REPRODUCTIVE PHENOLOGY IN A LOWLAND DIPTEROCARP FOREST AND ITS CONSEQUENCES FOR SEEDLING RECRUITMENT

by

YU-YUN CHEN

(Under the Direction of Stephen P. Hubbell)

ABSTRACT

We carried out weekly surveys of flower and seed rain and annual censuses of seedling recruitment and survivorship using a network of 336 sampling locations in a mapped 50 ha plot of lowland dipterocarp forest in Peninsular Malaysia. The study ran between August 2001 and September 2006 and included four general flowering (GF) events of varying magnitudes. With the analysis of time series auto cross correlation, we found that 50.8% and 74.6% of the 126 study species exhibited supra annual flowering pattern and flowering synchrony with dipterocarp species in genus *Shorea* section *mutica*, respectively. Moreover, many of the supra annual species were synchronized in their flowering with species of the genus *Shorea* section *mutica*, which are the classical signature GF species. Flowering periodicity was significantly related to dispersal modes, the types of rewards offered by fruits to dispersers, and growth forms. However, fruiting periodicity was only related to reward types. The relationship of phenological patterns and functional traits supports the hypothesis of predator satiation, but also the hypothesis that species in the upper and lower canopy layers have different microclimatic triggers for flower induction. Among *Shorea* species there was no evidence of staggered flowering, but there was significant fruiting synchrony. Published methods using the flowering pattern of *Shorea* species in the section *mutica* to estimate floral induction time did not yield consistent dates for induction (5 or 7 weeks before the appearance of the first flower in *Shorea macroptera*, the first *Shorea* species to flower in a given GF season), but these methods assume that all species have the same trigger. Mortality was more strongly and negatively density dependent during the transition from seed-to-established seedling that during the transition from established seedling to yearling. However, we detected no difference in density dependence among various phenological groups. We also found no compensation in the strength of density dependence between the two sequential transitions. The loss in species diversity over time, as measured by Fisher's α, was greater in the seed-to-established seedling transition than in the established seedling-to-yearling transition. The one cohort of seeds produced in a non GF year lost more species diversity and evenness than the GF cohorts, and it remained in the lowest in diversity and evenness after the second year.

INDEX WORDS: Lowland tropical forest, Pasoh Forest Dynamics Plot, Malaysia, dipterocarp forest, Dipterocarpaceae, *Shorea*, *mutica*, the predator satiation hypothesis, the pollination facilitation hypothesis, dispersal saturation, the density dependence hypothesis, phenology, periodicity, synchrony, general flowering, auto cross-correlation function, D metric, evolution, diversity, evenness.

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DEDICATION

To Fauzi Mhd. B. Hassan

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TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS iv

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW 1

2 ASSEMBLY OF GENERAL FLOWERING AND THE EVOLUTIONARY IMPLICATION 10

3 REPRODUCTIVE PHENOLOGY OF *SHOREA* SPECIES AND THE TRIGGERS OF GENERAL FLOWERING EVENTS IN A LOWLAND TROPICAL FOREST 54

4 DENSITY DEPENDENT MORTALITY AND CHANGES IN SPECIES DIVERSITY AMONG GERMINATING SEEDS AND FIRST-YEAR SEEDLINGS DURING AND FOLLOWING GENERAL FLOWERING EVENTS IN A LOWLAND DIPTEROCARP FOREST 78

5 CONCLUSIONS 106

REFERENCES 115

APPENDICES 124

A TIME SERIES DATA AND AUTO CROSS CORRELATION FUNCTIONS (ACF) FOR 183 FOREST SPECIES 125

B ASSIGNMENTS OF PHENOLOGICAL PATTERNS AND ECOLOGICAL FUNCTIONAL TRAITS 217

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Background

Various phenological studies on plants, particularly trees, have shown that reproduction can be highly variable among years. Despite strong seasonality in temperate and some seasonal tropical forests, the reproductive performance of many species in these forests still fluctuates from year to year, and the patterns of fluctuation vary among species as well. Synchronized, supra annual seed production is observed in some temperate species such as in oaks of eastern North America, a phenomenon known as masting. This is synchronous fruiting within a single species population, resulting in much greater abundance of fruits in some years than in others. However, the aseasonal South East Asian lowland dipterocarp forests not only exhibit reproductive synchrony at species level, but also at the community level. This community-wide synchronized plant reproduction, often referred to as general flowering (GF), takes place at an irregular interval and involves many canopy species (Appanah, 1985; Sakai *et al.*, 1999b; Wich & van Schaik, 2000). Previous studies have also reported that GF events are synchronized not just in local forests, but also geographically throughout the aseasonal South East Asia region (Curran, 1994a; Maycock *et al.*, 2005; Numata *et al.*, 2003; Wich & van Schaik, 2000). However, most of these studies were based on only a few species in the family Dipterocarpaceae, and other studies only provided qualitative data or anecdotal evidence for GF events (Ashton *et al.*, 1988). Furthermore, many studies only conducted phenological surveys during GF periods (Appanah, 1985; Maycock *et al.*, 2005; Medway, 1972; Ng, 1977) or included only a single GF event in the study period (Sakai *et al.*, 1999b).

Previous attempts to study phenological patterns in GF events on the community level were made by trapping flowers and fruits under focal trees (Curran, 1994a) and scoring tree reproductive magnitude along transects (Sakai *et al.*, 1999b). A study on 54 dipterocarp species in west Borneo between 1985 and 1993 confirmed the irregular interval and infrequent occurrence of GF events (Curran, 1994a). Over a four-year period of observation of trees along forest transects in Lambir, Sakai *et al*. (1999) showed that more than 50% of the trees were reproductive during a single GF event in 1996. Although Sakai *et al*. (1999) attempted to identify periodicities for 305 species, they only observed a small number of individuals per species and one GF event in the study, and so the results were inconclusive. To thoroughly understand the ecology and evolution of synchronized supra annual reproductive phonological patterns in South East Asian forests, we need longer term studies on reproductive phenology across multiple GF and non GF events, and studies involving larger samples of the populations and species in the community of both flowering and fruiting phenology. This need motivated the present research.

Proximate cues

Many hypotheses have been put forth to explain the proximate cues for general flowering. Several studies have analyzed time series data of GF events and weather data to attempt to identify which climatic cues might be responsible for triggering flowering (Ashton *et al.*, 1988; Sakai *et al.*, 2006; Yasuda *et al.*, 1999). Among possible meteorological cues, three have bee the focus of most discussion: prolonged drought, increase of insolation, and drop of minimum temperature. Drought has been proposed as a GF trigger since the mid-20th century (McClure, 1966; Medway, 1972). However, evidence for and against drought as a trigger has been found in different studies using long term weather and GF records (Sakai *et al.*, 2006; Yasuda *et al.*, 1999). An increase in direct sunlight (reduced cloud cover) was also proposed as a cue by Ng (1977), but conflicting supports for this hypothesis was provided in the later studies (Ng, 1981;

van Schaik, 1986; Wright & van Schaik, 1994; Yasuda *et al.*, 1999). A drop in the minimum temperature (or low night-time temperature, LNT) was associated with GF events in studies at Pasoh, Malaysia (Ashton *et al.*, 1988; Yasuda *et al.*, 1999). However, Sakai (2006) did not find such correlations between LNT and GF events in a similar study conducted in Lambir National Park, Sarawak. All of these tests tacitly assume that the same cue operates on all species, but this might not be the case. All that is required is that the cues themselves be temporally autocorrelated for those species that participate in GF events. To the extent that participation of species in GF events is itself variable, this would also relax the necessity for all species to share the same flower induction cue. Local microclimatic conditions may also differ within the layers of a forest and between the forest and the surrounding area, due to a variety of factors, including topography. Microclimatic conditions inside forests are influenced by light intensity and spectral quality, humidity, and air movement. Therefore, the microclimate conditions experienced by an individual plant are inevitably affected by its immediate environmental conditions. If plant reproductive decisions are indeed affected by the microclimatic conditions the plant experiences, one would expect to find differences in reproductive performance, not only among individuals, but also among different canopy layers and/or forest patches. Any such variation in reproductive performance may provide insights into the triggers of GF events. The primary significance of climatic cues to flowering is likely to be a direct effect on the induction time of flower primordia.

Evolutionary causes

Hypotheses for the natural selective forces that led to the evolution of the GF phenomenon have been based on the argument of the economy of scale (Kelly & Sork, 2002). The two leading hypotheses are the pollination facilitation and the predator satiation hypotheses. The pollination facilitation hypothesis (Kelly, 1994; Sakai, 2002) argues that community-wide synchronous flowering attracts migratory pollinators to the flowering site. Moreover, the supply of a large quantity of food resource also allows short-lived pollinator populations to multiply several fold after feeding on flowers (Appanah, 1993). However, mass flowering at the community level could lead to pollen wastage and contamination, and to pollinator competition among related species, all of which could lower pollination success. Several mechanisms could also promote more effective pollination. A synchronized flowering within a given species minimizes pollen contamination from other species. In addition, segregated flowering peaks in close-related species could reduce the degree of competition for pollinators if pollinators are limiting (Ashton *et al.*, 1988; Lafrankie & Chan, 1991).

The predator satiation hypothesis (Janzen, 1974), focuses mainly on seed predation after seed fall. This hypothesis asserts that synchronized heavy seed production during GF events "satiates" seed predators, such that a greater proportion of seeds escape seed predation when tree species drop seeds synchronously than asynchronously because there are more seeds available in a short period of time that can be eaten before they germinate. The hypothesis asserts that the satiation of predators is more effective when fruit production only occurs at long and irregular intervals. This will keep seed predator populations low in the non GF periods due to a very low food supply, assuming that the seed predators do not have alternative foods to sustain them during these non GF periods. However, synchrony of fruiting may not be advantageous for frugivore-dispersed seeds. Short seed fall time provides a short window for the service of seed dispersal agents (Herrera *et al.*, 1998). Thus, temporally concentrated seed production may satiate seed dispersers and reduce effective seed dispersal distances or result in no dispersal, especially when species share the same seed dispersers, or when a disperser for one species is a seed predator on other species. Poor dispersal may lead to high mortality near parent trees at seedling stage due to negative density dependence (Connell & Green, 2000; Janzen, 1970). To achieve a better understanding of how predator satiation selects for synchronous reproduction, one must compare fruit availability and seed survival rates between GF events and non GF periods. Moreover, species having different fruit types and dispersal syndromes may experience different ecological costs and benefits from different seed predators and disperses, and thus are under different selection pressures. The joint effects of predator satiation and dispersal saturation mechanisms may therefore be complex, leading to tradeoffs in selection for reproductive periodicity and synchrony among species differing in fruit type and dispersal syndrome.

Density dependence and forest diversity

The density dependence hypothesis is one of the leading hypotheses proposed for the maintenance of species diversity in tropical forests (Janzen, 1970; Connell, 1971). This hypothesis proposes that there is an interaction between seed survival and seed dispersal, such that there is hither per capita and absolute survival for seeds traveling greater distances from the maternal parent. Most trees drop more seeds close to the mother, and the hypothesis asserts that these seeds suffer higher absolute and percent mortality because the dense concentration of seeds attracts more seed predators and grazers. Conversely more of the low-density, dispersed seeds escape from being found and eaten. Besides seed predators, pathogens spread faster in densely packed seedling patches than among seedlings occurring at low density (Augspurger & Kelly, 1984). This spatial pattern of mortality maintains tree diversity, according to the hypothesis, by reducing the probability that species replace themselves in the forest in the same locations, thereby opening space for other species. If the hypothesis is correct, then one expects populations of locally abundant species in the seedling layer to decrease more than populations of locally rare species (Webb & Peart, 1999). This effect prevents any species from dominating the seedling pool and evens out the probability of which species wins a given site (Blundell & Peart, 2004a; Harms *et al.*, 2000). However, the predator satiation hypothesis predicts higher per capita seed survival after massive seed production (Andersen, 1989; Curran & Webb, 2000). The net result of these two opposing ecological forces has not yet been examined simultaneously.

Objectives and approaches

The objectives of this dissertation are: (1) to understand the assembly of GF events, by which we refer to the temporal patterning of community-wide reproductive phenology and the participation, or lack thereof, of species in the community in GF events; (2) to attempt to evaluate triggers for GF and ultimate causes of the GF phenomenon; and (3) to examine effect of density dependence on seed and seedling survival and the change of diversity over time. In this study, I adopt the conventional approach and use the reproductive phenology of species from the genus *Shorea* section *mutica* to define GF events. I used two types of data in this study. First I used 336 passive seed traps, each measured to 0.5 m^2 in area, to document flower and seed rain in weekly survey in the Pasoh 50-ha Forest Dynamics Plot (the Pasoh FDP) for the past five years. In addition to seed traps, three 1 m^2 seedling plots were set out on three sides of each trap. Seedlings in seedling plots were recorded annually. The seed trap and three surrounding seedling plots constitute what is hereafter called a “trap station”, which becomes the basic unit for my analyses in the subsequent chapters. The data were collected over a five-year period and on relatively large spatial scales (50 ha), which allowed me to tackle each chapter's questions at broader scales compared to previous studies by other researchers. Detailed objectives and approaches for each chapter are described below.

In chapter 2, I used data collected from traps to identify basic phenological patterns in periodicity and synchrony of *Shorea* species in the section *mutica*, along with their time of reproduction, and lastly, the temporal variability of flower and fruit production. To achieve these, I first used an autocorrelation approach for the detection of periodicity. The second approach in this chapter was the use of the so-called D metric. This metric detects the degree of reproductive synchrony of any given species with *Shorea* species from the section *mutica*. Additionally, I used circular statistics to identify the seasonality of reproduction for the forest species at Pasoh. Lastly, I measured annual variability in reproduction by the coefficient of variation. A second part of this chapter examines the relationship between phenology and functional traits of Pasoh tree species, using a contingency table analysis. The functional traits evaluated in this study are pollination syndromes, dispersal modes, reward types in fruits, and plant growth form (adult tree height). In these tests, there were two pollination syndromes, animal and wind pollination, three dispersal modes, wind, ballistic, and animal dispersal, and three reward types, endozoochorous, dyszoochorous, and nonzoochorous, based on fruit morphology. Endozoochorous are types meant for passage through the guts of dispersal agents; dyszoochorous are seeds and nuts that are consumed by seed predators, but are not dispersed actively by animals' and nonzoochorous are seeds that are not dispersed or eaten by animals (typically they are wind dispersed, small seeds). The growth forms of plants distinguished in the analysis include lianas, emergent trees, main-canopy trees, and sub-canopy trees.

In chapter 3, I examine the extent of staggered flowering in *Shorea* species to assess whether there is evidence of character displacement. This test was done with a randomization test on the mean overlap of flowering among species. The same approach was applied to testing for synchronous fruiting among *Shorea* species. I used the regression approach of Ashton *et al*. (1988) to attempt to identify floral induction time for *Shorea* species. The floral induction time was estimated two ways, one based on presence-absence flower data, and the other based on phenology weighted by number of flower records. I then evaluated the calculated dates of estimated floral induction in light of weather data to attempt to identify possible proximate cues for GF events. Finally, I discuss possible physiological causes for the variable fruit development time that results in highly synchronized fruiting in *Shorea* species.

In chapter 4, I evaluated the strength of the density dependence in mortality affecting two transitions in the early life stage of plants: the seed-to-germinated seedling transition and the seedling-to-yearling (one-year-old) transition. I also tested for differences in the strength of density dependence among various phenology groups. Finally, I measure the changes in species diversity that occur over these early life stages and discuss the implications these diversity changes for the evolution of the GF phenomenon and the maintenance of tree diversity in the Pasoh forest. In the concluding chapter (Chapter 5, I give an overview of the results of the thesis bearing on the evolution of the GF phenomenon, as well as the evidence for GF triggers and selective forces. I speculate about other possible mechanisms for the community wide synchronous reproduction. I also discuss on the strength and weakness of the approaches applied in this study and limitation from our data to conclusion.

CHPATER 2

ASSEMBLY OF GENERAL FLOWERING AND THE EVOLUTIONARY IMPLICATIONS[1]

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Abstract

General flowering (GF) in Southeast Asian forests is thought to be a phenomenon that has arisen by natural selection from improved survival of seeds when reproductive phenology among individuals and species of trees is highly synchronized. The leading hypothesis for the selective mechanism of enhanced seed survival is seed predator satiation. There are two important elements to this hypothesis: (1) scarcity of seeds in the intervening periods between GF events, which reduces the size of seed predator populations, and (2) sudden, massive increases in seed abundances during the GF events, making seeds too numerous to all be eaten before they germinate by the limited number of seed predators that are present (predator satiation). Four general flowering events were recorded in a lowland dipterocarp forest between 2001 and 2006. Time series auto cross-correlation analysis allowed objective classification of 126 species into flowering periodicity classes (annual, biennial, supra annual) and of 100 species into fruiting periodicity classes. This analysis revealed that at least half and two thirds of the species in the study, respectively, flower and fruit supra annually. Furthermore, 74.6% and 63% of the species, respectively, showed synchronized flowering and fruiting with *Shorea* species in the section *mutica*. Flowering periodicity was significantly associated with growth form, dispersal mode, and reward type, whereas fruiting synchrony was significantly related to reward type, but not to growth form or dispersal mode. The results are consistent wit the hypothesis that frugivore-dispersed species are under selection for less synchronized reproduction because of competition for dispersal agents (dispersal saturation). Additionally, the relationship between flowering periodicity and growth form suggests that species in different canopy strata may receive different microclimatic flower induction cues that lead to different reproductive responses. The greater fruiting synchrony in large-seeded species vulnerable to seed predators,

compared with species whose seeds are dispersed by animals or wind, is strong support for the predator satiation hypothesis. The hypothesis was also supported by the fact that the greatest contributors to GF events were supra annual species. Fruits that suffer from seed predation were most common during GF events, whereas frugivore-dispersed seeds were more important in non GF years.

Introduction

General flowering (GF) is the term used to describe synchronous reproduction by many species at irregular, multi-year intervals in forests dominated by trees from the family Dipterocarpaceae in Southeast Asia (Appanah, 1993; Ashton, 1988; Curran, 1994b; Sakai, 2000). Synchronized flowering and fruiting events are distinct from non GF periods among both dipterocarp (Curran, 1994) and non dipterocarp species (Appanah 1985; Sakai et al. 1999), during which there is little or no flowering and fruiting. Interest in the GF phenomenon has focused mostly on the question of identifying the proximate cues triggering GF events. The hypothesized cues that have received the most attention are climatic fluctuations such as drop in minimum temperature (Ashton *et al*., 1988; Yasuda *et al*. 1999), drought (Sakai *et al*., 2006), and an increase in solar radiation (Ng, 1977). Analyzing a 19-year meteorological record and GF records for Peninsular Malaysia, Yasuda *et al*. (1999) concluded that low night time temperature (LNT) was responsible for triggering GF events. However, a study in a Bornean forest showed a high correlation between drought and GF events but no sign of a strong link between air temperature and GF (Sakai *et al*., 2006). Wright *et a*l. (1994) and van Schaik (1986) suggested that there might be a relationship between an increase in irradiance and GF events, based on a review of data from seasonal and aseasonal forests. However, most of the supportive evidence of an effect of irradiance on high reproductive performance came from seasonal forests, and Ng (1981) rejected the increased irradiance hypothesis with a reanalysis of data from a Malaysian forest.

The other major theme in the interest in the GF phenomenon is to understand the ultimate forces driving its evolution. The two leading proposed selective mechanisms are the hypothesis of pollination facilitation and the hypothesis of seed predator satiation (Curran & Leighton, 2000; Sakai, 2002). Pollination facilitation hypothesizes a buildup of local populations of generalist pollinators through immigration of nomadic species such as giant honeybees, followed by local recruitment as the GF event progresses (Sakai 2002; Appanah, 1993). Seed predator satiation hypothesizes starvation of seed predators during multi-year periods having very low levels of community-wide seed production so that their populations decline, followed by predator swamping and satiation by synchronous community-wide seed production during the next GF event (Curran *et al.*, 1999; Janzen, 1974).

The two hypothetical mechanisms work best with somewhat different levels of synchrony, and they operate on different stages of reproductive phenology. Pollination facilitation works when the community-wide floral display is large enough to attract nomadic pollinators and then continues long enough to allow local recruitment of pollinators. Flowering synchrony attracts immigrant pollinators, but prolonged flowering allows local recruitment during the GF event. On the other hand, seed predator satiation works best when community-wide seed production is so tightly synchronized that both resident and nomadic seed predators are overwhelmed. This difference in the degree of synchrony can be accommodated if early flowers take more time and later flowers take less time to develop into mature fruit. Exactly this happens within *Shorea* section *mutica* wherein early and late flowering species nevertheless disperse their seeds synchronously (Ashton *et al*. 1988, Chan & LaFrankie, 1991).

Although GF events may cause high seed survival due to predator satiation and safety in numbers, GF events may be disadvantageous for seed dispersal particularly in animal-dispersed species. For animal-dispersed seeds, synchronous seeding may lead to satiation of seed dispersal agents, resulting in less effective seed dispersal. GF events may also be disadvantageous if the populations of dispersers, not just the seed predators, are also kept low during the interval between GF seasons. Therefore, one would expect animal-dispersed species to exhibit more frequent and more regular seed reproduction rather than participating in sparse and irregularly spaced supra annual GF events. On the other hand, wind-dispersed, ballistic-dispersed, and gravity-dispersed seeds do not compete for seed dispersal agents. These mechanically dispersed species might reap the advantages of seed predator satiation during GF events without a concomitant cost in seed dispersal. Thus we expect wind-dispersed species to exhibit strong synchrony and high interannual variation in see production.

Temporal variation in community-wide plant reproduction underpins the two economy of scale hypotheses as well as the disadvantages that might be associated with them. Both pollinators and seed predators include generalists that are able to switch among host plant species, and the selective advantage of synchrony will be diluted if other potential host plant species reproduce between GF events. On the other hand, to increase dispersal efficiency, animal-dispersed species need to compromise on the frequency and intensity of reproduction and annual seeding variation.

There are at least two reasons that GF is potentially advantageous for the dispersal of pollen and disadvantageous for the dispersal of seeds. First, successful pollination requires directed pollen movement from a source flower to a target flower located on a different conspecific individual while successful seed dispersal only requires undirected movement away from the source tree. For this reason, successful pollination requires some minimal level of intraspecific synchrony. Both pollinators (i.e., giant honeybees) and seed dispersal agents (e.g., birds) immigrate to general flowering events. Many tropical forest plants are pollinated by small insects with short generation times that are able to reproduce and recruit a new generation during a single flowering event. On the other hand, primary seed dispersal away from the source tree is almost invariably by vertebrates (birds, bats and other mammals) that have much longer generation times and are unable to reproduce and recruit new individuals during a single fruiting season.

Community-wide studies of plant reproduction are needed to evaluate temporal variation at the appropriate scale. Most studies of GF have recorded the presence or absence of GF events or make quantitative measurements during GF but not during the long intervals between GF events. Exceptions are the quantitative monitoring of seedfall in dipterocarps for 8 years at Gunung Palung National Park, Borneo (Curran, 1994b) and qualitative monitoring of the reproductive status of 576 individual trees of 305 species at Lambir Hills, Borneo (Sakai *et al.*, 1999b). However, these studies did not have adequate sample size to answer the fundamental questions about the species participation and temporal organization of GF events and non GF flowering events, questions which are potentially important to forest dynamics and the maintenance of tree species diversity in these forests. There has been no attempt to monitor flowering and seedfall throughout the entire community. Lianas, for example, have been completely overlooked.

We used 336 passive seed rain traps to monitor community-wide flower and seed production from August 2001 through September 2006 at the Pasoh Forest Reserve, Malaysia. Following Ashton *et al*. (1988), we used species in section *mutica* genus *Shorea* as an indicator of GF events because these species only reproduce during general flowering events at Pasoh. Our record includes four GF events in August 2001, April 2002, November 2004, and April 2005. In the 2001, 2002, and 2005 events, flowering occurred in 19.8%, 35.7% and 65.1%, of all trees of the family Dipterocarpaceae > 30 cm in diameter at breast height (DBH) in the Paso 50-ha forest dynamics plot (Sun *et al.*, 2007), respectively. There were two exceptions: *Neobalanocarpus hemii*, which flowers annually, and *Hopea mengarawan*, which has no individual greater than 30cm DBH.

Here, we use the flower and seed rain data to answer the following questions:

1) What proportion of the species in the Pasoh forest reproduces continuously, biannually, annually, and supra-annually? We call these "periodicity groups".

2) When are the flowering and seeding times of these periodicity groups?

3) What proportion of the species in each periodicity group produced seed synchronously with the core *Shorea* section *mutica* species?

4) How do these phenological traits associate with the life history traits such as: i) seed dispersal mode, ii) fruit reward type, or iii) growth form?

To answer these questions, we examine the timing and quantity of flowers and fruits produced to determine how general flowering events are assembled in the hyper-diverse Dipterocarp forest of Pasoh Forest Reserve, Malaysia. We evaluate the periodicity of reproduction, the timing (mean date) of reproduction, within-species synchrony of reproduction, and among-species synchrony, to identify species that contribute to general flowering events, versus species that reproduce on other schedules. Periodicity can be classified into four categories: continual, biannual (twice each year), annual or supra-annual. Species can contribute to GF events in several ways. Continuously reproducing species might nevertheless produce their largest numbers of flowers and fruits during GF events. Biannual and annual species that reproduced at one or both of the two times of year when general flowering events occur might also produce larger numbers of flowers and fruits during GF events. Finally, supra-annual species that reproduce on the same schedule as the GF species of *Shorea* section *mutica* will most clearly contribute to GF events, but supra annual species that reproduce on some other schedule will not. We consider each of these possibilities.

We then evaluate three attributes of species that contribute to GF events versus species that reproduce outside general flowering events. The first attribute is fruit reward type, which is categorized as endozoochorous, dyszoochorous, or nonzoochorous. As the name implies, endozoochorous fruits offer a fleshy reward and eaten by dispersal agents, and the seeds are typically deposited after passage through the gut of the dispersal agent. Dyszoochorous species have seeds that not pass intact through the gut of the dispersal agent, and are typically dispersed as a byproduct of seed food hoarding. Nonzoochorous species are not adapted for animal dispersal. One might predict that GF species would have endozoochorous (berries and drupes) and dyszoochorous (nuts and legumes) fruits, whereas one would expect non-GF species to have nonzoochorous fruits (samaras and achenes). The second attribute concerns seed dispersal modes. We would predict that general flowering species will have seeds dispersed by mechanical means (wind, ballistic, gravity), while non-general flowering species will have seeds dispersed by animals.

Methods

Flowering and fruiting data collection

We used passive traps to collect the rain of seeds and flowers, and the traps were censused and emptied weekly. Each trap consisted of a square, 0.5-m^2 PVC frame supporting a shallow, open-topped, 1-mm mesh bag suspended 0.8 m above the ground on four PVC posts. There were 247 and 336 traps for weekly censuses 1-53 and 54-267, respectively. Traps were located at 13.5 m intervals on alternating sides of pre-existing trails and randomly between 4 and 10 m from the trail (320 traps) or in recent, natural tree fall gaps (16 of the traps added for census 54 on 1 September 2002).

All flowers, seeds, fruits, capsules, and other reproductive plant parts that fell into the traps were identified to species or to morpho-species and counted (only presence was recorded for flowers). Fruits and seeds were further categorized as aborted, immature, mature (endosperm filled), or damaged by insects or vertebrates. We estimated the number of whole fruits that were represented by fruit parts by dividing the number of seeds, capsules, fragments, and damaged fruits by the species-specific average part-to-fruit ratio; and we added this number to the number of undamaged fruits to estimate the total number of fruits of a given species falling into each trap. Identical methods have been used to monitor the rain of seeds and flowers on Barro Colorado Island (BCI), Panama for 19 years (Wright and Calderón 2006). We collected the data used in this study between August 20, 2001 and September 29, 2006. We summarize the flower and seed (in unit of fruits) rain data as a separate time series for each species in Appendix A.

Data anlysis

We report community-wide time series of the number of times flowers of a given species were present (henceforth records), the number of fruit captured, and number of species participating in reproductive activity at a given time. For statistical, sample size reasons, we limited single species analyses to species with a minimum of 30 records of flowers or fruits over the entire study period. A total of 162 species, including 127 tree and 35 liana species, met this criterion.

We assigned pollination syndrome, dispersal mode, and reward type to each species. The pollination syndrome was animal- versus wind-pollinated and was based on inferences from the flower morphology of the given species, rarely on genus or family level flower traits (Corlett, 2004). Dispersal mode included categories of animal-, ballistic-, and wind-dispersal. The ballistic- and wind-dispersal categories were later pooled as dispersal by mechanical means. Each assignment was based on fruit morphology and suggestions from other field observation (Corlett, 1998). Fruit reward type included endo-, non-, and dys-zoochorous fruits (Herrera *et al.*, 1998). Endozoochorous fruits provide a food reward to the visiting animals besides the seeds. Examples of endozoochorous fruits are berries and drupes. Nonzoochorous fruits, such as achenes, are usually small fruits that provide no extra nutritious values other than seeds but are so small that most vertebrates ignore them. Dyszoochorous fruits are large fruits that provide no extra reward other than the seeds themselves. Dyszoochorous seeds are likely to suffer from seed predation during animal visits although some seed dispersal could occur via scatter hoarding or accidental loss during transport by animals (Jansen *et al.*, 2004; Wells & Bagchi, 2005). We followed suggestions from the Forest Research Institute of Malaysia on the assignment of growth forms of emergent, canopy, understory treelet, and shrub. However, to increase effective sample sizes for categorical analyses, we pooled the categories of understory and shrub as understory trees.

Periodicity

We used auto correlation analyses to help identify periodicity for each species. Each time series data vector contained the number of flower records or the number of fruits for all 267 weeks. The auto correlation analysis involved lagging each time series by $1 \leq x \leq 215$ weeks and then calculating a Pearson correlation coefficient (r) for the number of flower records or the count of fruits for the $267-x$ weeks of overlap between the original and lagged time series. To help visualize periodicity patterns, we created plots of correlation coefficients versus time lags (auto correlation function, ACF, hereafter) (Appendix A). ACF plots often have a local maxima at $x=1$ and decline quickly toward $r=0$. We used subsequent local maxima in each ACF and the observed time series to evaluate periodicity (Appendix A). Continuously reproducing species lacked subsequent local ACF maxima, had records in four or more years, and had records in each quarter of the year. Biannual species had records concentrated at two times of year and tended to have local ACF maxima near $x=26$ weeks and at larger multiples of 26 weeks. Annual species had records concentrated at one time of year and tended to have local ACF maxima near $x = 52$ weeks and near larger multiples of 52 weeks. Supra-annual species had the largest local ACF maxima near 2.5 or 3 years and lacked records for extended periods. The ACF maxima near 2.5 years will be explained below. We made independent decisions on flowering and fruiting periodicities for each species.

Mean vector

We used circular statistics to calculate mean vectors of flowering and fruiting dates for each species. A mean vector combines all records as individual vectors and provides an angle and a length from the final vector as the overall measures of mid-date as day of the year and the relative duration of the reproductive events. Dates from the records of a species were converted into days of the year and then to a corresponding circular angle (Φi) in radians (Hamann, 2004; Wright & Calderon, 1995). A vector length (r) combines the strength of all individual vectors (records) and represents the joint strength; it is calculated with formula (3). Combined angle is then calculated with formula (4).

$$x=\sum \cos(\Phi i) \qquad (1)$$

$$y=\sum \sin(\Phi i) \qquad (2)$$

Mean vector length (duration): $r = (x^2 + y^2)^{1/2} / \sum n_i$ (3)

Mean vector angle (mid-day): $\Phi = \mathrm{atan}(y/x)$ if $x > 0$

or $\Phi = 180 + \mathrm{atan}(y/x)$ if $x < 0$ (4)

The overall angle of each vector can be converted back to actual dates of the year to provide the information of the mid-flowering/fruiting dates. Mean vector calculations are problematical for species that reproduce at more than one time of the year. For example, a species that flowered on 1 January and 1 July would have a mean vector angle that fell arbitrarily on 1 March or 1 September and a mean vector length of zero. All biannual species and many supra annual GF species reproduced at two different times of year. To avoid problems with mean vector calculations, we calculated mean vectors for 26-week subsets of the entire time series for these species. We calculated mean vector lengths with the first 26-week subset beginning at a lag of 0-25 weeks. The lag, *x*, associated with the largest mean vector lengths was then used to determine the beginning of the reproductive year for all biannual and many supra-annual GF species, with the reproductive year beginning *x* weeks after 20 August (the date of the first census). The same date was used to divide years to calculate coefficients of variation of seed production (see Methods: Coefficient of variation).

Synchrony with mutica species

To identify species that reproduced during GF events (henceforth GF species), we evaluated the temporal association between reproduction for each species and the pooled reproduction of the six species of *Shorea* section *mutica* present in the 50-ha plot at Pasoh. These six species only reproduce during GF events (Ashton et al. 1988). Four flowering windows and three fruiting windows of the GF events were defined in formula (5) below. We evaluated temporal association using randomizations and time series cross correlations for species with no less than 30 or more records of flowers or fruits.

We performed cross correlations for the number of flower records (or seeds captured) for lags of −10 to +10 weeks. The cross correlations were between the number of flower records (or fruits captured) for each non-*mutica* species and the equivalent numbers summed over the six *mutica* species. Significant positive cross correlations identify species that reproduce with similar timing as *Shorea* section *mutica*. The lag indicates whether the species flowered simultaneously (lag = 0), before (lag < 0) or after (lag > 0) the pooled species of *Shorea* section *mutica*.

We performed randomizations using metrics designed to complement the cross correlation analyses by varying the importance assigned to timing and intensity. To evaluate lags, we recalculated the observed metric after shifting the windows of flowering (or fruiting) for

Shorea section *mutica* by −10 to +10 weeks. Each randomization had 267 possible values obtained by shifting the number of flower records (or seeds captured) by one census week for the species being evaluated with the final census, wrapping around to become the first census. The temporal association with *Shorea* section *mutica* was significant if the observed metric fell in the appropriate extreme 5% (a one-tailed test) of the 267 randomized metrics for each lag.

The metric D_s removed the effect of the intensity of reproduction as follows:

$$D_s = \begin{cases} \sum\limits_{t}\sum\limits_{c} N_{stc}, & \text{if } 1<c<10 \text{ or } 33<c<49 \text{ or} 165<c<176 \text{ or } 188<c<205 \\ 0, & \text{otherwise} \end{cases}$$

where N_{stc} represents the number of flower records for species *s* in trap *t* and census *c*. The censuses 1-10, 33-49, 165-176, and 188-205 included 95% of all *Shorea* section *mutica* flowers. The metric D_s is simply the number of flowers of the species being evaluated captured in censuses that included less than 5% of all *Shorea* section *mutica* flowers. The following formula calculates the number of fruits in the *mutica*-defined windows.

$$D_s = \begin{cases} \sum\limits_{t}\sum\limits_{c} N_{stc}, & \text{if } 20<c<27 \text{ or } 48<c<59 \text{ or } 204<c<214 \\ 0, & \text{otherwise} \end{cases}$$

Coefficient of variation

The coefficient of variation (CV) provides information on year-to-year variation in plant reproduction. It is calculated as the ratio of the standard deviation to the mean of flower or fruit production in a given species. In calculating annual CV, we explored CV variation within a yearly time frame with time lags of 0-25 weeks. A lag of zero weeks defined the years with the first week of our study as the first week of the first year; a lag of one week defined the years with the second week of our study as the first week of the first year; and so on. We chose a maximum lag of 25 for this study because it is the limit of detection for biannual species and possibly in supra annual GF species. We also calculated community maximum annual CVs of flowers and fruits. In addition to maximum CV, we calculated seasonal CV for biannual species, which had two reproductive events each year. We also calculated biannual CVs for supra annual GF species because some GF events occurred in two seasons which were approximately six months apart in our records. We used the species-specific cutting point derived from the mean vectors to define the two halves of a year for each species. We report the maximum annual CVs for all species, and the biannual CVs for biannual species and supra annual GF species. Seasonal CV for each species was the annual CV for continuous, annual, and supra annual nonGF species and the biannual CV for biannual and supra annual GF species. We calculated flowering and fruiting CVs independently.

Relationship of phenology to reward type, dispersal mode, and growth form

We performed contingency analyses to evaluate possible associations between fruiting phenological patterns, fruit reward type, seed dispersal mode, and growth form. Phenological patterns showed significant as well as insignificant associations between seedfall and general flowering events, as determined by the D-metric described above. Fruit reward types were endozoochorous (berries and drupes), dyszoochorous (nuts and legumes), and nonzoochorous (samaras and achenes). I also condensed seed dispersal modes into two classes to improve sample sizes; these dispersed by animals (birds, mammals) versus those dispersed by mechanical means (wind and ballistic). Similarly, I condensed growth forms into three classes: climbers (vines, woody lianas), sun-exposed trees (canopy, emergent), and shaded trees (mid-story trees, understory trees, shrubs). Species in the former two life forms reproduce when their crowns are in full sun, whereas specie in the third life form reproduce in the shade of taller trees. Sample size requirements are stringent for contingency analyses. All expected values must be greater than one and 80% of expected values must be greater than five. Thus, the number of species with known fruiting patterns (N = 101) precluded a four factor analysis. Moreover, two types of structural zeros complicated any analysis that included fruit reward type and seed dispersal mode. Structural zeros occurred because the seed of all endozoochorous fruits are dispersed by animals and the seeds of all nonzoochorous fruits are dispersed by mechanical means.

In addition, we examined the relationship of temporal variation of flower and seed production to the ecological functional traits of species. We carried out an analysis of variance to investigate the discrepancy of annual CVs between groups of pollination syndrome, reward type, dispersal mode, and growth form. A significance level of 0.05 was used.

Results

We recorded the presence of a species as a flower, a seed or fruit on 35,408 and 67,438 occasions, respectively, in 84,995 trap weeks spread over 267 weekly censuses. We identified 410 species of trees and 124 species of lianas. Some liana species were only morpho-species, whose flowers and fruits were associated with an adult plant in the field, but the adult plant remained unidentified. We recorded an additional 870 morpho-species of flowers, seeds or fruits that could not be associated with an adult plant in the field. The latter 870 morpho-species comprised just 1.76% of all reproductive records and were excluded from all analyses.

The temporal distribution of flower and fruit records suggests four periods of elevated reproductive activity (Fig. 2.1A). Numbers of flower records were elevated between August 20 and December 10, 2001, March 25 and July 19, 2002, September 6 and December 27, 2004, and March 7 and July 25, 2005. Numbers of fruit records were elevated shortly after each peak of flower production. Numbers of records were greatest in the spring of 2002 and 2005 for both flowers and fruits. The same four peaks were evident for the number of species recorded (Fig. 2.1B). The number of species recorded was also high at other times, however, including the first half of 2004 for both flowers and fruits and the first half of 2006 but only for flowers.

Periodicity

We evaluated flowering periodicity for each species with 30 or more flower records and fruiting periodicity for each species with 30 or more records, for mature fruit, seeds, capsules and fruit fragments. These criteria were fulfilled for 142 species for flowers, 102 species for fruit, and 82 species for both flowers and fruit. We were unable to assign periodicity for flowering and fruiting for 13 and 2 species, respectively. Not surprisingly, those species tended to have smaller numbers of records (Fig. 2.2). We still retained the minimum sample size criterion of 30 records because periodicity was clearly evident for 84% of the assessments based on 30 to 39 records (Fig. 2.2A and B).

We found 8 (6.3%), 17 (13.5%), 37 (29.4%), and 64(50.8%) of the 126 flowering species exhibiting continuous, biannual, annual, and supra annual patterns, respectively (Fig. 2.3A). There were 4 (4%), 11 (11%), 19 (19%), and 66 (66%) of the 100 species exhibiting continuous, biannual, annual, and supra annual patterns, respectively, in fruiting (Fig. 2.3B). Supra-annual flowering and fruiting characterized slightly more than half and two thirds of the species, respectively.

Among 79 species that have both flowering and fruiting periodicity assignments, 69 species were the same in periodicity class based on flower and fruit production (Table 2.1). Among the 10 species with incongruity between flower and fruit periodicities, eight species had more frequent flowering than fruiting while two species showed a biannual flowering pattern and continuous fruiting pattern. Among the 10 species, eight exhibited more frequent flowering but less common fruiting. *Ardisia crassa* (ARDICR) and *Durio grifithii* (DURIGR) displayed a biannual flowering pattern and a supra annual fruiting pattern. *Archidendron bubalinum* (ARCHBU), *Grewia miqueliana* (GREWMI), *Paropsia vareciformis* (PAROVA), *Trigoniastrum hypoleucum* (TRI1HY) flowered annually but only showed supra annual fruiting. Additionally, a liana species (CLM011) and a tree species (POL1RU, *Polualthia rumphii*) changed from a continuous to an annual pattern and from a biannual to an annual pattern, respectively. Several factors could contribute to this change. For instance, an unsuitable environment for fruit development and predation before seed maturation could eliminate the majority if no whole crop before seeding. On the other hand, one tree species, *Gironniera parvifolia* (GIROPA), and a liana species, CLM070 showed a biannual flowering pattern but a continuous fruiting pattern. This could be due to high variation in fruit development time within an individual plant. Despite some failure in fruit development, most species were consistent in periodicity throughout the study in their reproductive pattern.

Mean day and width of reproduction

The mean flowering day of species in each periodicity class showed differentiation among classes (Fig. 2.4). Flowering seasonality was determined by the flowering rhythm of a species, independent from a calendar season or year. This calculation yielded a mean Julian day of the year over all years of the study. We then calculated the overall mean of these per-species mean Julian days as the mean flowering day. The classes of continuous and annual species exhibited a unimodal distribution of mean flowering days for the species. On the other hand, species in biannual and supra annual classes showed a bimodal distribution. In this case, each species may be represented by two values for each of the flowering seasons. Continuous species had a scattered distribution of records (Appendix A) and most species had a mean flowering date between June and August (Fig. 2.4, first column), but with little central tendency (short vector length). A more concentrated flowering pattern with larger vector length on flowering dates was evident in annual species (Fig. 2.4, third column). The peak month with the highest number of species was in July for the class of annual species. In contrast, species in the biannual and annual classes both had more species in flower in two seasons: April to May and August to October (Fig. 2.4, second and fourth column).

The number of species with continuous fruiting is low (2) and these two species showed short vector length and the fruiting season as July. This was likely due to their scattered records. Following flowering, annual species exhibited a single peak in fruiting, whereas biannual and supra annual species showed a bimodal pattern in fruiting (Fig. 2.5). Annual species also exhibited shorter vector lengths than the biannual and supra annual species.

Synchrony with Shorea section mutica

Species of *Shorea* section *mutica* are believed to reproduce only during GF events at Pasoh (Ashton *et al*., 1988, LaFrankie & Chan, 1991). We encountered just one flower and no seeds or fruits of species of *Shorea* section *mutica* outside the four periods of peak production in fig. 2.1A. For these reasons, we used the overlap in the timing of reproduction by the six pooled species of *Shorea* section *mutica* to identify species that participated in GF events. Overlap of flowers was measured as the proportion of flower production that coincided with seed from *mutica* species (flower records with *mutica* windows/ total flower records). All evaluated for time lags of -10 to +10 weeks. The same procedure was applied to fruit counts. Each species with significant overlap for any lag was identified as a general flowering species. Significant general flowering species included 88 of 129 (68.2%) species evaluated for flowers and 58 of 100 (58%) species evaluated for seeds and fruits (these numbers exclude *Shorea* section *mutica* species).

We then combined assignments to the four periodicity and two general flowering categories (Fig. 2.3). Surprising numbers of species that reproduced continuously, biannually and annually had significant overlap in flower and/or fruit production with *Shorea* section *mutica* because levels of production were greater during GF events when *Shorea* section *mutica* also reproduced. The percentages of continuously, biannually, annually and supra-annually flowering species that overlapped significantly in time with *Shorea* section mutica was 62.5%, 70.6%, 45.9% and 93.8%, respectively. The percentages of continuously, biannually, annually and supra-annually fruiting species that overlapped significantly in time with *Shorea* section *mutica* was 50%, 54.5%, 52.6% and 68.2%, respectively. Nine out of ten *Shorea* species fell into the supra annual-GF category in flowering. The only exception was *Shorea ovalis*. However, all *Shorea* species exhibited supra annual-GF fruiting pattern.

Coefficient of variation

The uneven temporal distribution of flowers and fruits is shown in Fig. 2.1. The maximum annual CVs of flowers and fruits were 141.37 and 141.11 across all species including morpho-species. At the species level (162 species), fruit CVs were generally higher than flower CVs (Fig. 2.6). In the 162 species examined, maximum flower and fruit annual CVs were neither congruent nor interrelated (Fig. 2.6) in three of the four periodicity groups (continuous, biannual, and annual; general linear regression, df = 2, 13, and 17 for each group, respectively. P-values > 0.05 for all groups). The exceptional class in which species flowering and fruiting CVs were significantly correlated was the supra annual species (General linear regression, df = 45, $p<0.05$). Most species exhibited higher CVs in fruits than in flowers. Similar trends were found among GF and nonGF species in each periodicity class (data not shown).

Examination on the relation of annual and biannual CVs in biannual and supra annual GF species showed a significant correlation between the two sets of CV values (General linear regression, df = 72, $p < 0.0001$ for flowering, fig. 2; df = 77, $p < 0.0001$ for fruiting).

Among the different periodicity classes, mean CVs were calculated and compared among the four classes (Table 2.2). Only the supra annual species showed a significantly higher CV than the rest of the more frequently flowering species. This was true in both maximum annual CVs (ANOVA, df = 87, $p<0.0001$ for GF species; df = 27, $p<0.05$ for nonGF species) and seasonal CVs (ANOVA, $p<0.0001$ for GF species; $p<0.01$ for nonGF species). The same trend of variations was evident in fruiting among the groups of GF species (ANOVA, df = 66, p<0.001 for max. CV; p<0.0001 for seasonal CV) but not the nonGF species (df = 14, p>0.05).

Relation of flowering patterns to phylogeny, dispersal mode, and life history traits.

We included all species with assignments of phenological types and ecological functional traits in this analysis. Traits under examination were growth form, dispersal mode, and reward type. Temporal periodicity of flowers was significantly related to all three traits. GF feature in flowering, defined as synchronized flower production with species in *Shorea* section *mutica*, was not associated any of the three ecological functional traits. Growth form, mode of dispersal, and reward type were not associated with fruiting periodicity. We found only reward type significantly related to GF feature in fruiting (Table 2.3).

We further examined the distribution of species into periodicity classes of 128 and 113 species in flower among the four growth forms and three reward classes. Disproportional high number of supra annual species occurred in the liana class and emergent tree layer than the two lower canopy layers (Fig. 2.7A). More annual species than species with other periodicities were observed in the understory layer. The dyszoochorous and nonzoochorous classes of fruits had more species exhibiting a supra annual pattern, whereas more annual and biannual species were evident among endozoochorous species (Fig. 2.7B). Examination of the distribution of these classes among GF events indicated that species in dyszoochorous group differed significantly among low and high GF events (Fig. 2.8). No clear difference was evident in the other two classes.

At the species level, we examined four classes of CV: Maximum CVs and seasonal CVs for flowers and maximum CVs and seasonal CVs for fruits, to explore the association of within-species variation in flower and fruit production and ecological functional traits. Examination of the means of the CVs in the two classes of pollination syndrome (Table 2.4) showed no significant difference between the two classes either in flowering or fruiting. Dispersal modes, on the other hand, showed an effect in three out of four tests on flower CVs but not on fruit CVs (Table 2.4). When breaking the dispersal mode into more detailed classes (animal-, ballistic-, and wind-dispersed), we found that the effect of dispersal on flower CV became insignificant with maximum flower CVs (P-value = 0.058). Mean CVs were significantly different in the reward classes in both maximum and seasonal CVs, with the highest mean CV in the dyszoochorous group and the lowest mean CV in the endozoochorous group (P = value < 0.05).

Assembly of community reproductive pattern

Based on the periodicity assignment, we examined the relative contribution of each periodicity class to the community (Fig. 2.9). Species flowering fluctuated the most in the supra annual class and the least in the continuous class (Fig. 2.9, upper panel). Annual CV of number of flowering species in the continuous, biannual, annual, and supra annual classes were: 7.4, 8.8, 23.3, and 49.6, respectively. A larger difference between the supra annual classes and the other three classes was shown in flower production indexed with flower records (Fig. 2.9, lower panel). The annual CVs of flower records were 65.2, 65.7, 62.3, and 119.4 for continuous, biannual, annual and supra annual classes, respectively. In the high flower production seasons, supra annual species contributed the most of the reproduction during the seasons. However, during the low seasons, higher contribution came from biannual and annual species. Continuous species were rare and contributed less than the other three classes at all time except when compared to supra annual class in the low seasons. A similar trend was evident in fruiting (Fig. 2.10).

We also examined the contribution of reward types to the fruiting pattern in the Pasoh forest (Fig. 2.11). At the species level, participation of endozoochorous and dyszoochorous species was of similar importance during GF period. However, endozoochorous species were relatively more important in the nonGF seasons compared to the other two types. Nonzoochorous species showed higher participation in GF years but the number of species participating was lower than the other two groups during the events and its species participation was at a similar level as dyszoochorous species in nonGF seasons (Fig. 2.11, upper penal). On the other hand, fruit production of endozoochorous and nonzoochorous types were of similar magnitude and pattern over time. Lower quantities of fruits from these two groups compared to fruits from the dyszoochorous species were caught in traps during GF events. In contrast, the endozoochorous and nonzoochorous species contributed higher quantities of fruit production in nonGF periods (Fig. 2.11, middle and lower panel).

Discussion

It has been reported that SE Asian tropical forests exhibit a weaker annual pattern in plant reproduction compared to the neotropical forests (Sakai, 2002). Sakai (2002) reported that more than 80% of the species in the Lambir forest could be classified as supra annual species. However, this study showed that 49.2% of the species exhibited annual pattern (with one, two, or continuous flowering event in a year) and 50.8% of the species exhibited supra annual flowering pattern. The low percentage of supra annual species at Pasoh could be attributed to the inclusion of rare reproduction. Species that reproduce frequently and regularly are more likely to generate enough flowers and fruits to meet the criterion set for our analyses, >30 records. In other words, under-sampling is more likely to occur in the infrequently flowering species. For many forest species in Pasoh, no flower or fruit was caught by traps although the trap system is surrounded by more than 600 tree species and is likely to sample all the lianas in this forest. We suspect that many species are rare in either their reproductive frequency or their abundance, or a combination of these two.

Proximate cues for GF

The evolution of GF has been explained by various proximate cues and ultimate forces, but no consensus has yet been reached. Drought, low night-time temperature, and increased irradiation along with other meteorological measurements were proposed as the candidates of proximate cues for GF. However, time series analyses from the region are scarce, and there is little confirmation of the role of particular cues in the triggering of GF events. Two studies reported LNT (or lower nighttime temperature) as the correlated cue to GF for peninsular Malaysia. However, these two studies proposed different mechanisms for the drop of temperature. Ashton *et al*. (1988) proposed a cooling effect results from the penetration of dry air into the forest during periods of low humidity and rainfall (cloudless days). The dry air is caused by the anomalous convection from El Niño Southern Oscillation (ENSO) obstructing the trade wind that usually brings rain to the East slopes of Malesia. On the other hand, Yasuda *et al*. (1999) proposed the La Niña-STR (northern subtropical ridge) mechanism for the drop of LNT. The argument of this mechanism builds upon two factors. Firstly, annual low temperature in this region often occurs in January under the influence of Asian winter monsoon. Secondly, the winter monsoon is intensified by La Niña with the anomalous increase of sea surface temperature in the west Pacific, through the local meridional Hadley Circulation, the rising air from the equator that sinks at the subtropics. During La Niña, the low-level northern subtropical ridge (STR) is intensified and this brings the cold surges from the north to SE Asian region. This cold surges plays an important role, if not the only, in cooling the air in this region.

Under the El Niño mechanism, we expect that the cooling effect operated through the reflection of heat to the space during the night. Furthermore, if cooling acts as a function of humidity of the air, we expect the strength of the effect to differ form the emergent layer to the understory layer. However, the cooling by cold surges suggested in the La Niña-STR hypothesis may lead to a more uniform temperature decrease in the forest, above and under the continuous canopy. If LNT is the trigger of GF, we would expect the higher canopy crowns to respond differently from the understory layer under El Niño mechanism. On the other hand, we should not see a difference between the higher layers of canopy and the understory is temperature cooling is via La Niña-STR mechanism. Our data indicated a significant discrepancy in proportion of Supra annual GF species between the upper canopy layers and the understory layer and trended towards the prediction under El Niño hypothesis.

Changes in levels of sunlight are strongly associated with the El Niño Southern Oscillation at Pasoh. During El Niño, there are fewer clouds, lower rainfall and lower humidity so that more sunlight penetrates the atmosphere and reaches the forest. On the other hand, enhanced cold surges during La Niña events bring rain to SE Asia, and increased cloud cover and humidity so that less direct sunlight reaches the forest. Clouds and water vapor in the atmosphere diffuse sunlight, however, and diffused light penetrates deeper into forest canopies than direct sunlight. As a consequence, the amount of direct plus diffused light that reaches understory plants may vary less between El Niño and La Niña conditions than does the amount of direct sunlight that reaches sun-exposed canopy trees. Thus, the sunlight hypothesis would predict a greater proportion of GF species in the canopy layer. Increased direct sunlight, however, coincides with the drop of LNT, under the El Niño hypothesis. The two could act as the co-triggers of GF unless more evidence could disentangle the fine difference between the two factors.

There are many complications relating drought as a proximate to GF. Firstly, intensity of drought could not be explained solely by the factor of rainfall but also the combination of soil and topography. Secondly, effect of drought on plants is complicated and is likely species- and tree size-dependent. Thirdly and lastly, plant reproduction could be triggered both by watering and lack of water in species in various regions. However, despite the complications, drought was proposed in many occasions, with and without strong support, as an important candidate for GF triggering factor. Our data could not, however, provide sufficient support for either hypothesis due to lack of spatial context. Direct long term monitoring of soil water potential in a wide spatial range is suggested in order to resolve the relation of drought to GF.

Ultimate selection forces

In the investigation of relations between phenological patterns and species' functional traits, we found supporting evidence for the predator satiation hypothesis and the dispersal saturation hypothesis. The predator satiation hypothesis predicts strong synchronization and high annual variation for dyszoochorous species that suffer from seed predation. On the other hand, dispersal saturation hypothesis predicts lower degree of reproductive synchrony and variation for endozoochorous species that rely on animals for dispersal. Supportive evidence for effects of reward type and dispersal mode on periodicity was found in the flowering stage. We discovered that more dyszoochorous species are supra annual species and these species exhibited highest annual CV among the three reward types. In addition, higher proportion of frequent flowering species and lower annual CV in endozoochorous species were consistent with the predictions from the dispersal saturation hypothesis. This suggested a strong selection through predator satiation and seed dispersal. In contrast to the flowering stage, effect of reward type and dispersal mode on periodicity of fruiting was not significant. We speculated that this insignificant pattern in fruiting might be due to various conditions in fruit development. For instance, resource limitation and heavy seed predation may eliminate some crops and reduce the others. This did not imply lack of effect from predator satiation. On the contrary, seed predation may be reducing the significance of the effect upon fruit maturation. However, result of selection via predator satiation during synchronous reproduction, in the form of high seed survival, was reflected in the flowering stage for it is the necessary stage of reproduction. The insignificant effects of traits on the fruiting pattern suggested that flowering may be a better indication of impact from natural selection than fruiting. This may be due to less noise from the environment during the flowering stage. Therefore, drawing conclusions on the evolution of GF from merely fluctuations of seed production may be biased and misleading.

On the synchrony feature, only reward types showed a significant relation with GF features. This was strong evidence supporting the predator satiation hypothesis, despite seed damage during development. Disregarding the periodicity types, seeds that suffered significant predation synchronized in a higher degree than seeds on the other end of the reward type spectrum.

