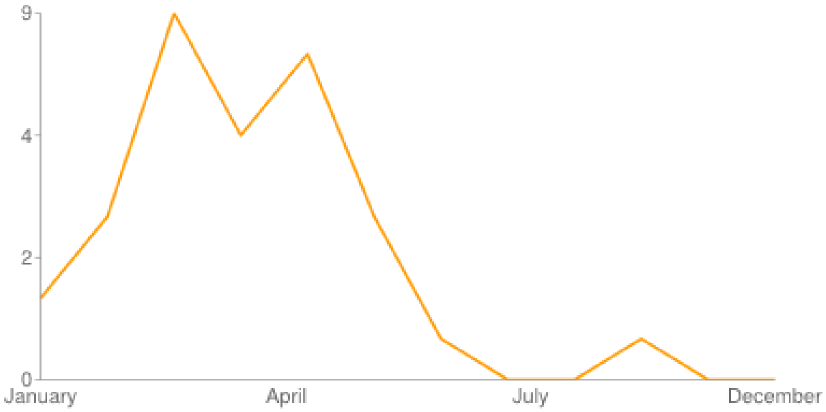
Hoffmannia congesta

Flowering Time



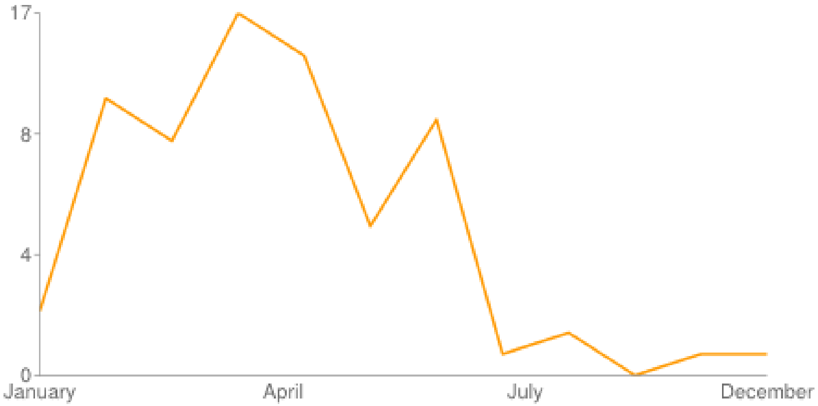
Psychotria carthagenensis

Flowering Time



Palicourea lasiorrhachis

Flowering Time



Notopleura uliginosa

Flowering Time