GF assembly

Flower and fruit production is highly variable over time in the SE Asian lowland forests. The distinguishing peaks of flowering and fruiting occurred during GF and were built upon the contribution of many plant species, with the highest contribution from supra annual species, followed by annual, biannual, and continuous species in a sequential order. On the other hand, the low level of flower and fruit production between GF events was maintained largely by annual and biannual species. This highly fluctuating plant reproduction shapes dynamics of plant species as well as animals in SE Asian forests. Seed availability largely determines regeneration of a species and the fate of animals that rely on the species. Therefore, it is important to learn the availability of flowers and seeds and the types of fruits provided by plants during and beyond GF events. In addition, for the evaluation of selection forces for GF, understanding availability of resources that may sustain animal populations is crucial. The prediction on seed survival by the predator satiation hypothesis requires the existence of an important element and that is the decrease of population sizes between GF events. The hypothesis proposed that shortage of food during the long intervening period should drive the seed predator populations low enough so that seed predation could not catch up with the seed production when GF takes place. The huge temporal variation in seed production provided some support for this element. Seed predators, which are likely generalists, are facing low food supply during the low seasons. Furthermore, we observed a more drastic fluctuation with long intervals between reproductive events in the dyszoochorous fruits, which face higher pressure from seed predation. On the other hand, reproductive events are more regular in the endozoochorous species. This implies a constant supply of food resource for frugivores, which is consistent with the prediction of dispersal saturation hypothesis.

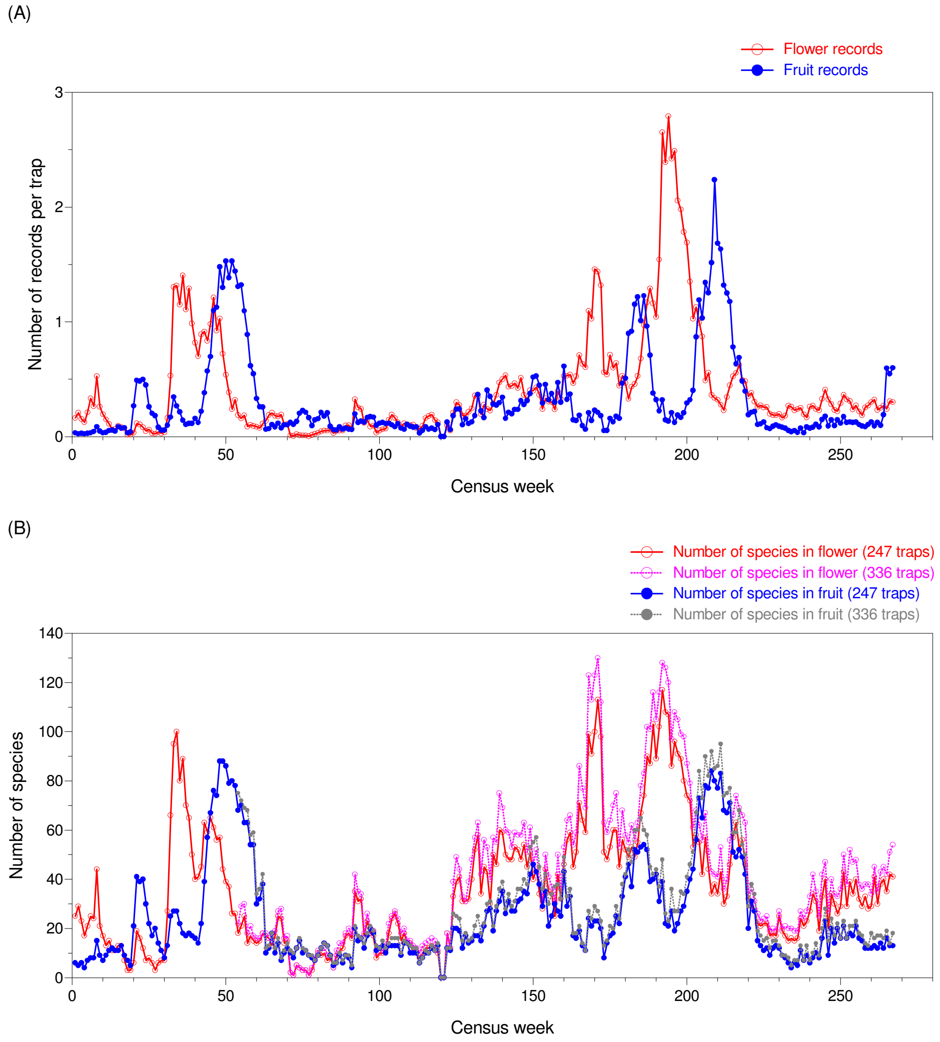
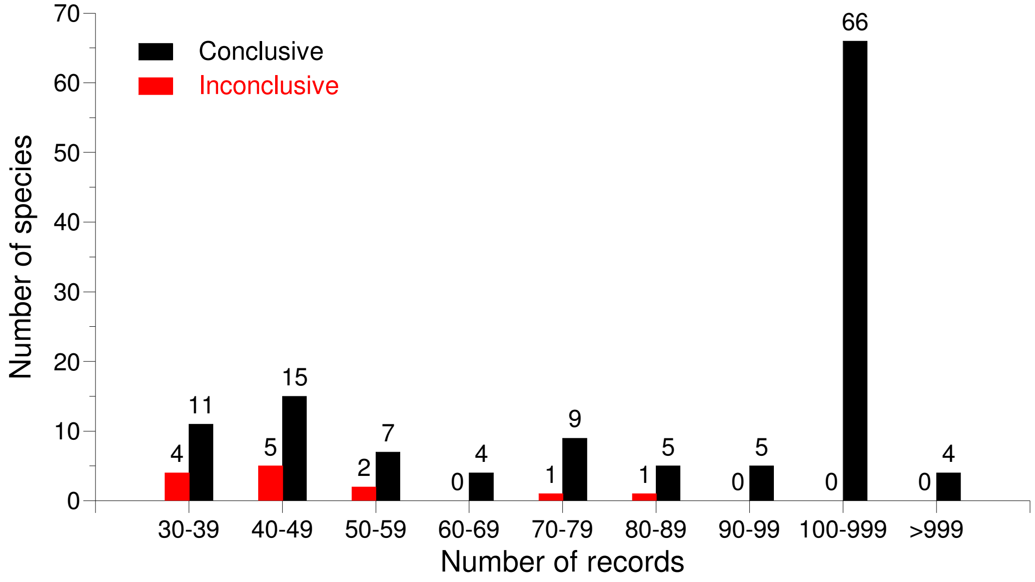


Figure 2.1 Temporal fluctuation in flowering and fruiting for the Pasoh Forest Dynamics Plot from August 2001 through September 2006. Flower and fruit records (A) and species in flower and fruit (B) were distributed unevenly over time. Only trees and lianas are included. Each record refers to the presence of a species or morpho-species in a passive 0.5 m^2 trap. There were 247 traps for censuses 1 through 53 and 336 traps thereafter.

(A) Flowers



(B) Fruits

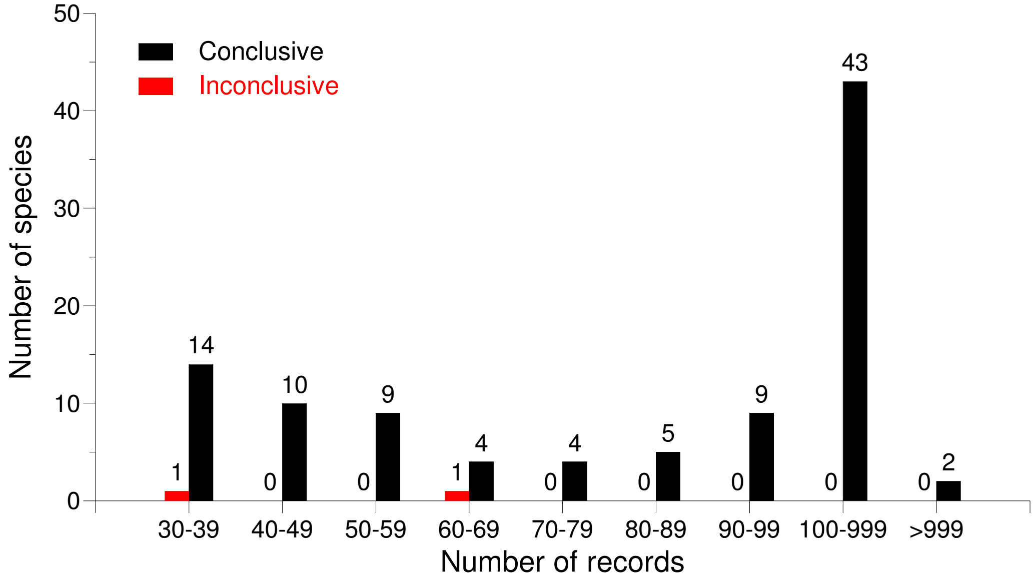
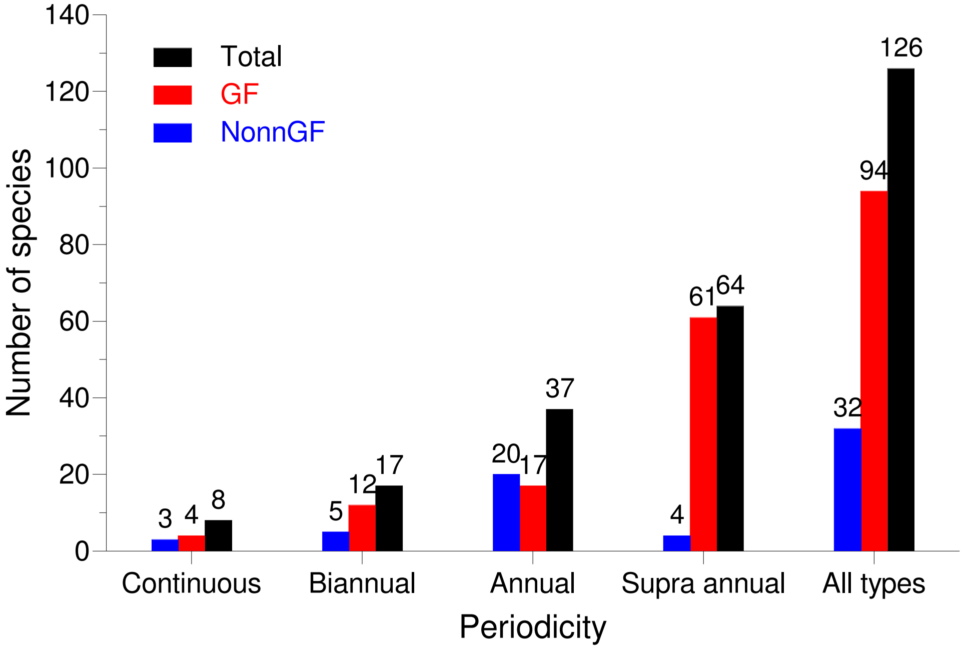


Figure 2.2 Evaluation on periodicity decisions. Number of conclusive and inconclusive flowering (A) and fruiting (B) periodicities decisions was plotted against sample size. Proportion of inconclusive patterns was higher in lower sample size classes. Classes with sample size greater than 100 records were pooled into two classed: 100-999 and >999.

(A) Flowers



(B) Fruits

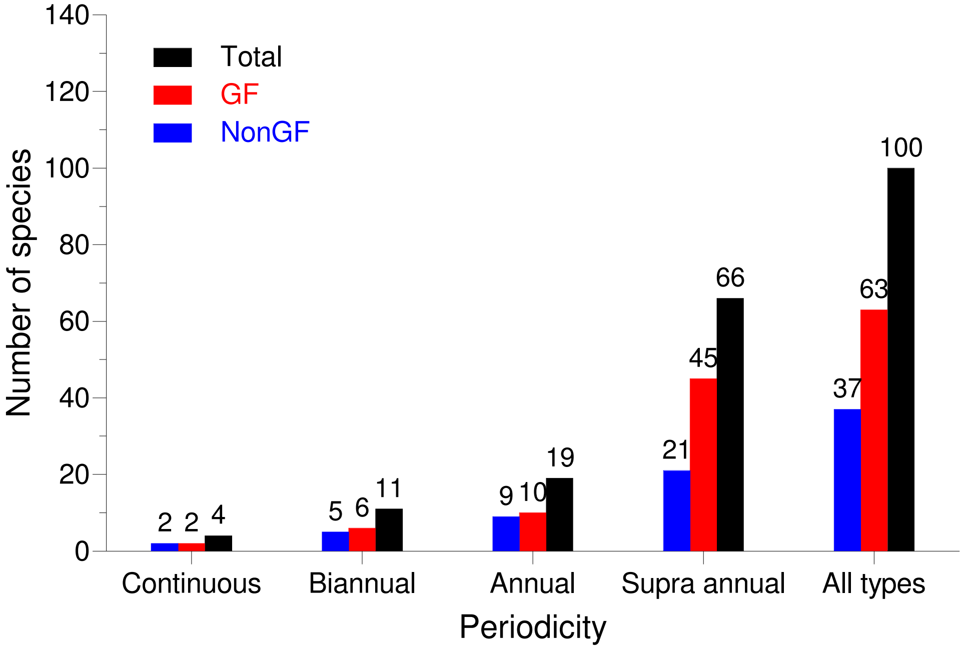


Figure 2.3 Periodicity types and synchrony. Species were placed into one of the eight categories (continuous-GF, continuous-nonGF, biannual-GF, biannual-nonGF, annual-GF, annual-nonGF, supra annual-GF, and supra annual-nonGF) based on periodicity assignment with ACF and general flowering feature from D statistic. Flowers and fruits were treated independently.

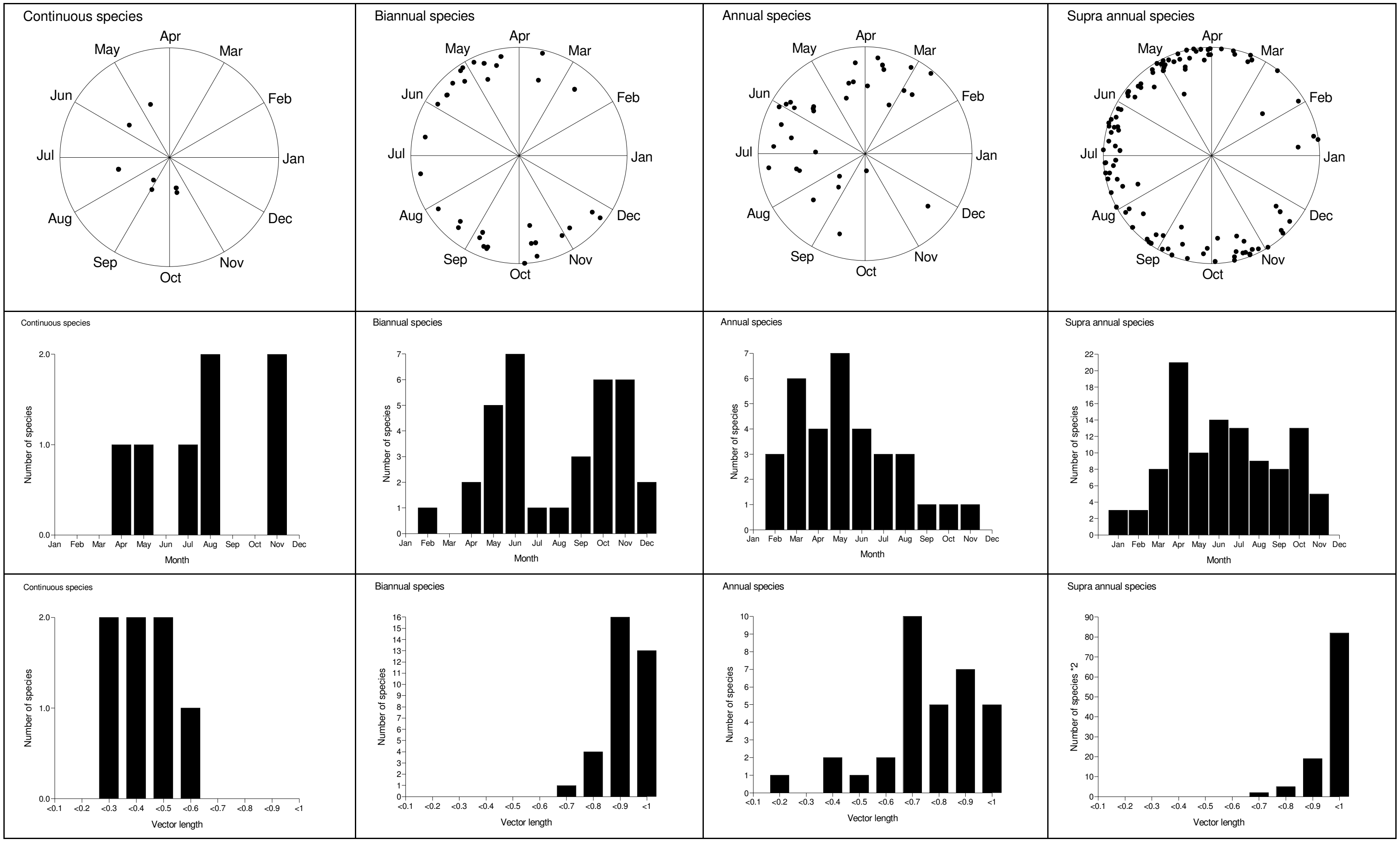


Figure 2.4 Mean vectors of flowers among four periodicity groups. Mean date and vector lengths of each species were averaged over values of four years data with exclusion of the year with less than 5 flower records. Samples size included in the continuous, biannual, annual and supra annual groups were 7, 17, 33, and 54 species, respectively. Two seasons of vectors were calculated for biannual and supra annual species and then pooled for graphing. Therefore each biannual and supra-annual species appears twice in the appropriate plots.

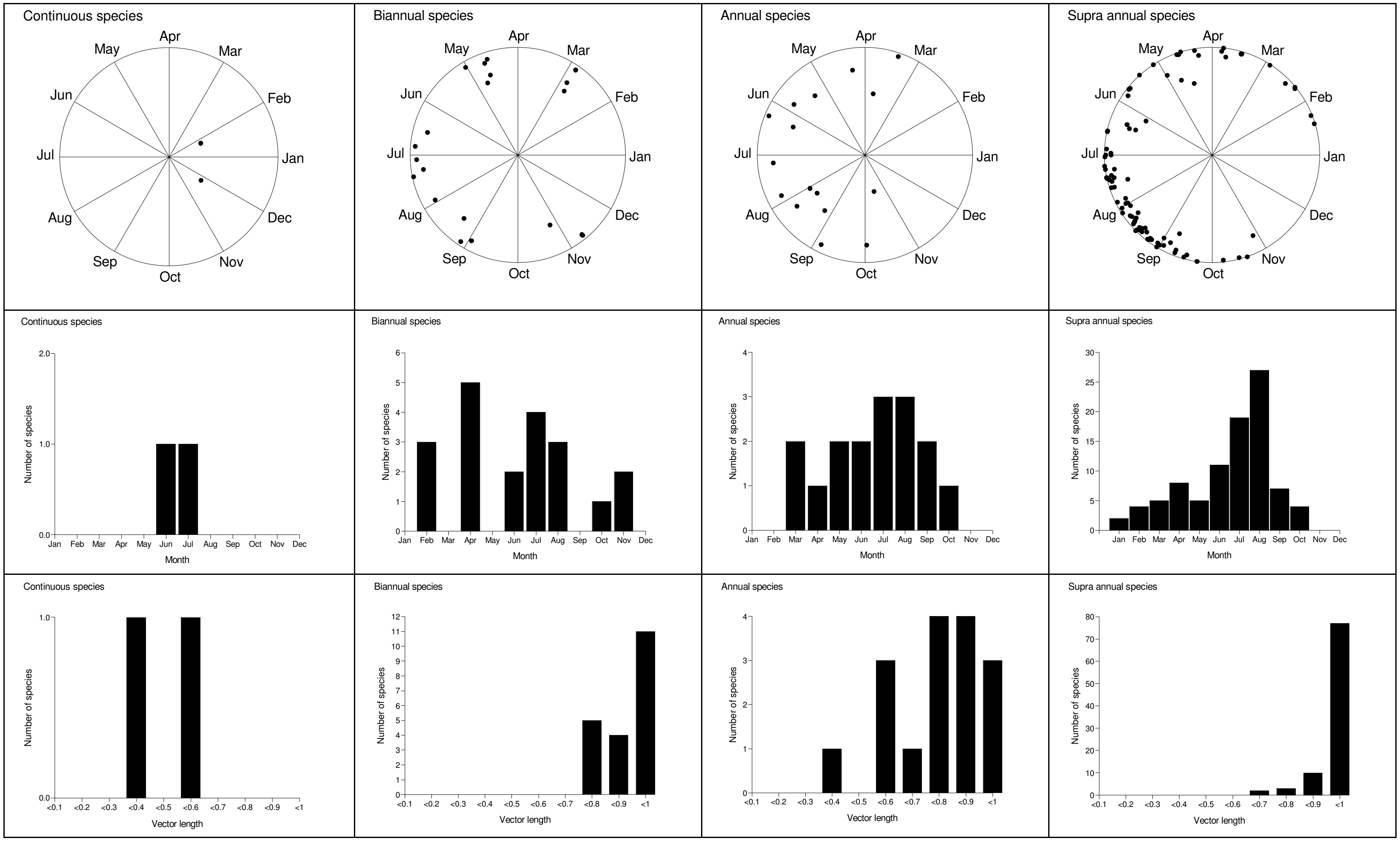


Figure 2.5 Mean vectors of fruits among four periodicity groups. Mean date and vector lengths of each species were averaged over values of four years data with exclusion of the year with less than 5 flower records. Samples size included in the continuous, biannual, annual, and supra annual groups were 2,10, 16, and 47 species, respectively. Two seasons of vectors were calculated for biannual and supra annual species and then pooled for graphing. Therefore the numbers of species shown on the graphs for these two groups were twice as many of the real number of species.

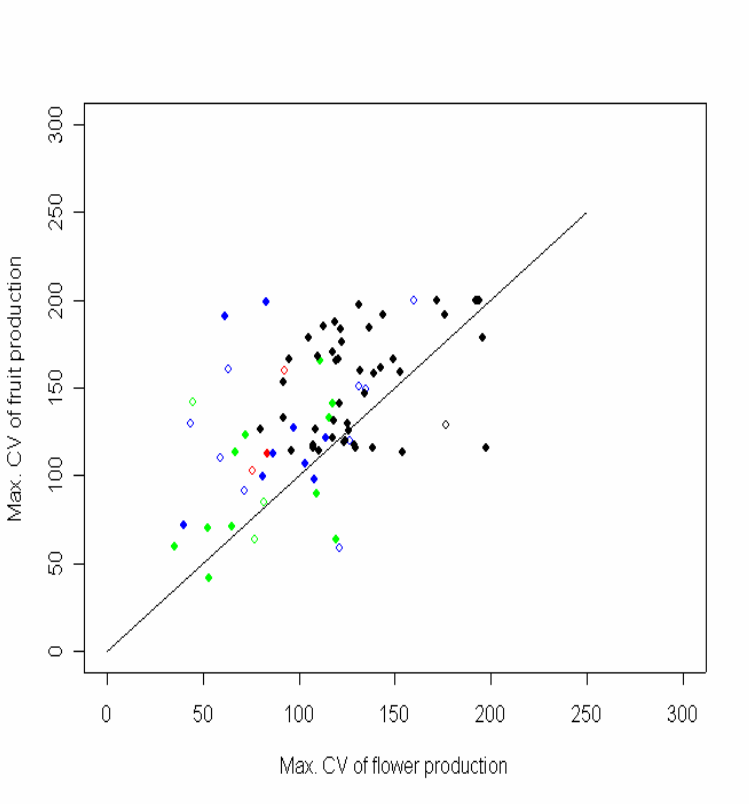


Figure 2.6 Relations between flower and fruit CVs. Maximum flower and fruit CV were plotted on the graph. Hollow circles were nonGF species and solid points were GF species. Red circles represented continuous species; green circles represented biannual species; blue circles represented annual species; black circles represents supra annual species. The straight line represented 1:1 relation of flower and fruit CVs. Most species exhibited a higher variability in fruiting than flowering.

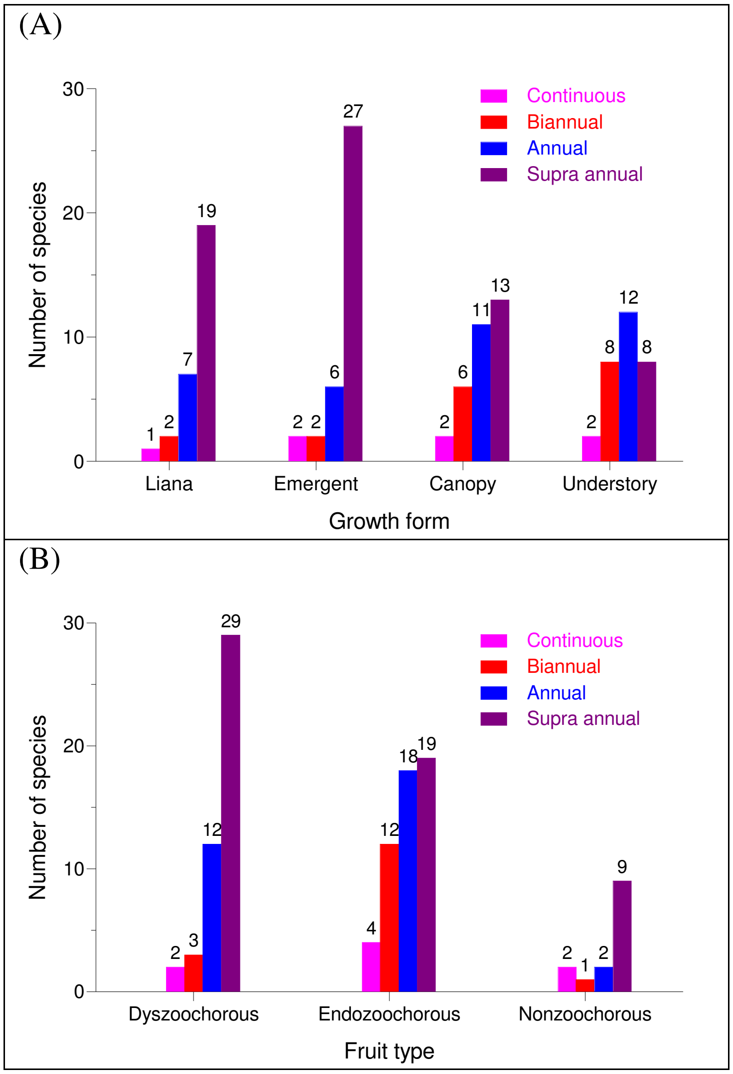


Figure 2.7 Distribution of periodicity types of flowering among growth forms (A) and reward types (B). Periodicity was assigned based on ACF results. Growth form of each species was from the FDP census data provided by Forest Reseach Institute Malaysia. We observed: (A) greater proportion of supra annual species occurred in the emergent layer while higher proportion of annual species was observed in the understory, and (B) relatively higher number of supra annual species in dyszoochorous and nonzoochorous fruits. A total number of 128 species was included in this analysis.

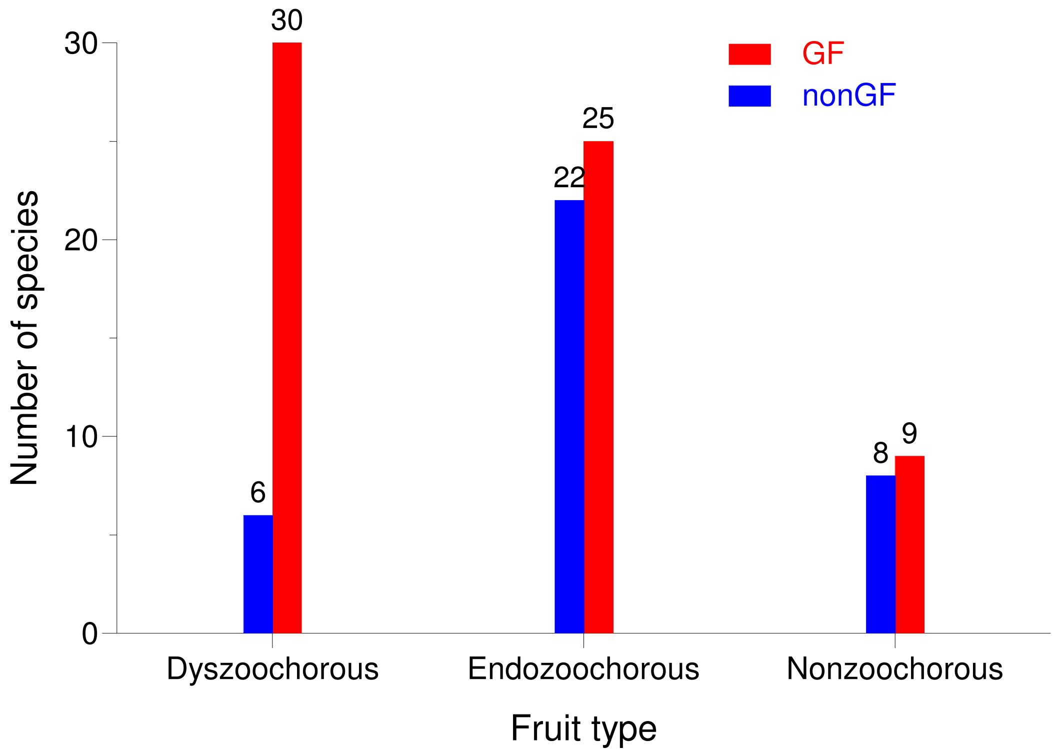


Figure 2.8 Distribution of GF feature in fruiting among three dispersal modes. Three dispersal modes were defined according to the type of rewards for visiting animals and principle dispersal type. A total number of 100 species were included in this analysis.

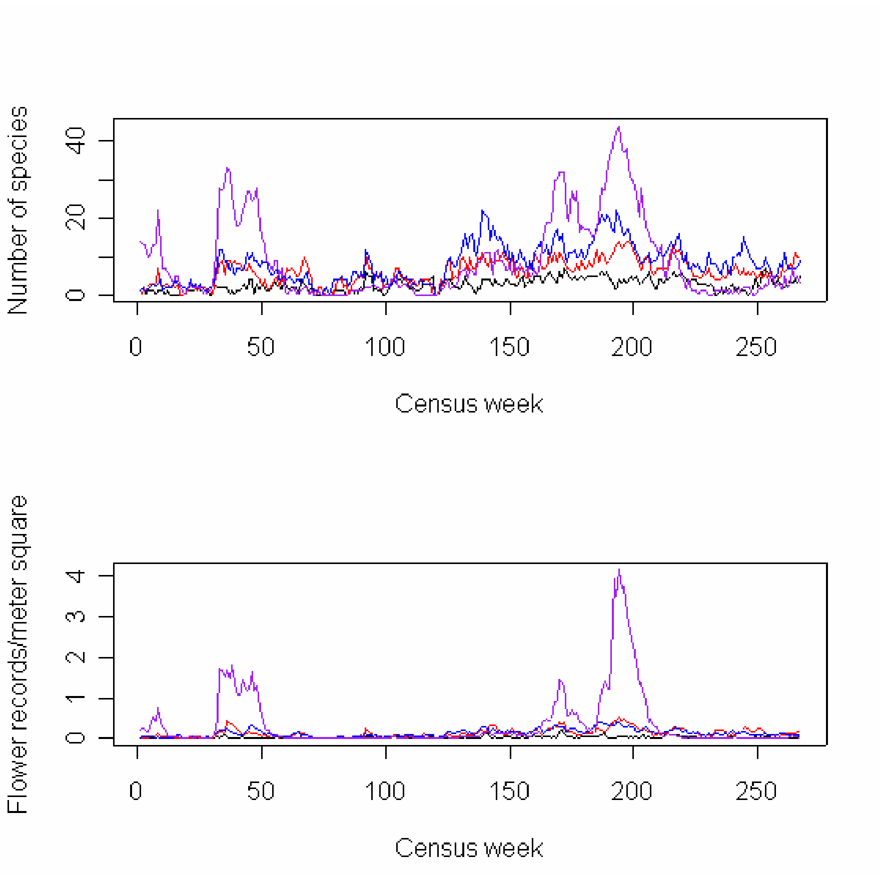


Figure 2.9 Contributions of four periodicity groups to the community-level fluctuation in flower production. The upper panel showed number of species from each periodicity group participating in flowering in the five-year period. The lower panel showed the contribution of flower production (number of records) from each group in each week. Supra annual species was important on contributions to the fluctuation in species number and flower record. Periodicity groups of continuous, biannual, annual, and supra annual species were represented with colored lines in the order of black, red, blue, and purple, respectively.

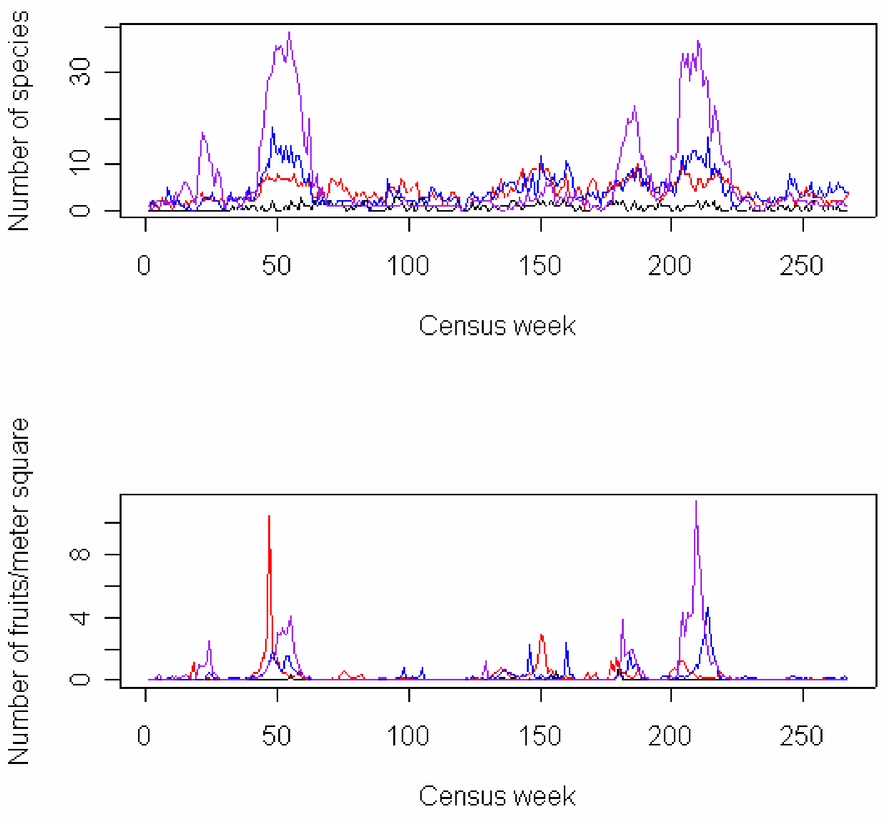


Figure 2.10 Contributions of four periodicity groups to the community-level fluctuation in fruit production. The upper panel showed number of species from each periodicity group participating in fruiting in the five-year period. The lower panel showed the contribution of fruit production (number of fruits) from each group in each week. Supra annual group was important on contribution to species number fluctuation. Continuous and supra annual groups were more fluctuating in fruit production. Periodicity groups of continuous, biannual, annual, and supra annual species were represented with colored lines in the order in black, red, blue, and purple, respectively.

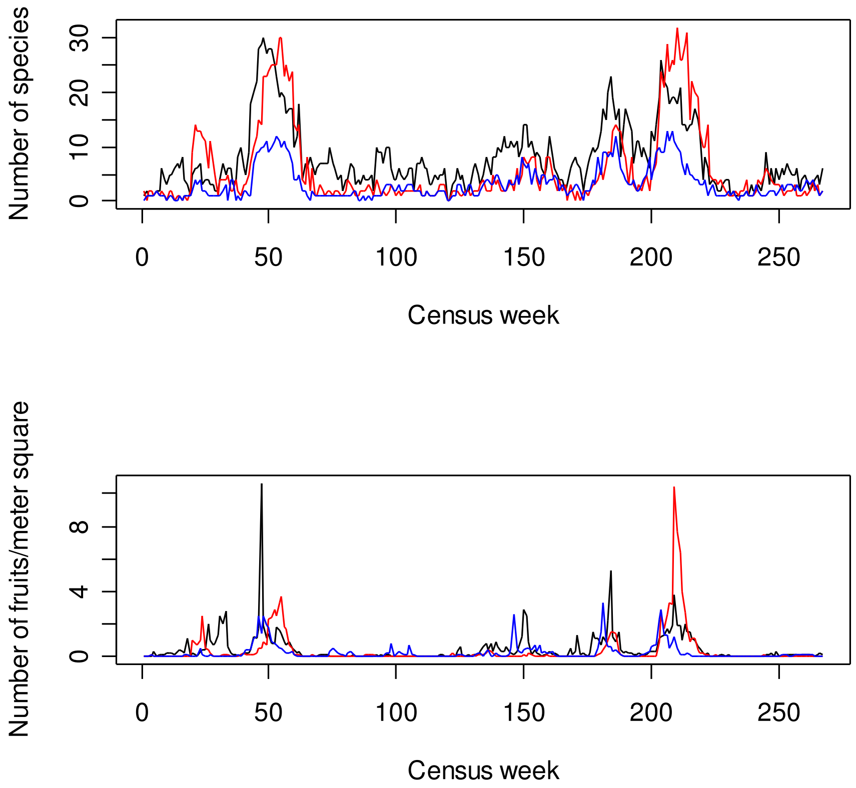


Figure 2.11 Contributions of endozoochorous, nonzoochorous, and dyszoochorous fruits to the fruit production in Pasoh forest. The upper panel showed number of species of each fruit type participating in fruiting in the five-year period. The middle panel showed the number of fruit records per trap. The lower panel showed the fruit density of each group in each week. Black, red, and blue lines represented endo-, dys- and nonzoochorous fruits in the panels. Endozoochorous and dyszoochorous fruits are more important in the forest than the nonzoochorous fruits.

Table 2.1 Independent assessments of the periodicity of flowering and fruiting for 79 species from the Pasoh Forest Reserve. Each species had 30 or more presences recorded for both flowers and fruits. Flowering and fruiting occurred with the same periodicity for 69 species (the bold diagonal). Two species flowered biannually and appeared to produce fruit continuously. Another eight species produced fruit less frequently than flowers. Three species are omitted because it was not possible to assign a periodicity to flowering or to fruiting.

		Flower			
		Continuous	Biannual	Annual	Supra annual
Fruit	Continuous	**2**	2	0	0
	Biannual	0	**9**	0	0
	Annual	1	1	**13**	0
	Supra annual	0	2	4	**45**

Table 2.2 Mean of CVs in all phenological groups. Result from ANOVA test was presented with groupings.

		Flower				Fruit			
		Max. CV		Seasonal CV		Max. CV		Seasonal CV	
	Periodicity	N	Mean	N	Mean	N	Mean	N	Mean
GF	Continuous	4	91.63a			3	88.34a	3	88.34a
	Biannual	12	80.55a	24	86.97a	6	97.06a	6	111.40a
	Annual	16	105.47a			10	118.89a	10	118.89a
	Supra annual	56	128.93b	112	162.39b	48	150.99b	48	185.65b
NonGF	Continuous	3	81.42a	3	81.42a	1	102.88	1	102.88
	Biannual	5	89.73a	5	89.87a	3	96.81a	3	109.94a
	Annual	17	102.97a	17	95.83a	8	119.69a	8	119.69a
	Supra annual	3	168.86b	3	168.86b	4	160.09a	4	160.09a

Table 2.3 Relations between phenology types and various functional traits. Significance level of 0.05 was used and significant relationship was indicated with *. Analyses did not include species exhibited continuous pattern.

	Flowers							
	Periodicity				GF feature			
	N	X^2	df	p	N	X^2	df	p
Growth form	121	19.543	9	0.003*	130	0.170	3	0.964
Dispersal mode	106	15.164	6	0.004*	113	1.092	2	0.870
Reward type	106	11.306	6	0.023*	113	0.749	2	0.863
	Fruit							
	Periodicity				GF feature			
Growth form	97	14.152	9	0.117	105	1.214	3	0.621
Dispersal mode	91	6.951	6	0.325	97	2.101	2	0.116
Reward type	91	10.710	6	0.098	97	9.126	2	0.020*

Table 2.4 Difference in means of CVs among various functional traits. Significant difference of mean CV was found seasonal flowering CVs among the dispersal modes and in flowering and fruiting CVs among reward types. A significance level of 0.05 is used.

	Flower				Fruit			
	Max. CV		Seasonal CV		Max. CV		Seasonal CV	
Pollination syndrome (p-values > 0.05 for all examinations)								
	N	Mean	N	Mean	N	Mean	N	Mean
Animal	99	112.06a	99	127.22a	89	134.58a	89	153.23a
Wind	8	120.26a	8	109.88a	10	137.51a	10	137.36a
P-value	> 0.05		> 0.05		> 0.05		> 0.05	
Pooled dispersal mode								
Biotic	71	106.26a	71	115.08a	62	132.76a	62	147.80a
Abiotic	37	124.87b	37	147.39b	38	138.85a	38	159.96a
P-value	< 0.05 *		< 0.05 *		> 0.05		> 0.05	
Dispersal mode								
Animal	71	106.25a	71	115.08a	62	132.76a	62	147.00a
Ballistic	10	125.01a	10	136.08ab	26	138.92a	26	149.38a
Wind	27	124.82a	27	151.58b	12	138.68a	12	164.84a
P-value	> 0.05		< 0.05 *		> 0.05		> 0.05	
Reward type								
Endozoochorous	51	102.40a	51	108.25a	47	130.86a	47	141.87a
Nonzoochorous	13	115.76ab	13	134.18ab	17	135.36a	17	145.34ab
Dyszoochorous	44	123.55b	44	144.53b	36	141.44a	36	168.17b
P-value	< 0.05 *		< 0.05 *		>0.05		< 0.05 *	

CHAPTER 3

REPRODUCTIVE PHENOLOGY OF *SHOREA* SPECIES AND THE TRIGGERS OF GENERAL FLOWERING EVENTS IN A LOWLAND TROPICAL FOREST[2]

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[2] Chen, Yu-Yun, Wright, S. Joseph, Sun, I-Fang, Hubbell, Stephen P., Nur Supardi Md. Noor. To be submitted to *American Naturalist*.

Abstract

Community wide, long term monitoring data on general flowering phenomenon are scarce. We used seed traps to gather data on seed rain in a lowland dipterocarp forest over a five-year period that included four GF events. The four events were paired in time, with a weaker event followed by a stronger event the following year in each pair. The investigations in this study (1) examined the degree of segregation of flowering and synchrony in fruiting, (2) explored possible mechanisms leading sequential flowering to synchronous fruiting, and (3) estimated floral induction time and the cues associated with the induction. The prediction of the pollinator competition hypothesis of staggered flowering with significant segregation was not supported; there was considerable overlap of flowering among the *mutica* section of *Shorea* dipterocarps. Fruiting among these species was highly synchronized, which is consistent with the predator satiation hypothesis, which postulates a strong pressure from seed predators. Consequentially, the mean duration of the period of fruit development was inversely related to the order of flowering among species. The length of the fruit development period was not correlated with seed size or with content of phenolic compounds. Estimates of the time of floral induction were not consistent across all GF events or different methods of estimation.

Introduction

General flowering (GF, hereafter) is a term used to describe synchronous reproduction by many species at irregular, multi-year intervals in lowland forests in Southeast Asia dominated by species from the family Dipterocarpaceae (Appanah, 1993; Ashton, 1988; Ashton *et al.*, 1988; Curran, 1994b; Sakai, 2000). This remarkable phenomenon was described in peninsular Malaysia, Borneo, and Sumatra more than a century a century ago (Appanah, 1985; McClure, 1966; Medway, 1972; Wich & van Schaik, 2000). Many studies of GF events have used the reproductive phenology of dipterocarps as an indicator of GF (Appanah, 1985; Curran, 1994a; Numata *et al.*, 2003). In western Kalimantan, eighty nine per cent of the fifty four dipterocarp species studied reproduced during the 1991 GF (Curran, 1994a). Two community level studies have also demonstrated a high degree of participation of non dipterocarp species in the GF events (Appanah, 1985; Sakai *et al.*, 1999b).

Researchers have attempted to explain the proximate causes of GF events by correlating their occurrence with environmental fluctuations (Wood, 1956). Correlations of GF events and ENSO (El Nino Southern Oscillation) have been studied at both large temporal and spatial scales to attempt to uncover the mechanistic causes to GF (Curran *et al.*, 1999; Yasuda *et al.*, 1999). Concurrence of GF with several different measures of meteorological fluctuations has been reported. (Ashton *et al.*, 1988; Yasuda *et al.*, 1999)) report an association of these massive reproductive events with a drop of minimum nighttime temperature. This correlation was observed in long term meteorological and GF records on Borneo and Peninsular Malaysia. However, these studies, El Niño and La Niña-STR hypotheses were proposed to cause the trigger(s) of GF, respectively. Nevertheless, other studies indicated prolonged drought associated with El Niño is a more important cue for GF (Curran *et al.*, 1999; Sakai *et al.*, 2006). In addition, an increase of insolation during the cloudless period of a drought could enhance the carbon gain of deep-rooted trees and allow a high investment in reproduction to take place (Ng, 1977; van Schaik, 1986; Wright & van Schaik, 1994). This hypothesis was supported by data from tropical forests in the new world, but it was not supported by Ng (Ng, 1981) based on a re-analysis of data for peninsular Malaysia.

The quest for the cue(s) of GF remains open. Ashton *et al*. (1988) argued that it is important to know the time of floral induction in order to determine climatic triggers for GF. They proposed that variation of flower development should increase with the length of time since floral induction due to the accumulation of differences in the rate of floral development over longer time periods. More variable rates of flower development should be reflected by long flowering periods in a species, whereas less variable rates should be reflected by shorter flowering periods. This leads to a positive correlation between length of flowering period and the mid-flowering time. The regression line between these two variables can then be used to determine the time of floral induction by extrapolate to the point when length of flowering period is zero.

Simultaneous reproduction in GF events could lead to benefits as well as costs to the trees that participate. Flowering of ecological analogues with similar floral morphology may experience intra-guild competition for pollinators (Ashton *et al.*, 1988). (Ashton *et al.*, 1988; Borchsenius, 2002)) reported that species sharing the same pollinators exhibited staggered flowering, which they attributed to avoidance of pollinator competition; but it could also arise in response to selection to reduce pollen wastage. On the other hand, synchronous fruiting benefits each member of the guild that share the same seed predators if synchrony enhances seed survival by satiating the predators (Augspurger, 1981; Janzen, 1974). The combination of staggered flowering and synchronized fruiting generates variable lengths of fruit development time for the species. Length of fruit development time may associate with factors such as climatic harshness (Sparks, 2005), time of the year (Corlett, 1996), nutrient content in fruits (Corlett, 1996), or resource availability in forests.

GF phenomena are, by their nature, difficult to study. The generally long, multi-year interval between adjacent GF events creates difficulties for any one study to include more than one event. Furthermore, without large field crews, it is difficult to quantitatively monitor GF events on more than a few individuals for each species (Appanah, 1985). Incorrect or biased conclusions may be drawn by not adequately sampling the phenological variation in a population. In order to obtain large-scale, quantitative information of forest phenology, we established a large distributed array of passive seed traps to monitor seed rain on a weekly basis over the long term in a lowland forest. In this paper, we report the phenological patterns of the *Shorea* community, especially in the section *mutica* and the temporal segregation of flowering and synchrony of fruiting in these species over the first five years of the study. Next we examine the variability in fruit development time for the *mutica* species. Finally, we estimate floral induction time with both qualitative and quantitative measures of flowering periods. We then examine the association of climatic fluctuation and the estimated times of floral induction.

Methods

Study site

Pasoh Forest Reserve (2 ^{o} 58’ 47” North, 102^{o} 18’ 29” East) includes 2,400 ha of lowland dipterocarp forest. The average elevation of the Pasoh forest is 80 m above sea level, with a topographical relief of less than 20 m (Lafrankie & Chan, 1991). Monthly maximum and minimum temperatures are 33.2 °C and 22.7 °C and are stable throughout the year. Annual rainfall averages 1571 mm and the minimum mean monthly rainfall is 93 mm in January (Losos *et al.*, 2004). The forest is characterized as aseasonal lowland Dipterocarp forest, and trees of the family Dipterocarpaceae, were estimated to comprise 10% of the forest stems. A 50-ha

Forest Dynamics Plot (FDP) was established in 1985 and all trees greater than 1 cm diameter at breast height (DBH) were tagged, mapped, measured in diameter, and identified to species or morpho-species. Tree censuses were carried out every five years, and 814 tree species were recorded in the first census (Kochummen *et al.*, 1990). We carried out the present study within the Pasoh FDP.

Data collection

We used passive seed traps with a PVC frame and 1mm mesh size fiberglass screen to collect plant reproductive materials. We established 247 traps along existing trails before August 13, 2001 and added 89 traps along three north-south trails and gaps before August 19, 2002. The first census with 247 traps began on August 20, 20001 and the first census with 89 additional traps began on August 26, 2002. The design of seed traps and distribution of these traps followed the design for the seed rain study on Barro Colorado Island (Wright & Calderon, 1995). We census traps weekly. We identified all parts to species or morpho-species and separated them into eight categories: complete fruit, complete seed, capsule, fragment, immature fruit, flowers, fruit bit by animals, and seed bit by animals. We counted all parts except for flowers which were recorded only for their presence. We identified species by referring to the tree identification in the FDP and herbarium collections in Forest Research Institute Malaysia and Singapore Herbarium.

We carried out 265 censuses in 267 weeks between August 20, 2001 and September 30, 2006. Two censuses were missed but these occurred during periods of low flower and fruit production between GF events and did not affect our analyses. The census effort was 247 traps per week for censuses 1-53 and 336 traps per week for censuses 54-267. All analyses were conducted after standardizing the data to a per trap basis.

Staggered flowering and synchronized fruiting

For the calculation of flowering overlap, we used standardized flower records within each *Shorea* section *mutica* species and GF event. Windows of GF events were defined to include 95% of all flower records of *mutica* species as a group. We defined the four events as the periods in August 20-October 25, 2001 (census 1-10, referred as GF 2001 hereafter), April 1-July 25, 2002 (census 33-49, referred as GF 2002 hereafter), October 13-December 29, 2004 (census 165-176, referred as GF 2004 hereafter), and March 22-July 21 (census 188-205, referred as GF 2005 hereafter). Narrow windows make it more difficult to detect segregation in flowering and synchrony in fruiting than when windows are wide. We calculated overlap of flowering as the sum of all weekly minimum flower records in each pair of *mutica* species within a season. Mean overlap (Pleasants, 1990) of all pairs for three GF events were calculated for each separate GF event. A wrap-around randomization test was used to test the null hypothesis that the degree of community-wide flowering overlap was equal to or higher than the degree of overlap produced by chance. In the randomization procedure, we randomly assigned different starting dates of flowering events to *mutica* species within each GF events and maintained the temporal structure within each species. The temporal structure and the length of flowering period were preserved by shifting all flower records according to the new starting dates. If part of the shifted flowering period exceeded the overall flowering period of all mutica species, we moved the remaining records to the beginning of the overall flowering period. This altered temporal flower distributions of among *mutica* species and allowed us to calculate randomized mean overlap. This random mean overlap was compared to the observed mean overlap for 1000 iterations and a p-value was obtained based on 1000 comparisons for all events separately. We applied the same overlap calculation and randomization procedure with a different null hypothesis for the statistical test for the community-wide overlap in fruiting. As with flowering windows, we defined fruiting windows using the central 95% of fruit records from *mutica* species. The weak flowering event in 2004 resulted in almost a complete failure of fruiting in early 2005, with only seven seeds (five records) from three *Shorea* species (only one from *mutica* section) were caught by 336 traps. Thus only three distinct fruiting peaks for *mutica* species were detected during our study: January 1-February 20, 2002 (census 20-27) for GF 2001, July 15-October 3, 2002 (census 48-59) for GF 2002, and July 11-September 22, 2005 (census 204-214) for GF 2005 (Fig. 3.1). The null hypothesis to be tested in fruiting was that the observed community-wide fruiting was equal to or less than the overlap expected by chance. We calculated P-values based on 1000 iterations for fruiting of GF 2001, GF 2002, and GF 2005, separately.

Fruit development time and seed mass

We calculated fruit development time as the interval between peak flowering and peak fruiting time for each species in unit of days counting from the first day of each census. Seed mass data were provided by YYC (unpublished data). We used general linear regression to investigate the relationship between time for fruit development and seed mass.

Estimation of floral induction time

We estimated floral induction time by the regression of mid-flowering dates and lengths of flowering period suggested by Ashton *et al*. (1988). To obtain a more objective measure for our community-level sampling, we replace mid-dates with mean weeks and lengths of flowering periods with standard deviations (SD) of weeks. Before proceeding to regression, we used two approaches to obtain mean weeks and SDs. The first approach used only presence of flower to retrieve the date measures in the unit of week (flower-presence data, hereafter) and generated similar measures to the previous study. We used 95% flower records of a species to define the flowering window of the species. We calculated the mean week and the SD of the weeks with the defined window without weighting by number of flower records. The second approach used all records for the date measures (flower-record data, hereafter) with the definition of flowering window described above. We calculated the mean week and the SD of the weeks with all weeks associated with the records. This weighted approach allowed the inclusion of more variation in a population. We performed regressions of mean weeks and SDs for *mutica* species (*S. macroptera*, *S. lepidota*, *S. parvifolia*, *S. acuminate*, and *S. leprosula*) with the flower presence and flower record approaches independently. Using linear regression of mean weeks and SDs, we obtained the regression lines and x- and y-axes, modified from Ashton *et al*. (1988). We estimated the floral induction date from the intercepts of these regressions. All intercepts reported here were corrected with the week of the first flower in *S. macroptera*, the first species to flower in *mutica* section of *Shorea*. A negative intercept indicated a cue took place some time before *mutica* flowering. We applied the same regression method to another 56 non *mutica* species to obtain estimates of floral induction time with these supra annuals GF species (Chen *et al*. unpublished).

Result

During the 5-year study period, we recorded flower presence 4724 times and 7315 fruits of *Shorea* species in 336 traps. A total of 3773 (79.9%) flower records and 5721 (78.2%) fruits were produced by species in the section *mutica*. Four flowering events of *Shorea* species in section *mutica* were evident during the study (Fig. 3.1). The flowering of *Shorea* exhibited a paired-event pattern consisting of two back-to-back events over a period of three years. The peak flowering times of GF 2001 and GF 2002 were eight months apart, and the peak flowering times of GF 2004 and GF 2005 were six months apart. However, GF 2004 was a weak flowering event for *Shorea* species and only three of the *mutica* species flowered. Among these three species, only *Shorea parvifolia* exhibited considerable production of flowers. Generally, flowering intensity reflected fruiting intensity. A linear regression between flowering intensity and fruiting intensity of all *Shorea* species from GF 2001, GF 2002, and GF 2005 revealed a strong relationship between intensities in flowering and fruiting (General linear regression, N = 32, $r^2 = 0.72$, $p < 0.001$).

Staggered flowering and synchronized fruit fall

The sequence of flowering species was consistent across all GF events, which began with *S. macroptera* and followed by *S. lepidota*, *S. parvifolia*, *S. acuminata*, and *S. leprosula* (Fig. 3.2A-D). An apparent exception to this pattern in *S. lepidota* in GF 2001 is most likely a small-sample problem due to the low flowering level and low record numbers (one week only) for this species. High temporal dispersion of median flowering time among *mutica* species was evident. Standard deviations of flowering weeks were 2.94, 3.87, and 3.39 weeks for GF 2001, GF 2002, and GF 2005, respectively. Despite the dispersion in median flowering times, there was substantial overlap of flowering intervals among the species. Mean flowering overlap in all pairs of *mutica* species in GF 2001, GF 2002, GF 2004, and GF 2005 were 21.8%, 25.3%, 18.5%, 34.0%, respectively.

We used the community mean overlap with all pairs of *mutica* species (Pleasants, 1990) to test whether segregation of flowering was occurring within the *mutica* section. Our randomization tests failed to reject the null hypothesis that the high overlap of flowering was due to chance in all events (p = 0.591, 0.774, 0.583, and 0.278 for GF 2001, GF 2002, GF 2004, and GF 2005, respectively).

Fruiting of *mutica* species exhibited a high degree of synchronization in GF 2001 (fruit fall in early 2002) and GF 2005 (Fig. 3.2E and 3.2H). All *mutica* species reached peak fruit fall in the same week for both events: census 24 for GF 2001 and census 209 for GF 2005. In GF 2001, 43.8% of all fruits were collected in traps in the single peak week, census 24. Fruiting of GF 2005 was more spread out in time with 48.2% of total fruit fall collected in two weeks (census 209-210). In GF 2002, the peak fruit fall of all *mutica* species was less synchronized (Fig. 3.2F). Peak fruit fall in the *Mutica* community during GF 2002 occurred in census 55, which had 15.7% of all fruits. Three weeks of fruit fall (census 54 to 56) amounted to 43.3%, less than that occurred in the peak weeks in GF 2001 and GF 2005. The GF 2004 event had a low number of species participating and too few fruit (7) for any analysis, and thus was not included. Compared to flowering, relatively lower temporal dispersion was observed in fruiting time, with standard deviations of 0, 2.94, and 0.55 for GF 2001, GF 2002, and GF 2005, respectively.

We examined fruiting synchrony with the same randomization tests for flowering with the null hypothesis described in the method section. Mean fruiting overlap in all pairs of mutica species in GF 2001, GF 2002, and GF 2005 were 82.2%, 53.1%, and 72.0%, respectively. The tests showed that synchrony in *mutica* fruiting in GF 2002 and GF 2005 was highly significant and was not due to chance (one tail, $p = 0.01$ and $p = 0.004$, respectively). However, the synchrony in *mutica* fruiting was not significant in GF 2002 (one tail, $p = 0.228$).

Fruit development time and seed mass

A consequence of staggered flowering and synchronous fruiting is that species must differ in the time available for fruit development. The order from long to short fruit development time followed the sequence of flowering (Table 3.1). Fruit development time ranged from 79.5 days in *S. bracteolata* to 135.3 days in *S. macroptera* among all *Shorea* species. We found no correlation between seed mass and fruit development time of *Shorea* species (general linear regression, df = 8, $p = 0.607$) or within *mutica* section (general linear regression, df = 4, $p = 0.277$).

Estimation of floral induction time

The regression between mean flowering weeks and SDs of flowering periods of *mutica* species from GF 2001 and GF 2005 resulted in similar intercepts while GF 2002 gave a different estimate. We demonstrated the result from regressions on *mutica* species and the estimated intercepts in Fig. 3.3 with the flower-presence data. The regression lines were: $y = 9.1774x - 7.1774$ (GF 2001, df = 3, $r^2 = 0.82$, $p = 0.047$); $y = 3.8121x - 1.5356$ (GF 2002, df = 4, $r^2 = 0.70$, $p = 0.078$); $y = 5.7669x - 7.2931$ (GF 2005, df = 4, $r^2 = 0.69$, $p = 0.08$). Sample size from GF 2004 was too small for the regression thus GF 2004 was excluded from this analysis. The intercepts of these regressions yielded estimates of the moment of floral induction as 7.2, 1.5, and 7.3 weeks prior to the first flowering day of the first species to flower, *S. macroptera*, for GF 2001, GF 2002, and GF 2005, respectively. These weeks correspond to the week of June 25, 2001, March 11, 2002, January 7, 2005 for each of the GF events, respectively. The induction date, March 11, 2002, is likely to be inaccurate due to the unclear flowering peaks in two of the species as well as an exceptionally long flowering time. We used the 7-week interval estimated from GF 2001 and GF 2005 to estimate of floral induction in GF 2002. This yielded an induction week of February 4, 2002. With the flower-record data, estimated floral induction times from GF 2001 and GF 2005 were 2-3 weeks later than the qualitative estimates (Table 3.2). All regressions with non *mustica* species resulted invalid estimates of floral induction time (positive intercepts). We then examined temporal fluctuations in monthly minimum temperature and monthly rainfall in relation to the time of floral induction estimated with the flower-presence data as well as from the flower-record data (Fig. 3.4). Rainfall in the Pasoh area generally exhibits a pattern with two peaks per year, one in March-April and one in September-November. Low rainfall usually occurs between December and February each year, with mean monthly rainfall at this time of about 50 mm. However, during our study, extremely low values with less than 10 mm per month occurred supra annually. Two of the stronger GF events coincided with these periods of low rainfall. On the other hand, only the floral induction time of GF 2002 fell in the month in which the low night time temperature (<19 °C) occurred. The floral induction time of GF 2005 fell in the month before the low night time temperature occurred, whereas floral induction of GF 2004 took place in a month during which the minimum air temperature was relatively high.

Discussion

Most reports of general flowering (GF) events in Southeast Asia suggested that they occur at irregular and usually long intervals. Back-to-back events, such as those we observed, are reported to be more common in East Malaysia (Sabah) but rare in West Malaysia (Ashton *et al.*, 1988). Nevertheless, we observed two sets of back-to-back events during the 5-year period in our study. A back-to-back event was also observed in Lambir National Park, Malaysia (Nakashizuka *et al*. personal communication). However, patterns such as flowering species composition and flowering intensity in each species were not consistent between the pairs of events (Fig. 3.2). The time of year for flowering in the two stronger GF events from each pair were close (March 25, 2002 and March 10, 2005) but the dates for flowering in the two weaker events were farther apart (August 20, 2001 and October 11, 2004). Dispersion of median flowering time was large among *mutica* species. The flowering sequence was consistent with previous observations (Appanah, 1985; Lafrankie & Chan, 1991). (Ashton *et al.*, 1988) suggest that this pattern evolved in response to competition for pollinator attention. An additional selective pressure for separation in flowering times would be to reduce pollen wastage. However, a subsequent research reported a considerable amount of overlap in flowering despite separation of the peak flower times (Appanah, 1993) although this overlap was not tested statistically. In addition, we also observed high overlap in the distributions of flowering times in our data. Ashton *et al*. (1988) concluded that flowering overlap was significantly lower than expected by random chance based on their observation on a few individuals. We found no statistical support in our data for the existence of ecological displacement. When evaluating the quantitative distribution of flower production in the community, not just flower presence-absence, the mean overlap increased, and we were unable to reject the null hypothesis of random overlap.

This result was consistent throughout all four GF events. An important assumption for staggered flowering is that species in the focal group share common pollinators. In Shorea species, it was reported that thrips pollinated 90% of the flowers (Appanah, 1993). However, Appanah (1993) did not confirm that all the *Shorea* species share the same thrip pollinators. Studies in Sarawak on *Shorea* species demonstrated that other insect species were responsible for pollination (Sakai *et al.*, 1999a). Differences in their pollinator community may allow the high degree of flowering overlap.

Fruiting in two events, GF 2001 and GF 2005, was significantly synchronized, although fruiting synchrony among species was not significant in GF 2002. In order for the species to synchronize in fruiting despite sequential flowering requires that late-flowering *Shorea* species develop their fruits faster than the early flowering species. This implies that selection has acted to adjust the time period for fruit development such that synchronous fruiting occurs. One might therefore expect longer fruit development times in large-seeded species due to time needed for nutrient deposition in seeds (Corlett, 1996). Furthermore, making investment of expensive defense chemicals may also prolong fruit development. However, the correlation between length of fruit development time and seed mass was not significant among *mutica* species in the Pasoh forest (Table 3.1). Furthermore, no relation was found in fruit development time and concentration of defensive phenolic compounds (Linear regression, df = 4, p = 0.928). This analysis incorporated published data on concentrations of phenolic compounds (Numata *et al.*, 1999). These results reject the hypothesis that nutrient and defense investments in seeds impose a constraint on seed development such as to cause the observed synchrony in fruiting as an accidental byproduct. Therefore, length of fruit development time was not controlled by the rate of accumulation of nutrition or other defensive chemicals in fruits.

Another possible physiological constraint may come from resource availability. Fruit development is more likely to depend on the photosynthates provided by leaves in the nearby braches. Under this assumption, one would expect large-leaved species to exhibit shorter fruit development time. We cannot evaluate this hypothesis with present data. However, we note that leaf size was not inversely related to the length of the period of fruit development. Another mechanism for fruiting synchrony is chronic selection from seed predators, who might consume a greater fraction of seeds when species fruit synchronously. Janzen (1974) proposed that synchronized fruiting can satiate seed predators, permitting more seeds to escape predation and germinate. Augspurger (1981) conducted an elegant experiment on a neotropical species, *Hybanthus prunifoliu,* which is triggered to mass flower and fruit by the first rains of the wet season. Augspurger showed, by watering some plants and causing them to flower and fruit out of synchrony with the rest of the population, that these individuals suffered much higher seed predation than in the synchronized individuals. A similar pressure from seed predators may have selected the pattern of temporal fruiting aggregation in *Shorea* species. Individual trees with early or late fruit fall could lead to lower relative seed survival in the progeny of these trees, and thus they would be selected against.

Another goal of this paper was to identify the time of floral induction and the possible cues for the induction. We assumed, following Ashton *et al*. (1988), that all *mutica* species share the same cue for floral induction and that mean flowering time and length of flowering period should exhibit a linear relationship that point back to the floral induction time. Two out of three events examined showed similar estimates for the timing of floral induction. However, we did not get the same answer when we used flower-presence or flower-record data to estimate the floral induction time. In the case of using presence-absence data, we obtained an estimate of the time of floral induction of 7 weeks prior to the first flower of *S. macroptera*, the first species of mutica to flower. This interval is shorter than the previously suggested interval of 9 weeks (Ashton *et al.*, 1988). However, the estimates based on all flower records from GF 2002 and GF 2005 yielded an even shorter interval, 4-5 weeks prior to the flowering of *S. macroptera*, for flower development in *Shorea* species. Taking these two estimates, of 7 and 5 weeks, respectively, from the two approaches, we examined the association between estimated floral induction time and climatic factors. For all four GF events, the estimated floral induction week fell into the dry period during which the monthly rainfall were below 10mm and had no more 2 rainy days (Fig. 3.4). This was also observed in Lambir National Park in Sarawak with 10-year data (Sakai *et al.*, 2006). However, the estimated floral induction week fell during different times of each dry period. Estimated floral inductions of GF 2002 (the week of January 4 or January 18, 2002) and GF 2005 (the week of February 7 or February 21, 2005,) fell in the early part of the dry months with monthly rainfall of 5.8 and 2.6 mm, respectively. The estimated floral induction of GF 2004 (the week of August 23 or September 6, 2004) fell in the latter part of the dry month having a monthly rainfall of 8.4 mm (YYC, unpublished data). The low minimum temperature (<19 ℃) did not coincide with the estimated time for floral induction precisely in 2004 and 2005. The low temperature occurred three months earlier than the estimated time in 2004 and one month later in 2005. If our estimate of floral induction time is correct, the result suggests that low rainfall might be more important for the floral induction than low temperature. On the other hand, solar radiation increases during dry, less cloudy periods, and so insolation may also contribute to floral induction: they are not mutually exclusive hypotheses. We currently lack data on solar radiation for any further tests of these possibilities.

We attribute the incongruence of estimated time of floral induction in our study to the fact that we did our analyses over large numbers of individuals of all *mutica* species in the community. In the previous study, these regressions were limited to the phenology of just one or two individuals in each *mutica* species. In this case, much of variation was derived from within an individual. Our approach included not only the within individual variation but also the variation of flower development among individuals. Inclusion of among-individual variation is important because general flowering is a community-wide phenomenon. The total variation from within and among individuals must allow flowering to exhibit synchrony with some variation. Under the assumption proposed by Ashton *et al*. (1988), we expected to have consistent estimates of floral induction time with both qualitative and quantitative approaches. We were unable to assess the accuracy of the estimates by the two approaches. Perhaps the weakest assumption of the regression approach to estimating floral induction times is the assumption that all species have the same cue. This could also lead to an inconsistency in induction times. A support may come from the estimates of floral induction time from the regressions on non *mutica* species were invalid for the induction time was estimated to be after the first flower of these species. This implies that some of the species, if not all, may have the flower primodia induced in a different time, and perhaps with a different cue than the *Shorea* species. However, this is not sufficient to evaluate the extent to this assumption is violated.

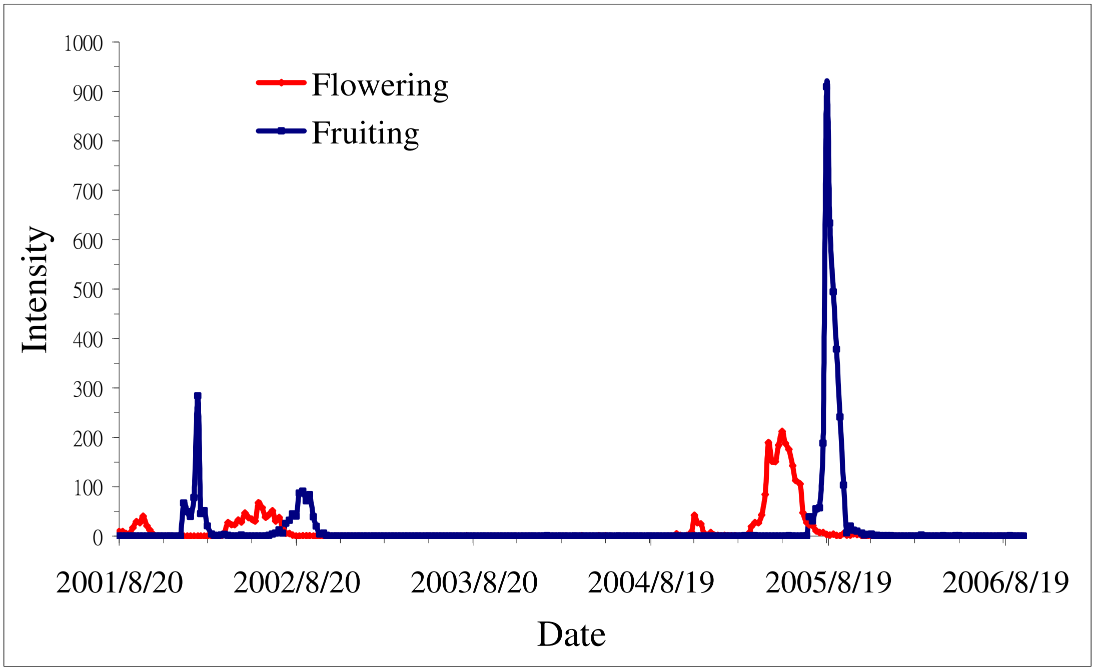

Figure 3.1 Temporal fluctuations in flowering and fruiting intensities of genus *Shorea* section *mutica* of Dipterocarpaceae. Flowering intensity is defined as the number of traps on a given census data that had flowers of mutica species (i.e. number of trap records). Fruiting intensity was the numbers of mutica fruits. Both intensities were calculated on 247-trap basis. For census 54-267, all flower and fruit records from 336 traps were renormalized to a 247-trap basis for graphing purposes and further analyses.

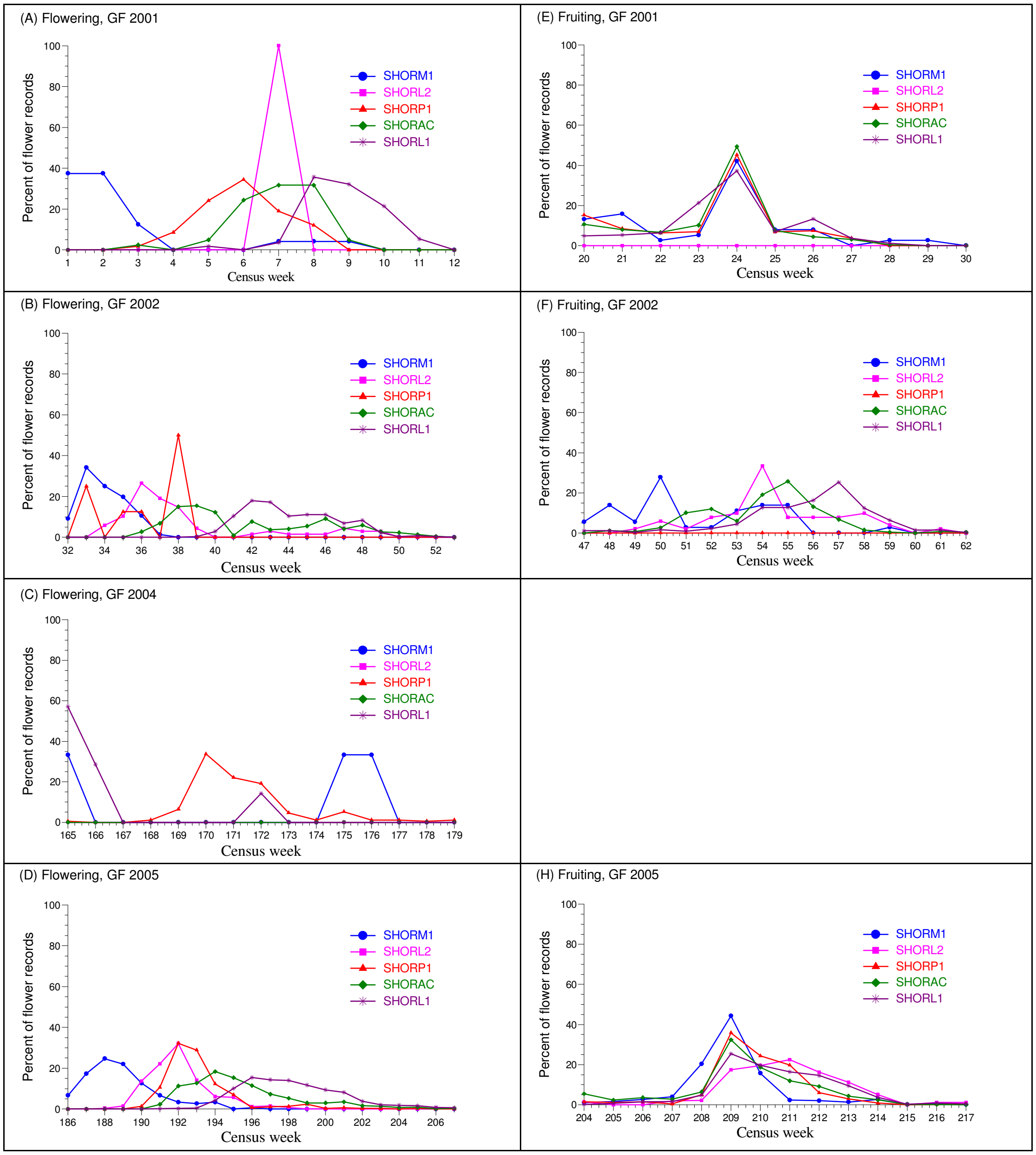

Figure 3.2 Staggered flowering and synchronized fruiting of species of the genus *Shorea* section *mutica*. A somewhat staggered flowering pattern is evident in all four fGF events, although there is considerable overlap. However, a high degree of fruiting synchronization only occurred in GF 2001 and GF 2005. The X-axis is the census week of each flowering and fruiting event. The Y-axis in flowering (panel A-D) is percent of flowering intensity (area under each curve is 100%), which was converted from absolute flowering intensity for each species within each defined event (see text). The Y-axis of fruiting pattern (penal E-H) is percent of fruiting intensity (area under each curve is 100%), converted from fruit numbers for each species in each event defined in text. Species were coded as SHORM1 for *S. macroptera*, SHORL2 for *S. lepidota*, SHORP1 for *S. parvifolia*, SHORAC for *S. acuminata*, and SHORL1 for *S. leprosula*.

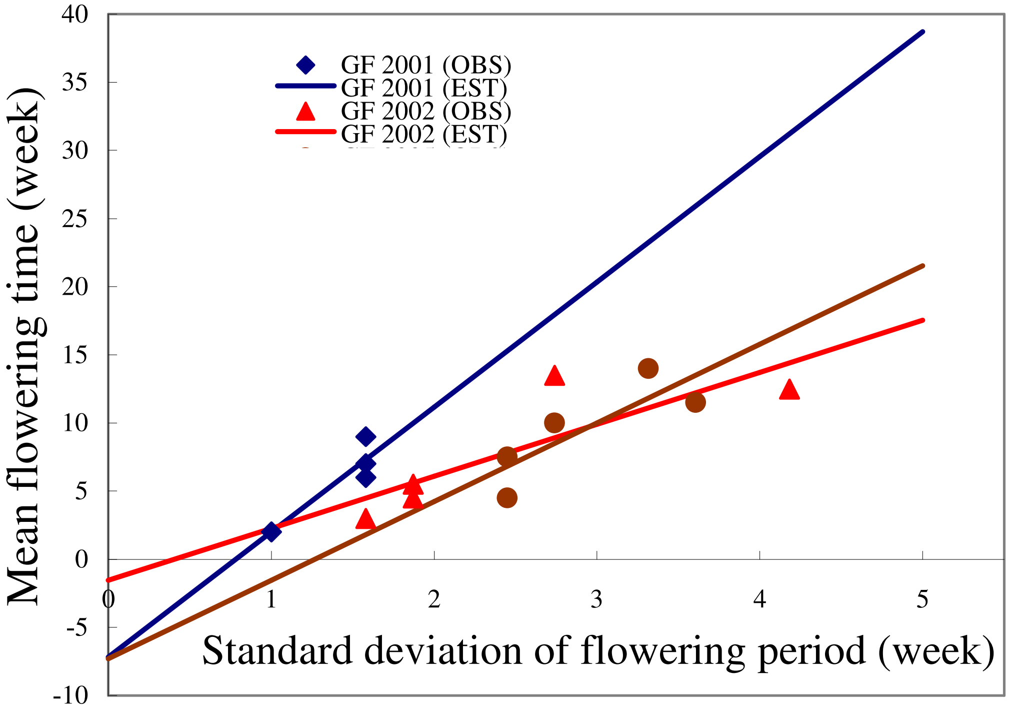

Figure 3.3 Regression method for estimating the time of floral induction using flower presence-absece data (the qualitative approach). The regression is of mean flowering time on the standard deviation of flowering time for GF 2001, GF 2002, and GF 2005. The intercepts of the regression lines indicate how long an interval occurred between the estimated floral induction time and the first flower of *S. macroptera*. The regression equations for the three events were: $y = 9.1774\,x - 7.1774$; $y = 3.8121\,x - 1.5356$; $y = 5.7669\,x - 7.2931$.

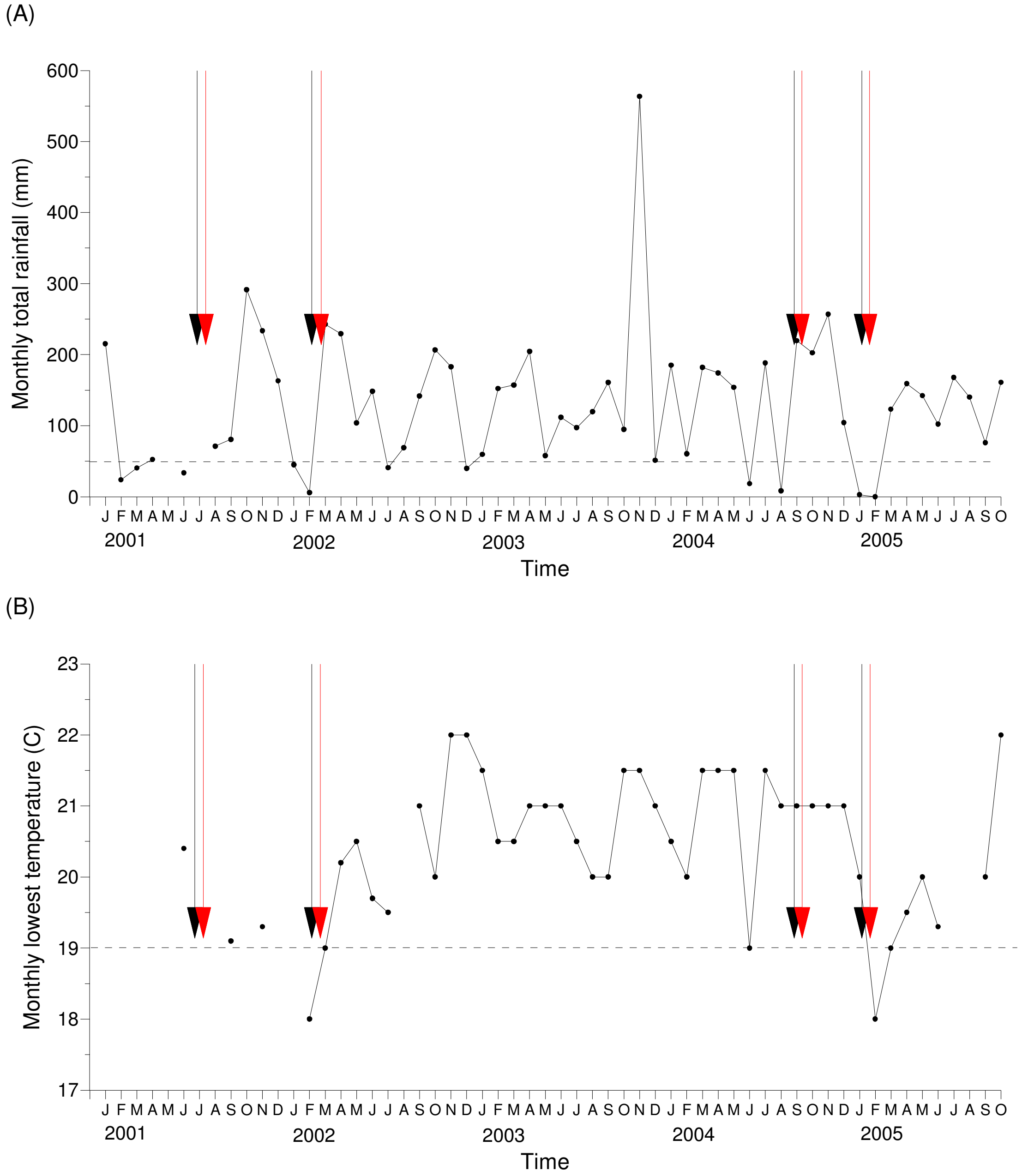

Figure 3.4 Climatic fluctuation and floral induction. Temporal variation of monthly total rain fall (A) and monthly minimum air temperature (B) from January 2001 to October 2005 are shown. Black arrows indicate the estimated floral induction time based on qualitative (presence-absence) flowering data. The red arrows represent the estimated floral induction time based on the quantitative data on species in *Shorea* section *mutica*. All four floral induction estimates occurred during low rainfall periods and only two fell during periods having low temperatures below 19 °C. Data for January 2001 to January 2002 were from the meteorological station in Kuala Pilah, Malaysia (30 km away from the research site), and were corrected for the average difference between urban and forest averages. Data for February 2002 to October 2005 were records from the weather station at the Pasoh field station run by FRIM.

Table 3.1 Fruit development time (FD) and seed mass. There was a strong correlation between mass of diaspores and mass of true seeds (R^2=0.93; seed mass data from YYC, unpublished.). We used mass of true seeds to evaluate the hypothesis of a significant correlation between seed mass and fruit development time in *Shorea* species. We found no significant correlation between fruit development time and seed mass (general linear regression, df = 8, p=0.607). Species codes were defined in the legend of fig. 3.2

Sp code	N	FD time (mean±SD)	Mean of seed mass (mg)	rank of seed size
SHORM1	3	135.3 ± 14.6	798.3	7
SHORL2	2	123.0 ± 12.3	1192.5	8
SHORP1	3	112.9 ± 9.0	200.8	2
SHORAC	3	98.0 ± 13.2	299.9	4
SHORL1	3	89.3 ± 9.7	364.4	5
SHORM2	3	86.4 ± 13.3	164.3	1
SHOROC	2	107.8 ± 5.9	265.1	3
SHOROV	1	85.5	734.7	6
SHORP2	2	91.3 ± 19.9	1407.5	9
SHORBR	2	79.5 ± 8.3	-	-

Table 3.2 Regression of mean flowering time on the standard deviation of flowering period. Four regressions yielded somewhat different result of the estimates of floral reduction time (intercept) in all years. These approaches were distinguished with flower-presence and flower-record data for *mutica* and non *mutica* species. Regressions were carried out using 95% of flower record of *mutica* species and non *mutica* species to define the flowering period in each season. Mean week and standard deviation of the defined periods were calculated with each type of data. Species with no less than 15 flower records in each season were included in the calculation.

	mutica species			non *mutica* species		
Year	Intercept	Slope	P	Intercept	Slope	P
Qualitative						
GF 2001	-7.1774	9.1774	0.0471	-3.5168	4.6316	0.0070
GF 2002	-1.5356	2.2248	0.1507	6.3532	1.0692	0.0378
GF 2004	NA	NA	NA	9.9796	0.5868	0.1431
GF 2005	-7.2931	5.7669	0.0573	6.9874	0.7529	0.0110
Quantitative						
GF 2001	-5.6131	12.0466	0.1510	-0.0514	4.1201	0.0124
GF 2002	2.9996	1.5424	0.2594	6.4764	0.8354	0.1361
GF 2004	NA	NA	NA	9.7194	0.3694	0.2241
GF 2005	-4.0232	4.9543	0.0461	6.2614	0.9959	0.0222

CHAPTER 4

DENSITY DEPENDENT MORTALITY AND CHANGES IN SPECIES DIVERSITY AMONG GERMINATING SEEDS AND FIRST-YEAR SEEDLINGS DURING AND FOLLOWING GENERAL FLOWERING EVENTS IN A LOWLAND DIPTEROCARP FOREST[3]

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[3] Chen, Yu-Yun, Wright, S. Joseph, Sun, I-Fang, Hubbell, Stephen P., Nur Supardi Md. Noor. To be submitted to *American Naturalist*.

Abstract

In dipterocarp-dominated SE Asian rain forests, supra annual general flowering (GF) that involves synchronous fruiting ("masting") in a large number of tree and liana species causes large interannual fluctuations in community seed production. In theoretical models, recruitment fluctuations, especially those that are independent among species, promote species diversity by giving rare species a frequency-dependent recruitment advantage. Synchronous masting that satiates predators should reduce density dependent seed mortality in those species joining the mast. However, GF events potentially could reduce species diversity by causing competitive exclusion of species that do not join the mast. Critical to the outcome is how density dependence operates in masting and non masting species. In this study we evaluated density dependent mortality over two transitions in the early life stages, the seed-to-seedling transition and yearling seed survival rates for tree species in a lowland dipterocarp forest. We found negative density dependence in both transitions with a stronger effect for seed-to-seedling transition than for the yearling survival. We also tracked changes in species diversity through time in different cohorts. Diversity of the seedling cohort resulted from a non GF year was consistently lower than cohorts from GF years. All cohorts lost diversity over time, but the loss of diversity was greater in both cohorts from non GF years but also greater in the strongest GF year.

Introduction

In the aseasonal dipterocarp forests of South East Asia, interannually highly variable plant reproduction, referred to as general flowering (GF), has been reported for more than a century (Appanah, 1985; Corlett, 1990; Curran, 1994a; Maycock *et al.*, 2005; Numata *et al.*, 2003; Wich

& van Schaik, 2000). GF have been reported to always involve many non dipterocarp tree species although few studies checked the flowering of these other species in non GF years. Janzen (1974) hypothesized that plant species that reproduce synchronously during GF achieve higher seed survival rates by satiating seed predators. Nonetheless, failure or low recruitment could occur during seedling establishment (Blundell & Peart, 2004b). Recruitment failure could be attributed to several sources: inability to reach suitable sites, unfavorable climatic conditions during periods of seedling establishment, and predation on seedlings. The later is usually hypothesized to be density dependent.

Janzen (1970) and Connell (1971) independently proposed that tree species diversity in tropical forests is maintained because trees are rarely replaced by an individual of the same species due to an interaction of seed dispersal and density- and distance-dependent seed predation. They proposed that seeds dispersing away from the maternal parent have a greater probability of escaping predation. The high density of seeds in the vicinity of maternal parent trees attracts host-specific seed and seedling predators and pathogens, leading to density dependent mortality, which lowers the rate of self-replacement of parent trees (Blundell & Peart, 1998) and consequently maintains forest diversity (Harms *et al.*, 2000). A number of studies in various forests have evaluated the Janzen-Connell hypothesis, with conflicting results. The majority of the studies testing this hypothesis addressed density-related questions for populations or communities in a spatial context (Wright, 2002). Few studies have recognized the importance of temporal fluctuations in recruitment at population level (Wright, 2002; Wright *et al.*, 2005). This is partly due to the scarcity of long term monitoring data at a community level.

A huge annual variation in seed production is evident in the Pasoh forest (Chapter 2). In Pasoh and elsewhere in SE Asia, high levels of seed production in GF events not only occur at the species level but also the community level, involving synchronous seeding among species (Sakai *et al.*, 1999b). We refer to such synchronous seeding hereafter as masting. At Pasoh there is evidence that the increased seed abundance during GF years increases because seed predators are satiated at the community level (Sun *et al.*, 2007). However, the question then is whether enhanced survival from seed predators during GF events leads to higher compensatory mortality in germinated seedlings or yearling cohorts (Blundell & Peart, 1998). Species reproducing annually might have an advantage over supra annual species, but not if they suffer seed predation due to the general scarcity of seeds in the forest during non GF years.

Studies evaluating the strength of density dependence during various life stages are scarce (Webb & Peart, 1999). Such studies are important, however, especially during the most vulnerable life stages of plants, when most mortality occurs, and they can potentially provide insights into how forest diversity is maintained. During a five year study, we evaluated density dependence in 38 species in the transition of seeds to seedlings and from established seedlings to yearling seedlings in the Pasoh forest in Peninsular Malaysia. We set out transects of seed traps across the 50 ha permanent plot at Pasoh (Manokaran *et al.*, 1992). Each trap had three associated seedling germination plots. Under the assumption that the seed rain into a given trap was the same as the seed rain in the immediately adjacent germination plots, we could evaluate the mortality of seeds before germination. We then followed newly germinated seedlings, and recorded whether they survived their first year. We addressed the following questions: (1) Does the strength of density dependence differ between (A) different life stages and (B) supra annual and annual fruiting species? (2) Is there evidence for compensatory mortality in the losses between different life stages? (3) How does diversity change over time and among cohorts?

Methods

Study site

The Pasoh Forest Dynamics Plot (Pasoh FDP onward) was established at the center of the Pasoh Forest Reserve, Negeri Sembilan, Malaysia (2^{o} 58' 47" North, 102^{o} 18' 29" East). All trees $\geq$ 1 cm in diameter at breast height were measured, tagged, and mapped in 1985 and have been recensused every 5 years since. A total of 814 tree species were recorded in the first tree census. It is estimated that the forest has at least 250 additional liana species (Yee-Chong Chan, pers. comm.). The forest is dominated by trees in the family Dipterocarpaceae, which comprised 10% of all stems, and is consequently characterized as a mixed dipterocarp forest. Mean monthly low and high temperatures in this forest are 22℃ and 32℃, respectively. Mean annual rainfall is approximately 1800 mm and is relatively evenly distributed throughout the year (Losos *et al.*, 2004). Therefore, the Pasoh forest is categorized as an aseasonal forest.

Data collection

Since August 13, 2001, a total of 336 passive traps, measuring 0.5 m^2 in area, were placed in the Pasoh FDP. We censused all traps weekly between August 20, 2001 and the present, and identified reproductive parts to species. We sorted these materials into eight categories: whole fruit, whole seed, capsule, fragment, immature fruit, flower, fruit bitten by animals, and seed bitten by animals. We identified all materials to species and morpho-species, and we counted all materials, with the exception of flowers, which we recorded as present or absent. This study is based on records on 89,032 seeds (whole fruit or whole seed) from 267 trap censuses.

We placed three 1 m x 1 m seedling plots two meters from each trap on three sides. We carried out the first seedling census between August 11 and December 8, 2001 on 741 plots.

We added 89 traps to the census in 2002, and this added 283 more seedling plots, which we first censused between June 1 and August 20, 2002. We tagged all seedlings below 50 cm in height and measured heights during the first census. We recorded the fate (survival or death), height growth of previously tagged seedlings, and new recruits in an annual census running from late May to July. We were able to identify 86.5% of all recruits to species or morpho-species. The numbers of new recruits for cohorts 2002, 2003, 2004, 2005, and 2006 were 1146, 4224, 3643, 1906, and 12775, respectively. The interval between the first census in 2001 and the second census in 2002 was 8 months.

We compared the strength of density dependence among various phenological groups. Phenological classes of species are considered in terms of periodicity and reproductive synchrony with *Shorea* section *mutica*. Categories in periodicity are continuous, biannual, annual, and supra annual. In addition, categories in synchrony feature are GF and nonGF (Chapter 2).

Data analyses

For present purposes, we define an annual period as the interval between the first days of two sequential seedling censuses, although the actual elapsed time is not precisely a year. We calculated the density of seeds (S), established seedlings (E), and yearling seedlings (Y) for each trap in each annual period. We measured annual seed rain as the total seed number over the annual period divided by the area of the trap and the length of time (number of seeds / m^2 yr^{-1}). We calculated densities of seedling recruits and seedlings surviving to the one-year-old stage (yearling seedlings) by pooling data from three seedling plots adjacent to a seed trap station and dividing by total area of the plots and the length of period (number of seedlings / m^2 yr^{-1}). We pooled the densities from all 5 years and all traps for each species for the tests of density dependence described in the next section. Two criteria were used to qualify a species for this test: (1) A species had to have records from no fewer than 5 traps; (2) A species had to exhibit at least four-fold variation in S, E, or Y.

Density dependence in seed-to-recruit transition

To estimate the strength of density dependence, we used the following formula to examine the relation between seed density (S) and recruit density (R) (Harms *et al.*, 2000):

$$E = a * S^{b} \tag{1}$$

Log transforming Eg. (1) gives a formula for simple linear regression and the addition of 1 allows us to include values of zero:

$$\log (E+1) = \log a + b * \log (S+1) \tag{2}$$

The slope b derived from the regression measures the strength of density dependence. A b value < 1 indicates negative density dependence, whereas a b value > 1 indicates positive density dependence. A value b of 1 indicates density independence.

Harms *et al.*, (2000) identified several potential sources of bias in estimating this slope. First, seed trap stations having many more seeds than could be physically fit into the limited space of the seedling plots could lead to a stronger (shallower positive or negative) slope in the regression. Second, stations having recruits but no seeds of a species will lead to a steeper slope or apparently weaker density dependence. Such cases tend to arise when there is a very low, Poisson probability of seed arrival in any given area the size of a seed trap or seedling plot. Third, empty stations with neither seeds nor seedlings of a given species will tend to inflate the apparent strength of density dependence. We included such stations in the regression under the assumption that the absence of seeds and recruits was due to a low probability of seed arrival in the tail of a dispersal kernel. Data were treated in the following ways to assess the biases: (1) Excluding stations with more than 132 seeds/m^2 yr^{-1}. We obtained this value from the densest seedling plot and use this as the limit of seed density. (2) Excluding stations with S values of zero and E values of non zero. (3) Excluding stations with S and R values that are both zero. Data from before and after these treatments were regressed using Eq. (2) and the results were compared.

Finally, addition of 1 in Eq. (2) in the log transformation of all data points could lead to a downward bias to the fitted slope b. To assess the impact of the addition of this constant before taking logarithms, we calculated the expected E and Y under the assumption of density independence. This can be done by summing all observed S, E, and Y to obtain the S-to-E and E-to-Y ratios. We then calculate expected E values by multiplying observed S values with the S-to-E ratio and expected Y values by multiplying observed E values with the E-to-Y ratio. Expected b values of the two recruitment stages were obtained by regressing expected E with observed S and expected Y with observed E. We compared observed and expected b values to assess the impact of the addition of 1 in the method.

Density dependence in the seedling-to-yearling transition

We tested recruit cohorts from the first four years for density dependence at the seedling stage independently. We calculated the relationship between density of recruits (E) and density of yearling seedling (Y or yearling hereafter) using Eq. (2), with S replaced by E and E replaced by Y. We found that the greatest source of bias in slope estimation was from empty stations where no first year recruit was found. An argument to include these stations in the analysis was that no census could be guaranteed to be error free. Zeros could occur because of overlooked individuals. We made an assessment of the impact of including the empty stations by conducting the same regression but excluding empty stations. Assessments of possible biases from empty stations and the addition of 1 were done in the same manner described above.

Change of diversity through time

Two weak GF events were identified in 2001 and 2004 and had resulted in cohorts 2002 and cohort 2005. In addition, two stronger GF events were identified in 2002 and 2005 and these events produced cohort 2003 and cohort 2006, respectively. The only cohort that resulted from a non GF year was cohort 2004. Fluctuations in flowering and fruiting resulted in variable numbers of recruits among years. To eliminate the effect of varying sample sizes, all indices were estimated with 5000 rarefaction iterations. Means of the indices were reported.

We chose Fisher's alpha (α) as the primary diversity index in this study (Magurran, 2003). The calculation of Fisher's alpha can be done using Eq. (3), where s is the number of species found in a sample of n individuals, and α is Fisher's alpha, the index.

$$s = \alpha * \ln (1 + n / \alpha) \qquad (3)$$

Fisher's alpha is less sensitive to the super abundant species compared to the other two commonly used indices, the Simpson index and the Shannon-Wiener index. In addition to the diversity index, we calculated evenness by using Pielou's evenness index (J) given in Eq. (4), where H is the Shannon-Wiener index and H_{max} is the H when all species are equal in abundance.

$$J = H / H_{max} \qquad (4)$$

We followed changes in diversities (α) and evenness (J) in the five cohorts over time. Due to the large differences in sample sizes among cohorts, we applied rarefaction to resample all cohorts before calculating diversity and evenness indices. The resampling size was chosen as the minimum number of live seedlings, x, found among all cohorts in the 2006 census. We randomly sampled x individuals from each cohort and each year independently. Seeds were also sampled with the resampling size, x. Diversity (α) and evenness (J) were calculated for these new samples. We carried out 5000 sampling iterations for all years and all indices. We calculated means of diversity and evenness indices from 5000 rarefaction runs.

Results

Density dependence

At the community level and across census stages and cohords, fitted b values from the linear regression with Eq. (2) ranged between 0.0 and 0.6 in the seed-to-established seedling stage, indicating strong negative density dependence. Thirty eight out of 40 regressions were significantly linear ($p<0.0001$). Fitted b values derived from fitting Eq. (3) ranged between 0.2 and 0.9 in the seedling-to-yearling stage and all forty five regressions were significantly linear ($P<0.0001$). Density dependence was more negative in the seed-to-germinated seedling transition that in the seedling-to-yearling transition (Fig. 4.1, two-tailed t-test, df = 81, $p < 0.0001$). However, comparing the means of b values for annual and supra annual groups for both life history stages, we found no difference (Fig. 4.2). At the species level, no clustering or linear pattern among phenological groups was found (Fig. 4.3).

Assessing biases in estimating the strength of density dependence

We assessed possible biases in the seed-to-established seedling transition by comparing b values fitted with and without various data transforms and eliminations. Eliminated sample stations with seed counts above a ceiling for seed density showed only a slight change to the distribution of b (Fig. 4.4, upper panels). On the other hand, excluding stations with no seeds shifted b values significantly higher (weaker negative density dependence) in seven out of thirty eight species. The dispersion of b values became larger when no-seed stations were excluded (Fig. 4.4, lower left panel). However, excluding null or empty stations significantly lowered b values (stronger negative density dependence) on twenty three out of thirty eight species. These treatments also change the range of b values at the community level (Fig. 4.4, lower right panel). Nevertheless, all treatments showed consistent negative density dependence at the community level.

We assessed possible biases on slope estimation in the regression for the seedling-to-yearling transition by excluding empty stations. The b values derived after exclusion did not differ significantly from the b values derived before exclusion in all species. However, the dispersion in b values widened, and in two species, slopes were > 1 (Fig. 4.5). These large b values could be explained as a mathematical artifact.

At the community level, the difference between means of b values in the two life history transitions was significant after exclusion of empty stations (Fig. 4.6, two-tailed t test, $p<0.0001$). However, we found no clustering or a linear relationship in slopes among the phenological groups by excluding empty stations in the seed-to-seedling transition (Fig. 4.7), consistent with results from regressions before station exclusion. At the species level, b values from before and after station exclusion showed linear relationships for both seed-to-established seedling and established seedling-to-yearling stages, with correlation coefficients of 0.7605 and 0.6982, respectively (Fig. 4.8).

Change of diversity through time

Changes in species diversity were consistently downward over time. The most significant drop was from year 0 (seed stage) to year 1 (first-year recruit) for all but cohort 2002 (Fig. 4.9). However, after recruitment into seedling stage, diversities within a cohort remained more or less constant through time thereafter. The diversity indices of cohorts produced by weak and strong GF events fluctuated at similar levels, whereas the diversity index for the cohort 2004 from a non GF year fluctuated at a significantly lower level (Fig. 4.9).

Simple species richness exhibited similar temporal patterns to the diversity indices (Fig. 4.10). In most cases, however, species richness was not statistically distinguishable among cohorts, except in the comparison between cohort 2002, cohort 2005, and cohort 2006. Although species richness in seedling stages among cohorts fluctuated, it did not differ among cohorts significantly (Fig. 4.10). On the other hand, evenness showed distinct temporal and among-cohort patterns. Cohort 2002 and cohort 2003 showed marginally significant drop of estimated evenness between year 0 and year 1 but not for all sequentially paired seedling stages. Cohort 2005 and cohort 2006 exhibited no difference in estimated evenness from seed to all seedling stages. In contrast, cohort 2004 experienced a significant drop of estimated evenness up to year 2. The evenness in the later stages of this cohort fluctuated at a significantly lower level.

Discussion

Density dependence

To answer whether the strength of density dependence differs between (A) different life stages and (B) supra annual and annual fruiting species, we compared the means of b between groups. Our study indicated more negative density dependence in the first life history transition (seed-to-established seedling) than the second transition. This suggested a strong effect to reduce the frequency of dominant species in the earlier stage to determine population abundance (Connell & Green, 2000) for the later stage. Our observations were inconsistent with the much longer (32-year) observation on *Chrysophyllum* sp. (Sapotaceae) in Australia (Connell & Green, 2000). Significant negative density dependence in both transitions strongly limited recruitment in the first year of seedling life in Pasoh. We were surprised to find no difference in the strength of density dependence between supra annual species and annual species in any of the stages. This result suggests the existence of similar density dependent effects on frequently and infrequently fruiting species.

To look for compensatory mortality, we examined the b values of the two sequential life history stages for each species. Compensatory mortality occurs when, if mortality is high in the first stage, it is low in the second stage, and vice versa. Compensatory mortality would show if there is a negative relationship between the sequential b values in the two transitions. Conversely, a positive relationship or not relationship between the sequential b values would be evidence against compensation, and a positive relationship would, in fact, indicate a strengthening of density dependence through time. We found no systematic evidence for compensatory mortality, or for a strengthening of density dependence, either at the individual species level, or among phenology groups. Compensatory mortality must occur at some life history stage, however, because of physical packing constraints as plants grow. Our failure to detect it is due in part to the short time period of the study (4 years), but it may also be that in these early life history stages, compensatory mortality effects are truly weak. In any event, no predictions about trends of dominance of species or phenological classes can be made from the current data. An important caveat to make here is that there are limitations to this regression method. We selected species for regression analyses that met criteria of adequate sample size (number of traps receiving seeds) and minimum seed density variation within species. Although this selection of species ensured the legitimacy of the regression with adequate sample size and variation, it also limited our ability to address the same questions for rare species, for species with infrequent reproductive events, or for species having a combination of the two. Most species in hyper diverse tropical forests such as Pasoh are rare (Okuda *et al.*, 1997; Whitmore, 1984). Moreover, SE Asian forests has more supra annual flowering species than the other frequent flowering types (Sakai, 2001). However, it is in rare species that one would like to look for evidence of a frequency-dependent, rare-species advantage. Thus, our inability to study these species by our regression approach may bias our conclusions at the community level.

Assessing bias in estimating the strength of density dependence

When large numbers of species are rare and/or flower infrequently, dealing with small sample sizes for many species is inevitable. Even if a species made it into our analysis, many sampling stations typically had null data—zero numbers of seeds, seedlings, or both. Despite these problems, when we estimated all possible biases, we only found six altered b values in the seed-to-established seedling transition out of 38 analyses, and 23 for the seedling-to-yearling transition out of 45 analyses. Moreover, all of these analyses that corrected for bias still indicated negative density dependence, and the b values estimated before and after bias correction mostly shifted in the direction of a stronger effect. Therefore, after considering the effects of bias, no change in the qualitative conclusions needed to be made.

In this study, we reported b values from regressions for all data, including observations of zeros. This decision implies that the zeros are meaningful. The inclusion of null stations especially had a strong effect in limiting slopes between 0 and 1. Values of b within this range could be interpreted from density dependence (b<1) to density independent (b=1). A b value greater than 1 can not be explained ecologically, but arises from a Poisson sampling process whenever there are more germinated seedlings than seeds at a sampling station. This situation did occur, but only in 2 cases out of a total of 85, so it was a minor problem.

Change in species diversity over time

The final goal of this study was to examine the change in species diversity through time against a backdrop of large fluctuations in seed production in the Pasoh forest. From the trap data (Sun *et al.*, 2007), we found high species and individual tree participation in major GF events, with heavy seed production in the 2001 and 2005 GF events, and much less seed production in non GF years. Previous studies have concluded that mast seeding has an important influence to forest diversity. For example, single-species studies have showed that the masting species were more successful in recruitment during masting years, from which the authors concluded that these species would achieve higher dominance level (Alvarez & Williams, 2002; Connell & Green, 2000). Moreover, variable seed production influences seedling recruitment at a varity of spatial and temporal scales, and the strength of this effect is likely to be species-specific (De Steven & Wright, 2002). However, the single-species studies could not answer the questions on the relative performance of other species that coexist with the focal species and thus could not predict the impact of mast seeding in one species to the whole community. To understand the influence of community reproductive performance on the temporal pattern of diversity, we investigated how several measures of species diversity changed over time in five cohorts.

In all 5 cohorts, including two cohorts from weak fall GFs, two cohorts from strong spring GFs, and one cohort from a non GF year, there was a large decrease in Fisher's alpha in the transition from seed (year 0) to established seedling. There were small variations in diversity within each cohort, but diversity estimates did not differ significantly from year to year after the seed to seedling transition. This suggested that the most important life history for determining the level of diversity was the seed-to-established seedling transition. This is the transition on which two opposing mortality forces act against each other: density dependent mortality with worsens seed and seedling survival, and predator satiation, which improves seedling survival. As argued by numerous authors, community masting generates positive density dependence by swamping seed predators with too much food to be eaten before seeds germinate into the relative safety of seedling stages (Andersen, 1989; Augspurger, 1981; Kelly *et al.*, 2000). At the same time, however, a high density of seeds may increase seed predation by pathogens and some specialized seed predators that are not satiated. These two counteracting forces are not mutually exclusive, and balance between them affects the resulting diversity in surviving seedlings. If effect of predator satiation is more important, the positive density dependence gives an advantage to the abundant species, and thus should tend to lower diversity. In contrast, if negative density dependence dominates, then locally abundant species should have lower per capita recruitment success than less common species, promoting higher diversity and higher evenness. Compared to cohorts 2002, 2003, and 2005, significantly bigger drop in diversity was observed in cohorts 2004 and 2006 from a non GF year and the strongest GF (Chapter 2; Sun *et al*. 2007), respectively. However, the later two cohorts differed in the trend of evenness.

The trend of positive density dependence was confirmed again with evenness for cohort 2004 but not for cohort 2006. A large decrease in species richness in cohort 2005 indicated why diversity decreased despite increases in evenness. Loss of species in either high (abundant species) or low end (rare species) of abundance spectrum increased evenness. Most of the effect on evenness was due to the loss of rare species in cohort 2006. On the other hand, cohorts from the other three GF years showed little change in diversity or in evenness between year 0 and year 1. This may suggest a balancing effect on density dependence between the counteracting forces of predator satiation and other factors causing negative density dependence.

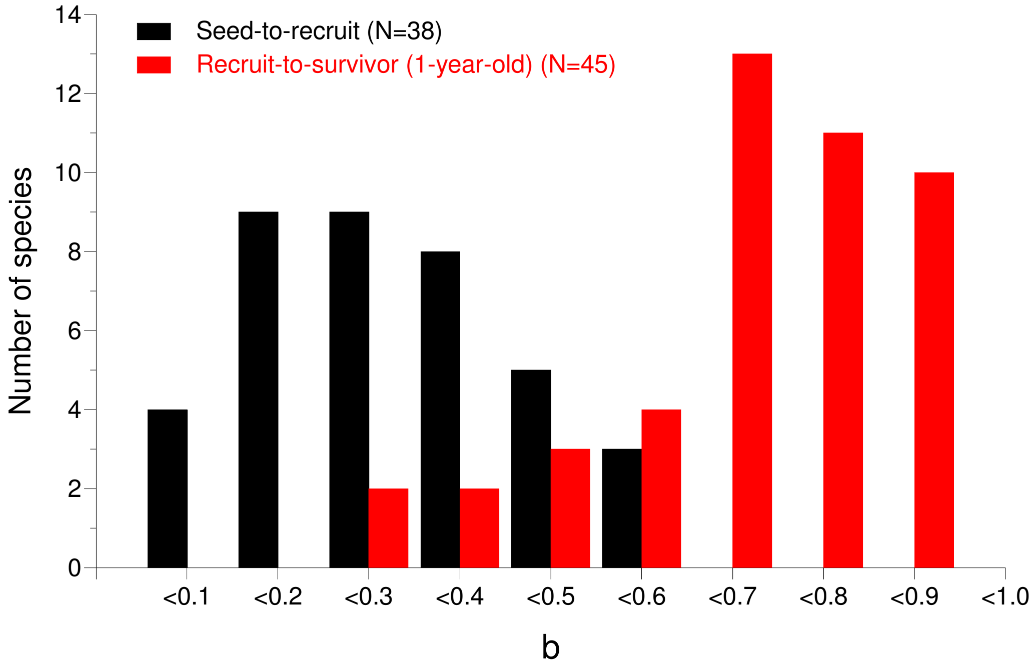
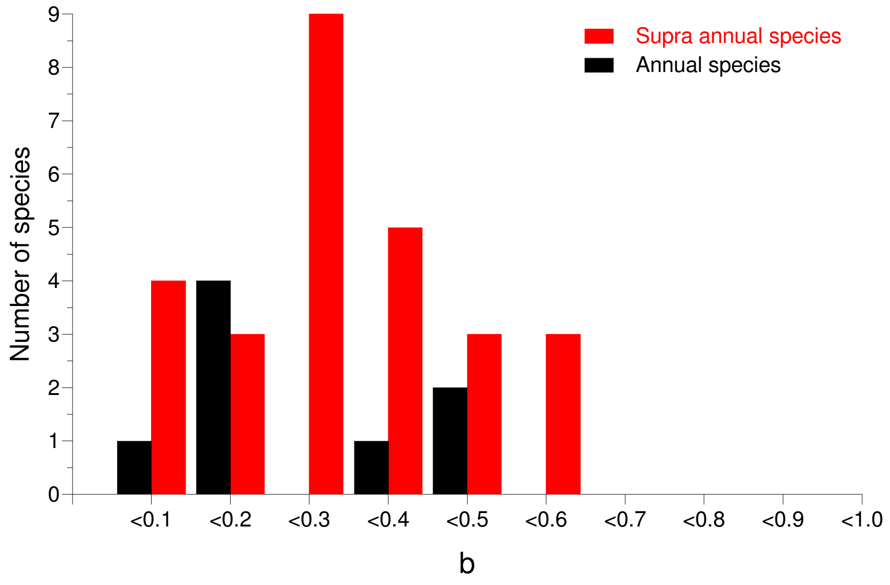


Figure 4.1 Distributions of b values in the seed-to-established seedling and seedling-to-yearling transitions. Histogram bars of b for the seed-to-germinated seedling transition are in black and seedling-to-yearling in red. Means of b values for the two transitions were significantly different (two-tail t test, $P<0.0001$). Numbers of species included in the regression were 38 and 45 for these two transitional stages, respectively.

(A) Seed-to-recruit transition



(B) Recruit-to-survivor (1-year-old) transition

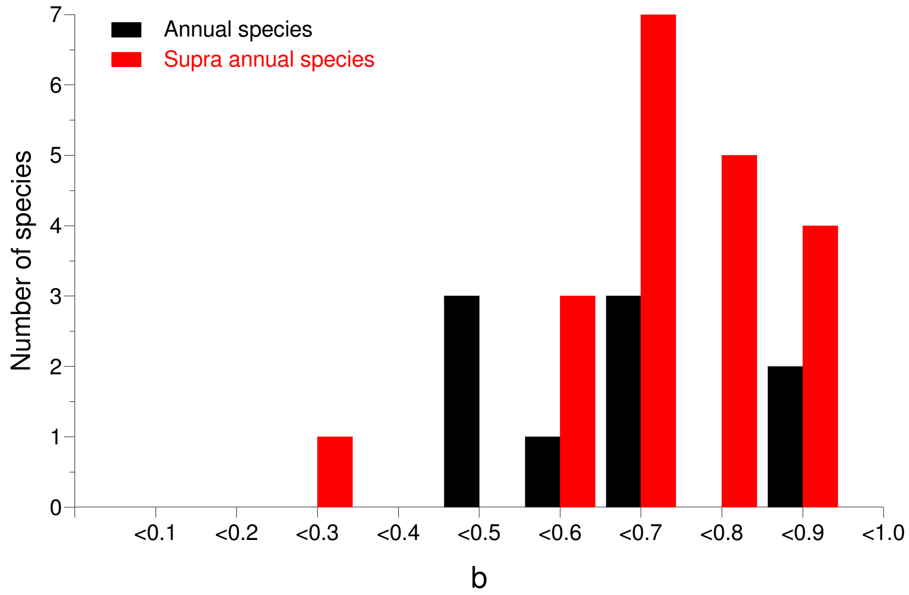


Figure 4.2 Values of b in two periodicity groups in seed-to-established seedling transition (A) and seedling-to-yearling transition (B). Means of b in the two periodicity groups were not distinguishable statistically for either transition. Three and one biannual species were excluded in pannel (A) and (B), respectively. Periodicity of each species was identified in chapter 2.

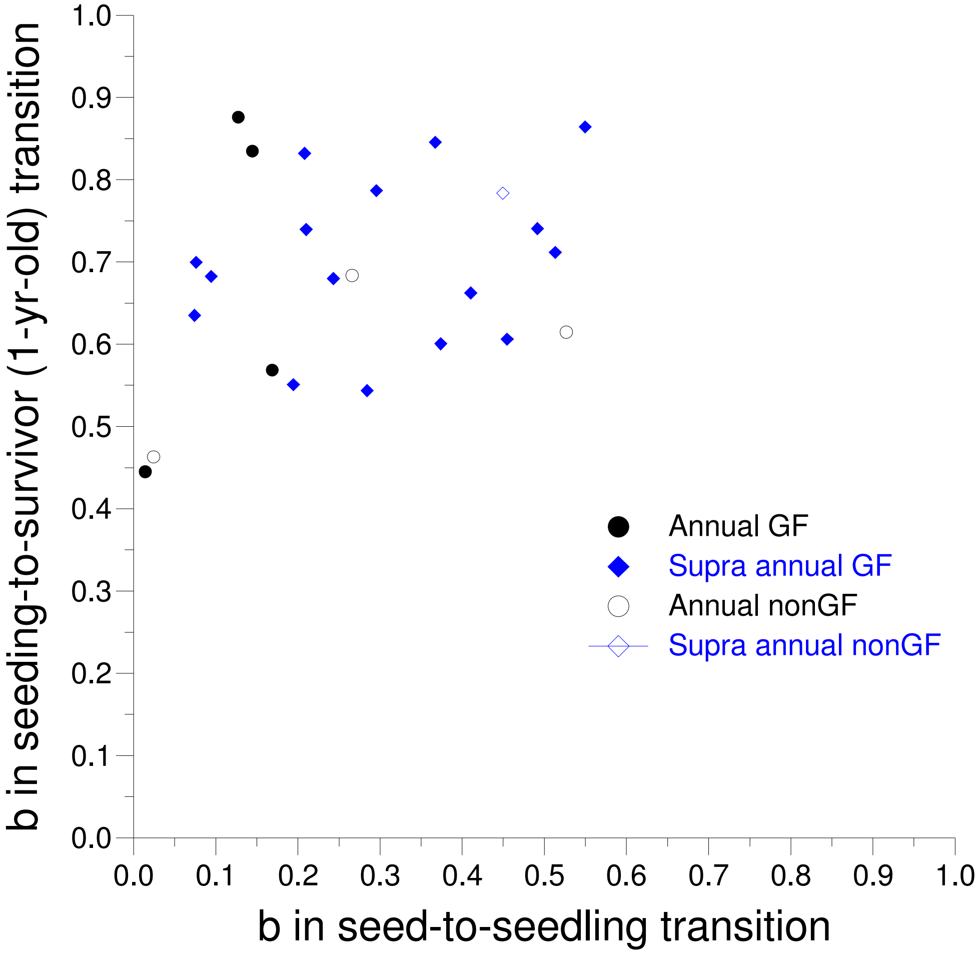


Figure 4.3 b values of two transitions among periodicity groups. No clustering pattern was found among 24 species from 4 phenology groups. Closed circle, closed diamond, open circle, and open diamond represented species from annual GF, supra annual GF, annual nonGF, and supra annual nonGF groups, respectively. All phenology patterns are defined in chapter 2.

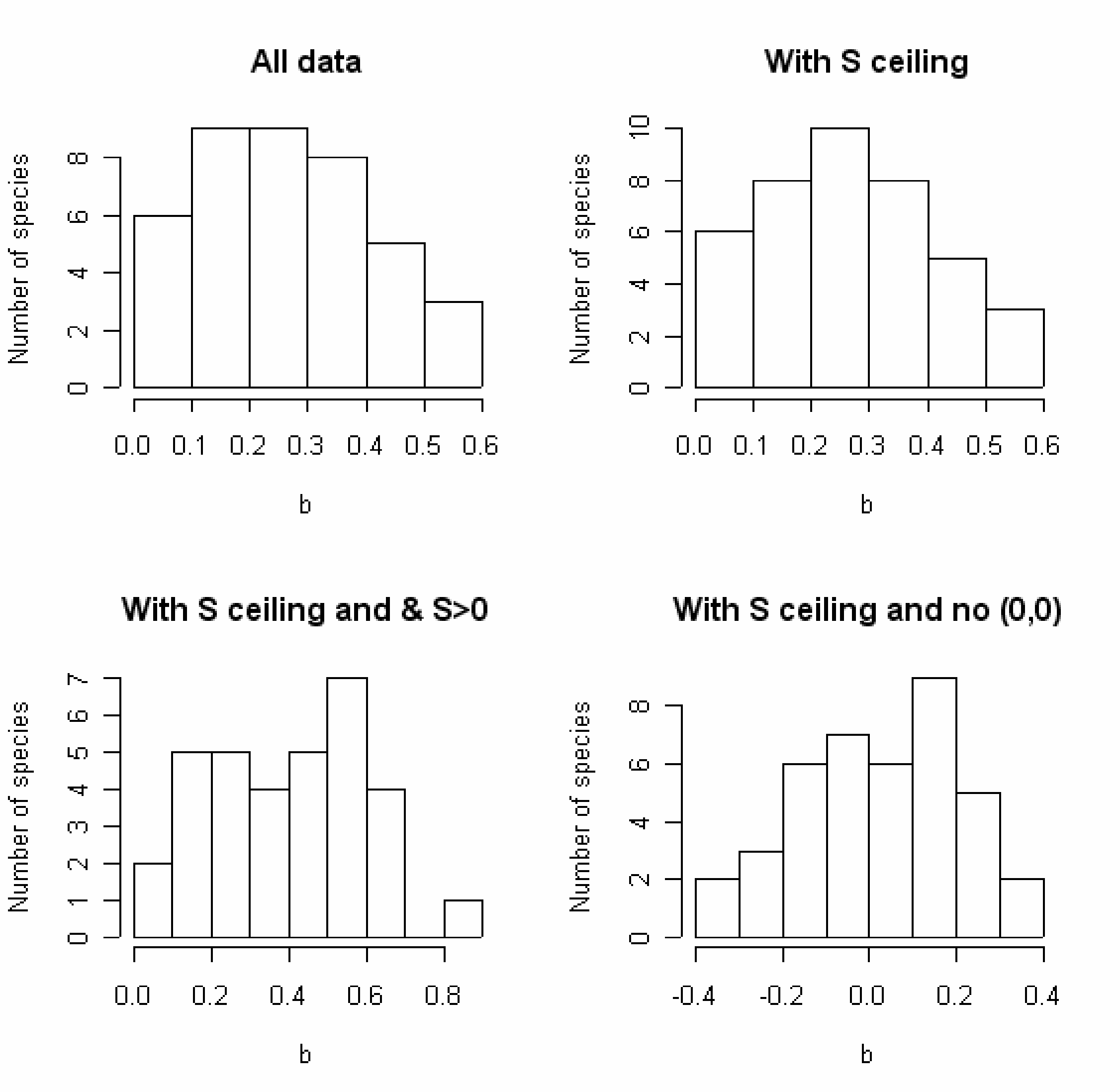


Figure 4.4 Distributions of b values in the seed-to-established seedling transition. Regressions were conducted with all stations included (upper left panel), after exclusion of stations with seed density exceeding 132 m^2 yr^{-1} (upper right panel), after combing the exclusion of stations with high seed density and exclusion of stations with seedlings of a species but no seeds (2) (lower left panel), and after exclusion of stations with high seed density and empty stations (lower right panel).

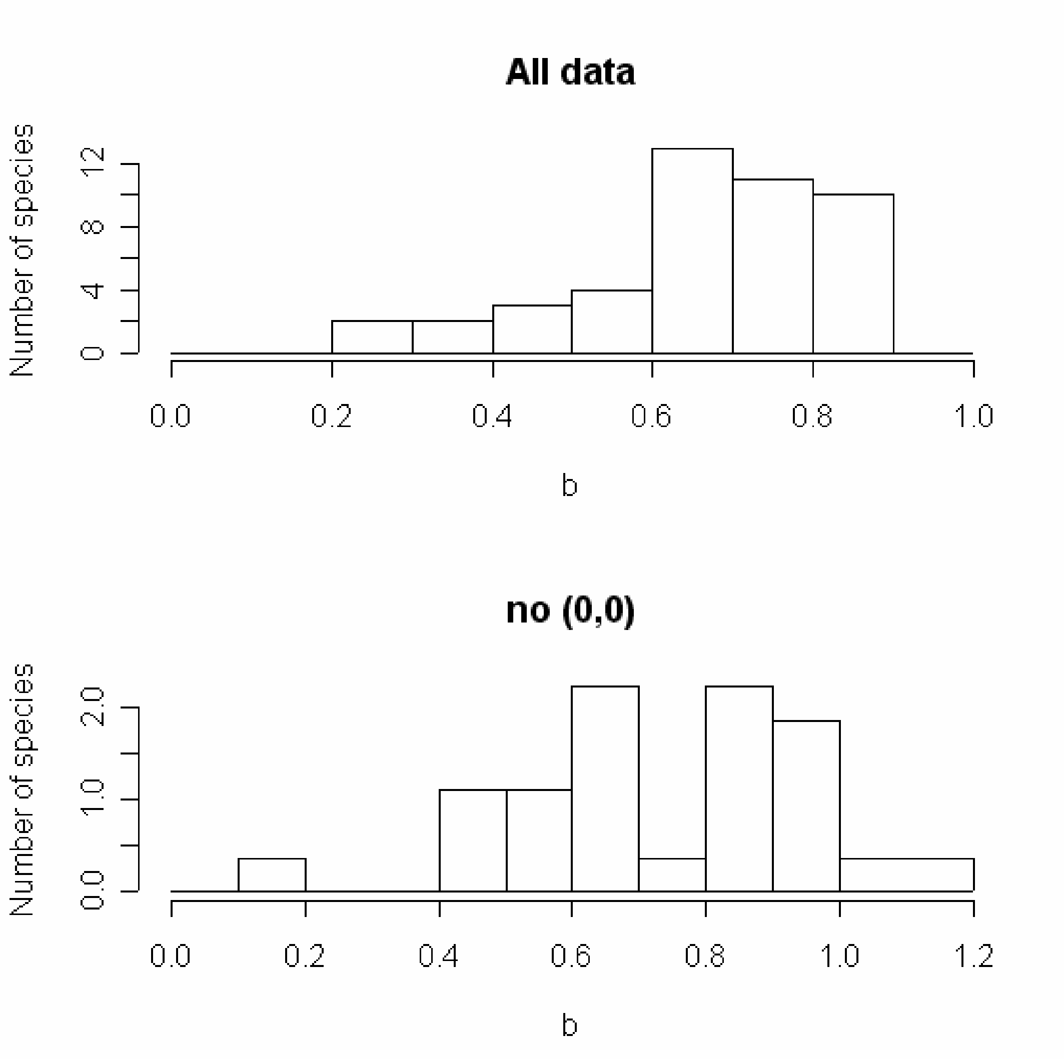


Figure 4.5 Distributions of b values in the seedling-to-yearling transition. Regressions were conducted with all stations included (upper left panel) and after exclusion of empty stations (lower panel).

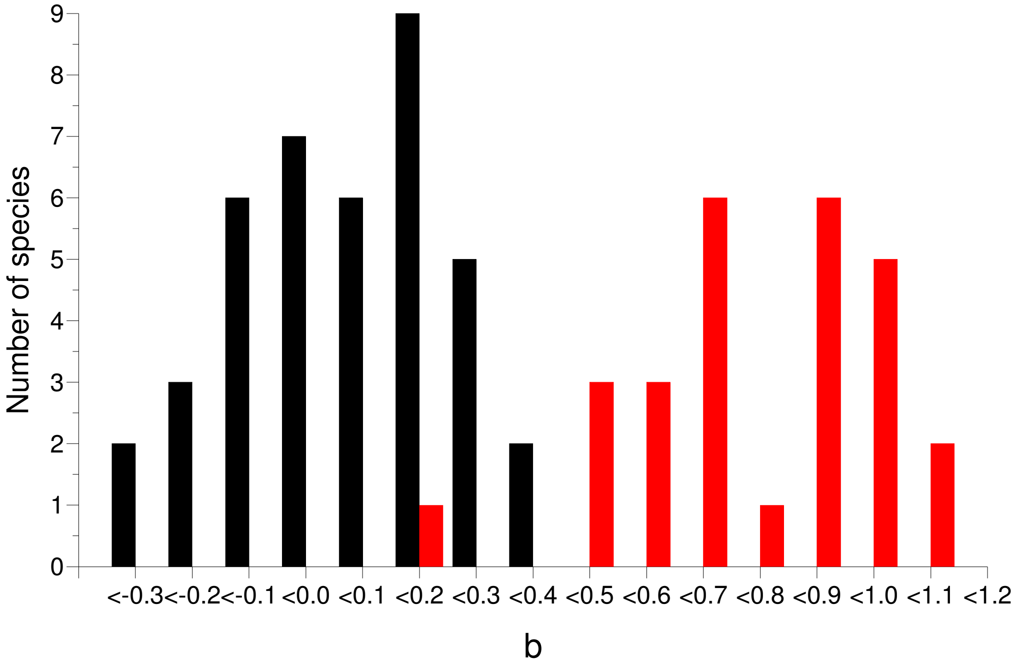


Figure 4.6 Distribution of b values from regressions excluding empty stations for seed-to-established seedling and seedling-to-yearling transitions. Ranges of b values expanded to a wider range in both transitions. Extremely negative density dependence was found in some species in seed-to-established seedling transition. In the seedling-to-yearling transition, 2 species showed slopes >1.

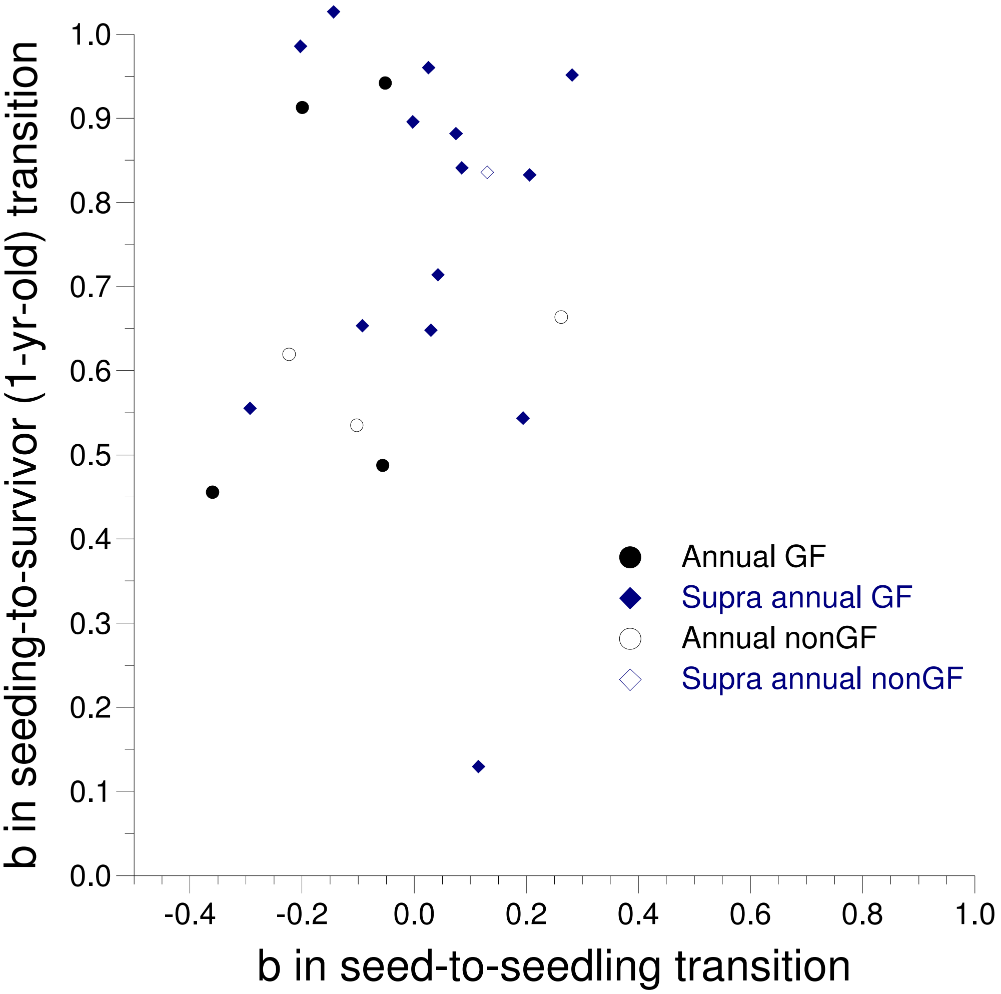
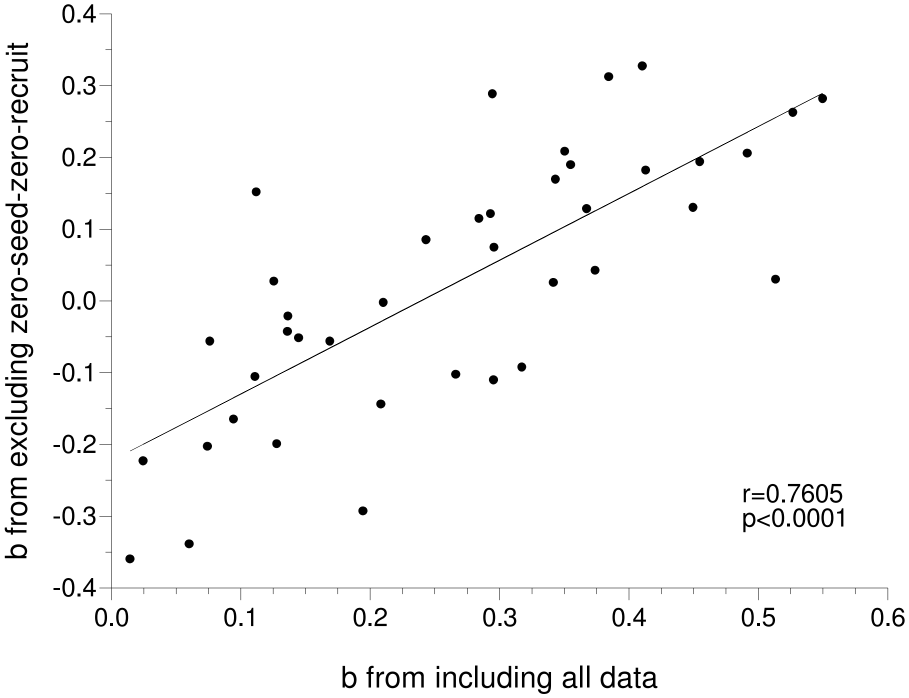


Figure 4.7 b values of seed-to-established seedling and seedling-to-yearling transitions among 24 species from 4 phenology groups. Slopes b were derived from regressions with exclusion of empty stations. No clustering patterns were found.

(A) Seed-to-recruit transition



(B) Seed-to-survivor (1-year-old) transition

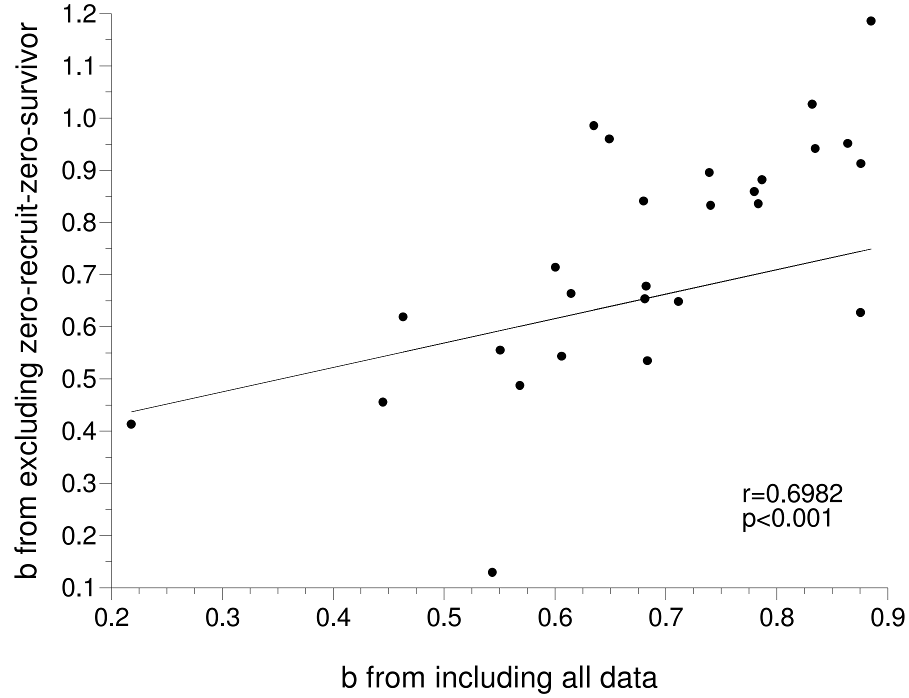


Figure 4.8 Relationship between b values obtained by including (x-axes) and excluding (y-axes) empty stations for seed-to-recruit (A) and recruit-to-survivor stages (B). Estimates of b from before and after exclusion of empty stations showed a linear relationship.

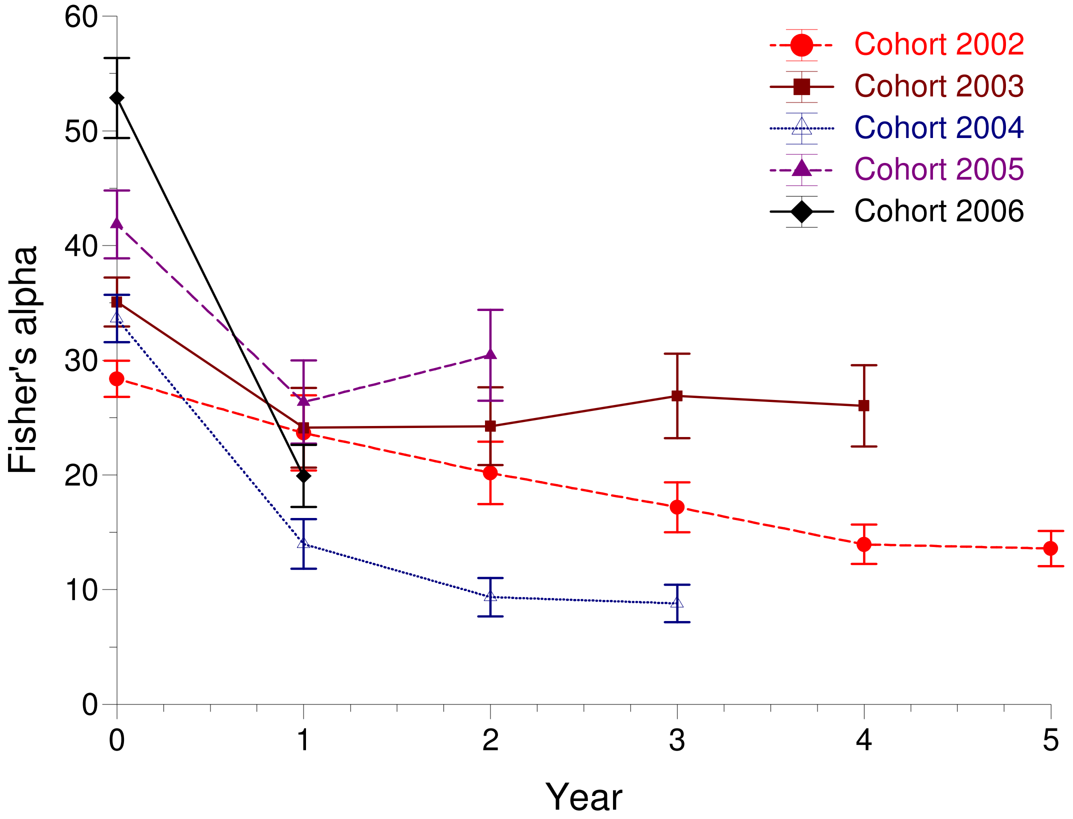


Figure 4.9 Change in diversity in each cohort through time. Five cohorts were treated independently. The only cohort resulting from a non GF year showed the lowest level of diversity among the five cohorts. Mean α and standard errors were estimated with 5000 iterations with rarefaction procedures. Cohort 2002 and 2005, shown by dashed lines, were from two weak fall GF events. Cohort 2003 and 2006, shown by solid lines, were from two strong GF events. The only cohort from a non GF year, cohort 2004, is shown by blue dotted line.

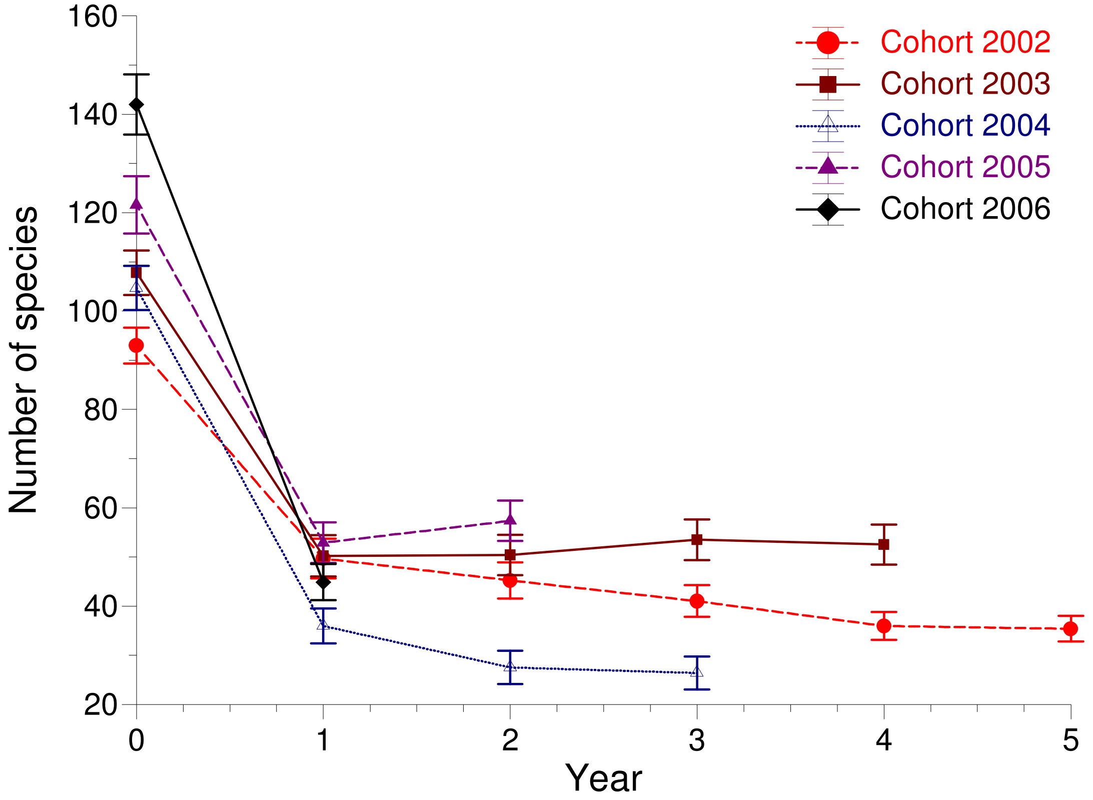


Figure 4.10 Change in species richness in each cohort through time. The largest change occurred in the seed-to-established seedling transition. Species richness remained at similar levels through time. Mean of estimated species number and standard errors were obtained with 5000 iterations with rarefaction procedures. Cohort 2002 and 2005, presented by dashed lines, were from two weak fall GF events. Cohort 2003 and 2006, presented by solid lines, were from two strong spring GF events. The only cohort from a non GF year, cohort 2004, is shown by the blue dotted line.

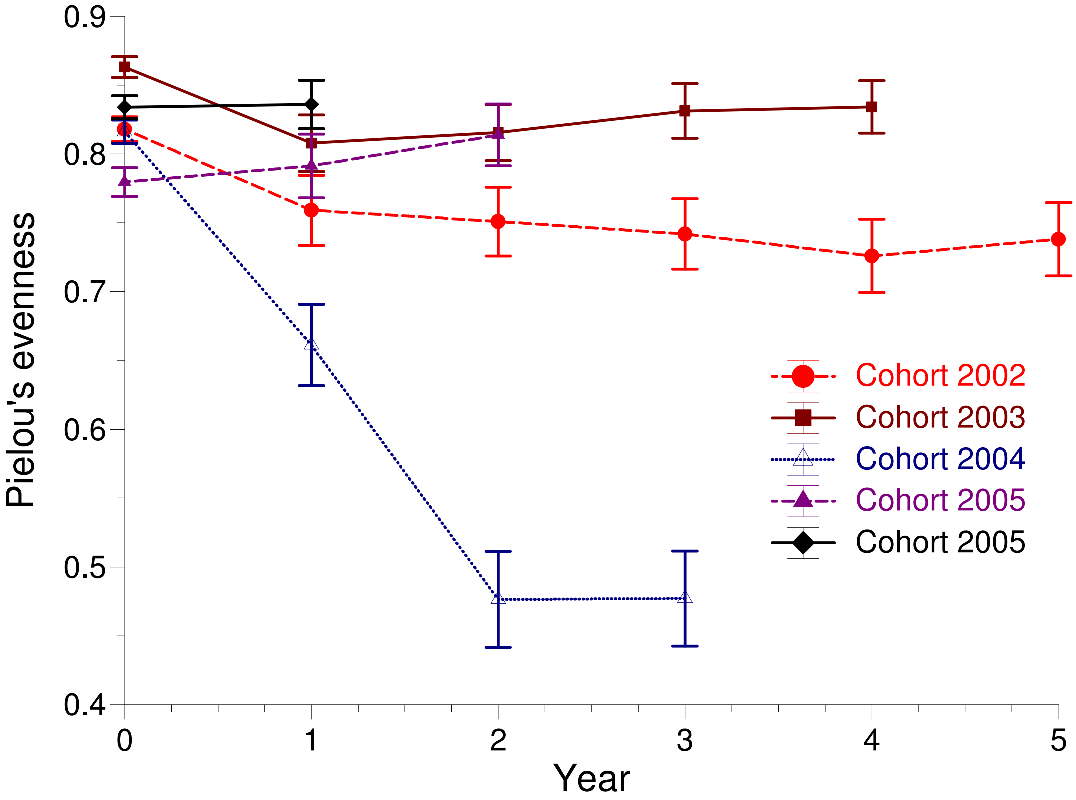


Figure 4.11 Change in evenness in each cohort through time. In the four cohorts recruited after GF events (close symbols), evenness remained relatively constant with minor fluctuations through time, whereas the evenness of the only cohort in a period without GF dropped significantly in the seed-to-established seedling transition.. Mean of the estimated number of species and standard errors were obtained with 5000 iterations with rarefaction procedures. Cohort 2002 and 2005, shown by dashed lines, were from two weak fall GF events. Cohort 2003 and 2006, shown by solid lines, were from two strong GF events. The only cohort from a non GF year, cohort 2004, is shown by blue dotted line.

CHAPTER 5

CONCLUSIONS

Significance

The general flowering phenomenon in Southeast Asia forests was first reported scientifically in 1901. For the past century, many observations on GF were collected and made available by Ashton *et al.*(1988). These records provided an understanding of the irregularity and regional pervasiveness of GF (Appanah, 1985; Sakai, 2002). Various studies also demonstrated that GF events were variable in magnitude and spatial distribution (Numata *et al.*, 2003; Sun *et al.*, 2007). In addition, thanks to long term weather data, researchers have been able to correlate the GF records to special climatic conditions, such as unusual dry spells and unusually low minimum temperatures in this region (Sakai *et al.*, 2006; Yasuda *et al.*, 1999). However, small sample sizes of the numbers of tree species and individuals, and the usual failure to include more than one GF event in any given analysis limited our full understanding (Curran, 1994a; Sakai *et al.*, 1999b), especially of the evolution of the phenomenon. For instance, there has been little attention to the temporal periodicity of reproduction in individual species and whether this periodicity determines species' participation in GF events. Furthermore, liana species, which comprise almost a quarter of the species, have been completely overlooked. In this project, I used systematic sampling methods in a long-term monitoring study of community-wide reproductive phenology at the Pasoh forest. In addition, I was fortunate to be able to observe four GF events during the study period. I applied objective and robust analytical approaches to identify periodicity and detect synchrony of reproduction. With a combination of long term quantitative data and objective approaches, we were able to provide, for the first time, information on periodicity for the most abundant species in the Pasoh forest and on the degree of reproductive synchrony with *Shorea* species in the section *mutica* (the GF feature).

In previous search for flowering triggers of GF events, researchers commonly applied time series analysis to correlate the fluctuation in climate with the occurrence of GF. Another approach was used by Ashton *et al*. (1988), who estimated the date of community-wide floral induction, assuming that variation of flower and fruit development was constrained by the requirement for synchronous seedfall in all species. This assumption allowed them to back calculate a date of floral induction, which could then be related to unusual weather events. However, the regression analyses were done with qualitative data on a few individuals per species without considering either the difference in flowering magnitudes of various events or source of variation at the population level. I repeated the same estimation for floral induction time with trap data, and my analysis included data on the reproductive phenology of much larger numbers of individuals per species. I compared the estimates of floral induction time based on weekly flower presence-absence data and based on data using all flower records. The two methods gave significantly different estimates. I attribute this inconsistency to unknown variation in phenology among individuals within populations. However, no one has ever evaluated the assumption underlying the Ashton *et al*. method, and the present study was not designed to do so. I can draw no conclusions regarding the triggering mechanisms, nor even conclude that a single triggering mechanism for all species is a valid assumption. The fact that species participation varied among the GF events in this study, however, is consistent wit the hypothesis that at least the intensity of the stimulus required may vary among species, if not the cue itself.

Various studies have evaluated the predator satiation hypothesis in both temperate and tropical regions (Burkey, 1994; Curran & Webb, 2000; Vander Wall, 2002). These tests were at single-species scales, and, with a few exceptions, on grass and herb species (Kelly *et al*., 2000).

Evaluating the predator satiation hypothesis is made more difficult by the co-occurrence of many different types of fruits, some of which are much more likely to be attacked by seed predators than others. Moreover, some species, particularly those that are drupes or small-seeded berries consumed by vertebrate dispersal agents, may face a problem with limited dispersal opportunities if they mature fruits synchronously, resulting in dispersal saturation (Herrera *et al.*, 1998). This thesis make the new suggestion that predator satiation only drives the evolution of synchronous reproduction in certain fruit types but not in others.

An important question about tropical forests is how forest diversity is maintained. The leading hypothesis for the maintenance of forest diversity, the Janzen-Connell hypothesis, has been evaluated in many forests (Blundell & Peart, 2004a; Harms *et al.*, 2000; Wright, 2002). However, tests on seedlings, the most vulnerable life stage, at the community level are scarce (Wright *et al.*, 2005). Moreover, most prior studies have not tracked survival and density dependence over time. I evaluated the strength of density dependence in two succeeding life history transitions, from seed to established seedling, and from seedling to yearling. I also examined how the patterns of reproductive phenology affect the strength of density dependence. If this density dependence is important to the maintenance of species diversity in the forest, there should be greater diversity associated with strong density dependence. I tracked the change of diversity over time and examined the difference of diversity at the seedling stage between GF and non GF cohorts. This was the first evaluation for the impact of GF on forest diversity. In the examination of density dependence, I found the strength of density dependence to be the strongest in the seed-to-established seedling transition. Furthermore, loss of species in this transition largely determined the drop of diversity in the later transitions and the levels of diversity in different seedling cohorts. Cohorts produced form a non GF year exhibited the lowest level of diversity and evenness after seedling establishment.

Summary of results

Chapter 2

The Pasoh forest experienced four GF events between 2001 and 2006. Of the 126 species included in this study, 50.8% showed a supra annual flowering pattern. Significantly synchronous flowering with *Shorea* species from the section *mutica*, the indicator group of GF, occurred in 74.6% of the 126 species. High percentages of 66% and 63% of the species examined exhibited supra annual and GF phenology, respectively, and a very small number of supra annual species was not GF species. Results from a contingency table analysis indicated that flowering periodicity, but not fruiting periodicity, was significantly related to growth form and ecological functional traits such as dispersal mode and reward type. In addition, fruiting, but not flowering GF phenology was significantly related to the reward type. This result is strong evidence for selection for supra annual flowering and synchronized fruiting by predator satiation. Examining the relation between phenology types and growth forms, I found a higher proportion of supra annual species occupying the higher canopy layers, which suggests an influence of microclimate on flowering periodicity. Because GF events were largely comprised by supra annual flowering and fruiting species, it is not unexpected that the most common fruit types in these events are the dyszoochorous fruits, followed by nonzoochorous and then endozoochorous fruits. Additionally, endozoochorous fruits were important in the non GF years when fruit production was low. This indicated a short supply of fruits between GF events and may lower predator populations before the ensuing GF.

Chapter 3

Examination of the flowering and fruiting sequence showed significant fruiting synchrony but no sign of significant staggered flowering. The lack of significantly staggered flowering cast doubts on the assumption that there is character displacement among *Shorea* species due to competition for pollinators. On the other hand, I did find very strong fruiting synchrony among these species, which supports the hypothesis of predator satiation. In addition, I conducted regressions to estimate the floral induction time for the *Shorea* species. I looked at estimated dates for floral induction in relation to concurrent fluctuations of rainfall and minimum air temperature in the Pasoh forest and tentatively concluded that dry spells are more tightly lined to the GF events than other suggested cues. However, as mentioned, I could not evaluate the validity of the assumption that all species use the same cue.

Chapter 4

In the tests for density dependence, I detected negative density dependence for the life history transitions, seed-to-established seedling and seedling-to-yearling (one-year-old). There was stronger negative density dependence in the first transition. However, I was surprised that I found no difference between annual and supra annual species. I was unable to divide species by trait class that related to the strength of density dependence they experienced. Moreover, there was no evidence of compensatory mortality or in the strength of density dependence from one life history transition to the next. Finally, the change in species diversity over time was greatest in the seed-to-established seedling transition. This was largely due to a reduction of species richness rather than to a change in evenness. The only non GF year seedling cohort showed the lowest diversity and lowest evenness at the seedling stage compared to all the GF cohorts. This may imply a higher loss of species richness and weaker density dependence for the non GF cohort. Alternatively, it may just reflect a lower participation rate of species in non GF years in the community, and therefore have little relevance to the maintenance of diversity question.

Need for more long-term phenological research

This study has demonstrated how the use of more objective approaches can be helpful in detecting periodicity and GF characteristics. These findings allowed us to make inferences about GF triggers and selective forces that may have shaped the evolution of the GF phenomenon. However, the evidence provided here was indirect and based on analyzing temporal patterns over several GF events differing in magnitude. To understand the proximate cures for GF, for example, it might be useful to have detailed information on seasonally changing water potentials in both soil and trees as well as measurements on the forest temperature profile, in the upper canopy as well as in sub-canopy layers.

The Ashton *et al*. (1988) approach to identifying floral induction time could be a useful tool for detection of GF triggers. However, the inconsistency in the estimated floral induction time that we found when we used different types of data suggests that there may be hidden assumptions, or that the assumption that there is a universal cue is incorrect. It is possible to disentangle the influence from within- and among-individual variation by studying the distribution of flower records for each individual and carry out the regression at the individual level with as many individual as possible. Furthermore, it will be necessary to independently evaluate the assumptions on which the regressions were based.

I found an interesting trend indicating a shift in mean abundance from relative rarity in the continuous flowering species to commonness in supra annual flowering species (Figure 5.1). If this pattern is confirmed, one could infer that supra annual species, mostly GF species, gain per capita advantages that lead to higher abundance. However, such inferences are to be taken carefully due to our limited ability to sample rare species that also may exhibit infrequent flowering. Rare species are inevitably undersampled. It is important to learn the performance of rare species because these species comprised a majority of the species richness in the SE Asian forests, if we define rarity we mean . A compensatory design to monitor rare species should be added to the long term phenological study in order to improve our understanding of the rare species.

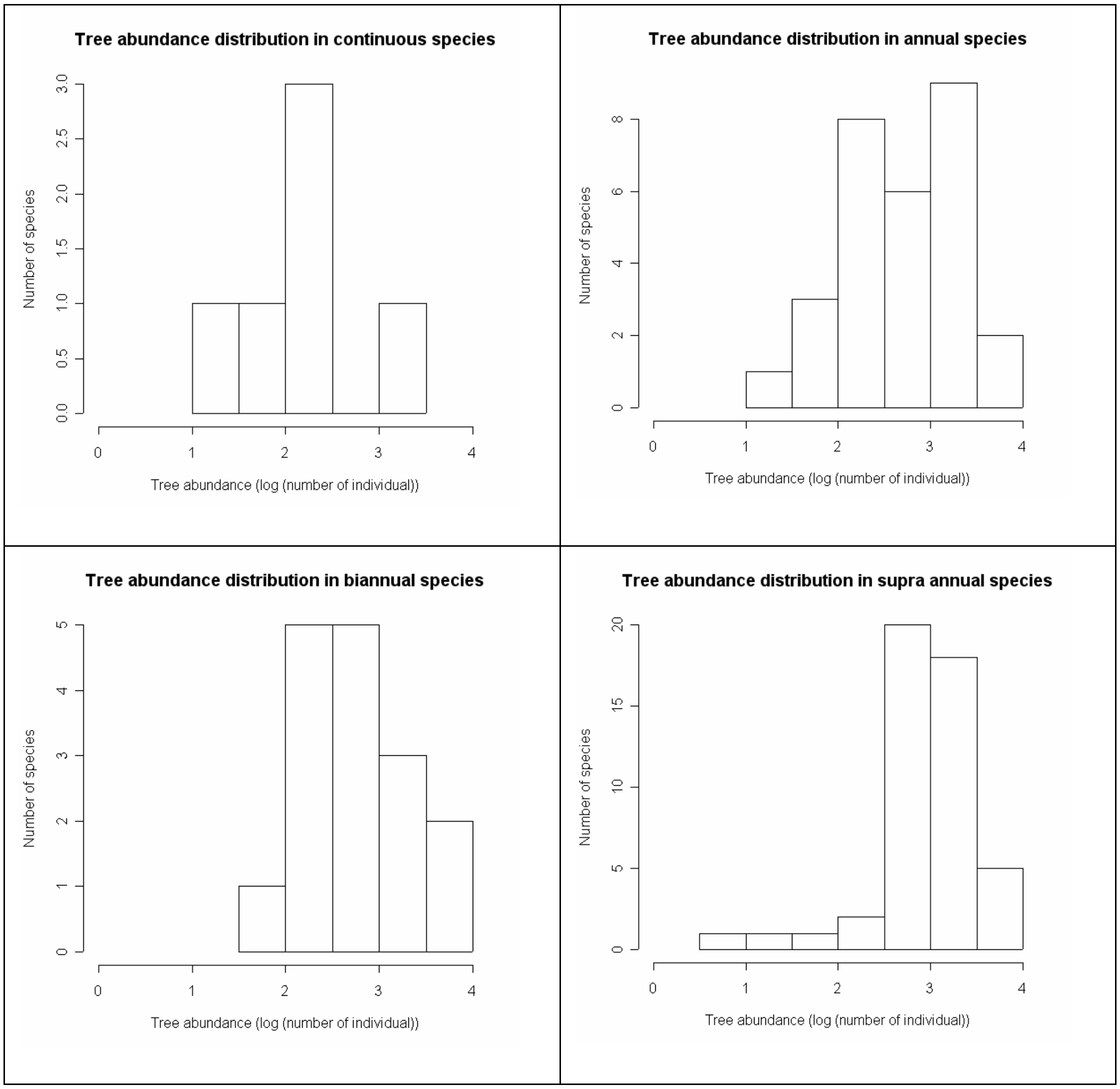


Figure 5.1 Distribution of abundances in the four periodicity groups. A trend is visible indicating that the supra annual species are relatively more abundant. Tree abundance was derived from the 2000 Pasoh FDP census data. Only 126 species were included in the grouping.

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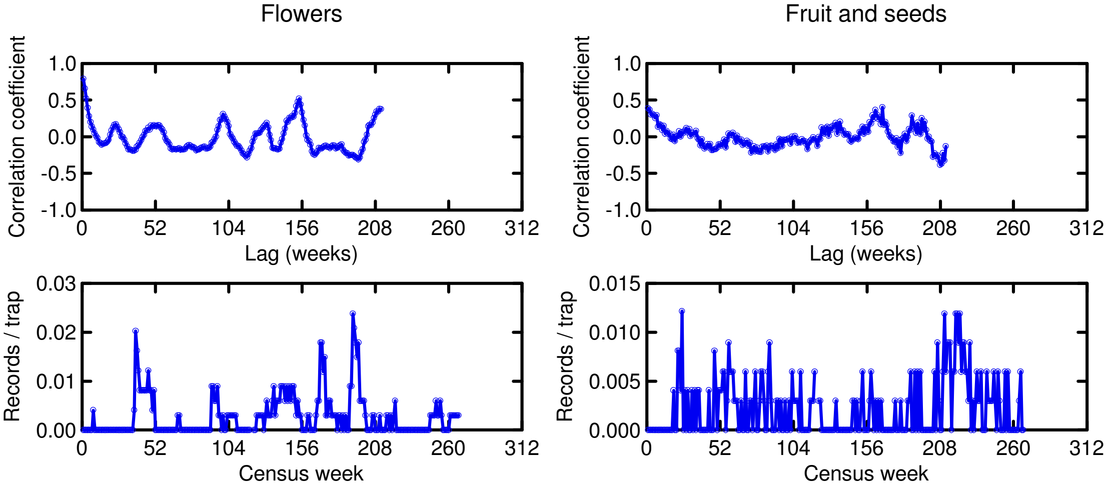
APPENDICES

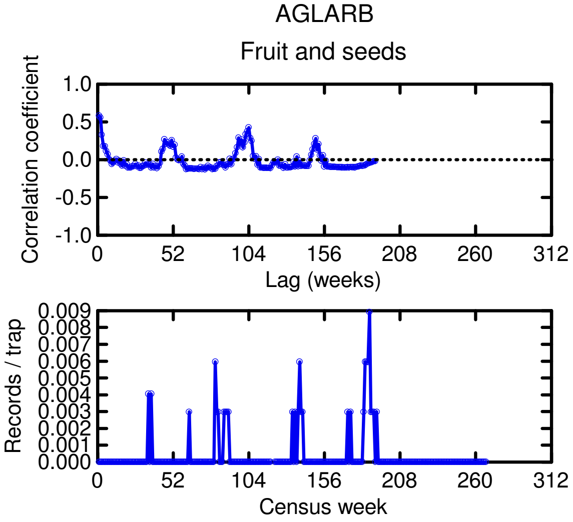
Appendix A Time series data and auto cross correlation functions (ACF) for 183 forest species. A set of four panels in two columns or two panels in one column represented the flowering and fruiting patterns of a species. Correlation coefficients for time lags of 1-215 weeks were showed in the upper panels. Original time series data of flowers and fruits in records per trap basis were shown in the lower panels. Species with sufficient sample size for only flower or fruit records have only one column of graphs for the qualified stage. We made judgments on periodicity based on corresponding lags to peaks of correlation coefficient. For example, in the first set of graphs titled as ADENBI, we detected flower and fruiting peaks at an interval of 26 weeks and assign periodicity of biannual to this species. Each set of panels followed a species code acting as the title of the graph set and all graphs were arranged alphabetically. Corresponding scientific names for species codes and assignments of periodicity were given in Appendix B. Species codes began with "CLM" are liana species and are mostly identified to morpho-species. Species codes began with "UNK" are morpho-species.

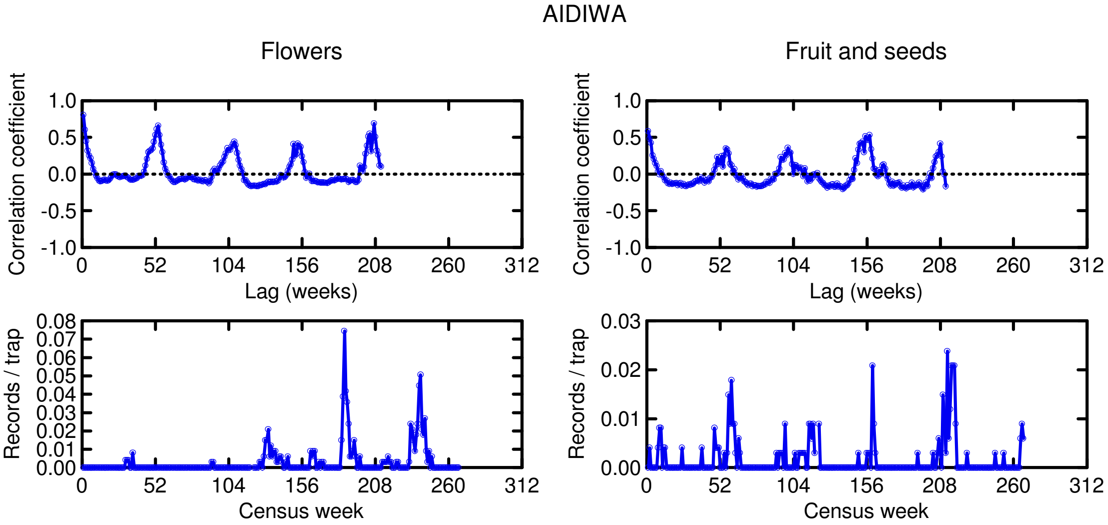
ADENBI



Flowers

Fruit and seeds


AGLARB
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
0
52
104
156
208
260
312
Census week


AIDIWA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
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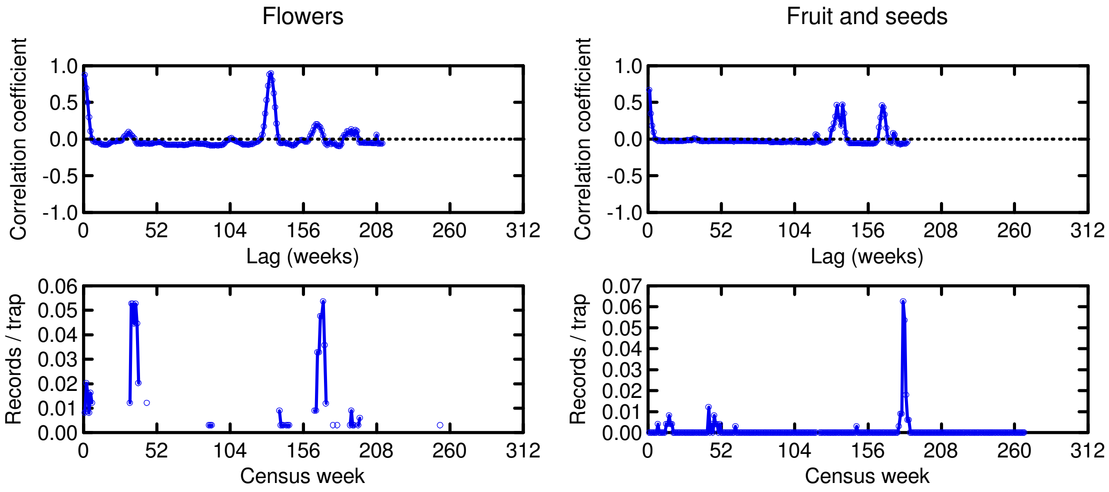
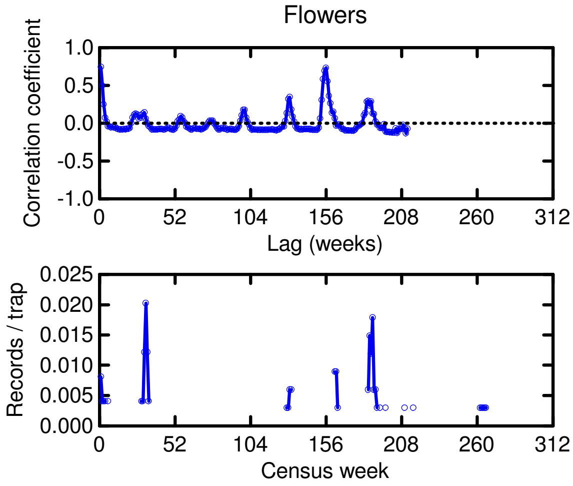
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

ALANEB



ALPHMA



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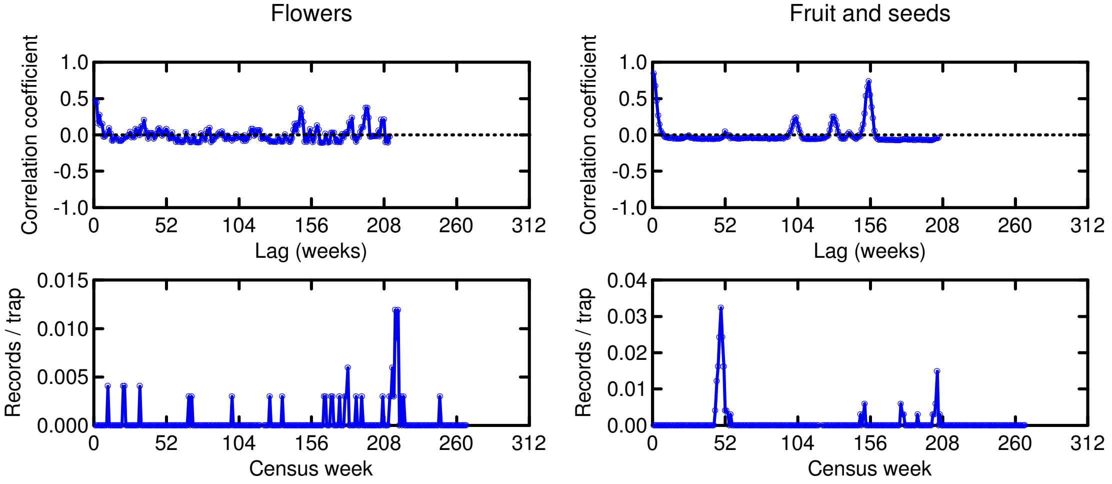

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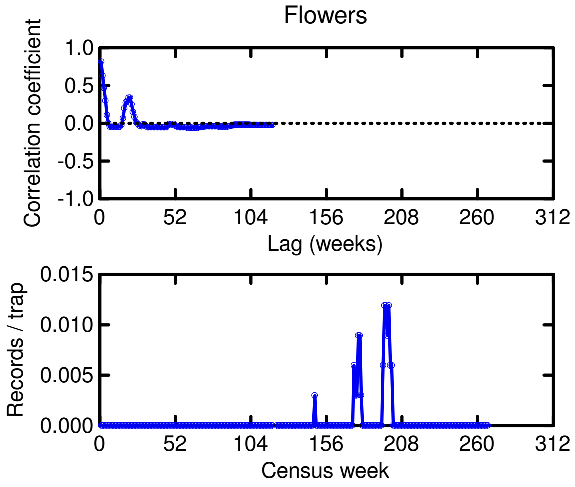
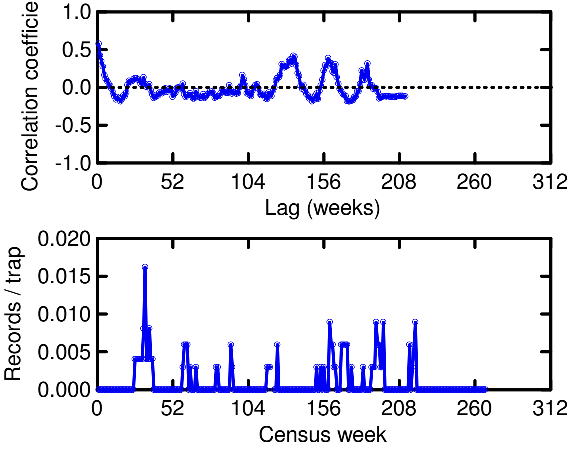
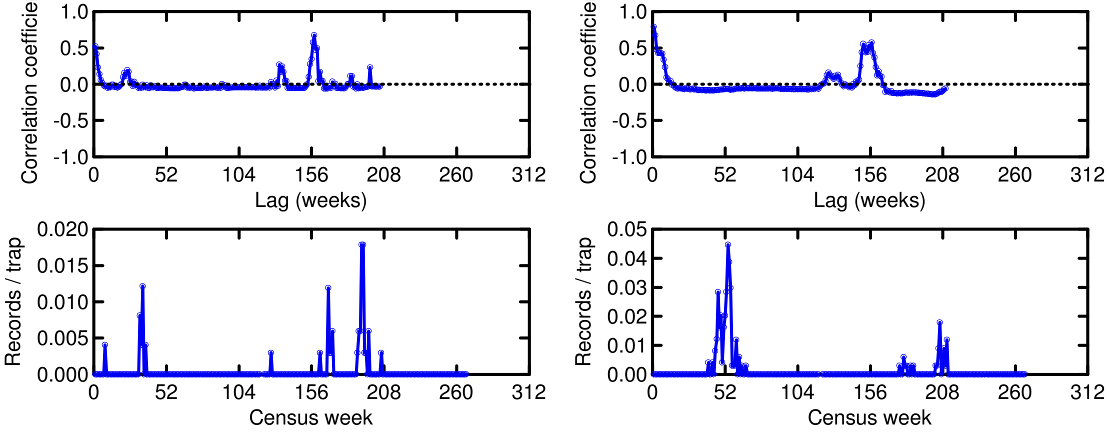


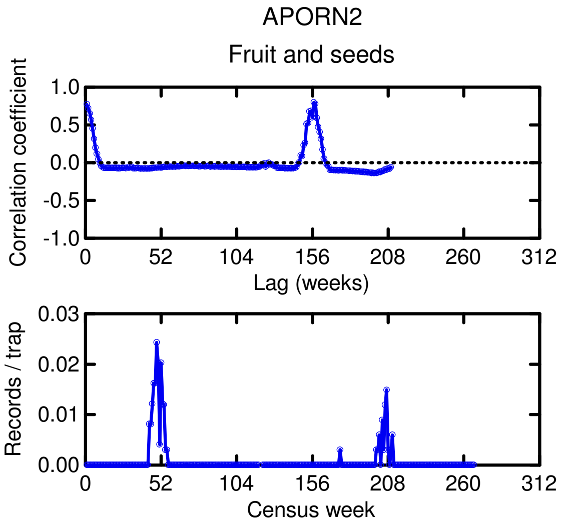

ANT1CU

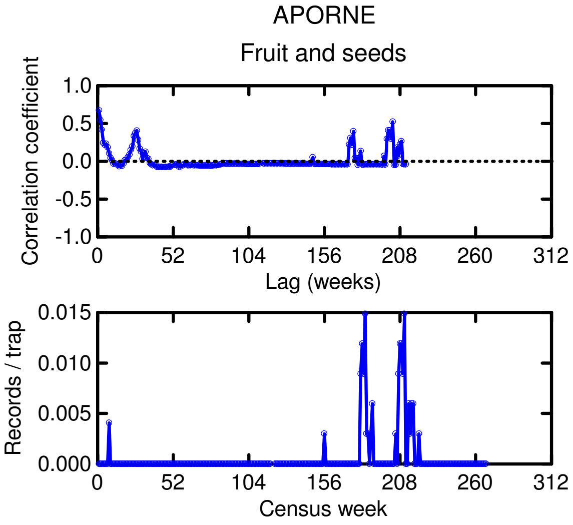
Fruit and seeds


APORM1

Flowers

Fruit and seeds


APORN2
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week


APORNE
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
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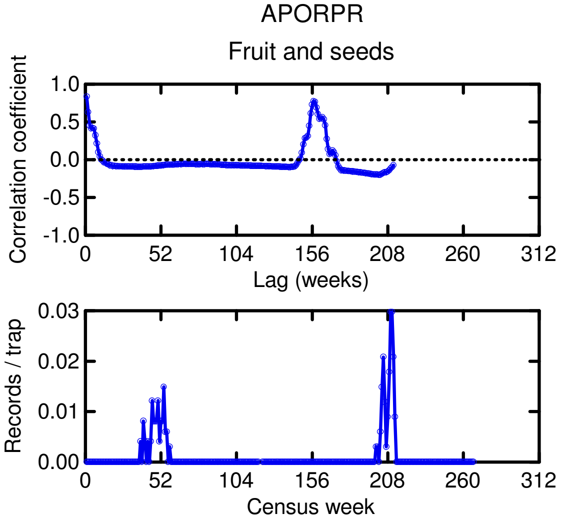
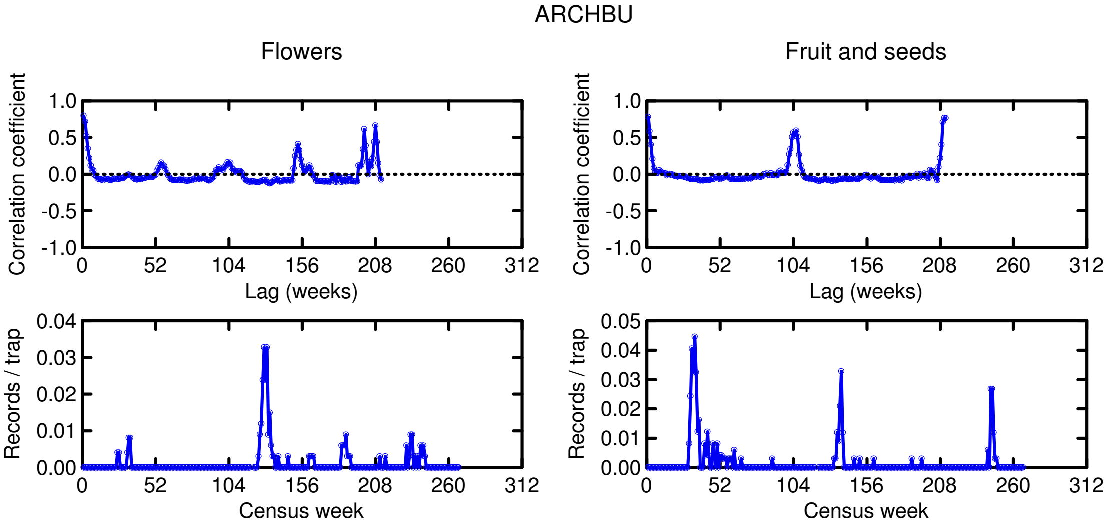
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


APORPR
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week


ARCHBU
Flowers
Fruit and seeds
Correlation coefficient
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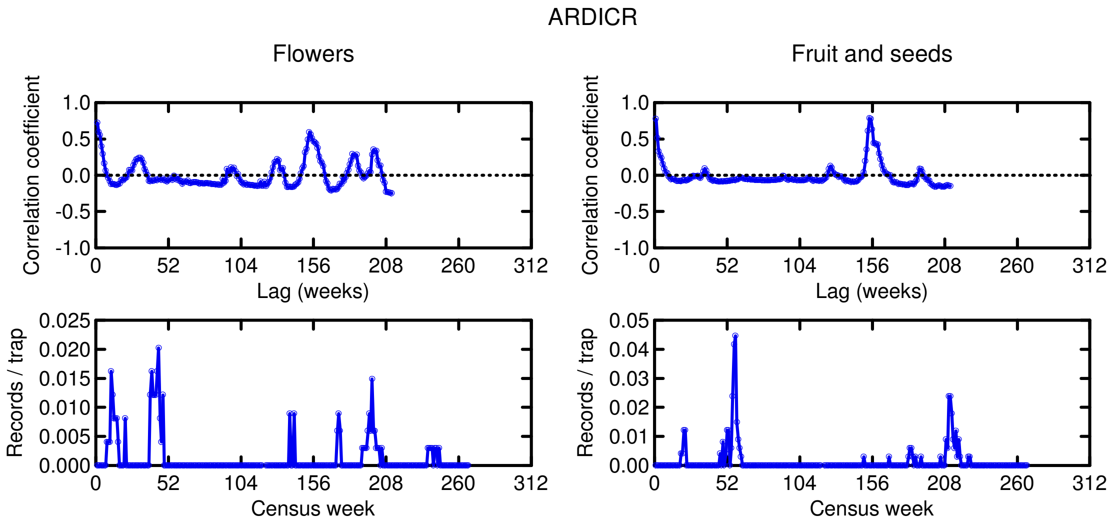
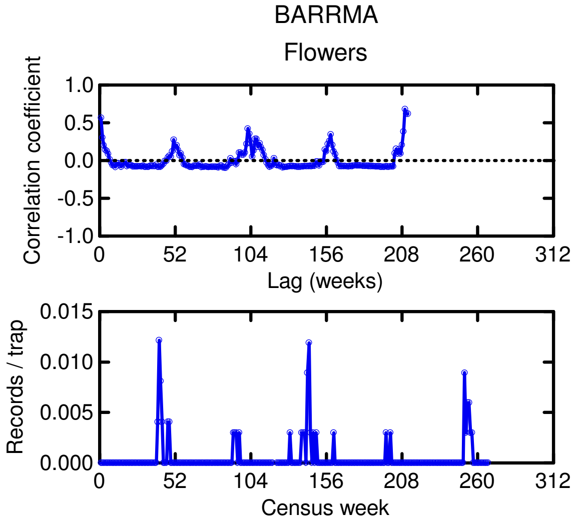
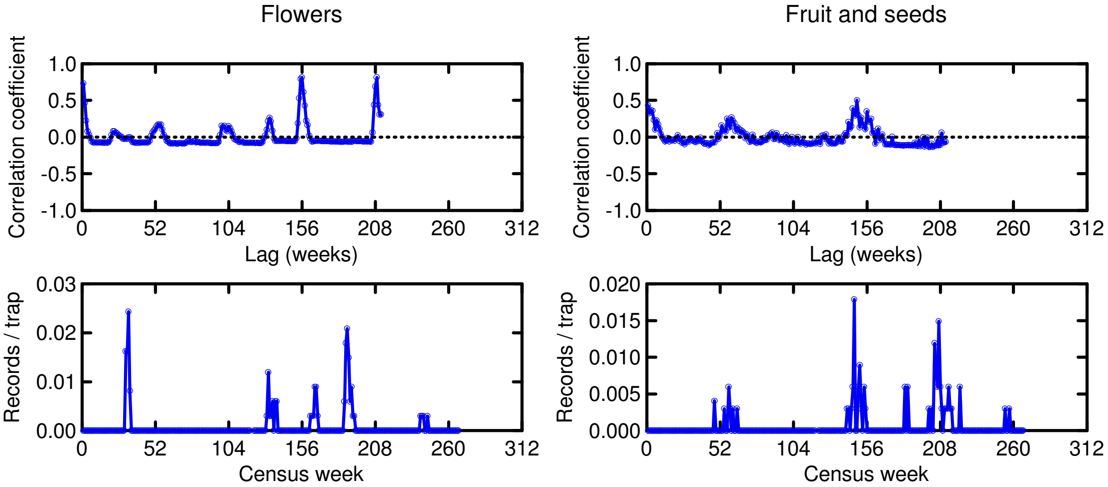
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.04
0.03
0.02
0.01
0.00
0.05
Census week

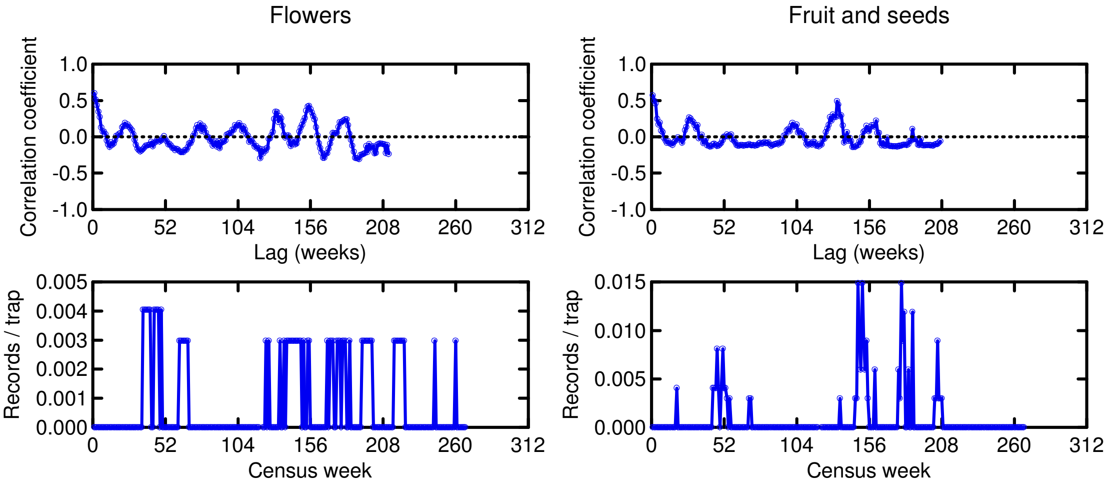

ARDICR
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.025
0.020
0.015
0.010
0.005
0.000
0.05
0.04
0.03
0.02
0.01
0.00
Census week

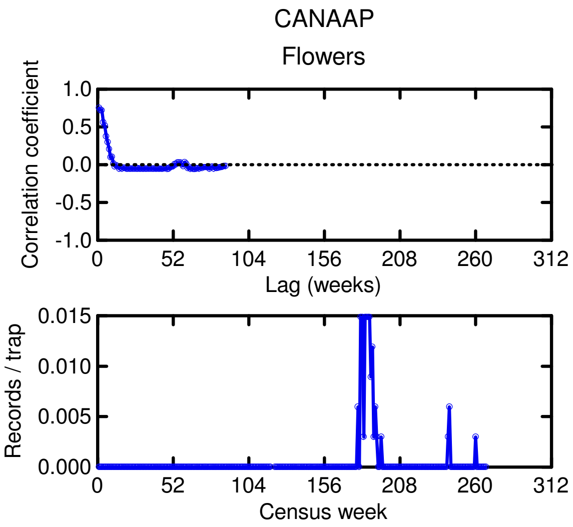

BARRMA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
Census week

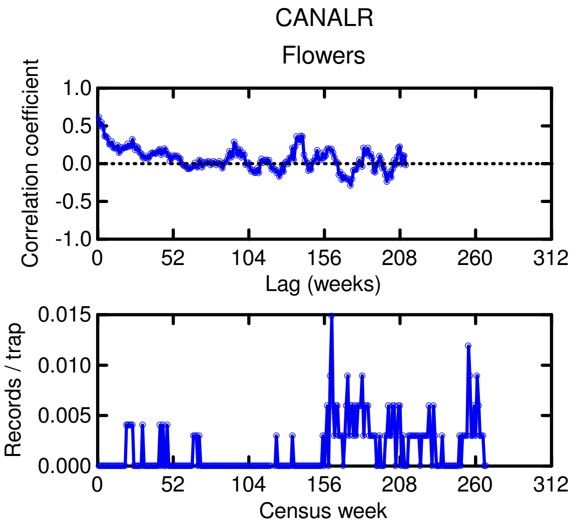
BUCHSE

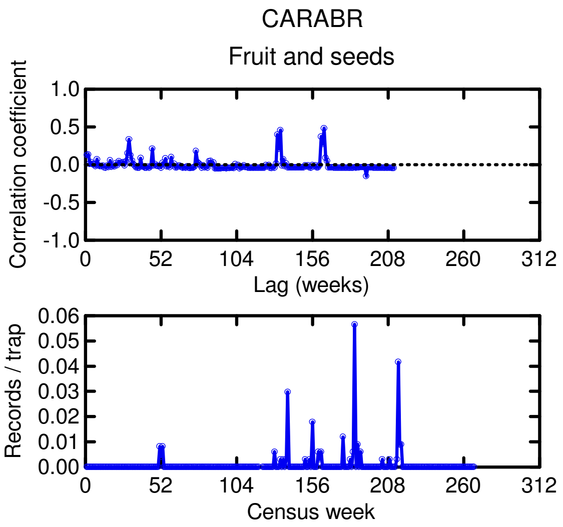


CALLMA



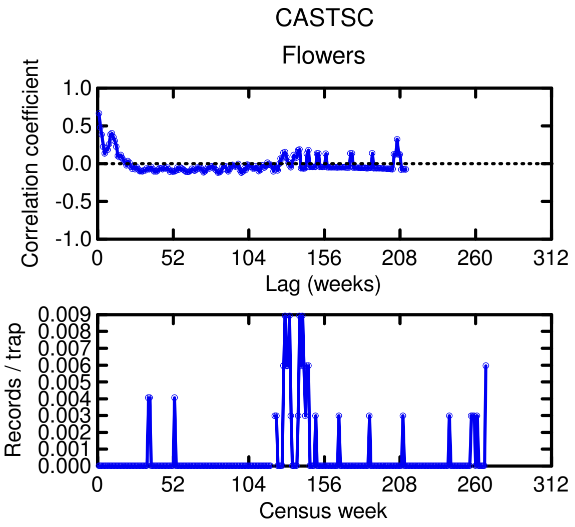

CANAAP
Flowers


CANALR
Flowers



CARABR

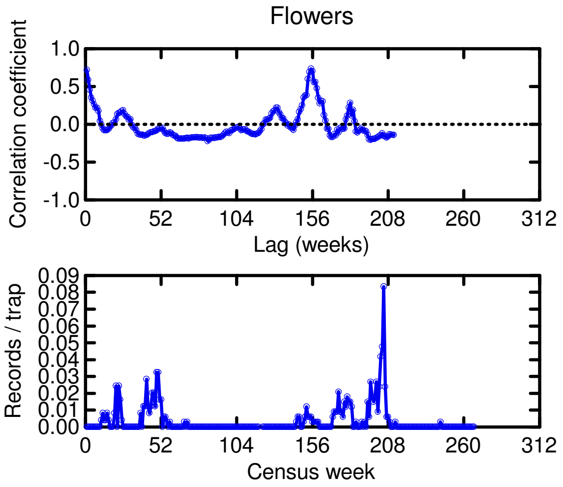
Fruit and seeds



CASTSC

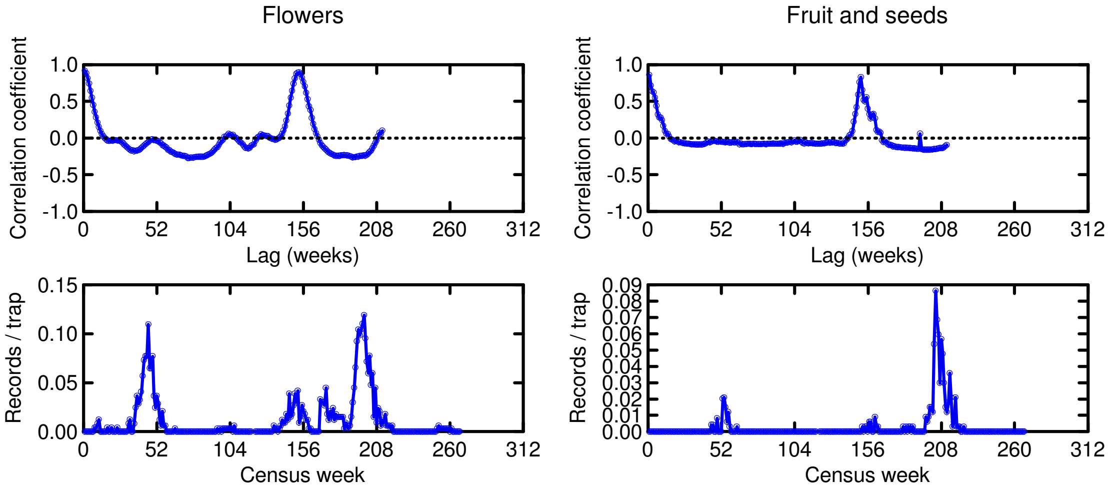
Flowers

CLM001



Flowers

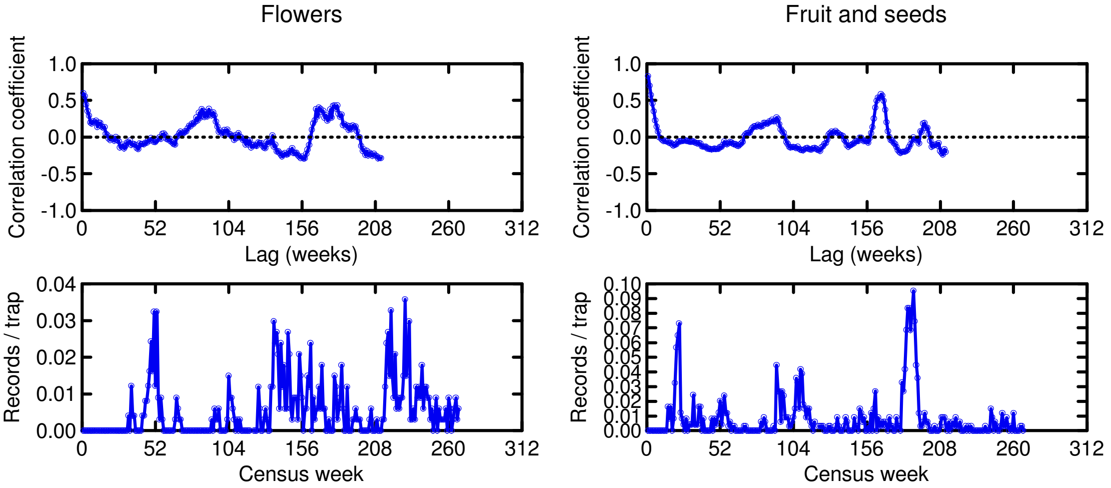
CLM002



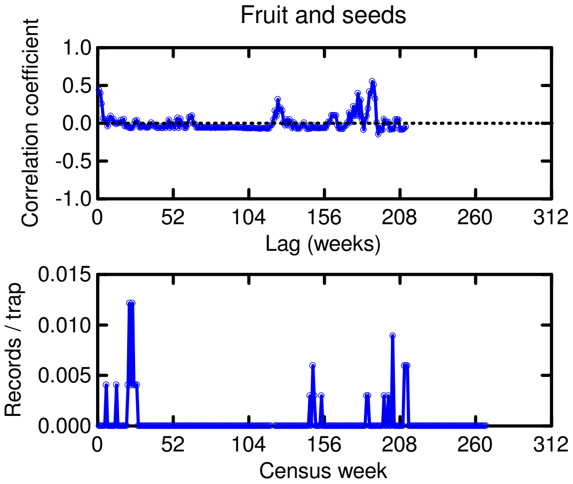
Flowers

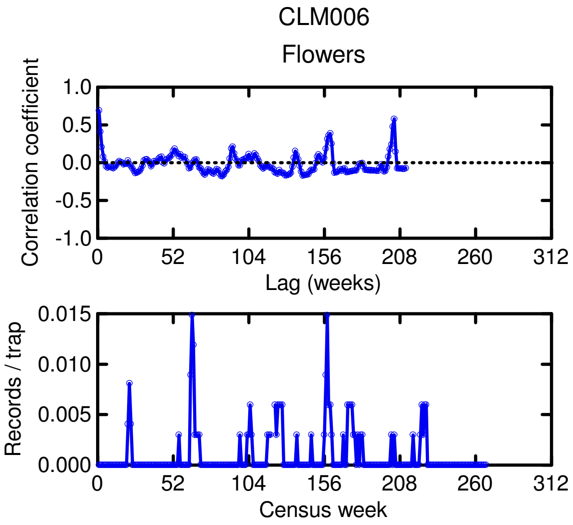
Fruit and seeds

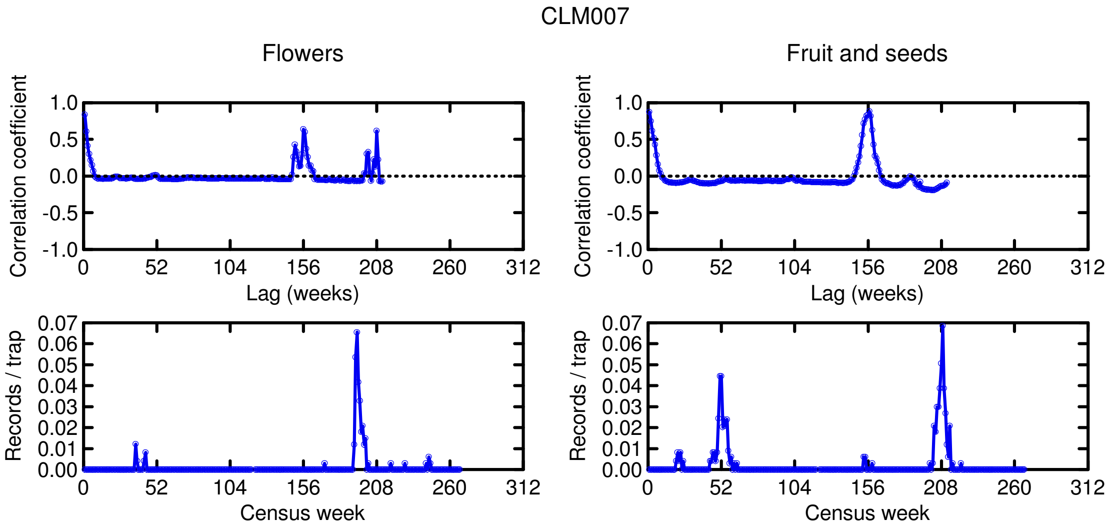
CLM004



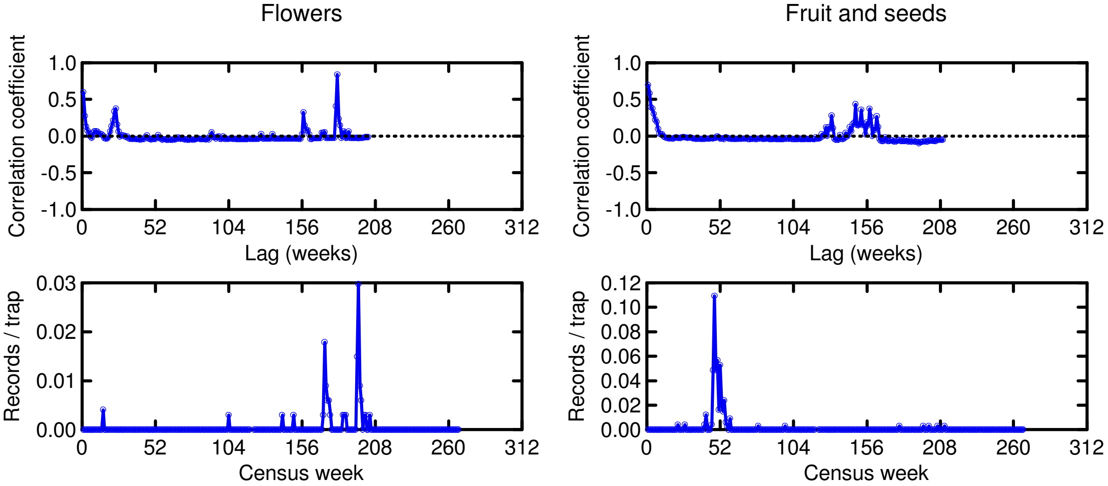
CLM005



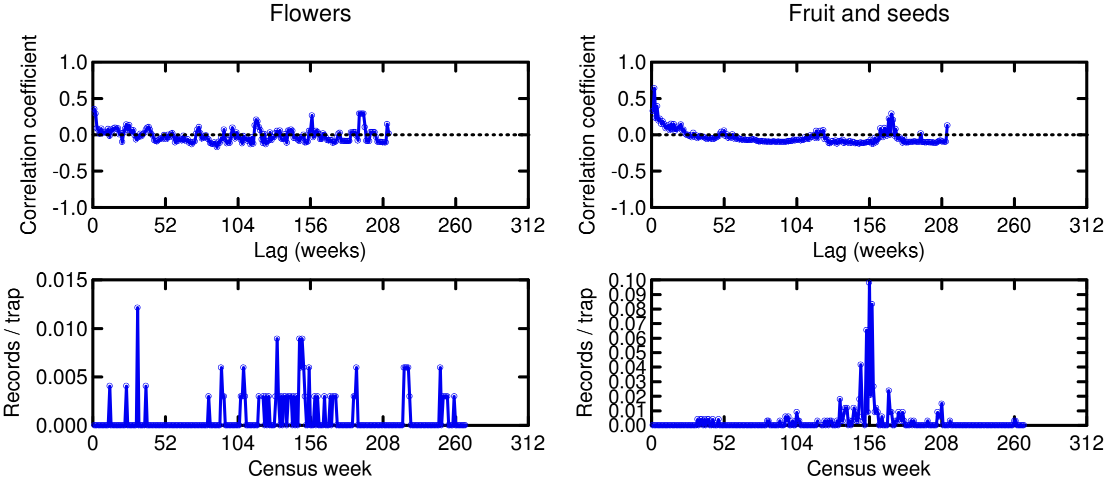

CLM006
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

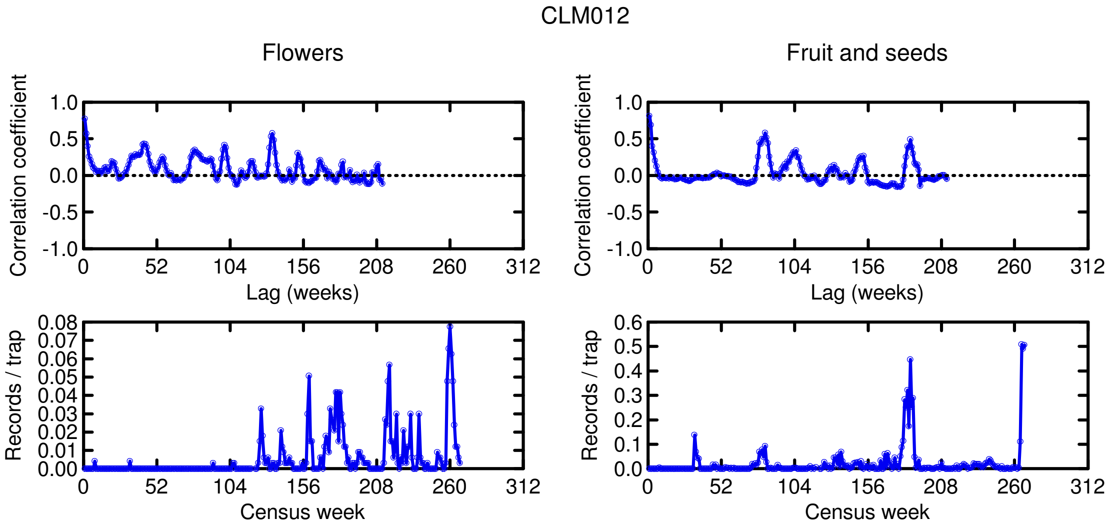

CLM007
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

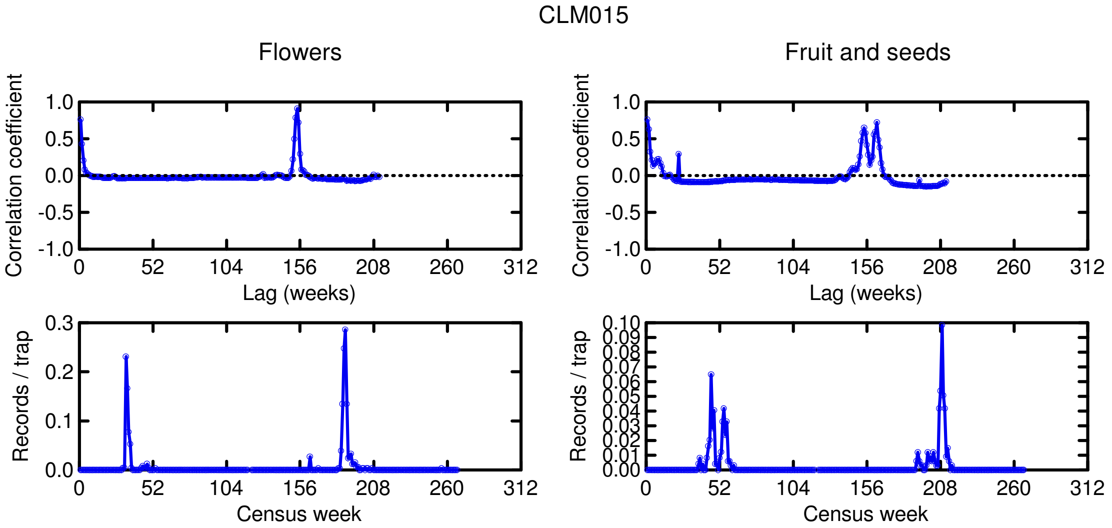
CLM009

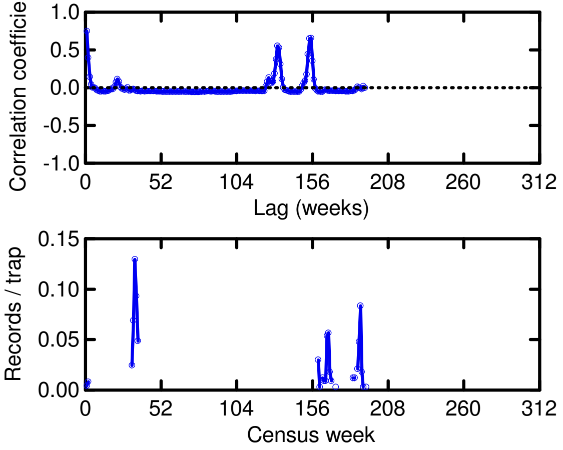


CLM011

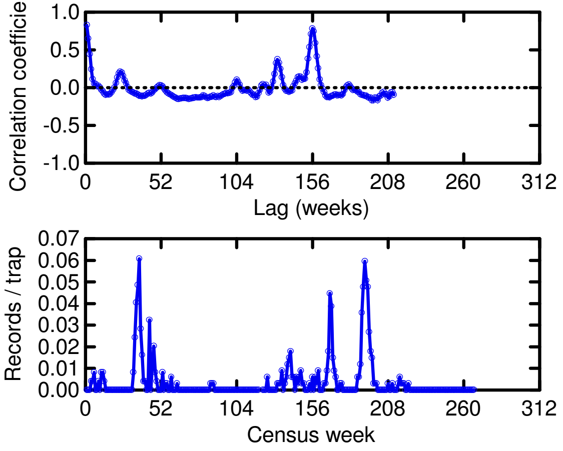



CLM012
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Census week

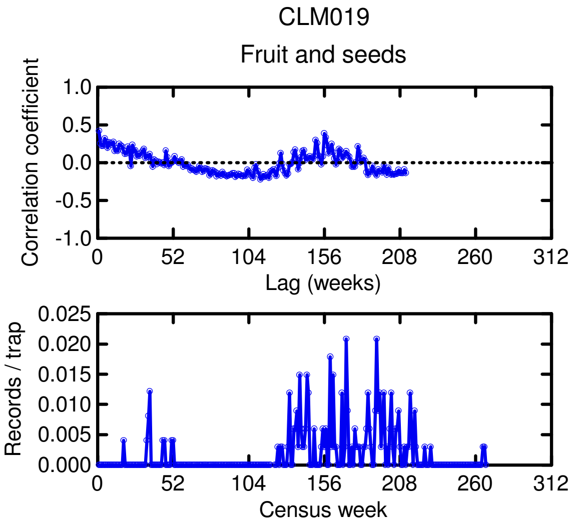

CLM015
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.3
0.2
0.1
0.0
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

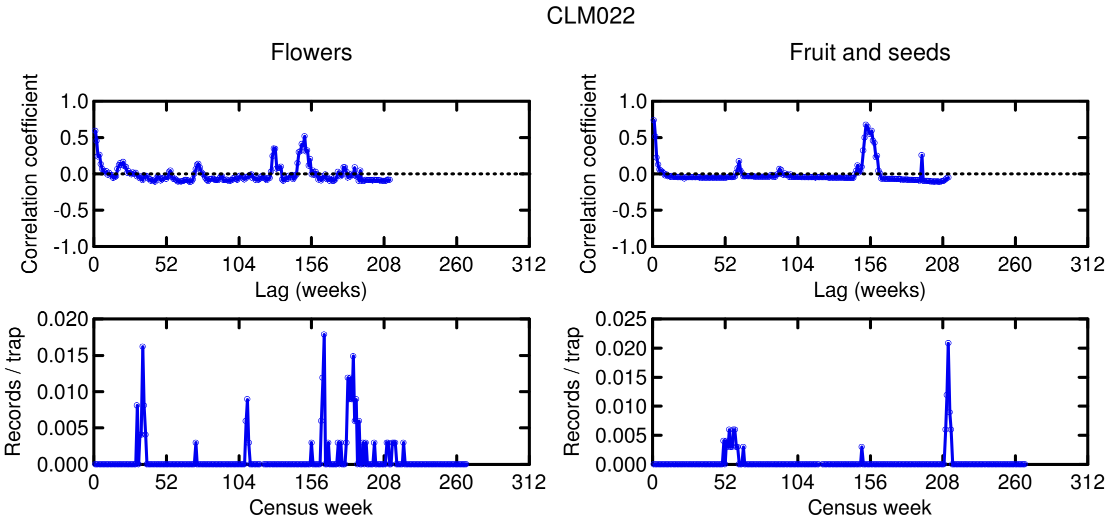

CLM016

Flowers

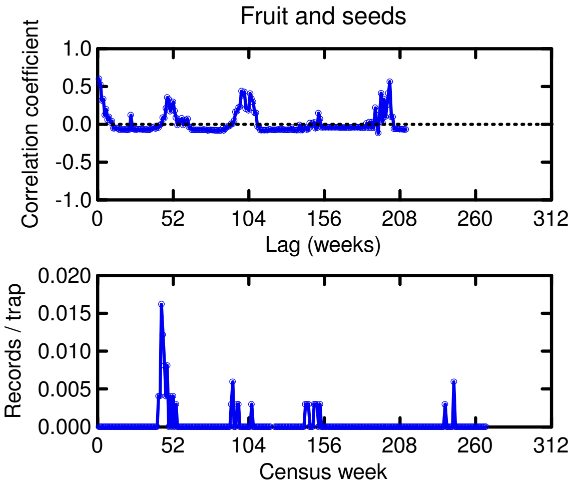

CLM018

Flowers

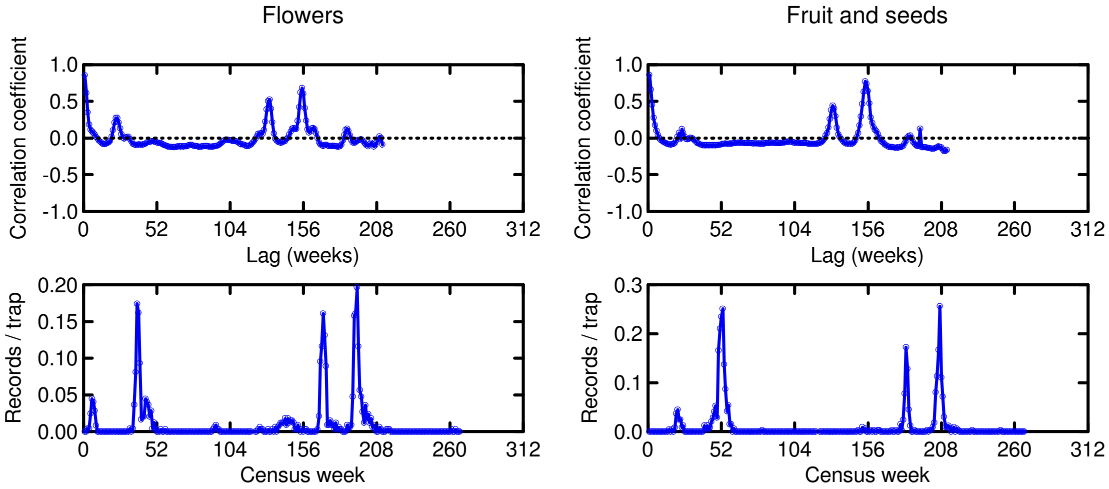

CLM019
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.025
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

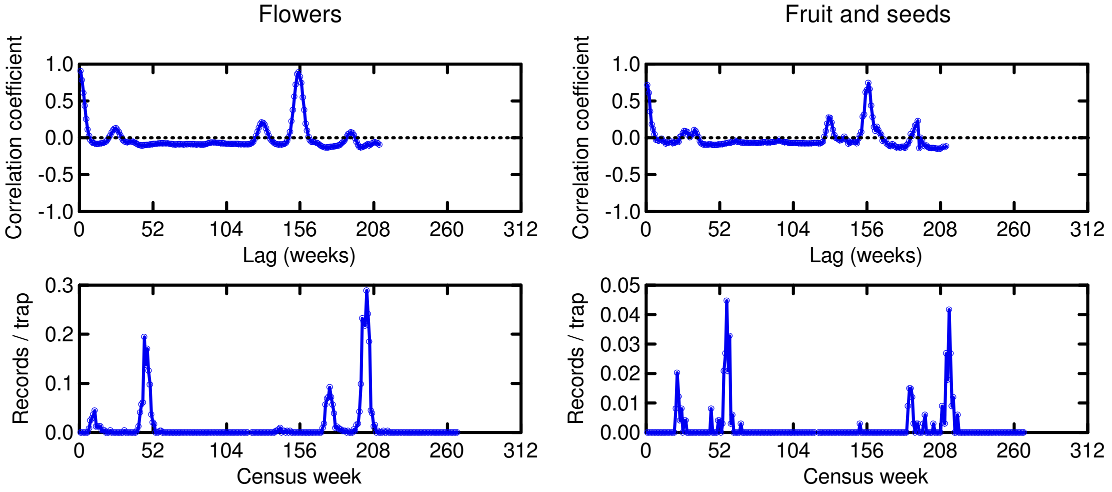

CLM022
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0.025
Census week

CLM024



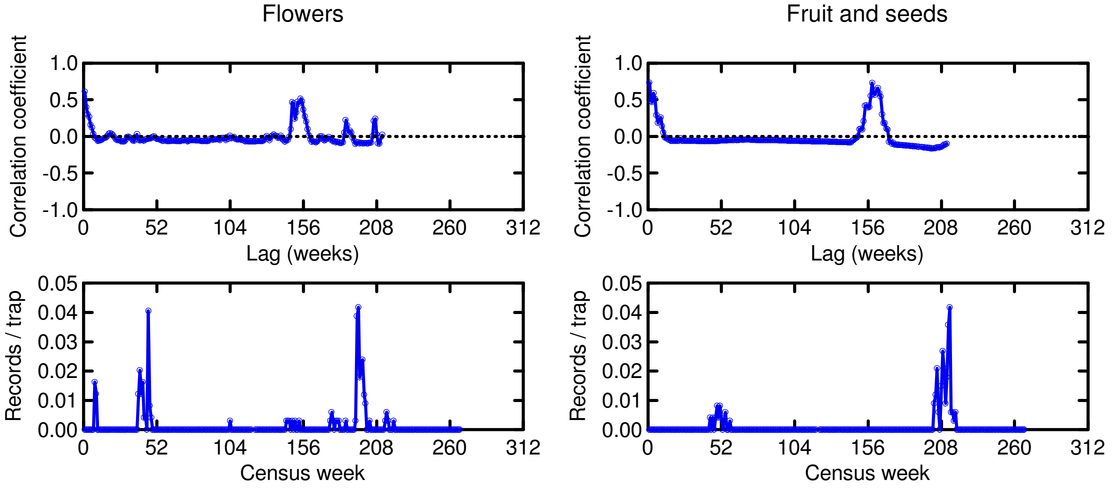
CLM025




CLM026

Flowers

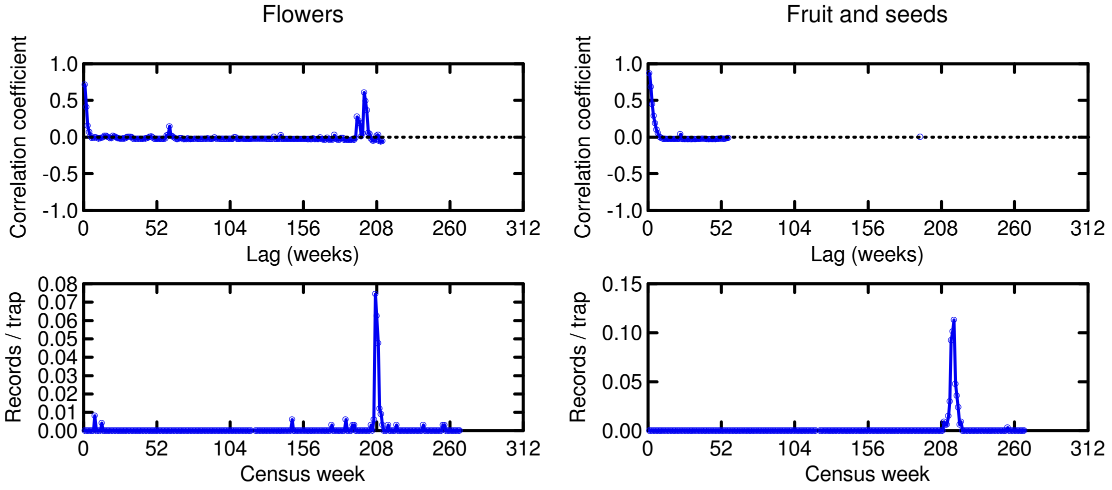
Fruit and seeds


CLM027

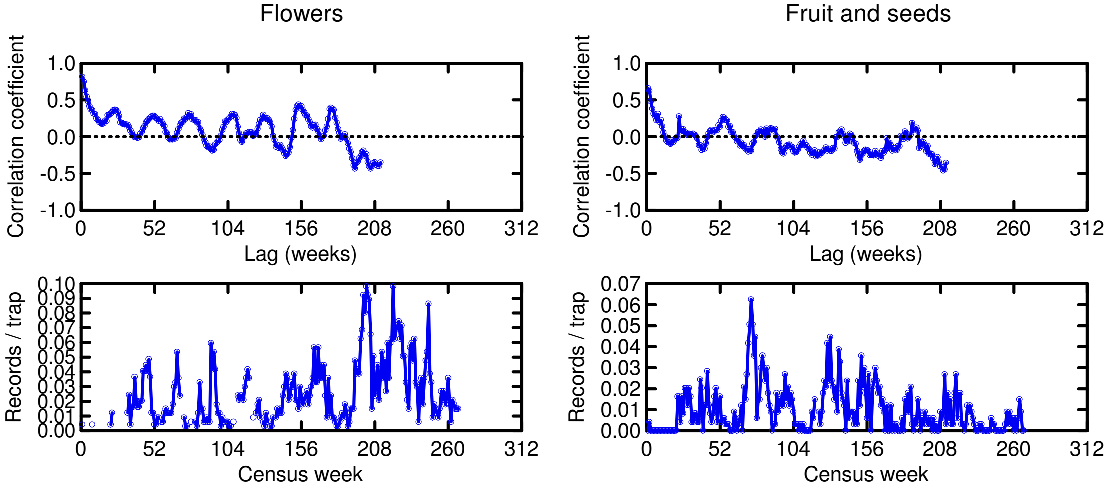
Flowers

Fruit and seeds

CLM030

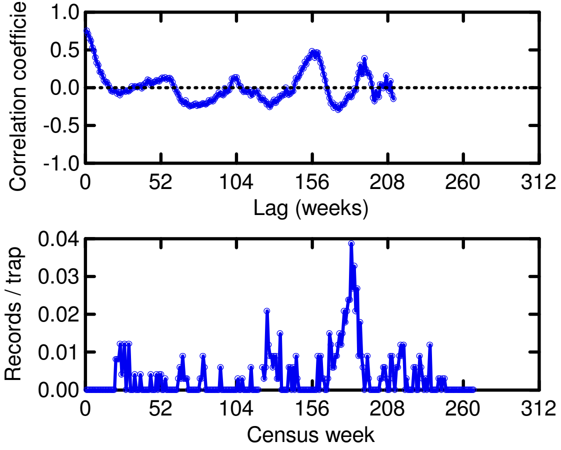


CLM032



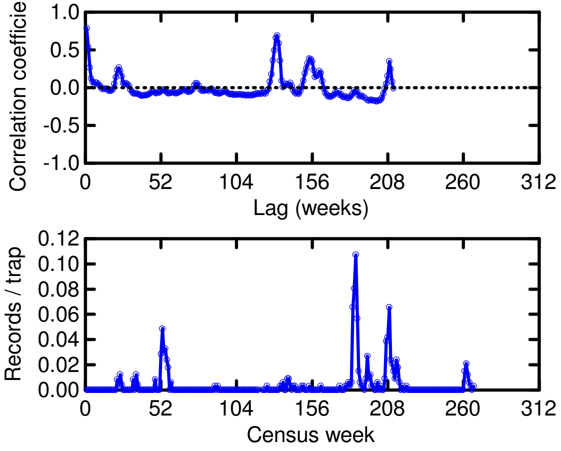
CLM033

Flowers

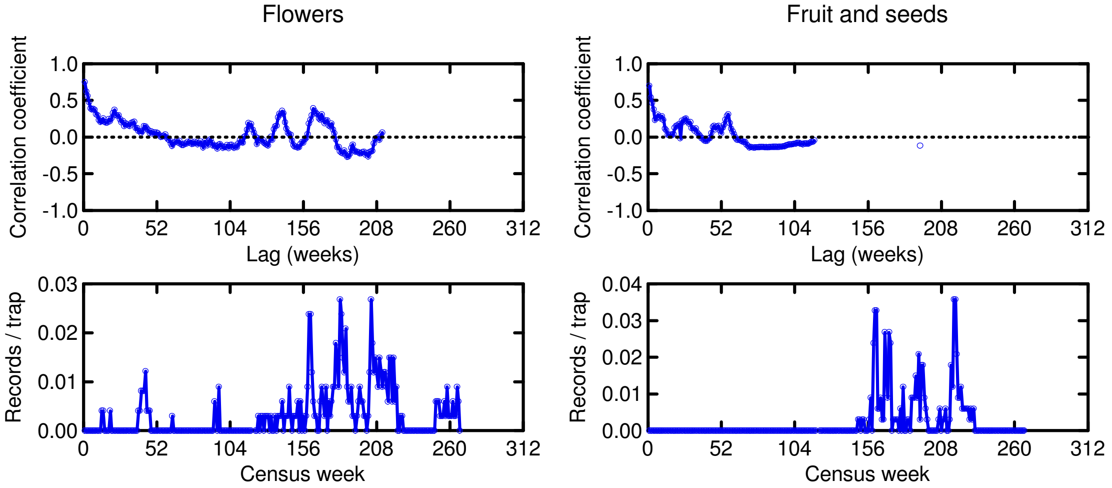


CLM034

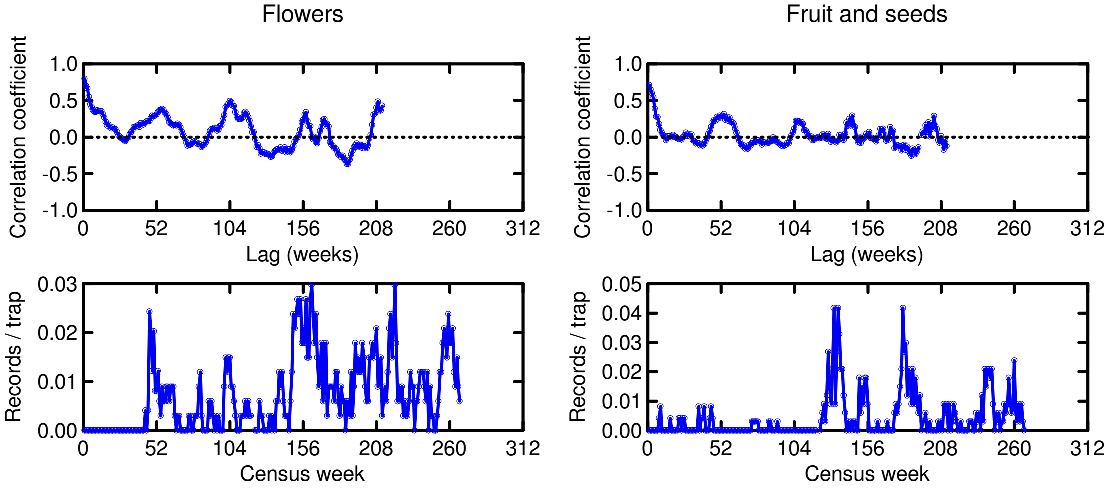
Fruit and seeds



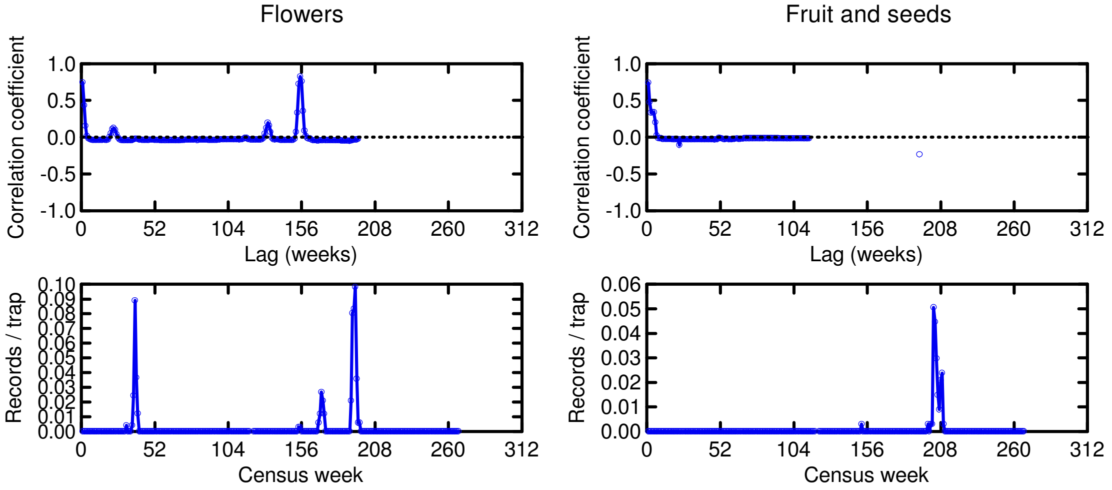
CLM036



CLM040



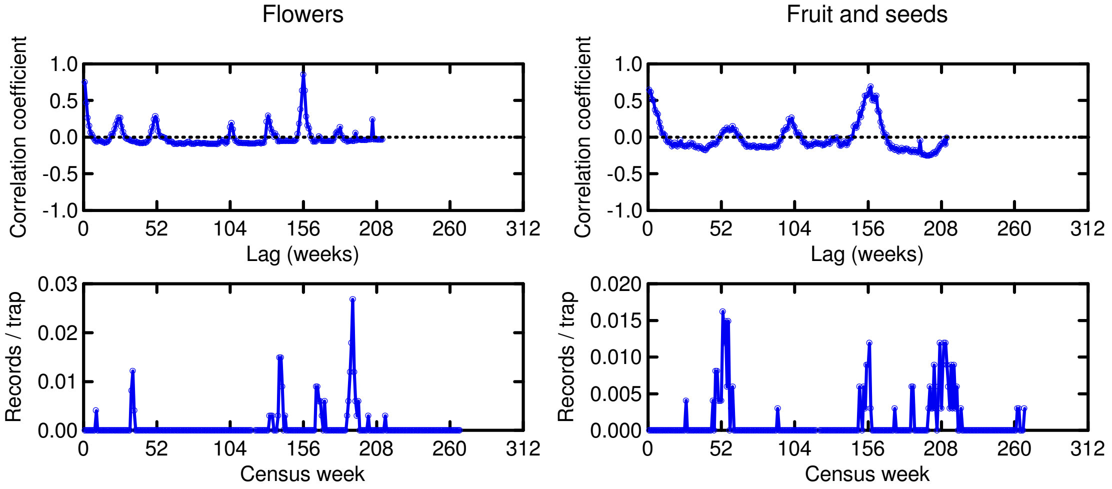
CLM041



Flowers

Fruit and seeds

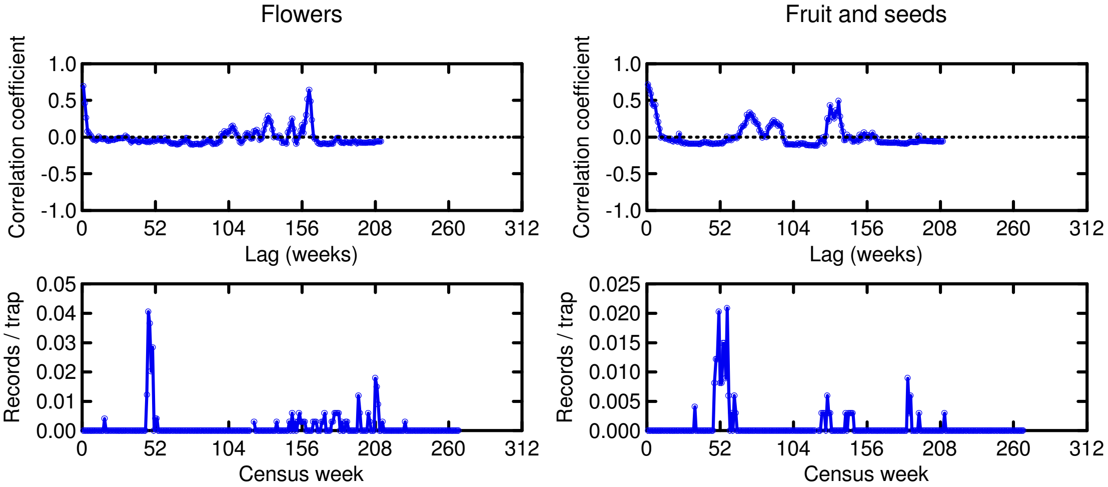
CLM042



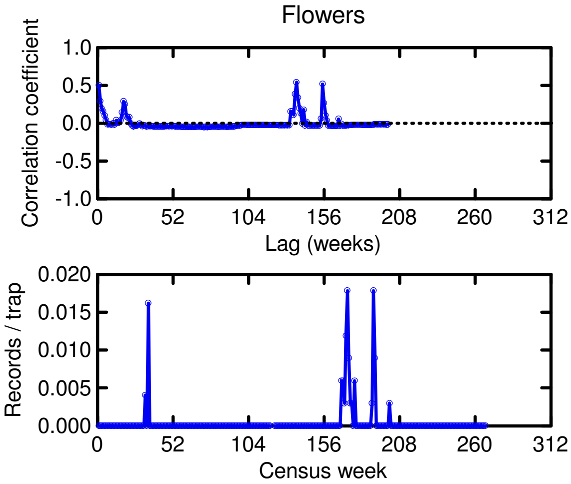
Flowers

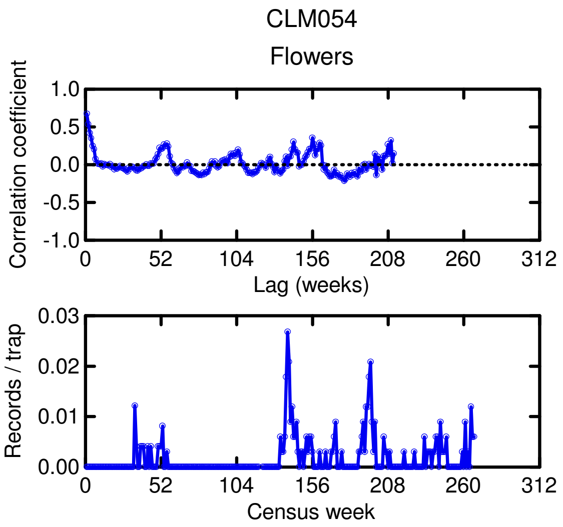
Fruit and seeds

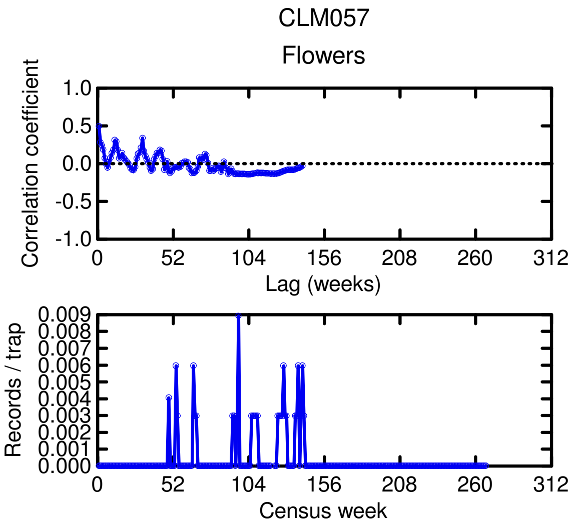
CLM044

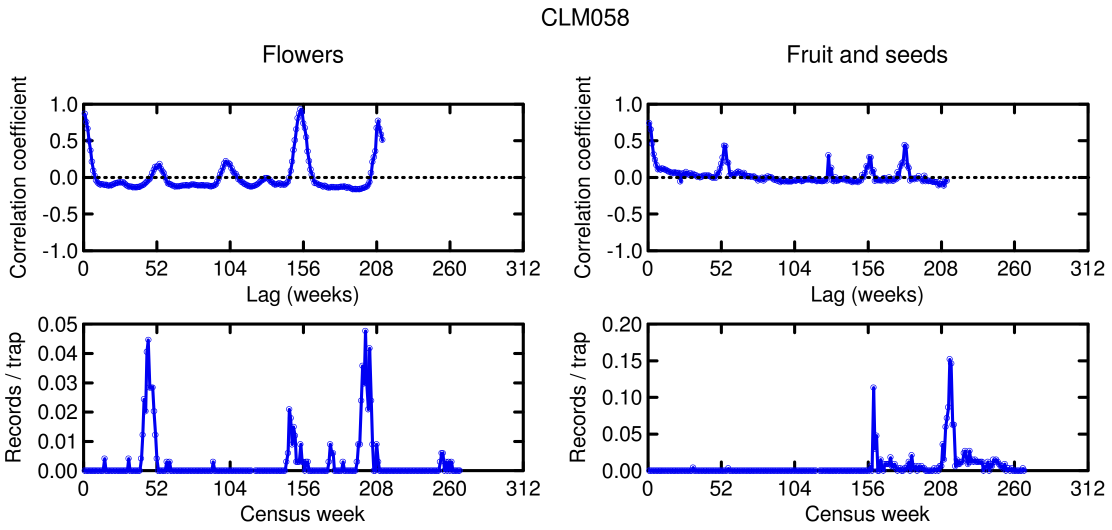


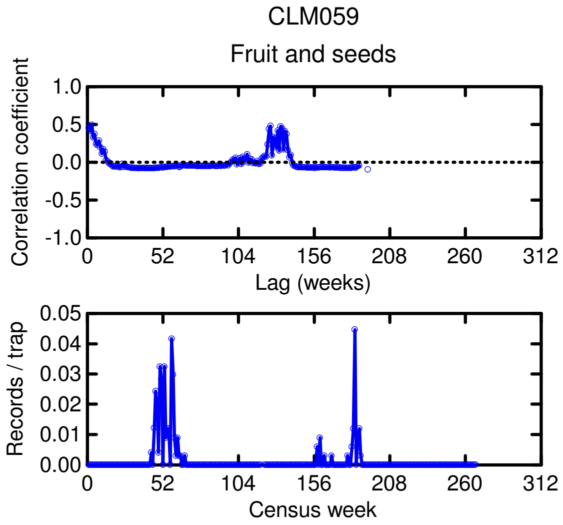
CLM049

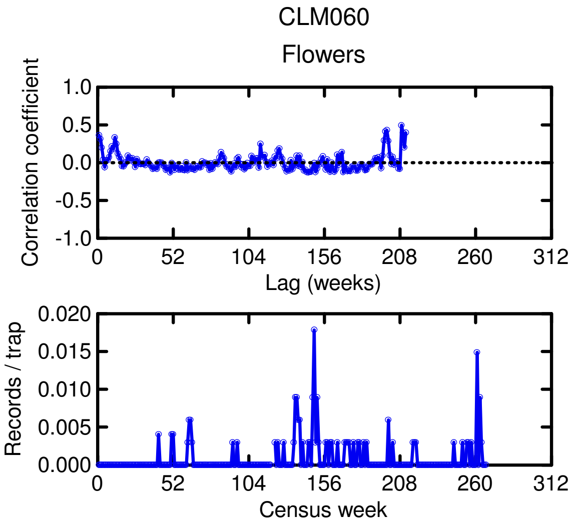


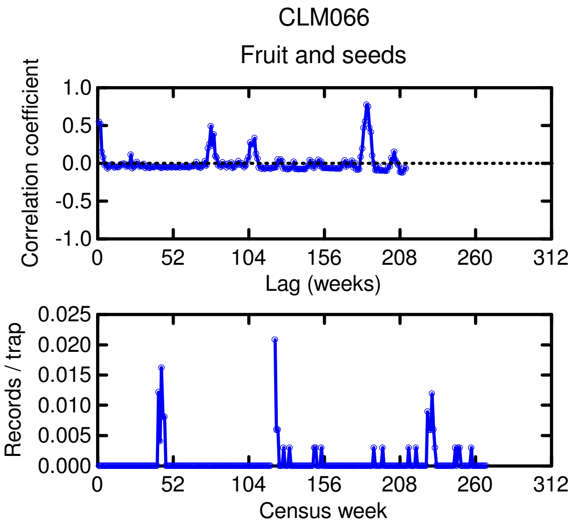

CLM054
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

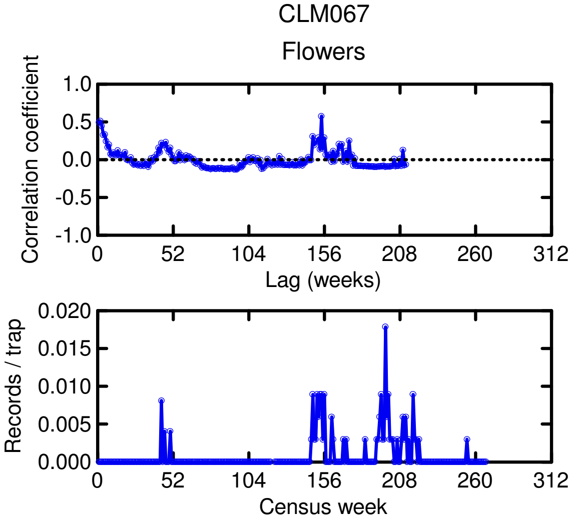

CLM057
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
0
52
104
156
208
260
312
Census week

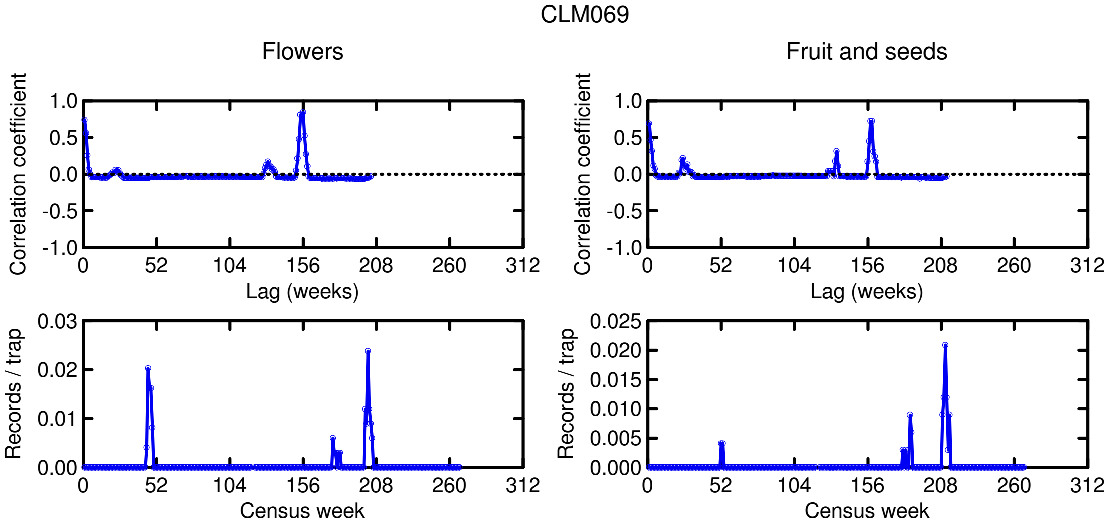

CLM058
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.05
0.04
0.03
0.02
0.01
0.00
0.20
0.15
0.10
0.05
Census week

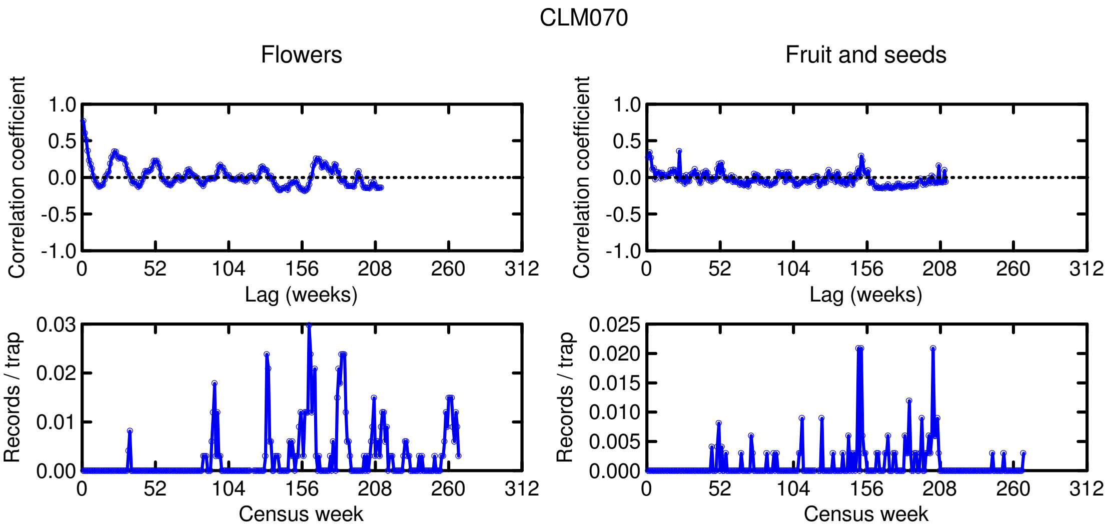

CLM059
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.05
0.04
0.03
0.02
0.01
0.00
Census week

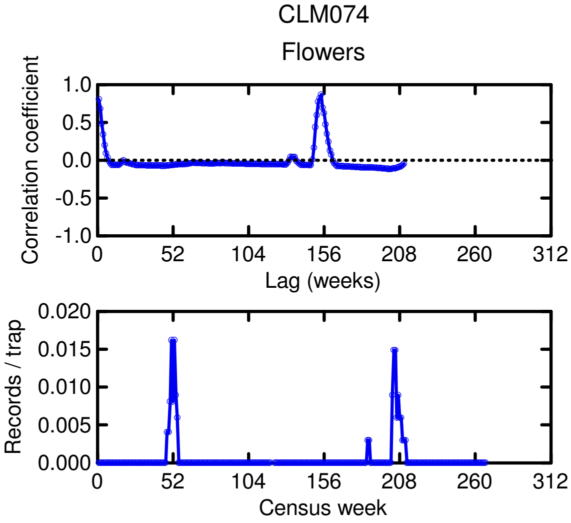

CLM060
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

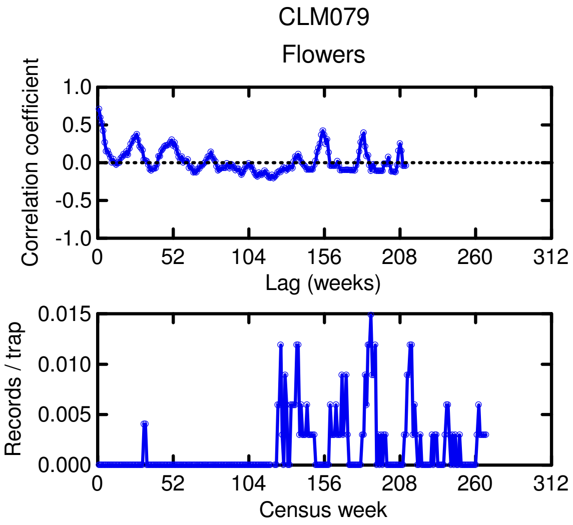

CLM066
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.025
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


CLM067
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


CLM069
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.025
0.020
0.015
0.010
0.005
0.000
Census week

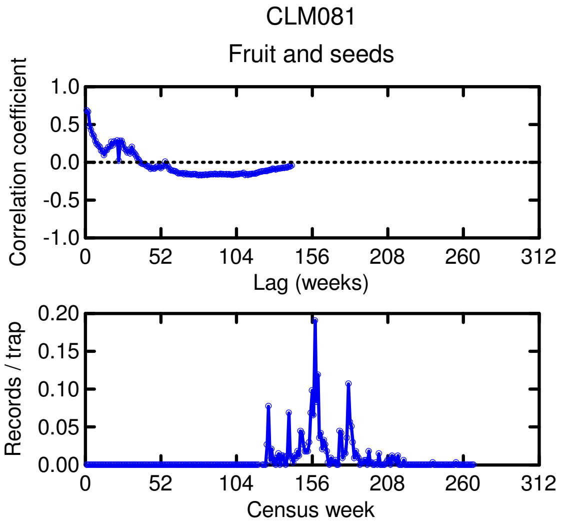

CLM070
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.025
0.020
0.015
0.010
0.005
0.000
Census week


CLM074
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
Census week



CLM079

Flowers

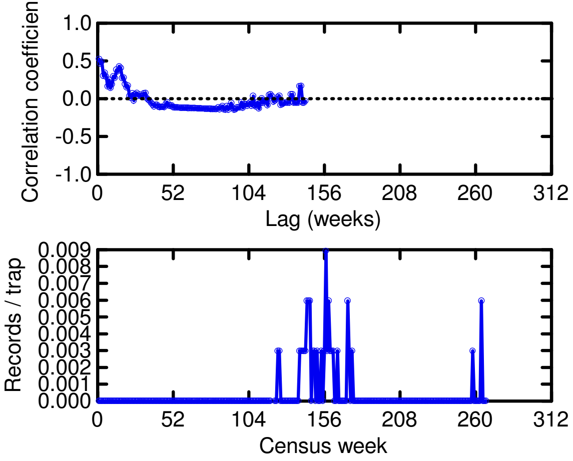


CLM081

Fruit and seeds

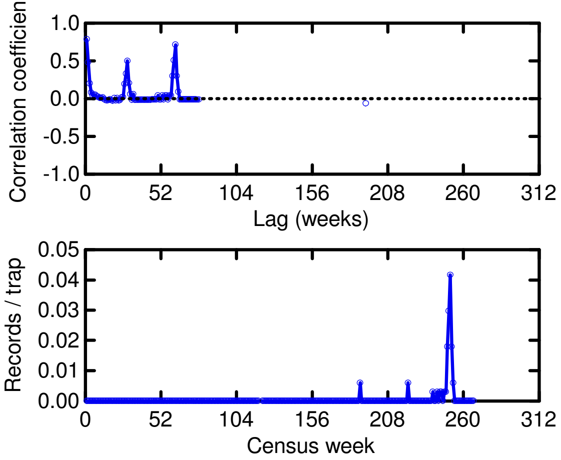
CLM084

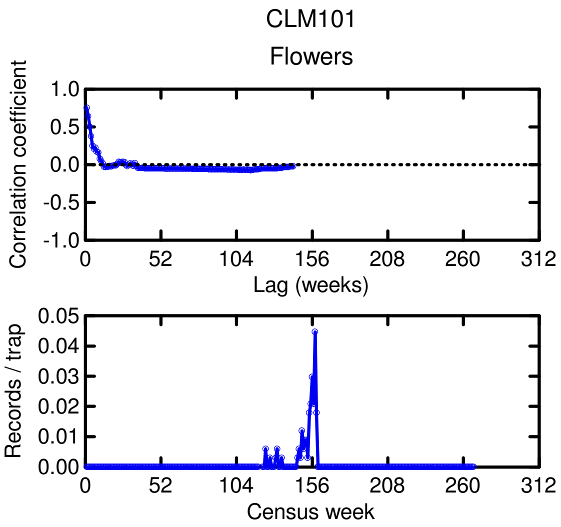
Fruit and seeds



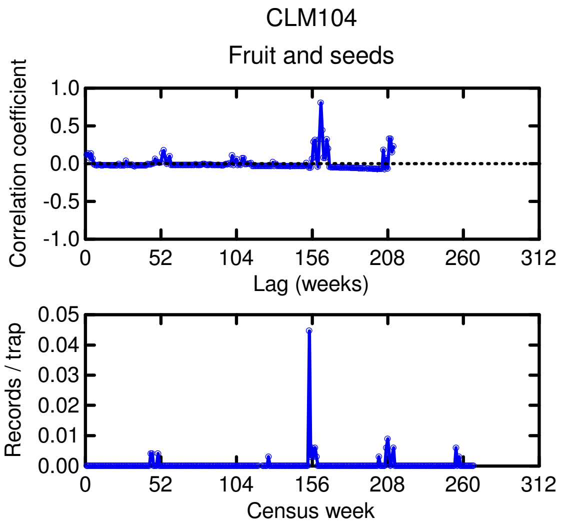
CLM091

Fruit and seeds



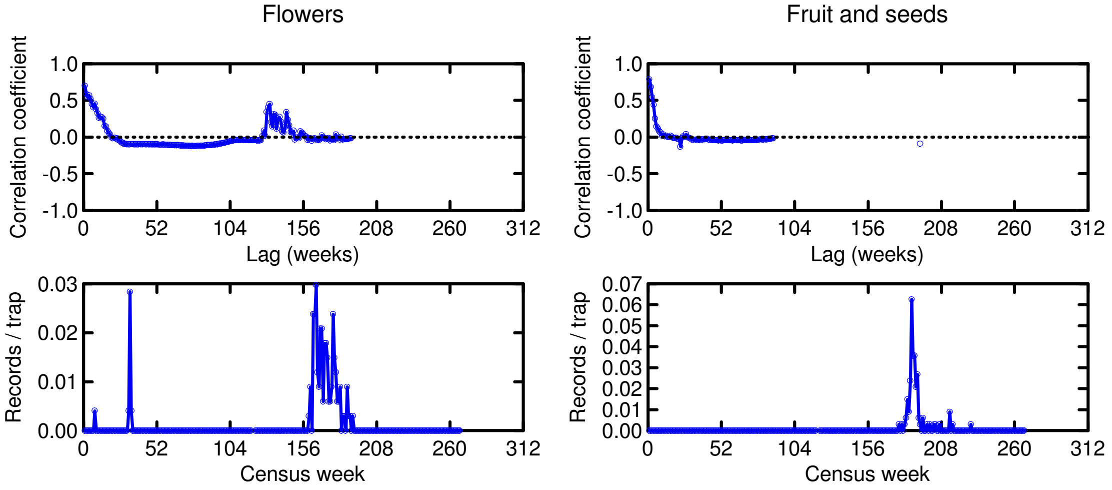

CLM101

Flowers

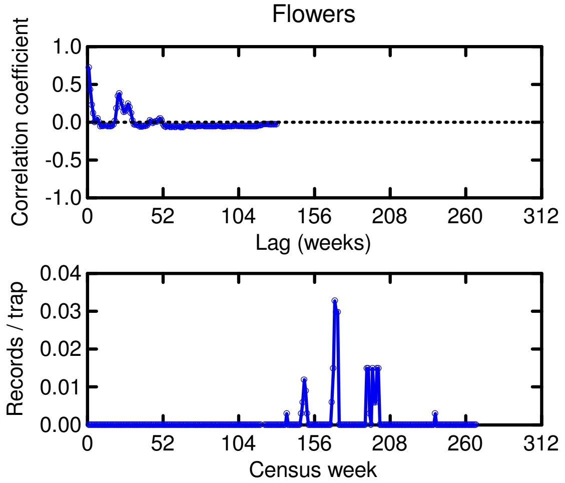

CLM104

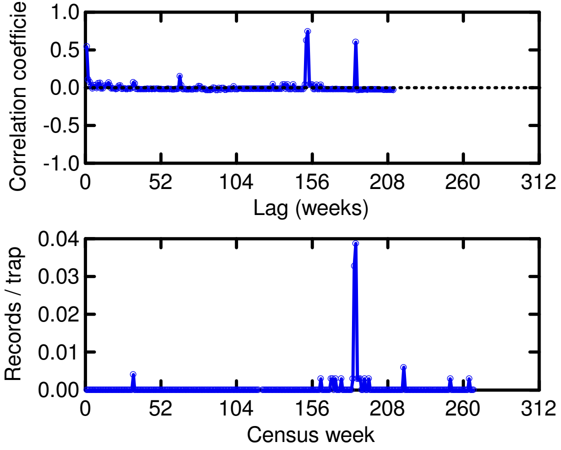
Fruit and seeds

CLM110



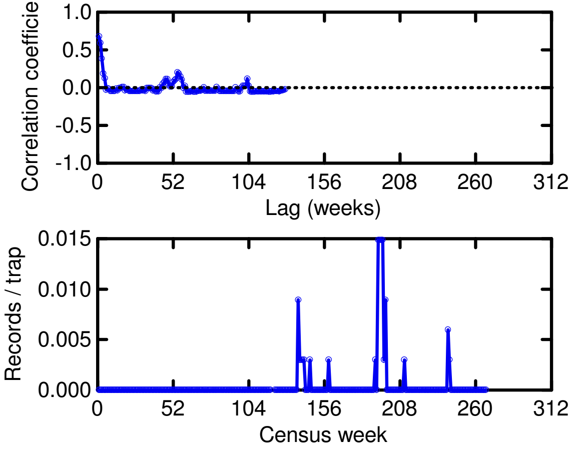
CLM113





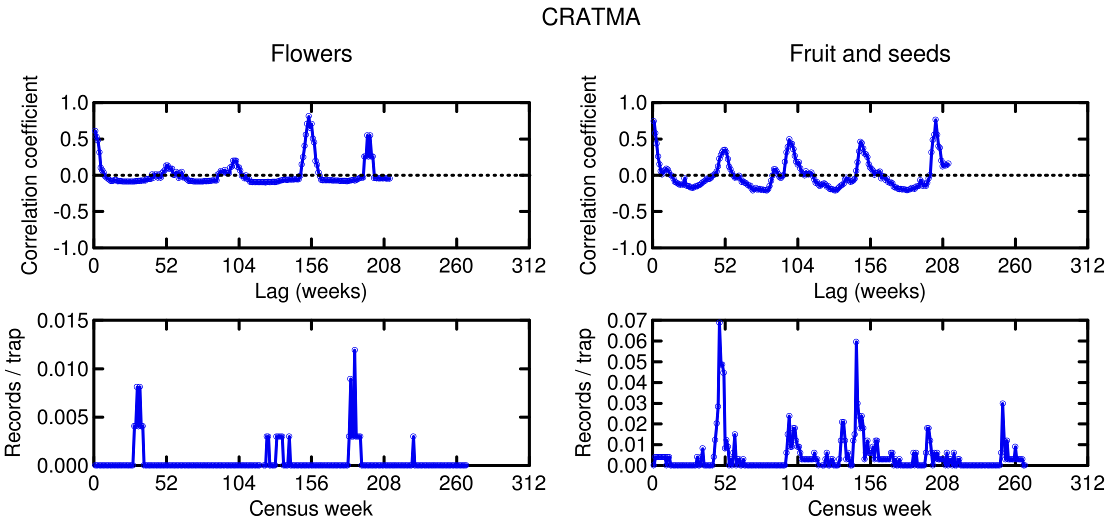
CLM118

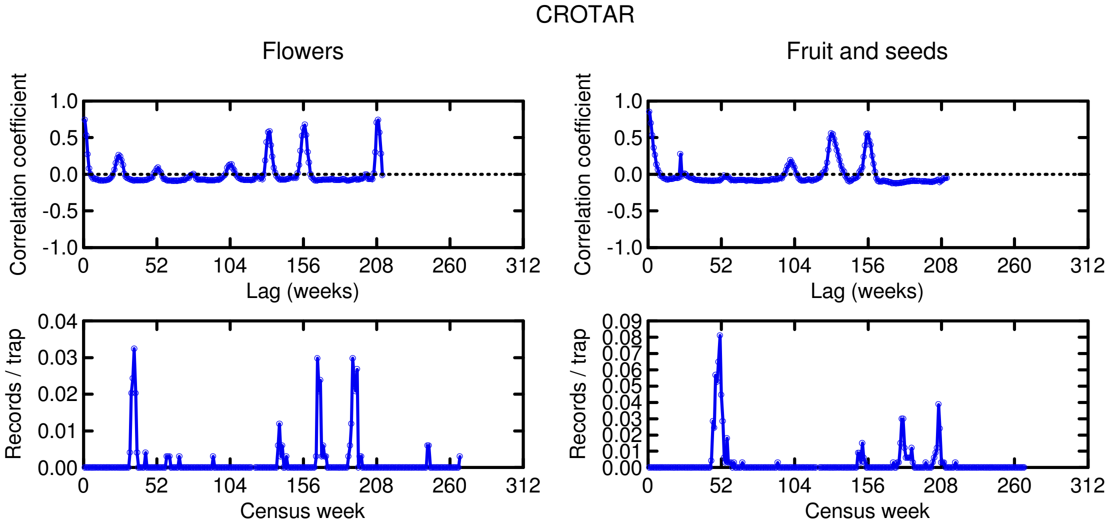
Flowers

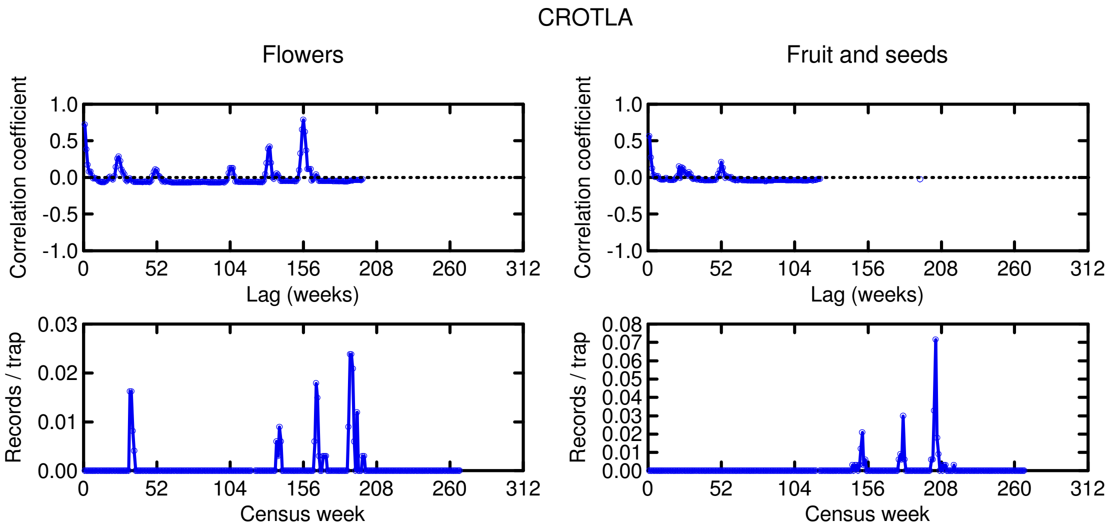


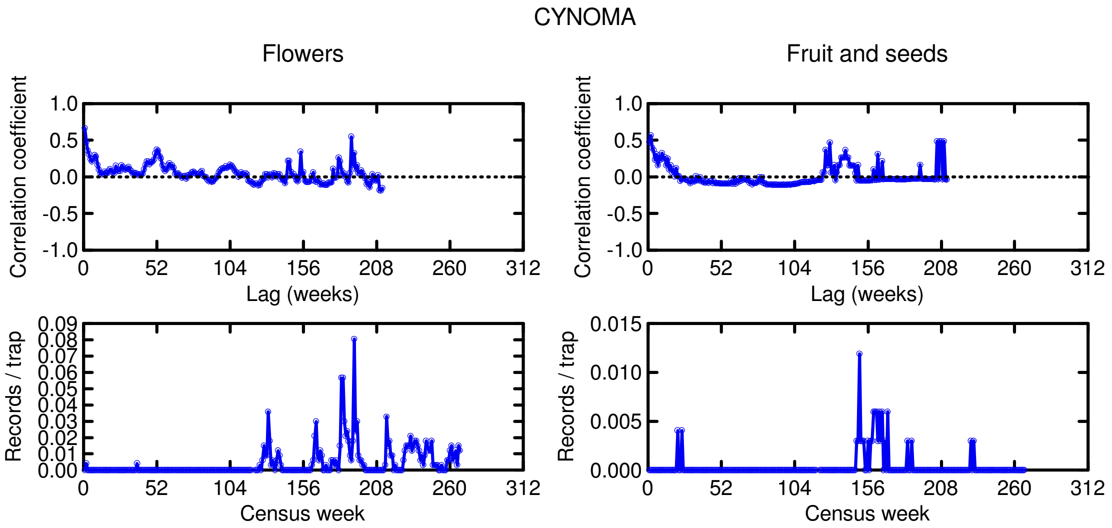
CLM126

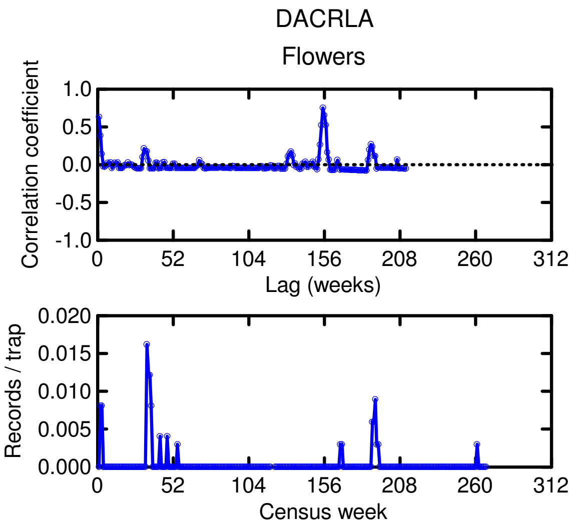
Flowers

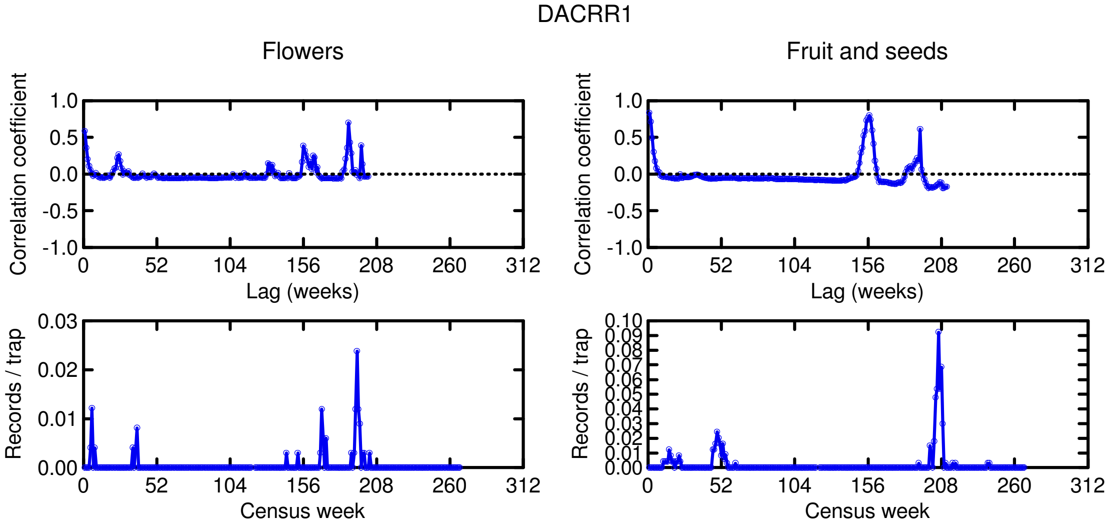

CRATMA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

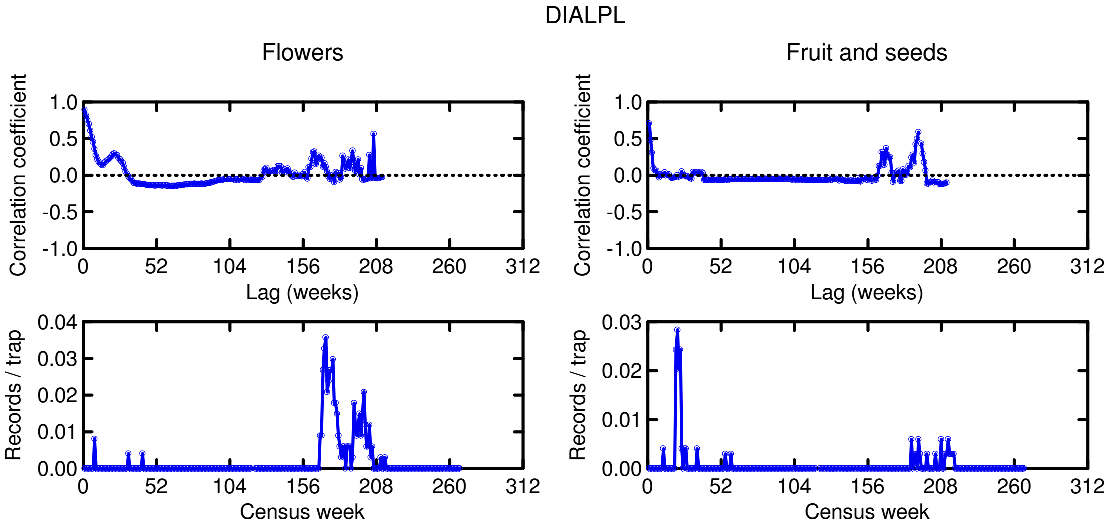

CROTAR
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.04
0.03
0.02
0.01
0.00
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

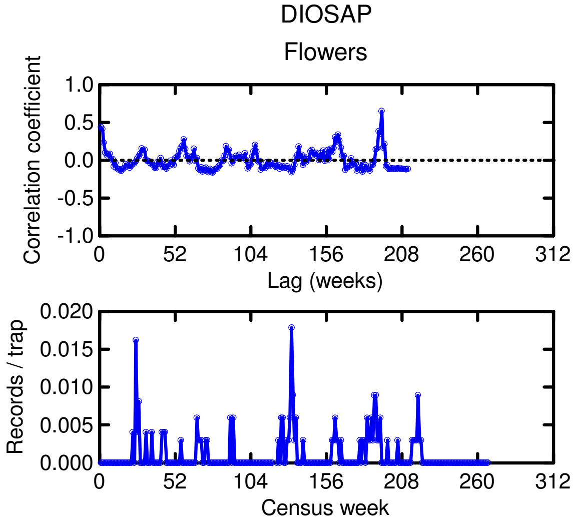

CROTLA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

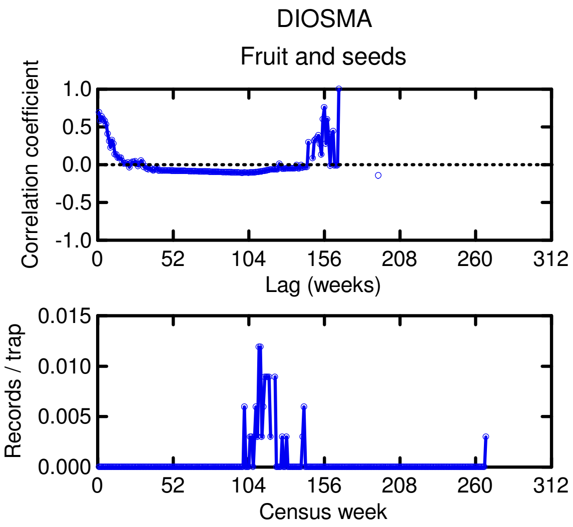

CYNOMA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.015
0.010
0.005
0.000
Census week

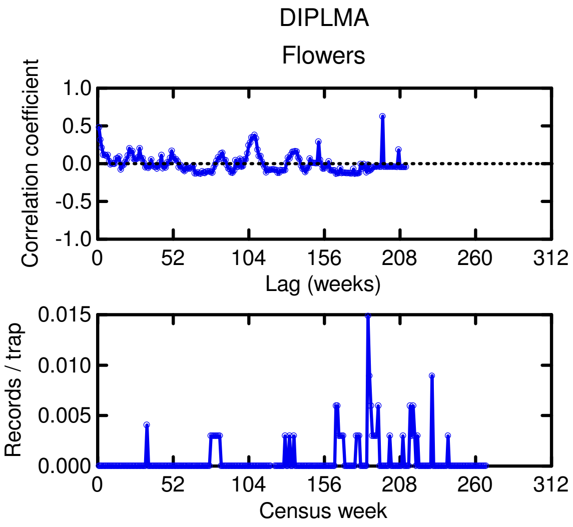

DACRLA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


DACRR1
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

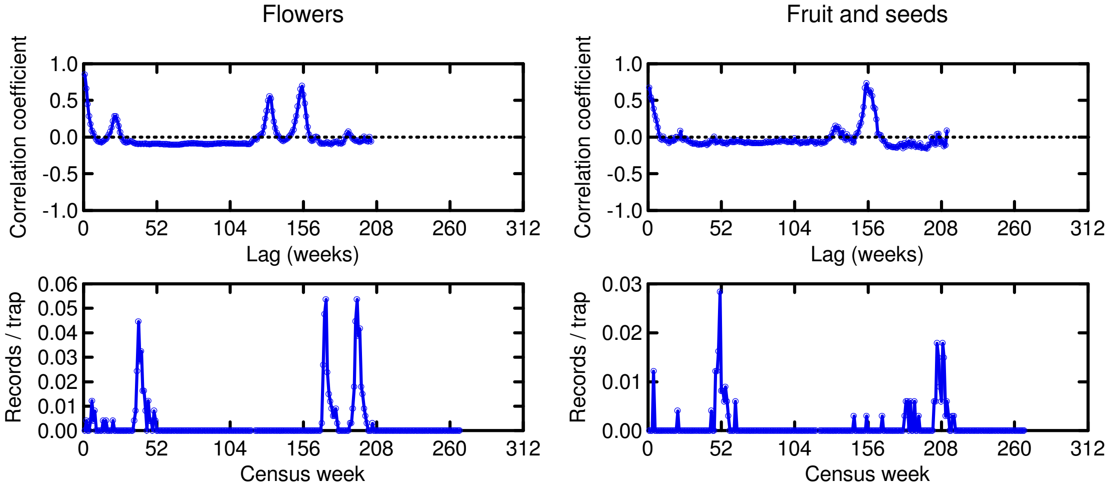

DIALPL
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
Lag (weeks)
0
52
104
156
208
260
312
Records / trap
0.04
0.03
0.02
0.01
0.00
0.03
0.02
0.01
0.00
Census week


DIOSAP
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
Lag (weeks)
0
52
104
156
208
260
312
Records / trap
0.020
0.015
0.010
0.005
0.000
Census week

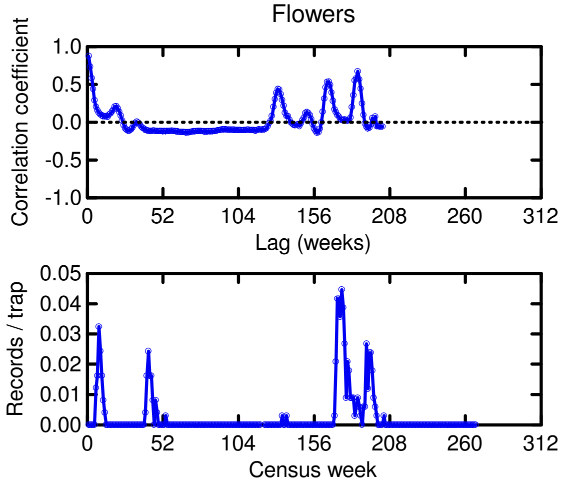

DIOSMA
Fruit and seeds


DIPLMA
Flowers

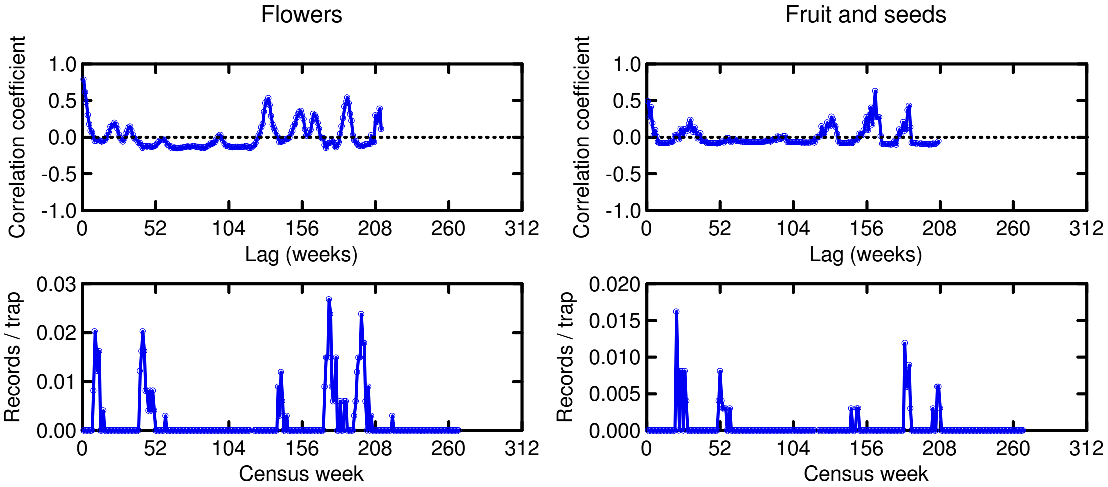
DIPTC1



DIPTC2

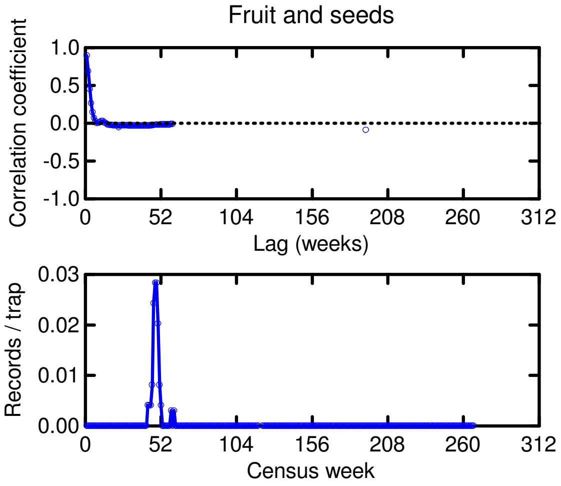


DIPTCR

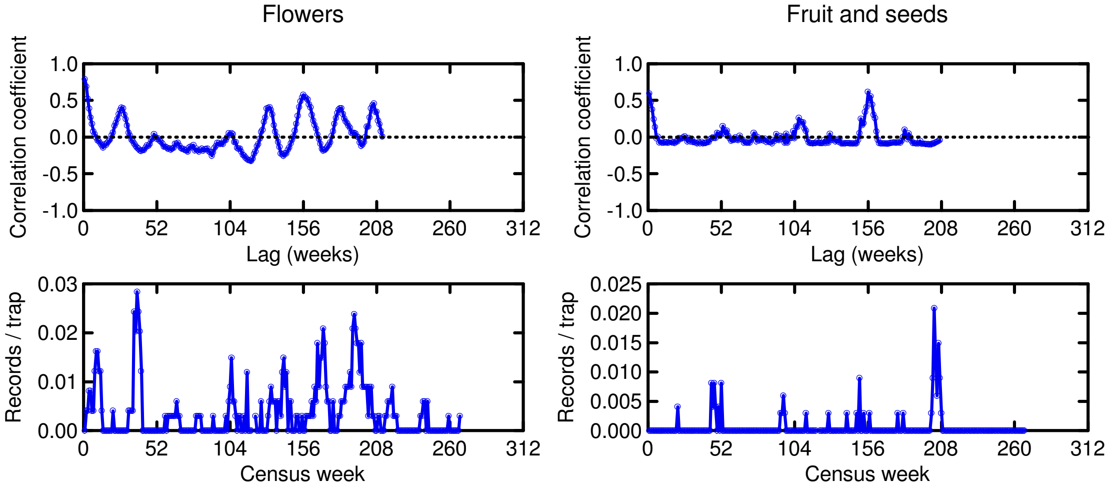

Flowers

Fruit and seeds

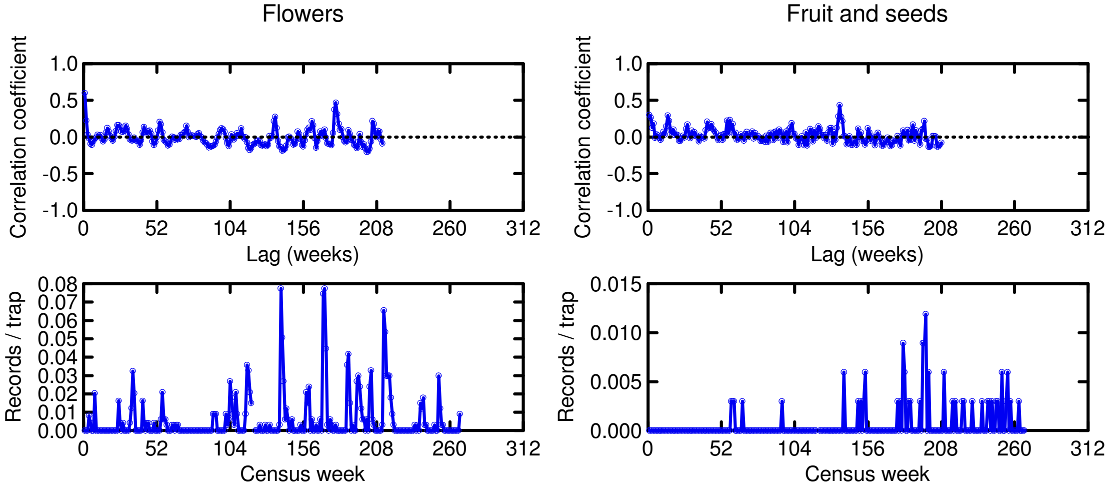
DRYPLO

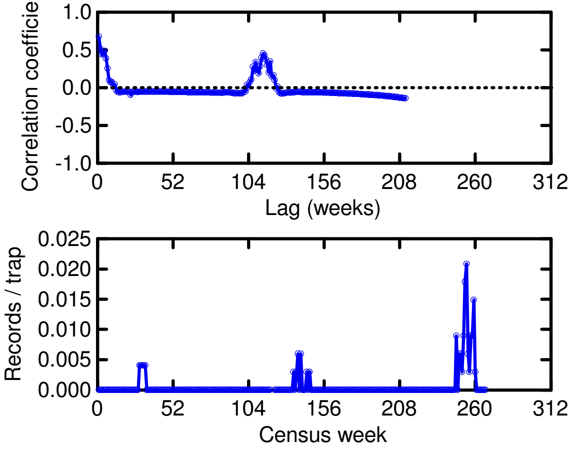

Fruit and seeds

DURIGR

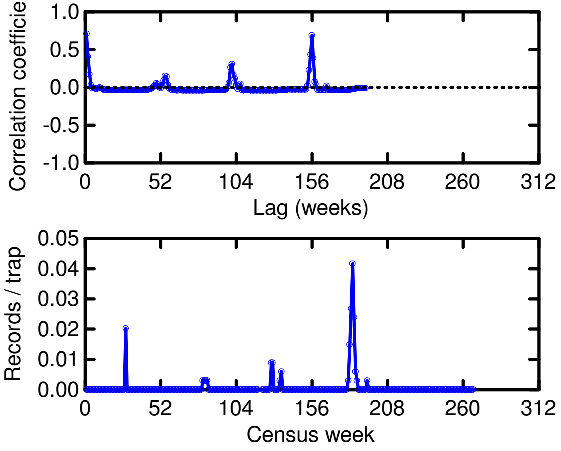


DYERCO

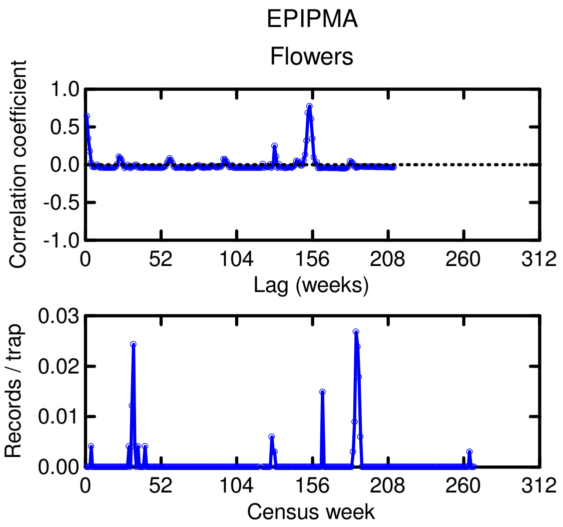


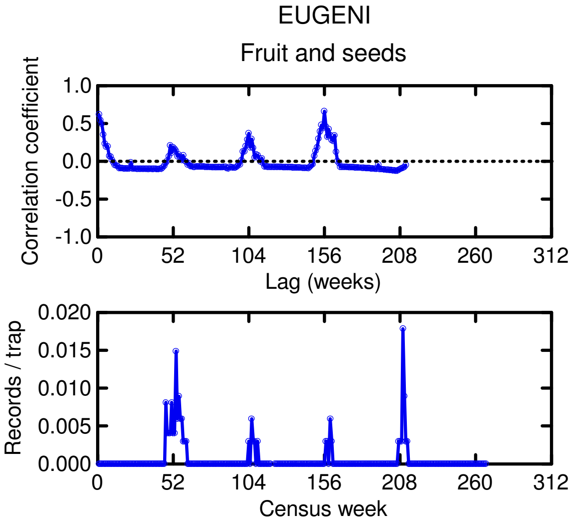

ELAEP3

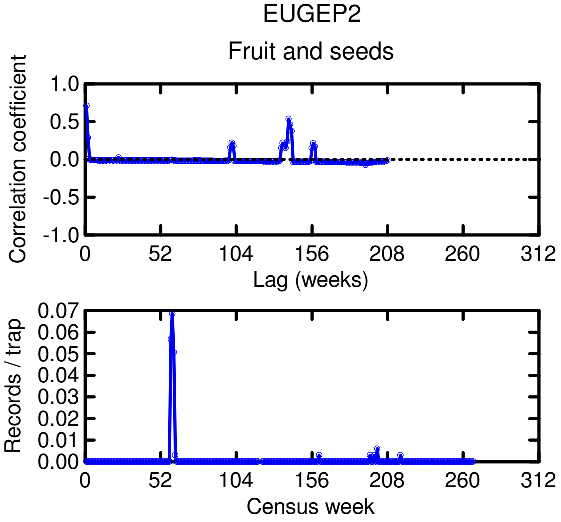
Fruit and seeds

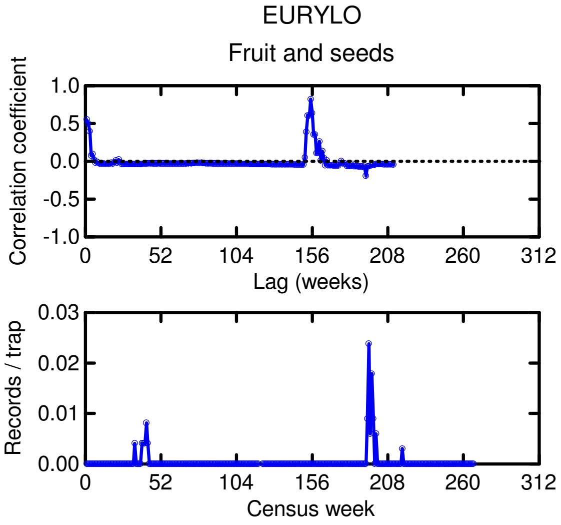

ELATTA

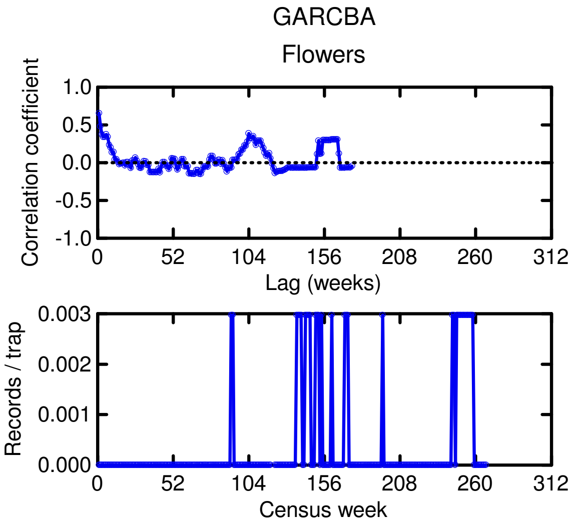
Flowers

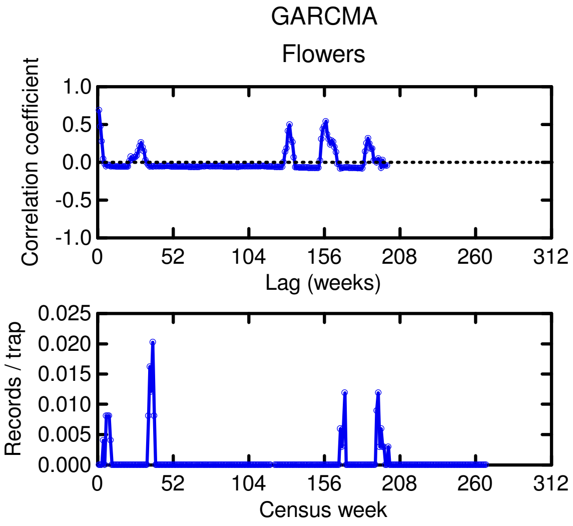

EPIPMA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

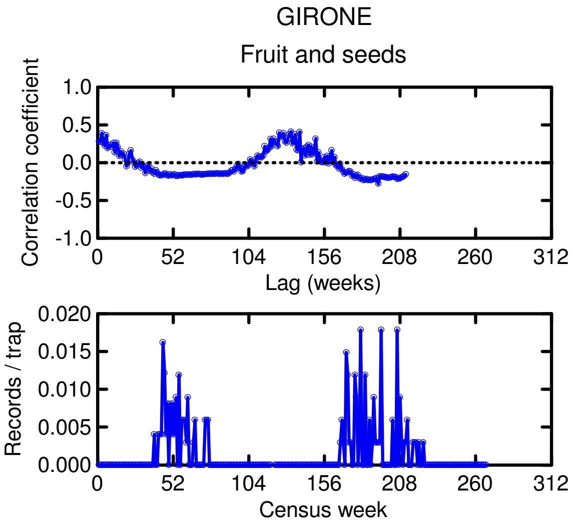

EUGENI
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

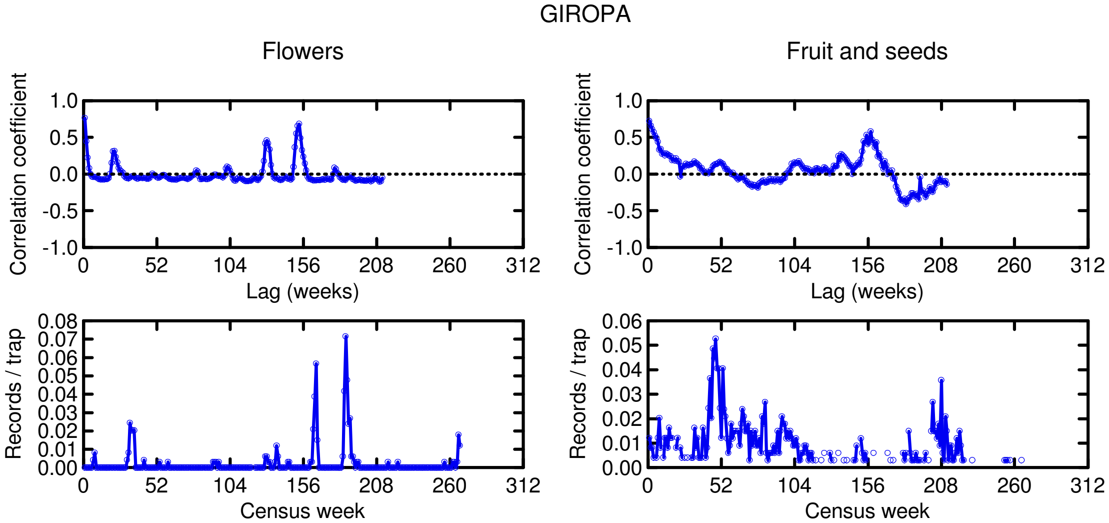

EUGEP2
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

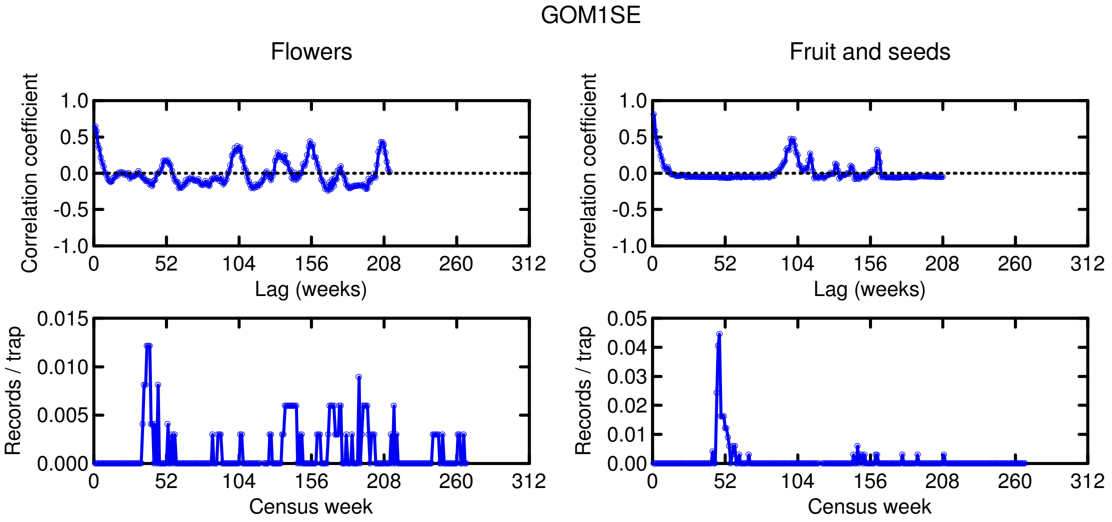

EURYLO
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

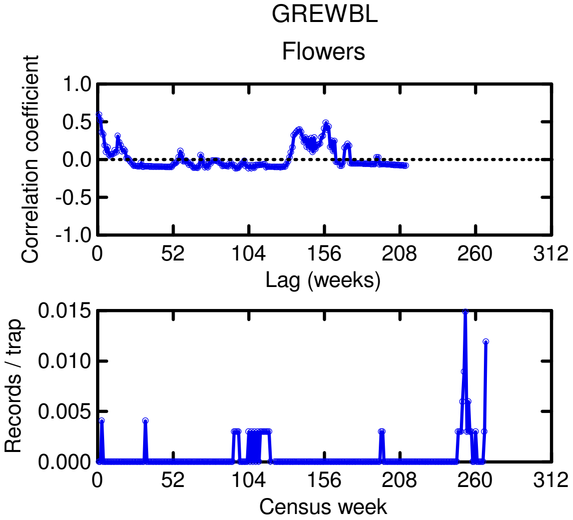

GARCBA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.003
0.002
0.001
0.000
0
52
104
156
208
260
312
Census week


GARCMA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.025
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

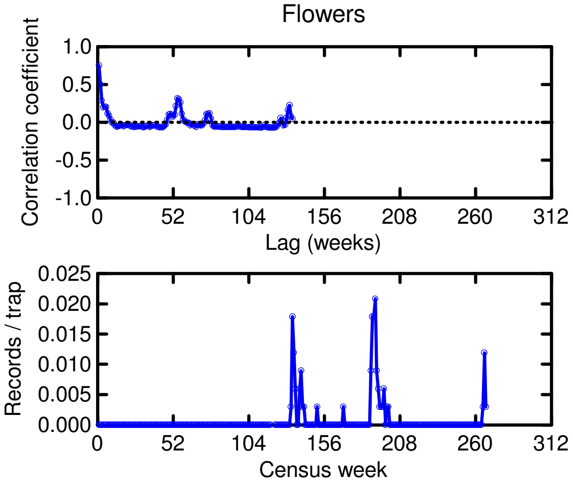

GIRONE
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


GIROPA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

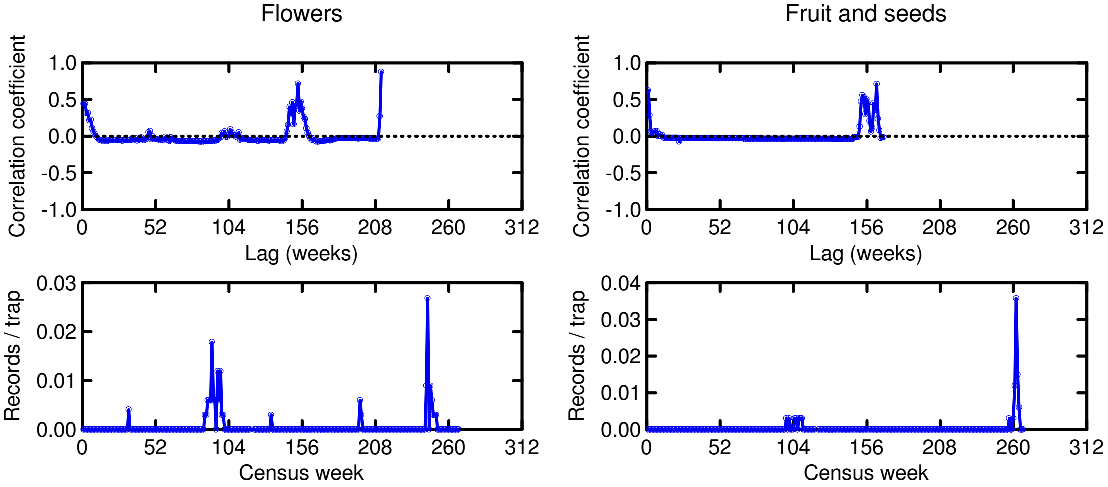

GOM1SE
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0.05
0.04
0.03
0.02
0.01
0.00
Census week

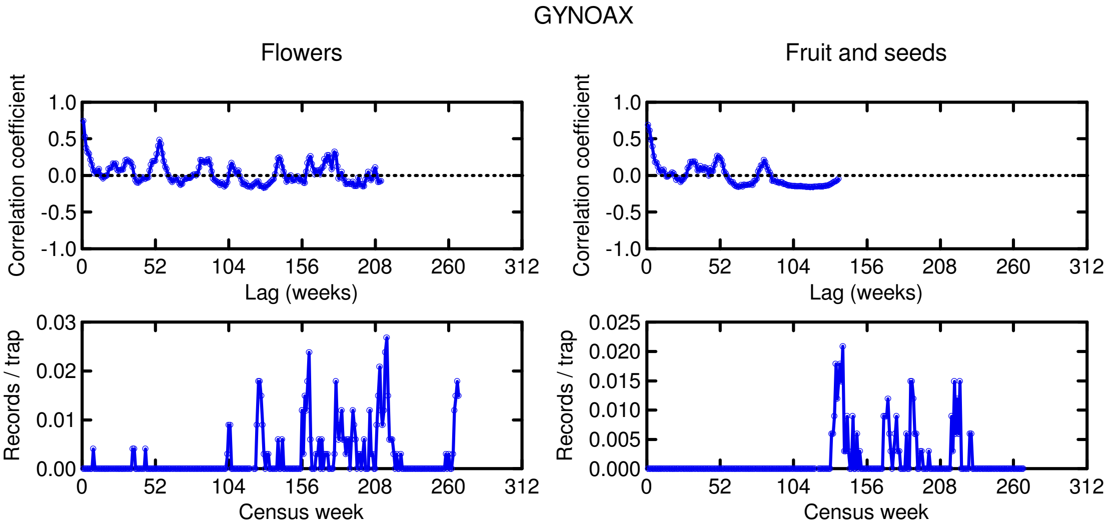

GREWBL
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
Census week

GREWLA



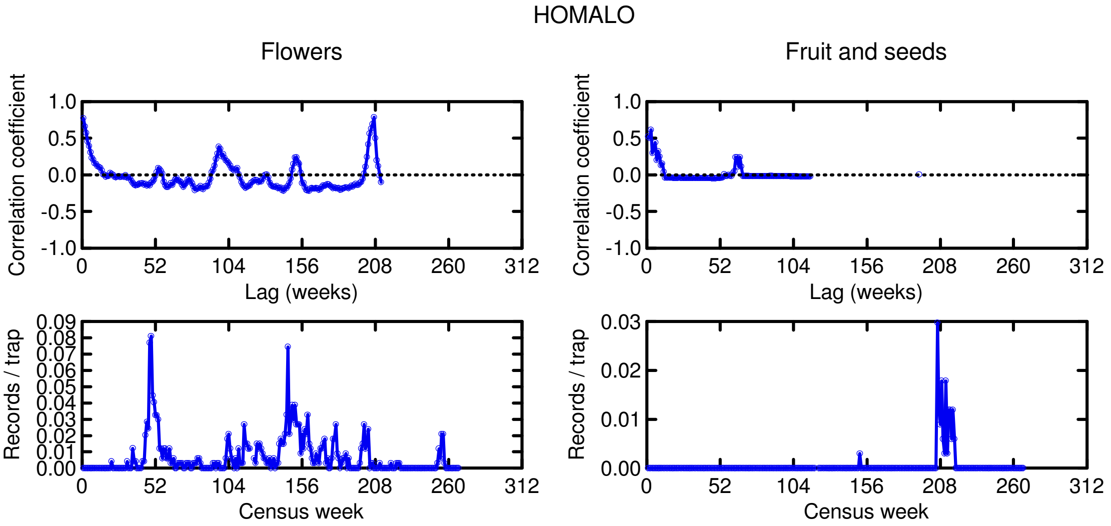
GREWMI




GYNOAX

Flowers

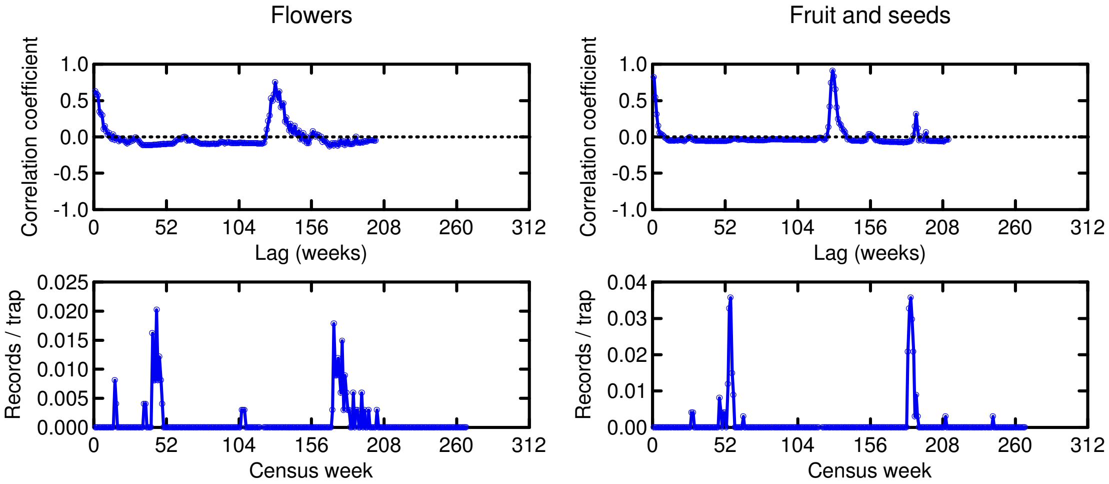
Fruit and seeds


HOMALO

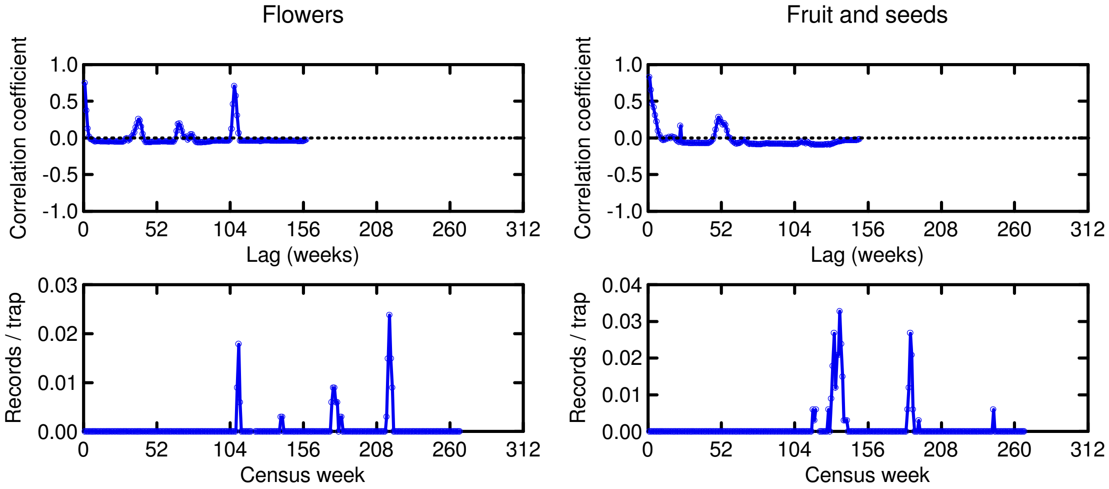
Flowers

Fruit and seeds

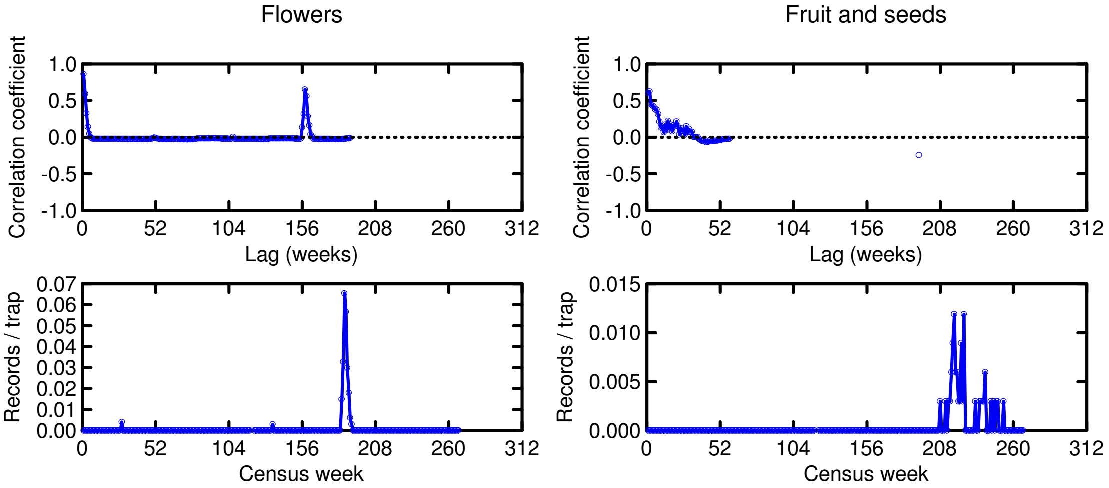
HOPEDR



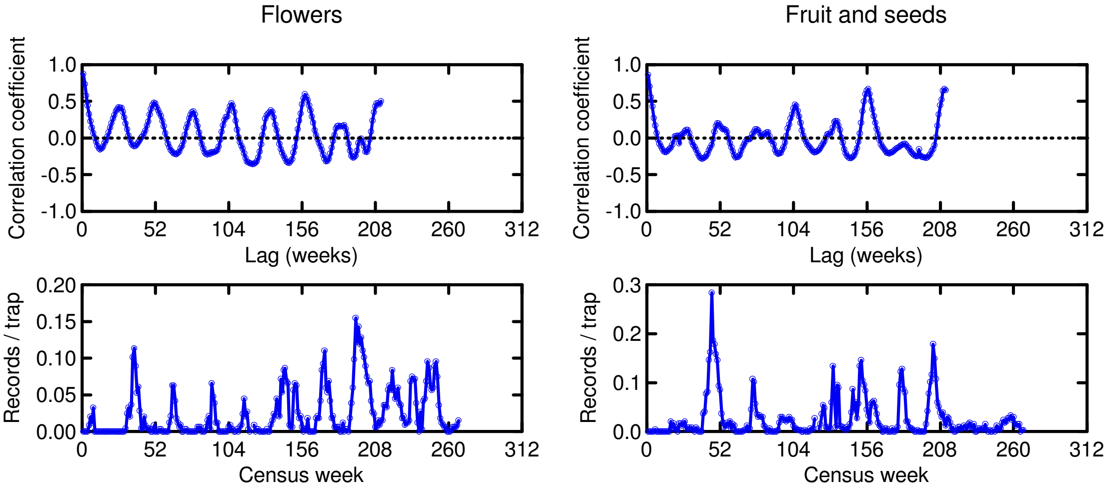
HOPEME

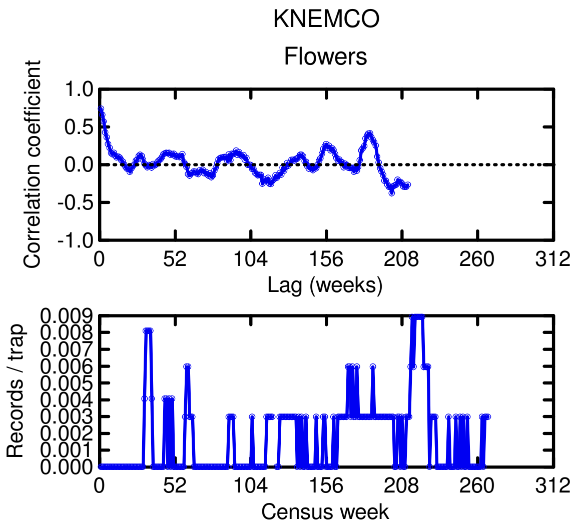


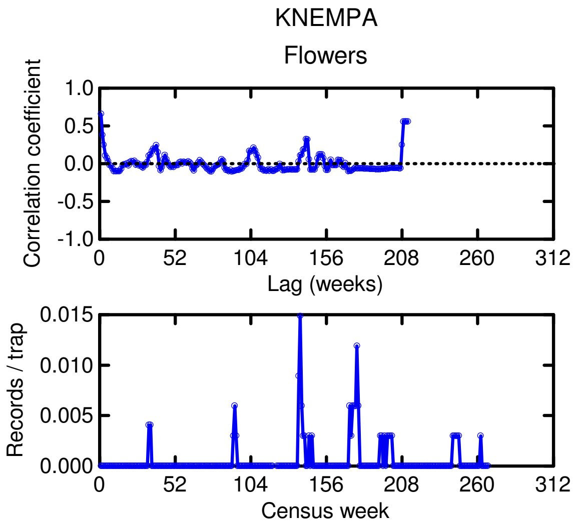
INTSPA

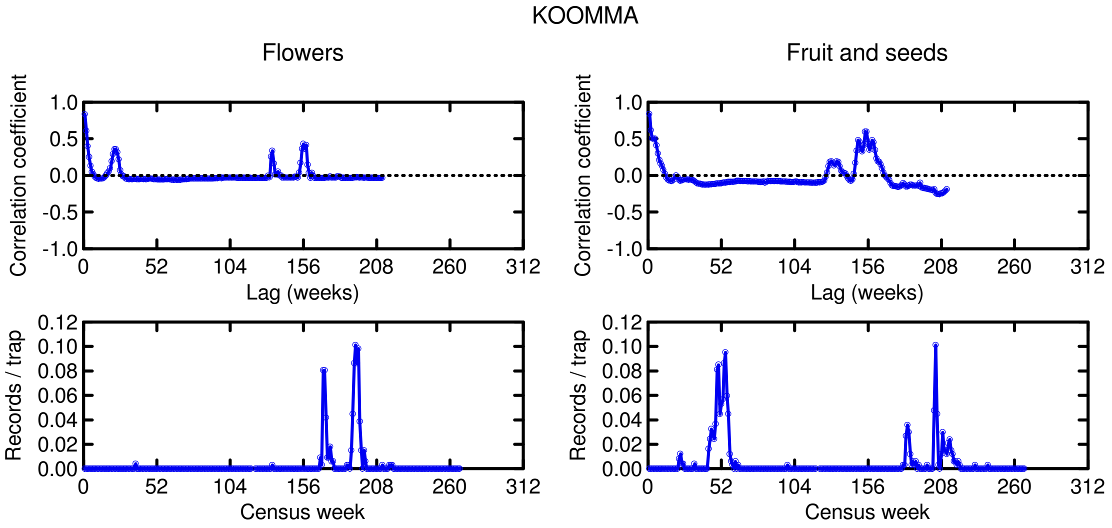


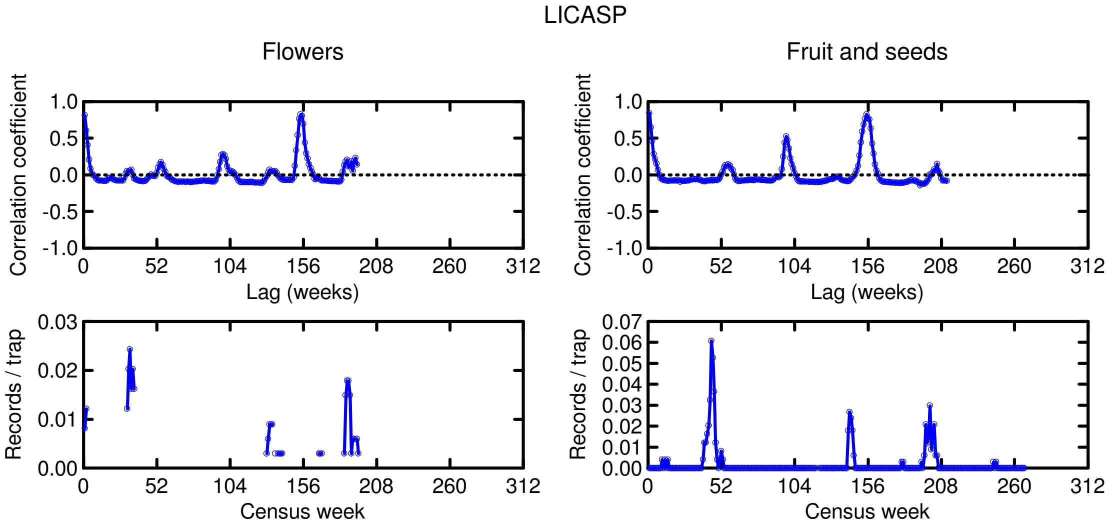
IXONIC

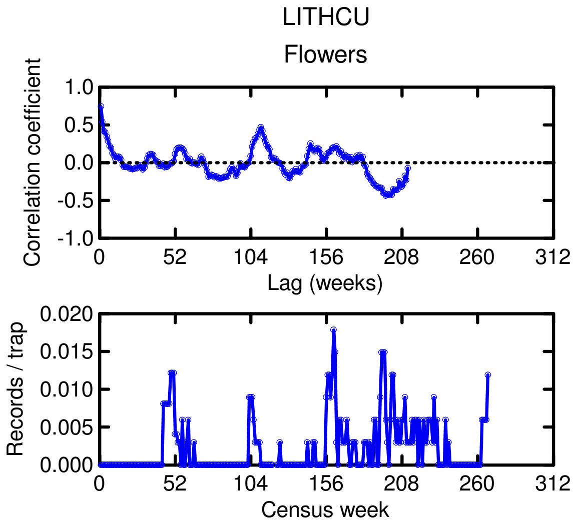



KNEMCO
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
0
52
104
156
208
260
312
Census week


KNEMPA
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

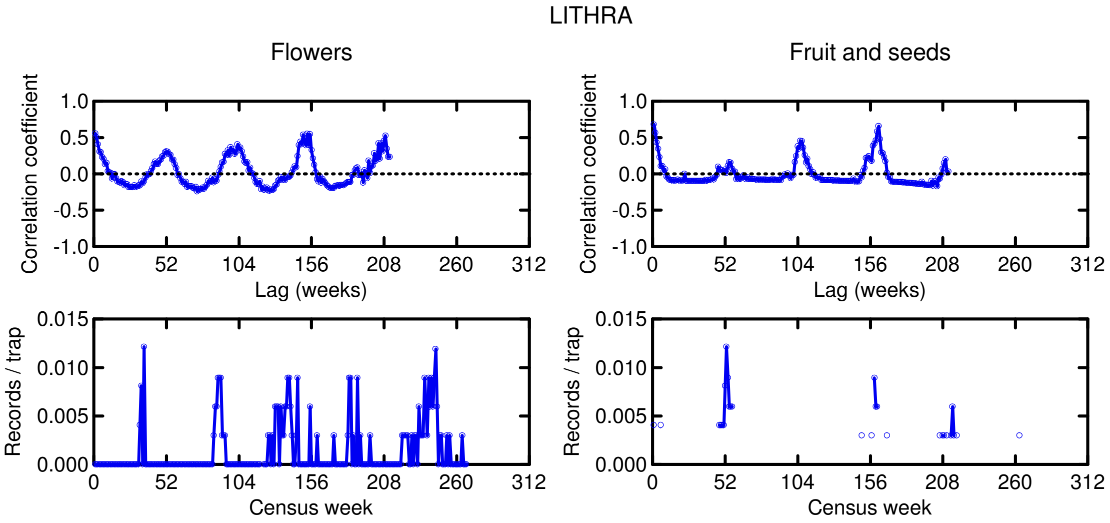

KOOMMA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Census week


LICASP
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week



LITHCU

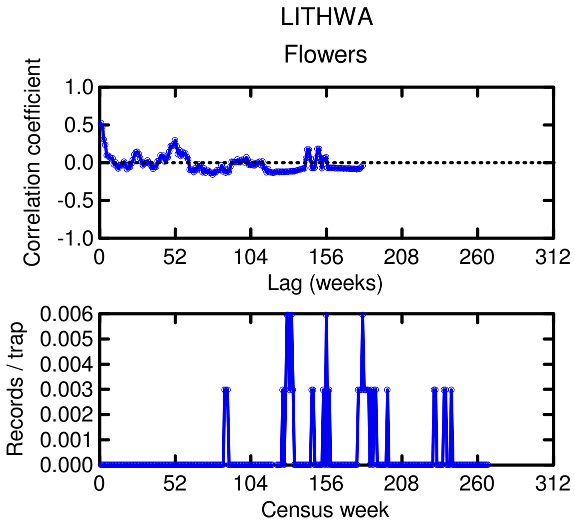
Flowers



LITHRA

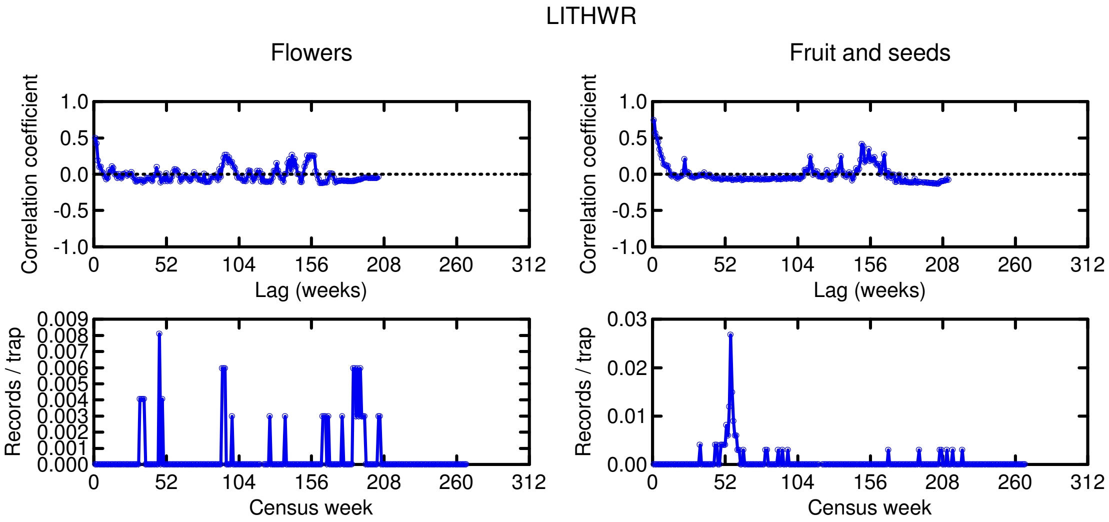
Flowers

Fruit and seeds



LITHWA

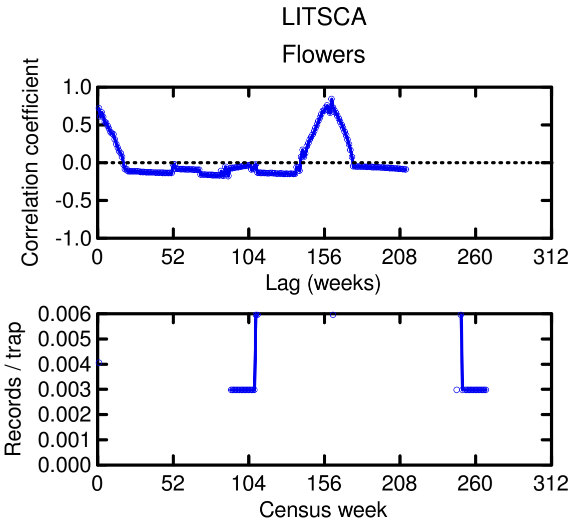
Flowers



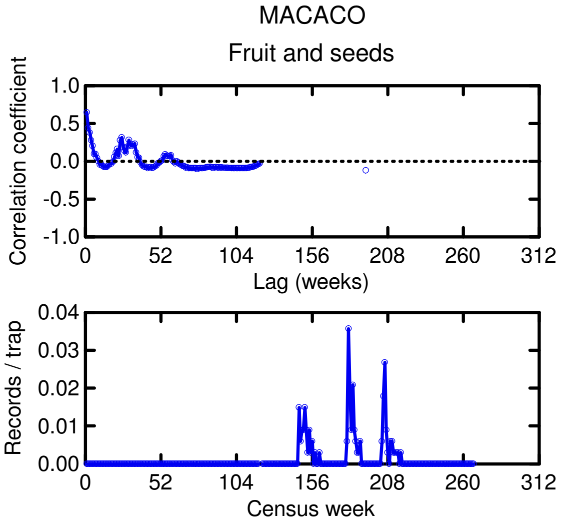
LITHWR

Flowers

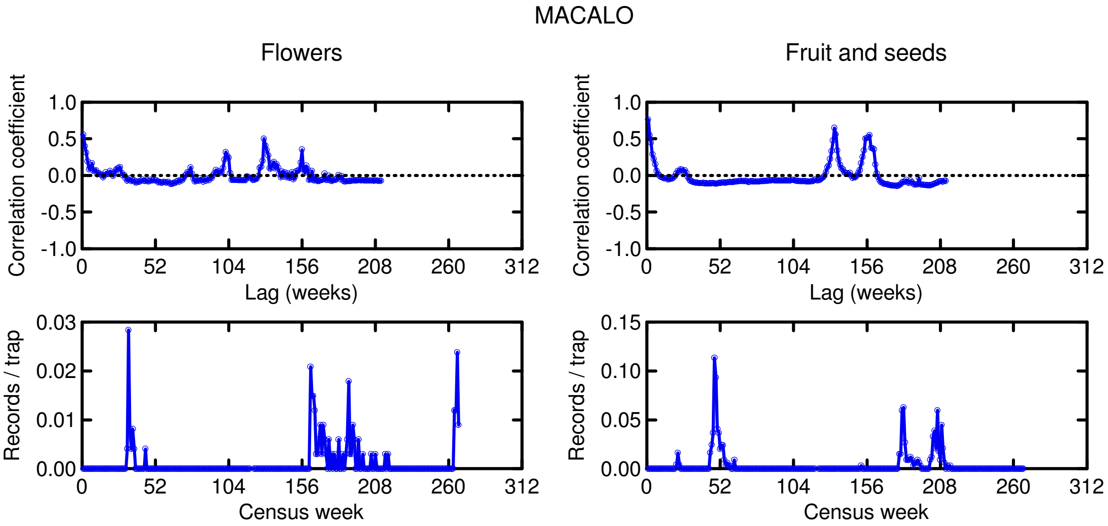
Fruit and seeds

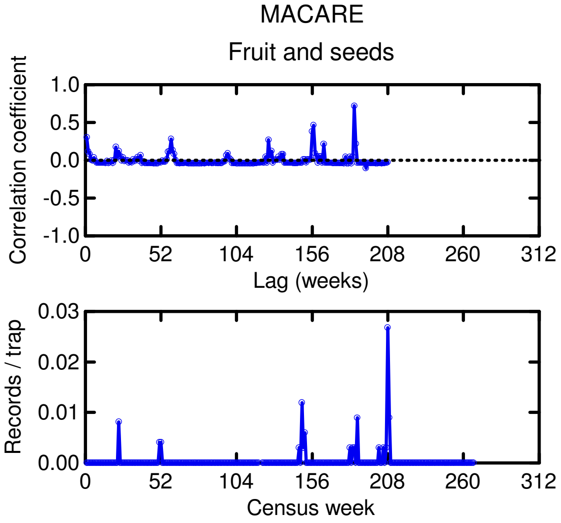

LITSCA

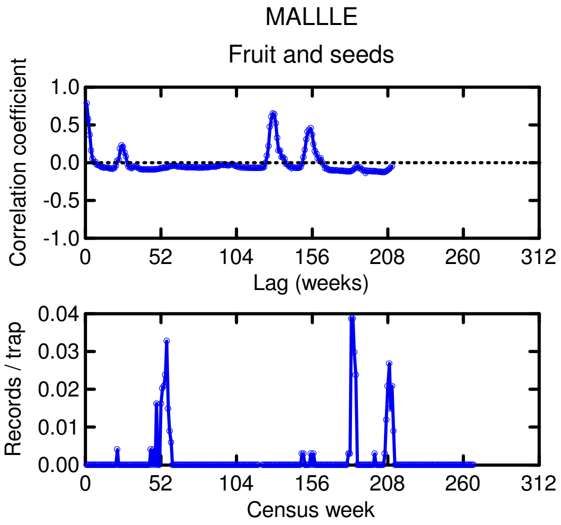
Flowers

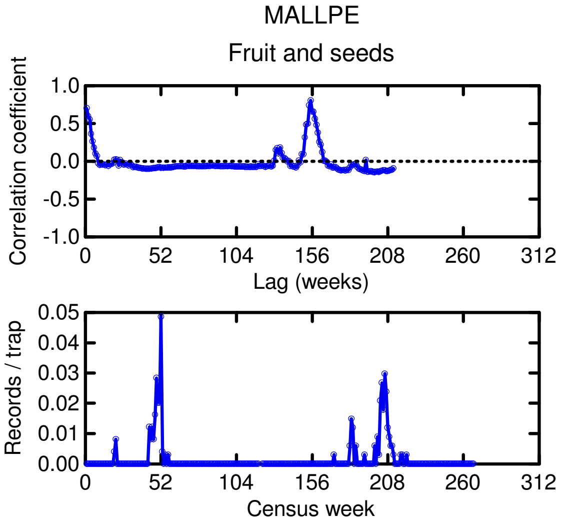

MACACO

Fruit and seeds

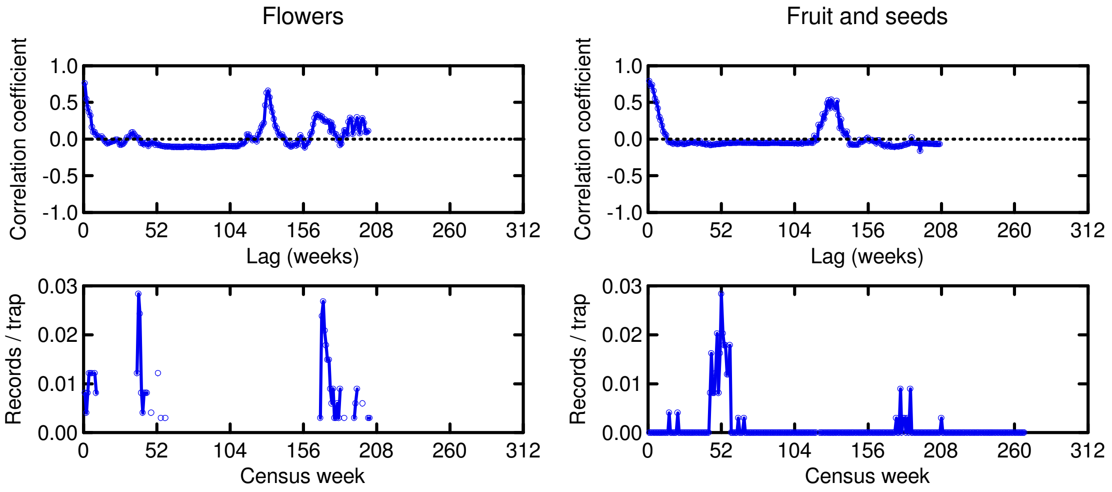

MACALO
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.15
0.10
0.05
0.00
Census week


MACARE
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
Census week

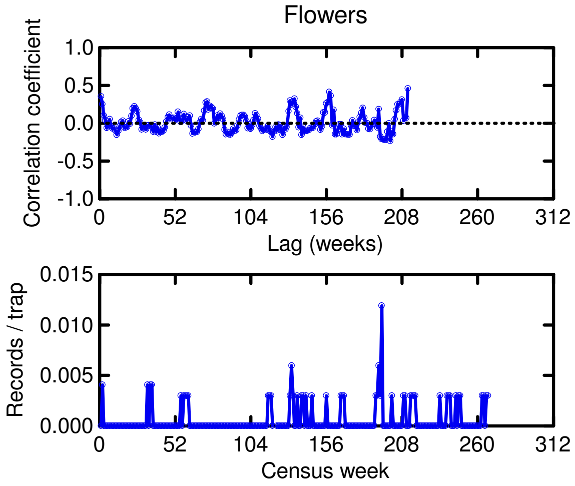

MALLLE
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

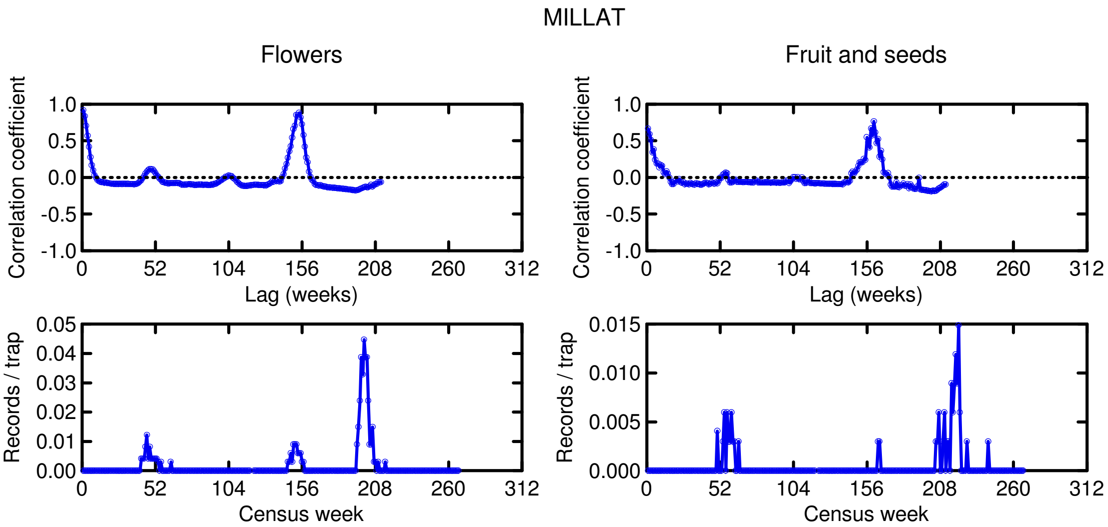

MALLPE
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.05
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week

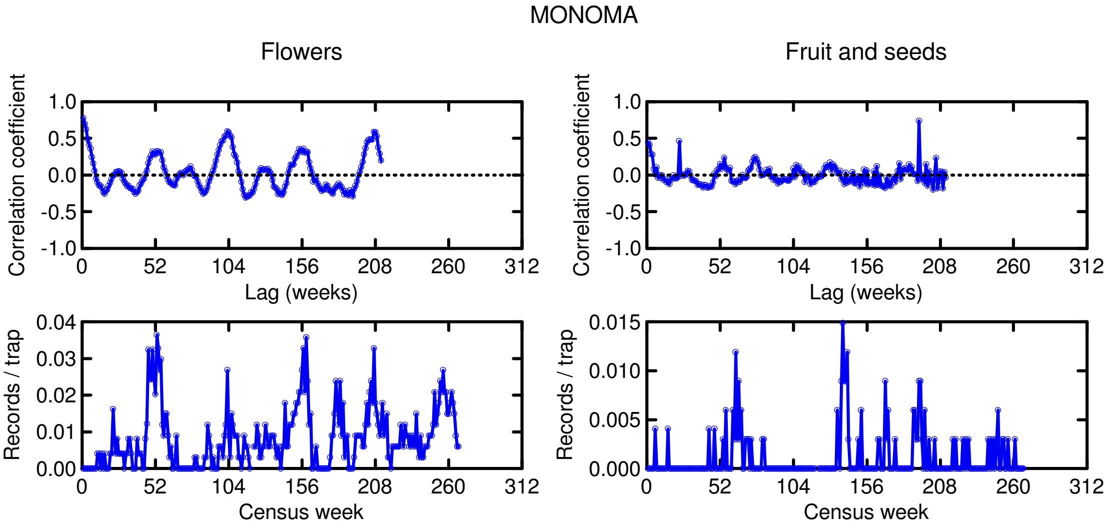
MESUFE

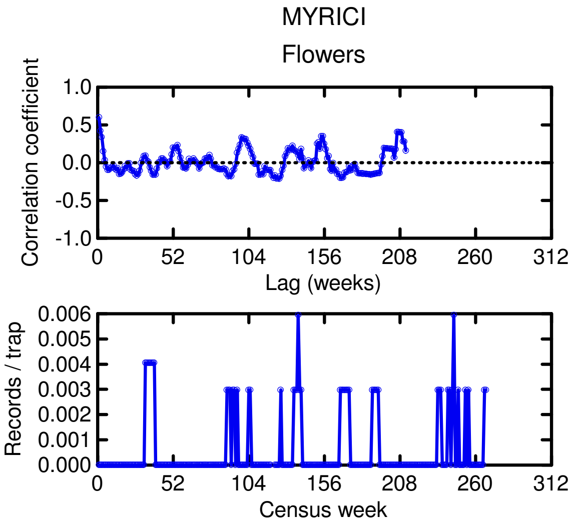


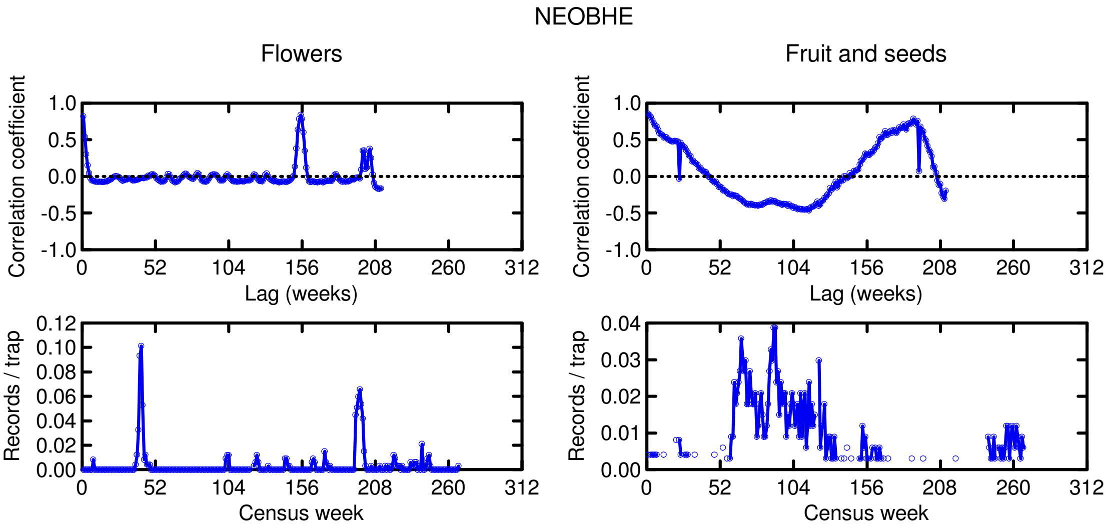
MIC1CA

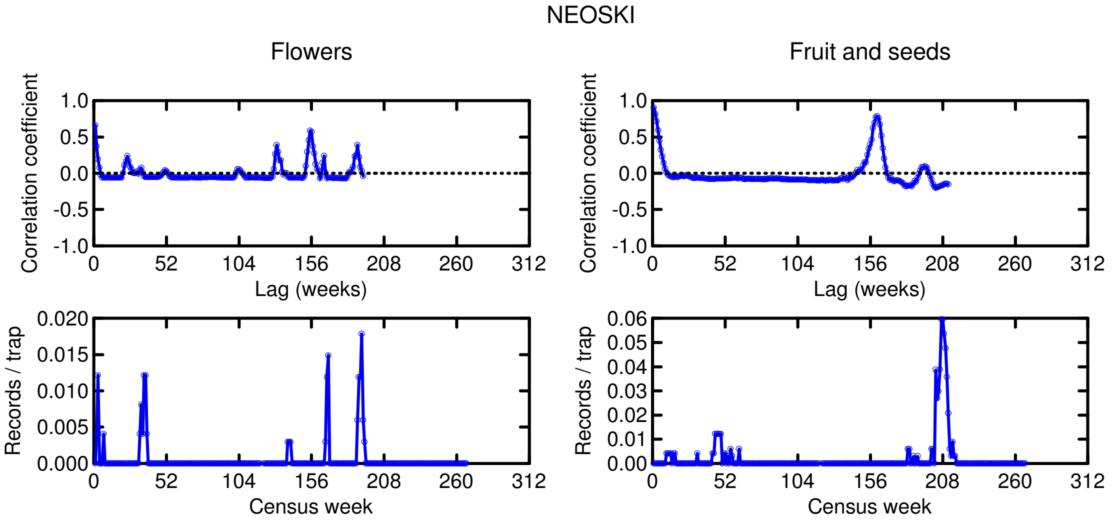


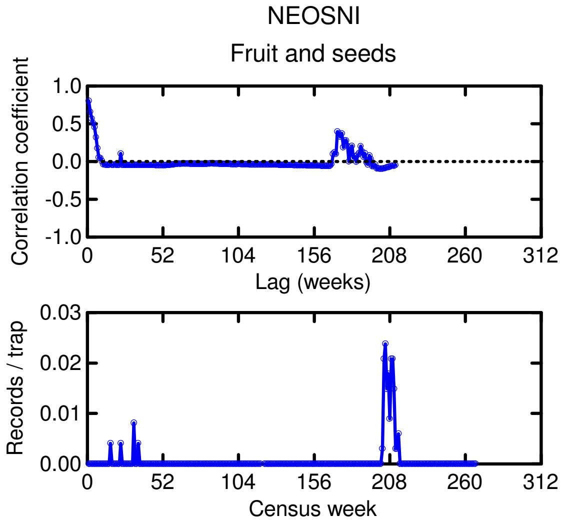

MILLAT
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
Lag (weeks)
Records / trap
0.05
0.04
0.03
0.02
0.01
0.00
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


MONOMA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
Lag (weeks)
Records / trap
0.04
0.03
0.02
0.01
0.00
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

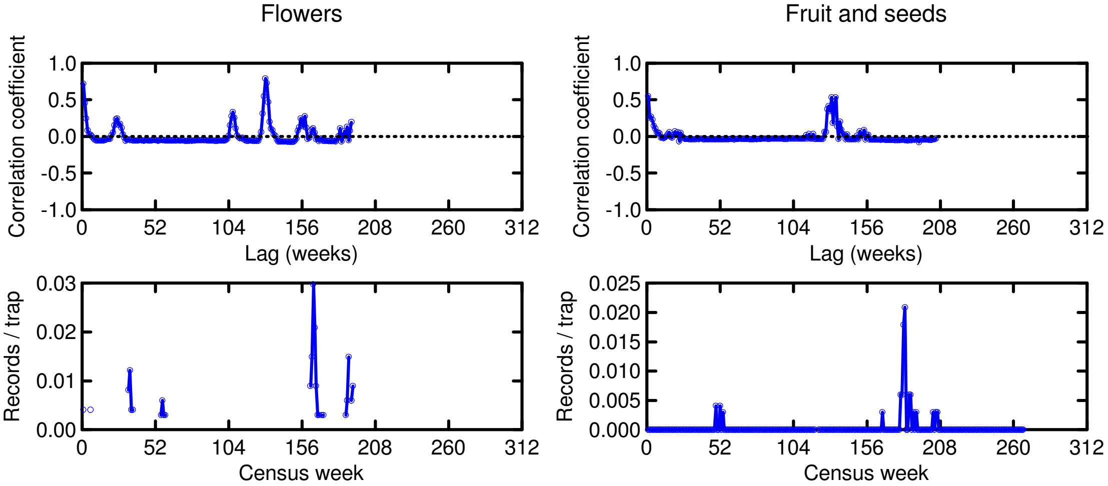

MYRICI
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.006
0.005
0.004
0.003
0.002
0.001
0.000
Census week


NEOBHE
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.04
0.03
0.02
0.01
0.00
Census week

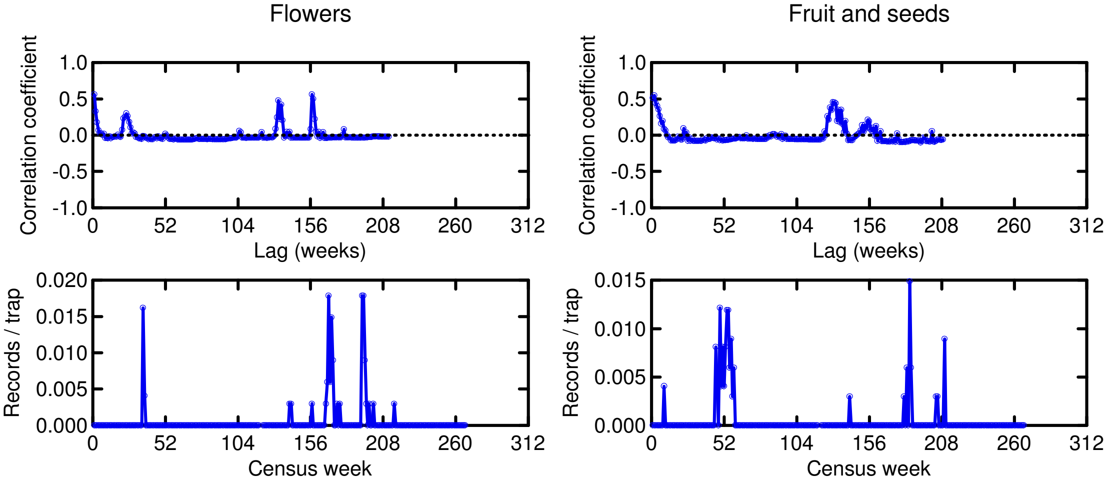

NEOSKI
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

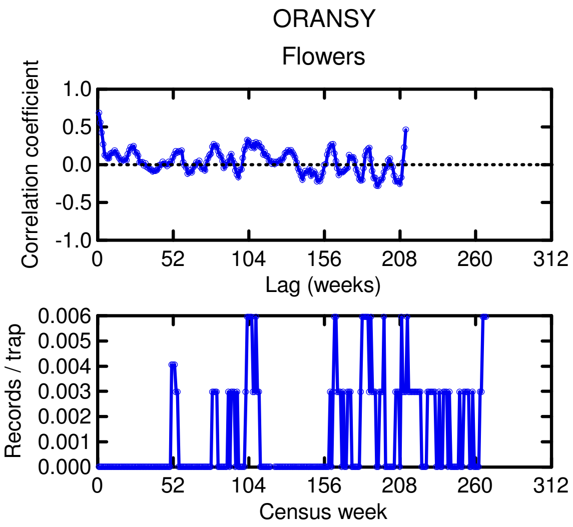

NEOSNI
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
Census week

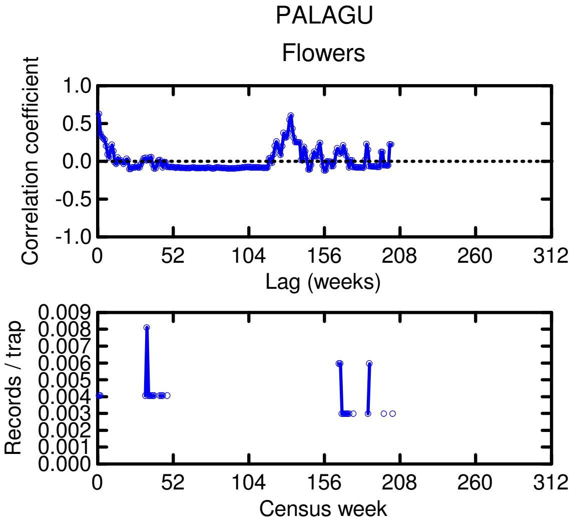
NEPHCO

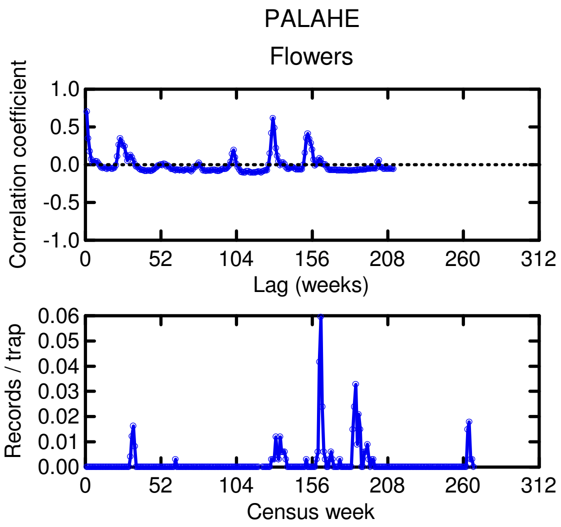


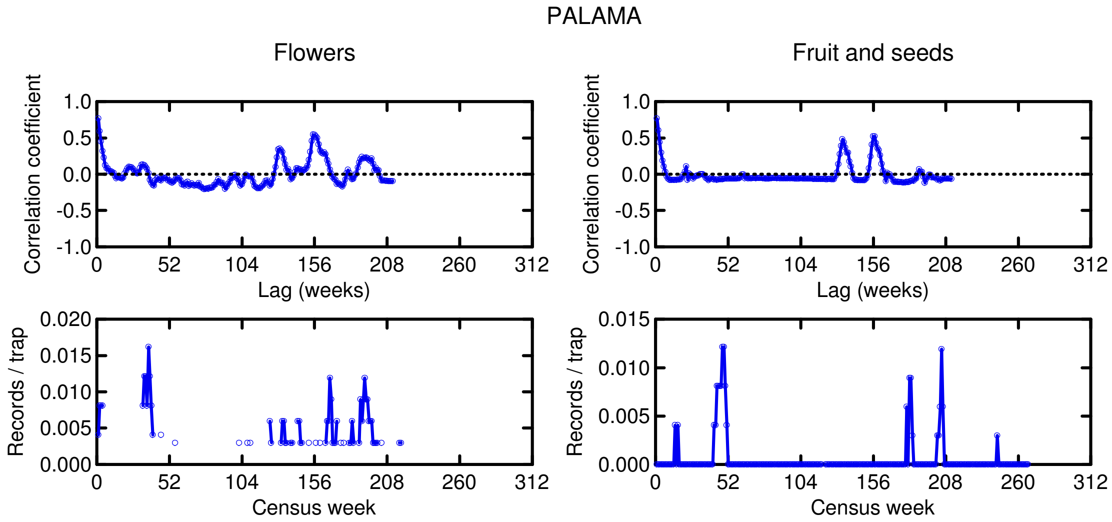
OCHAAM

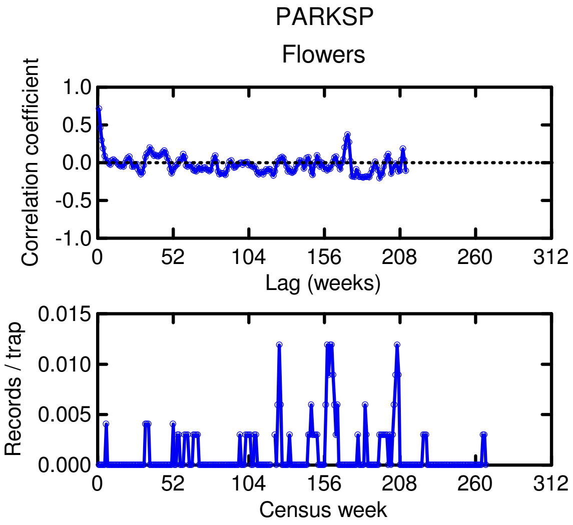


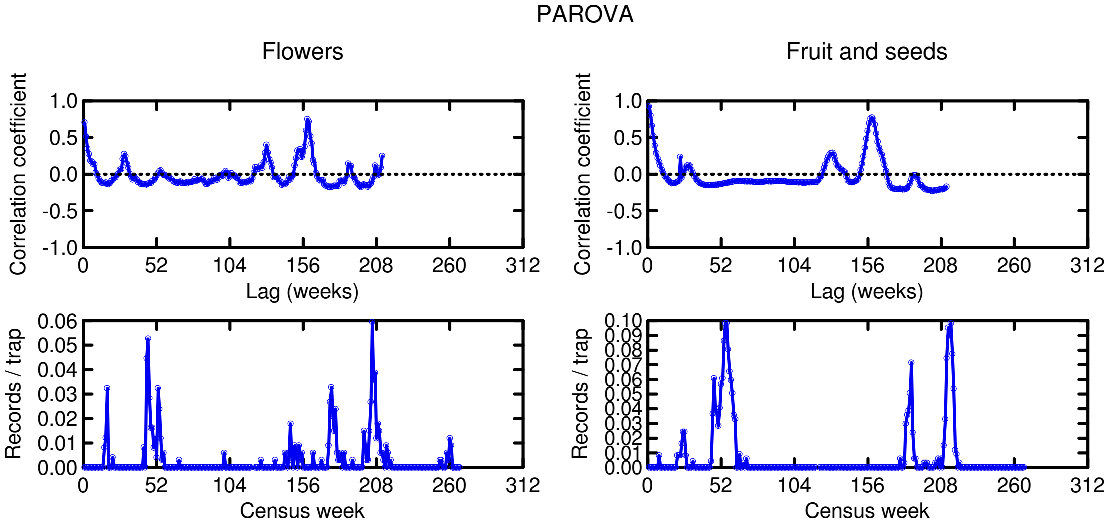

ORANSY
Flowers


PALAGU
Flowers

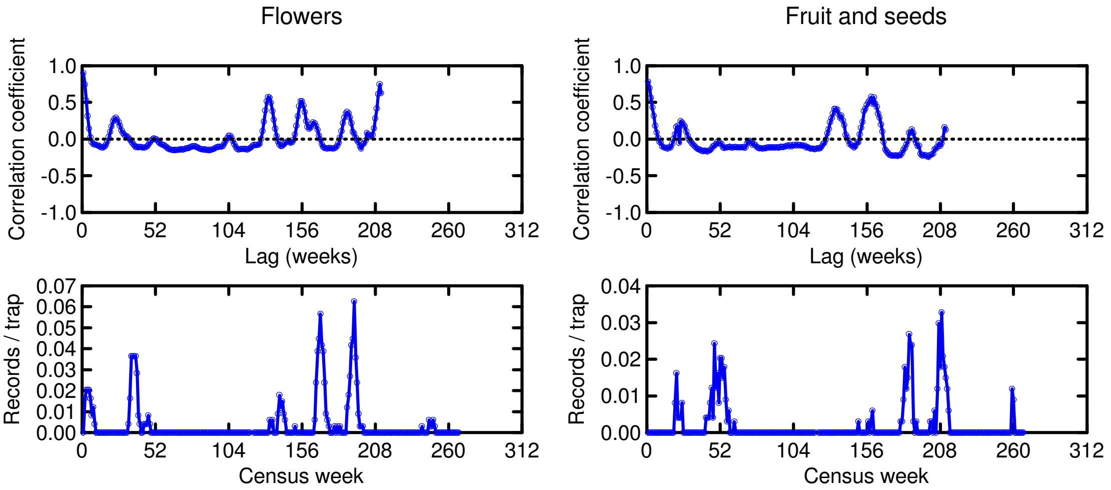

PALAHE
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
52
104
156
208
260
312
Census week


PALAMA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.020
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week
Records / trap
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

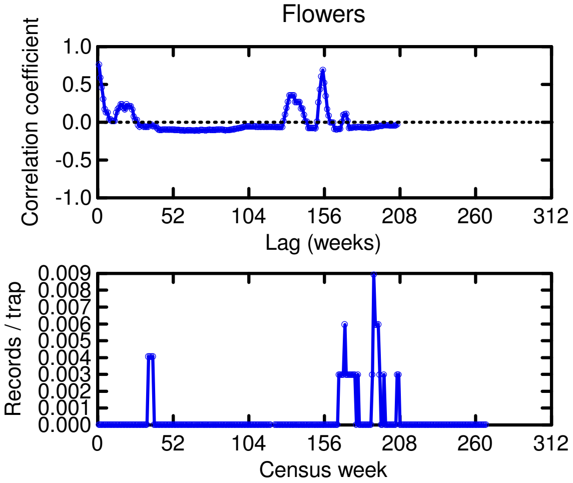

PARKSP
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week

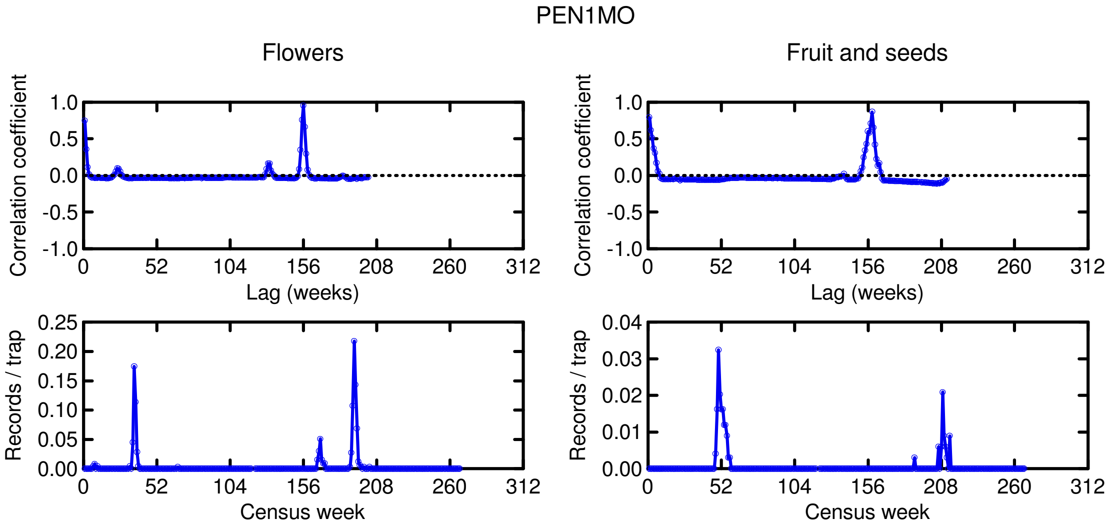

PAROVA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

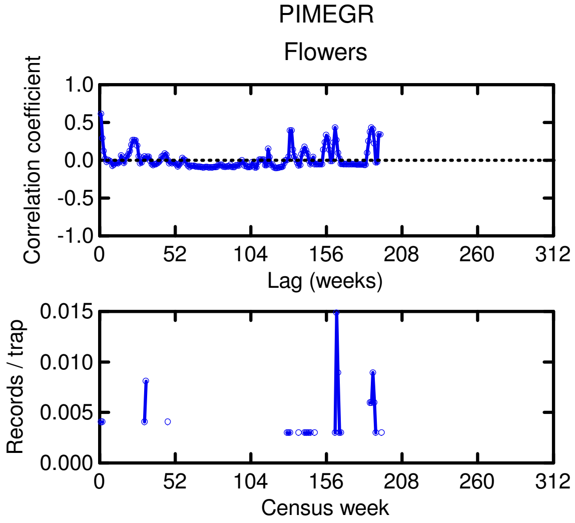
PAYELU



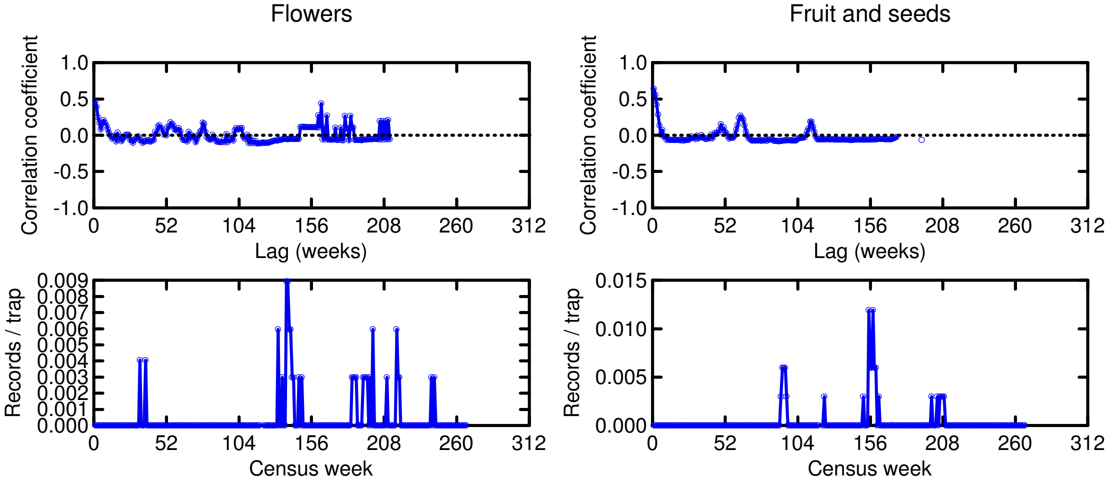
PAYEMA



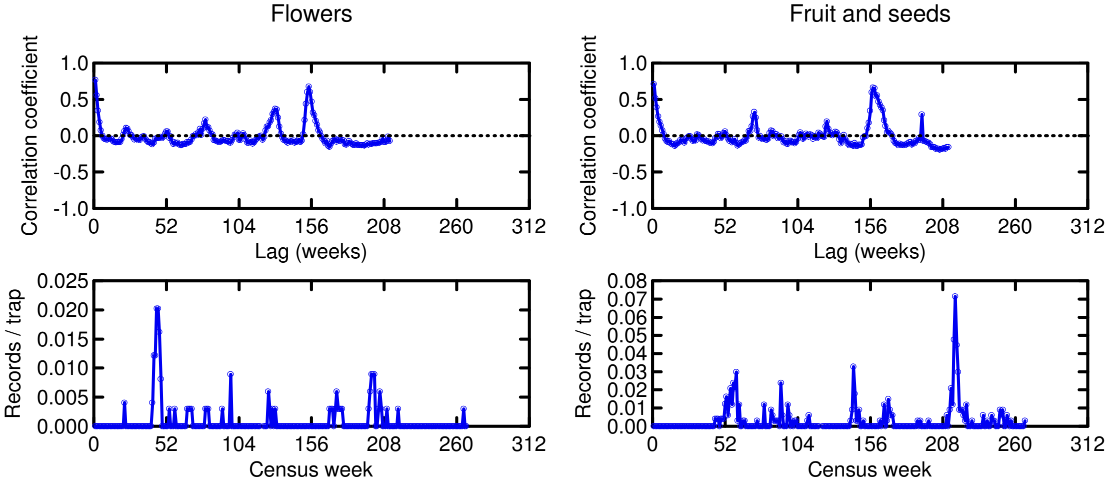

PEN1MO
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.25
0.20
0.15
0.10
0.05
0.00
0.04
0.03
0.02
0.01
0.00
Census week

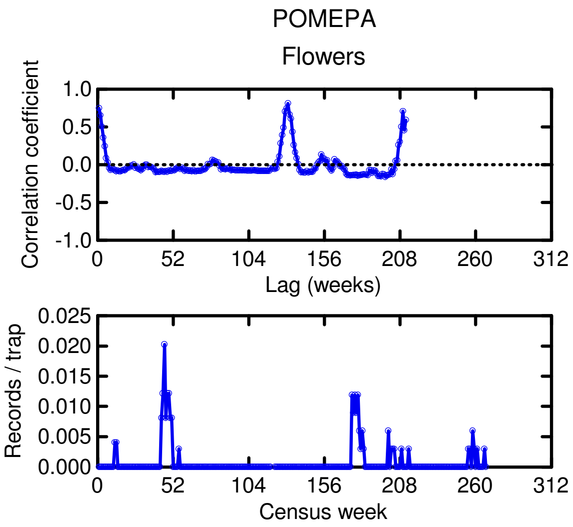

PIMEGR
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
Census week

POL1GL



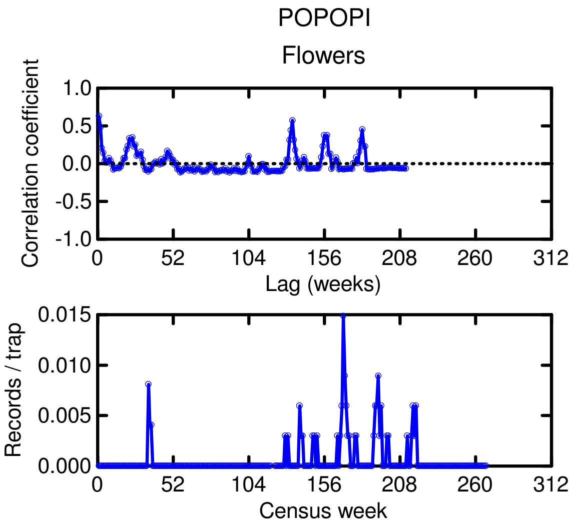
POL1RU





POMEPA

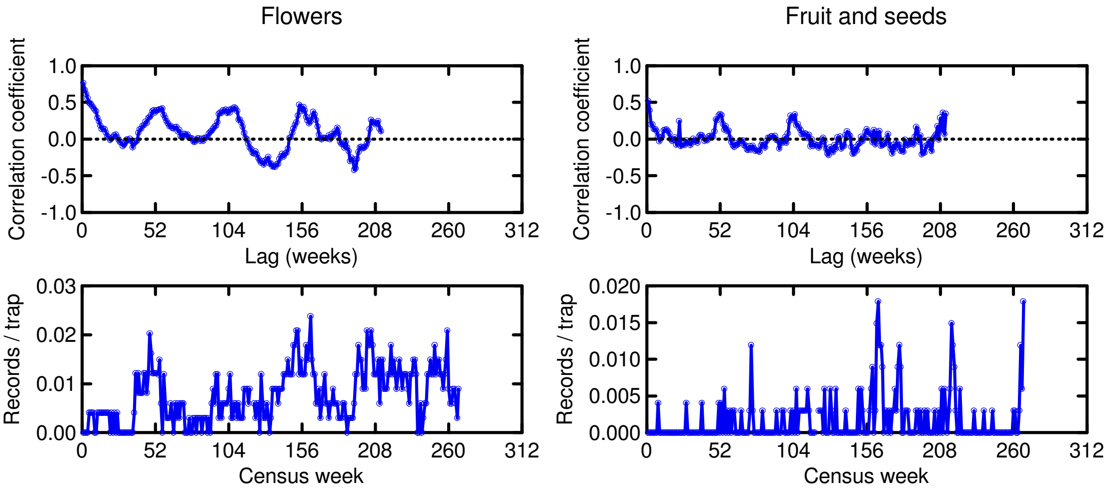
Flowers



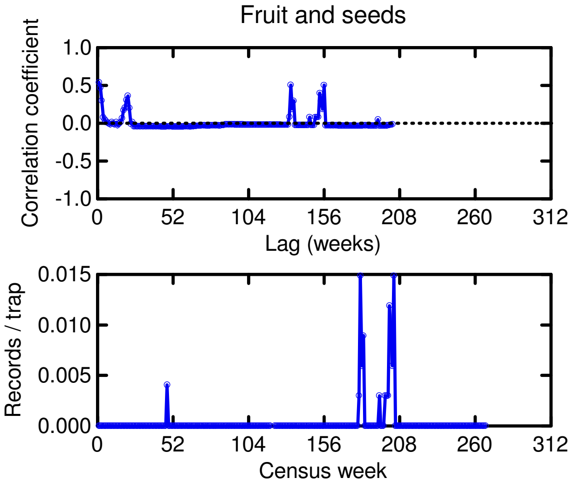
POPOPI

Flowers

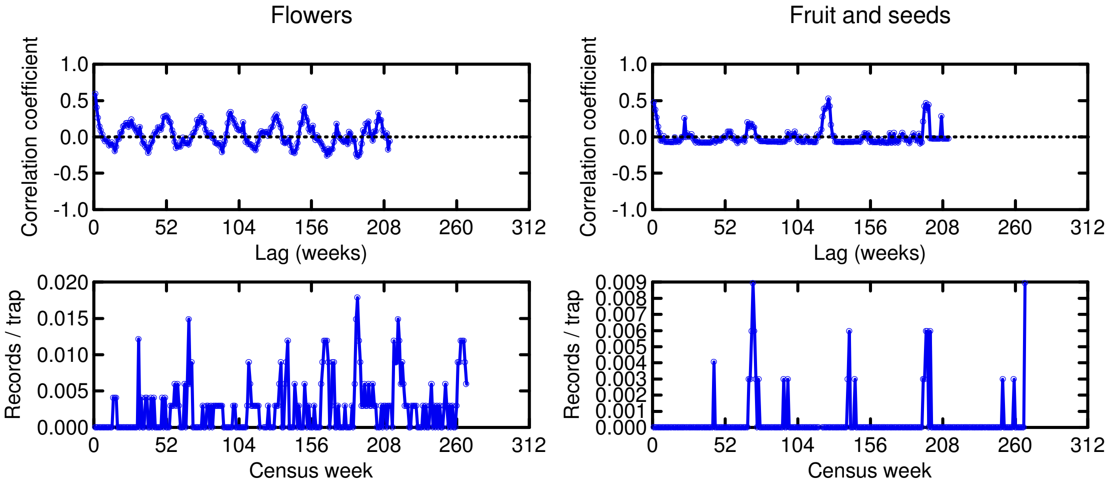
PORTAN



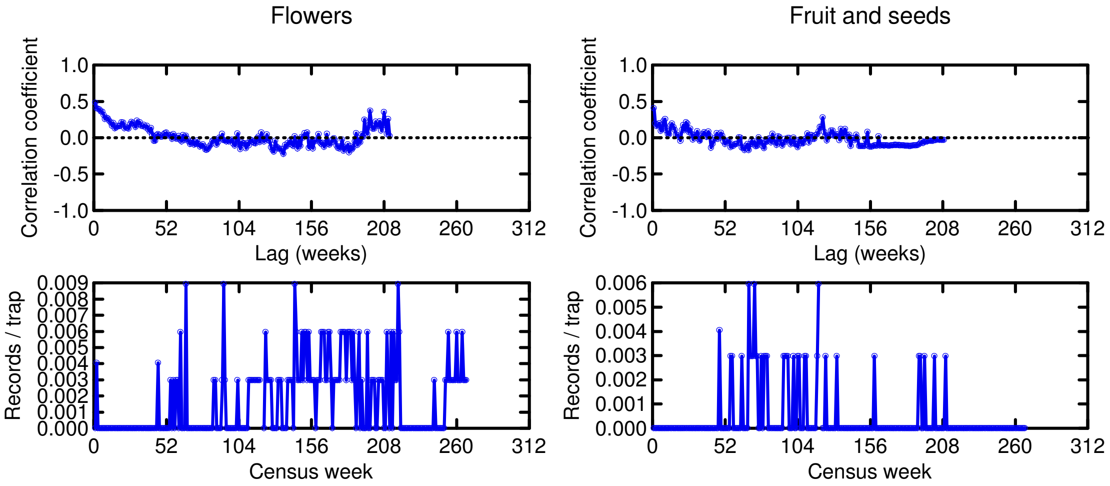
PSYDS8



PTE1CO

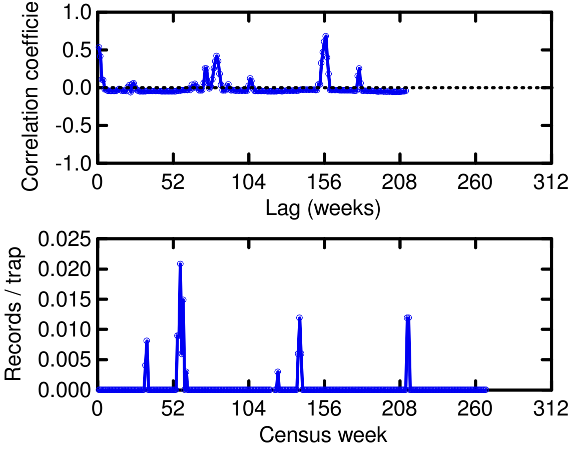


PTE1EC



PTE2TU

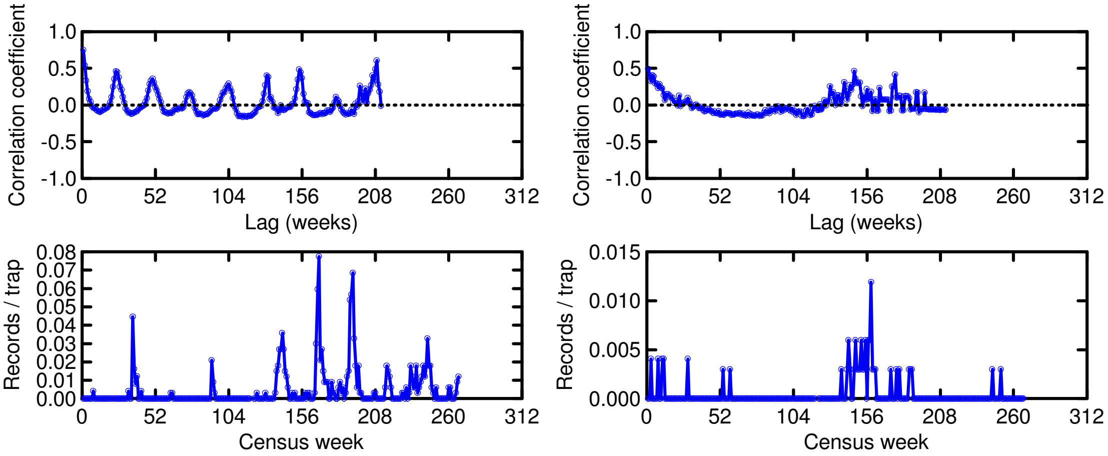
Fruit and seeds



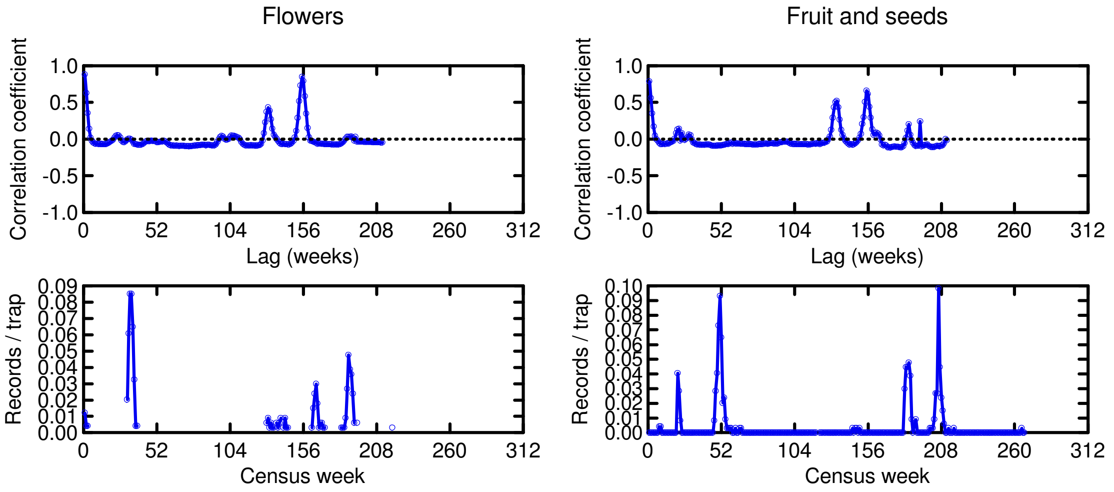
QUERAR

Flowers

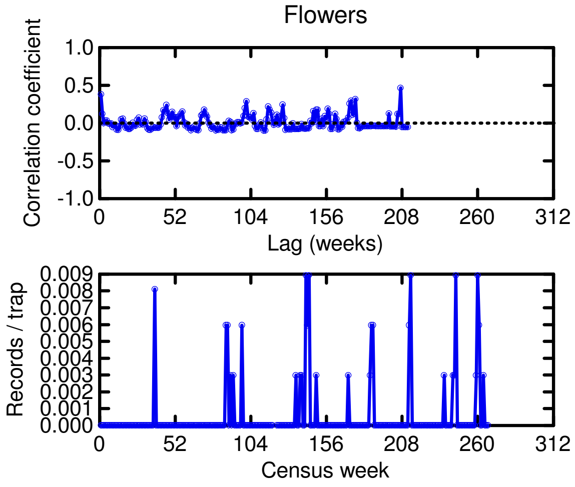
Fruit and seeds

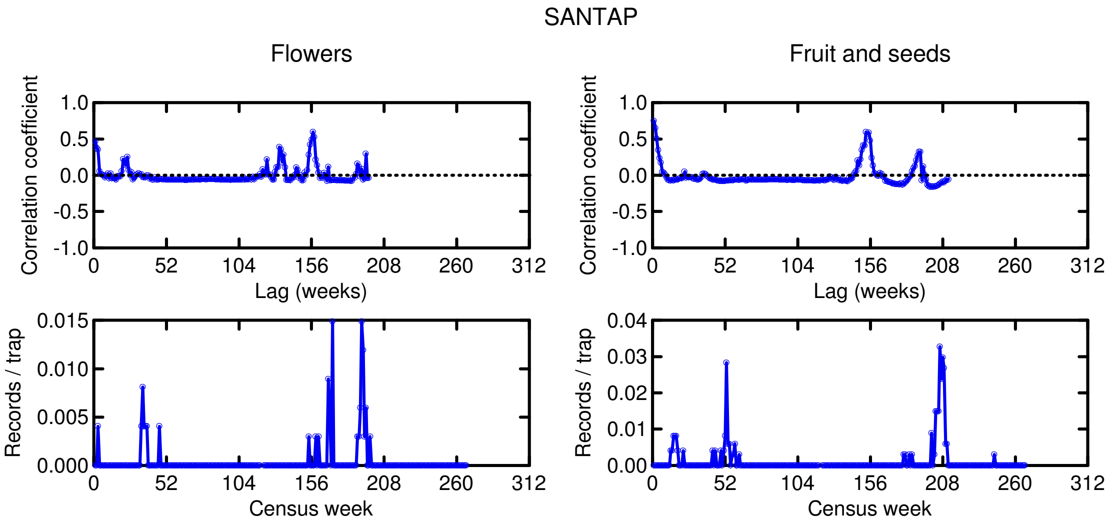


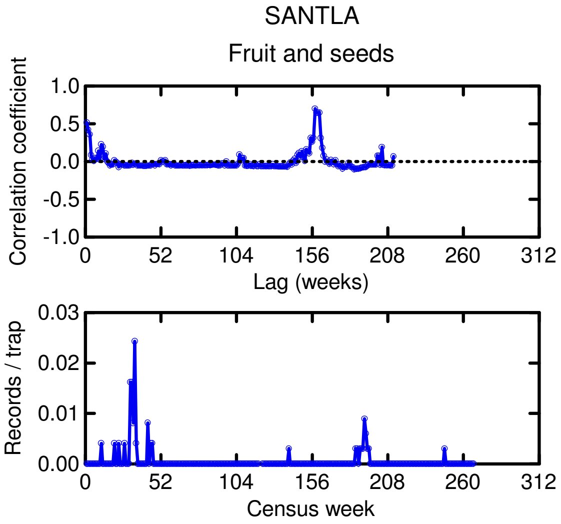
RINOAN

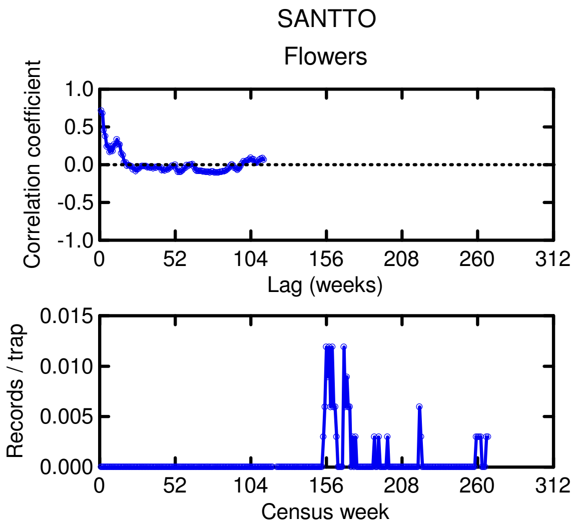


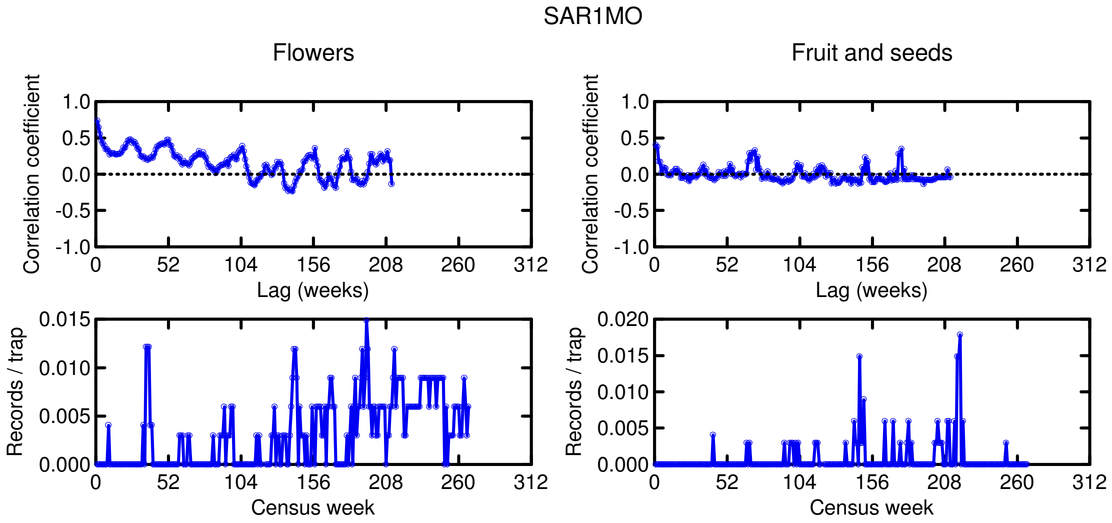
RYPAKU

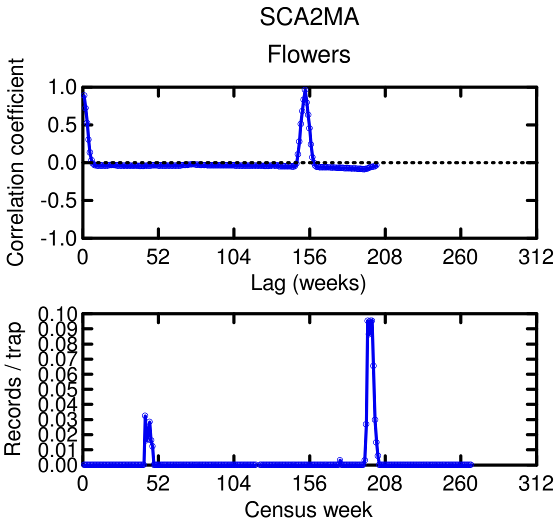



SANTAP
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0.04
0.03
0.02
0.01
0.00
Census week

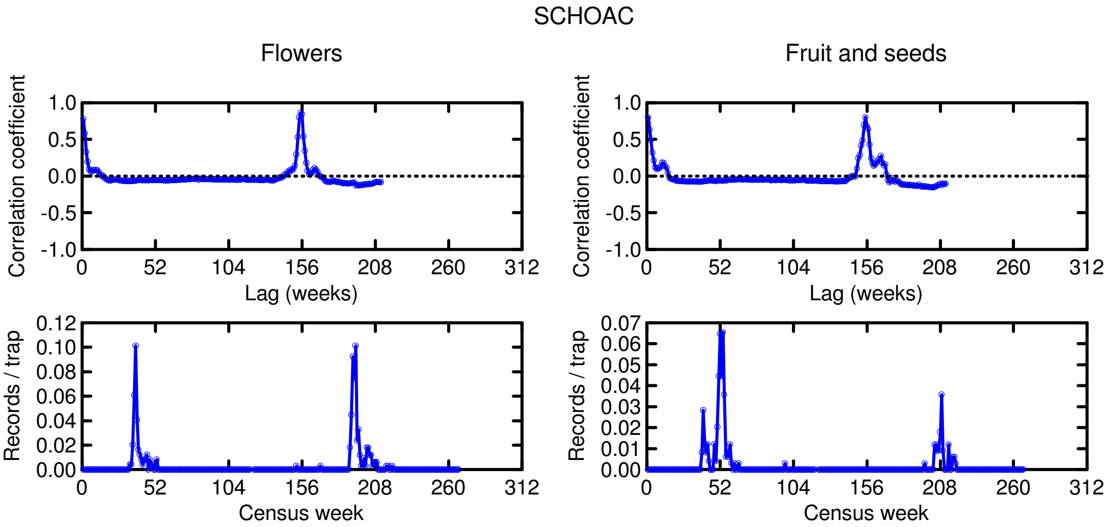

SANTLA
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
Census week


SANTTO
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0
52
104
156
208
260
312
Census week


SAR1MO
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.015
0.010
0.005
0.000
0.020
0
52
104
156
208
260
312
Census week

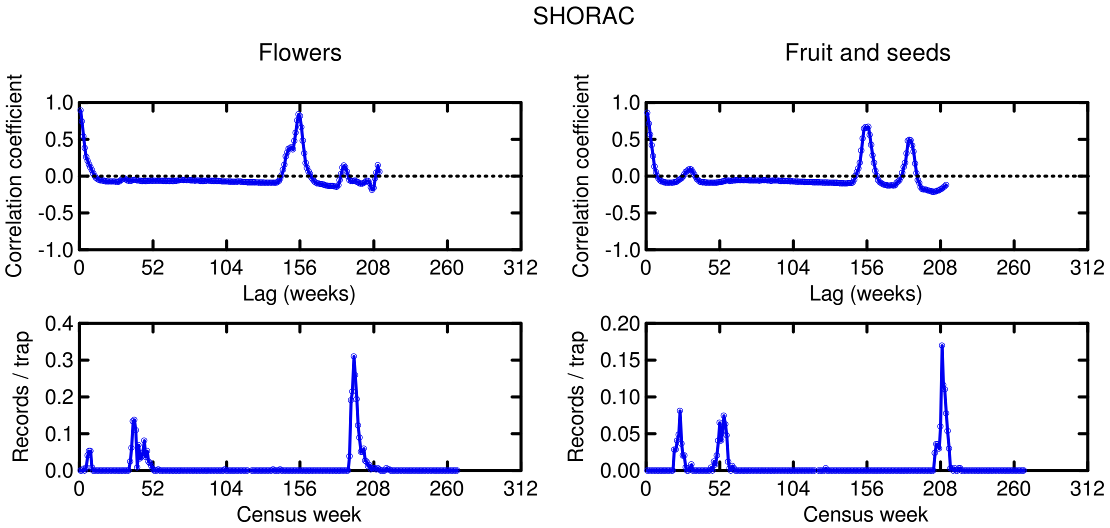

SCA2MA

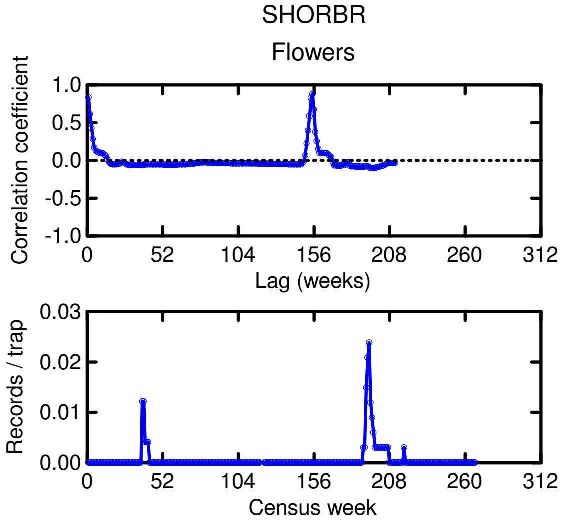
Flowers


SCHOAC

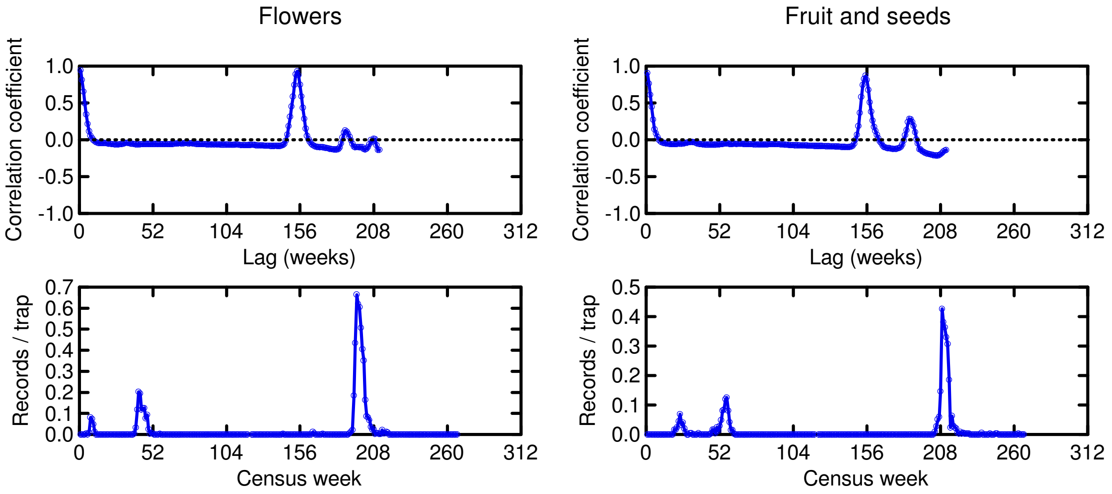
Flowers

Fruit and seeds

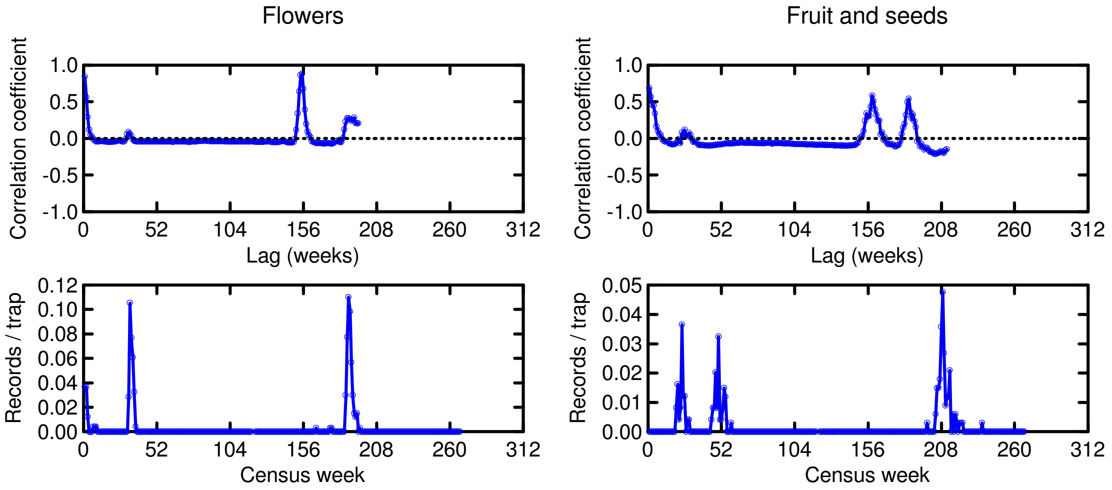

SHORAC
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.4
0.3
0.2
0.1
0.0
0.20
0.15
0.10
0.05
0.00
Census week

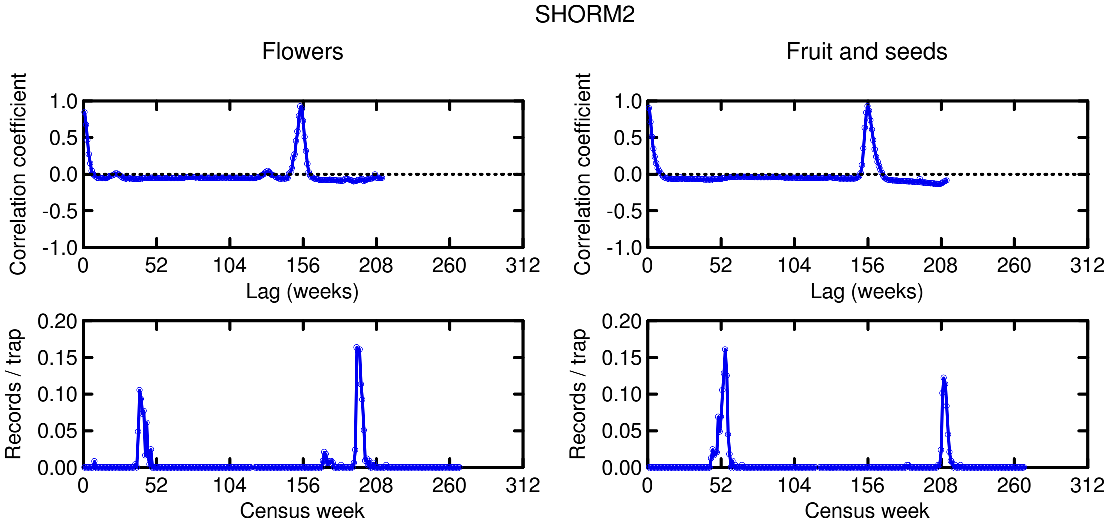

SHORBR
Flowers
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
Census week

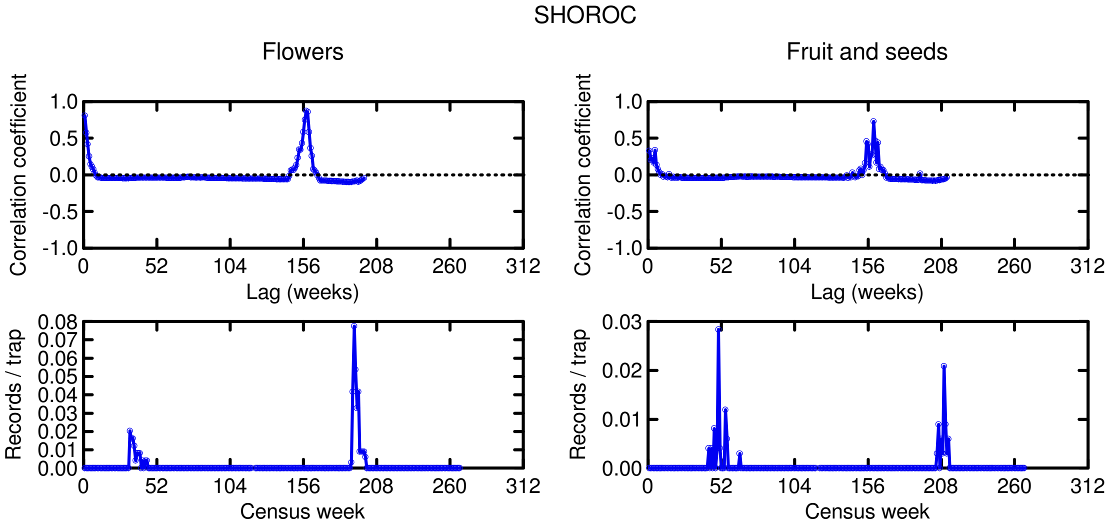
SHORL1

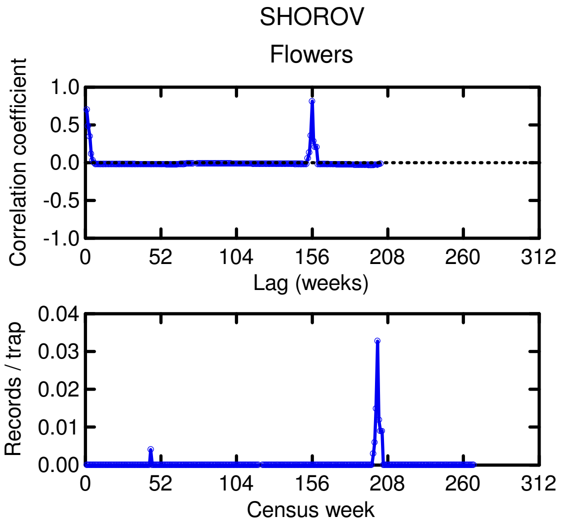


SHORM1

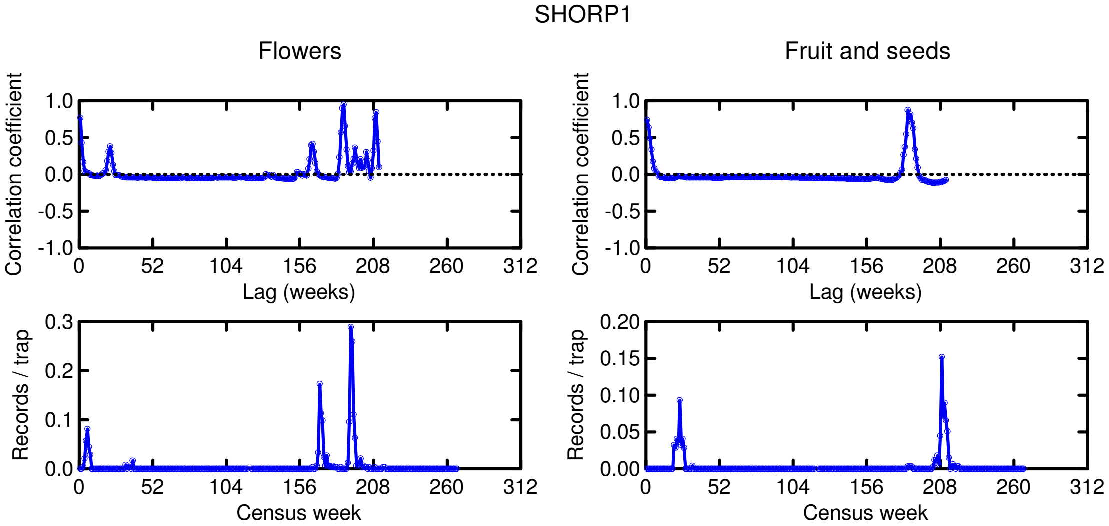



SHORM2
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.20
0.15
0.10
0.05
0.00
Census week


SHOROC
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week


SHOROV

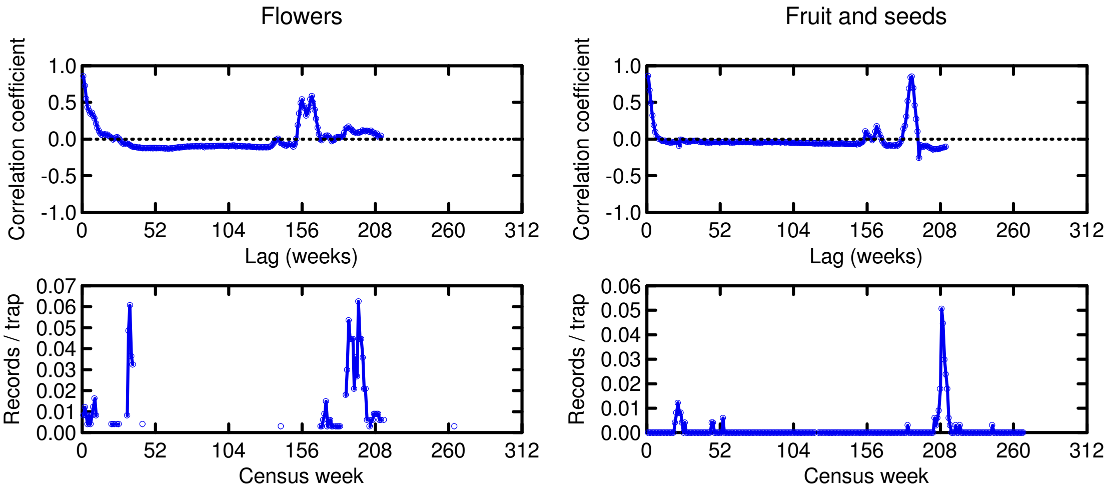
Flowers


SHORP1

Flowers

Fruit and seeds

SHORP2



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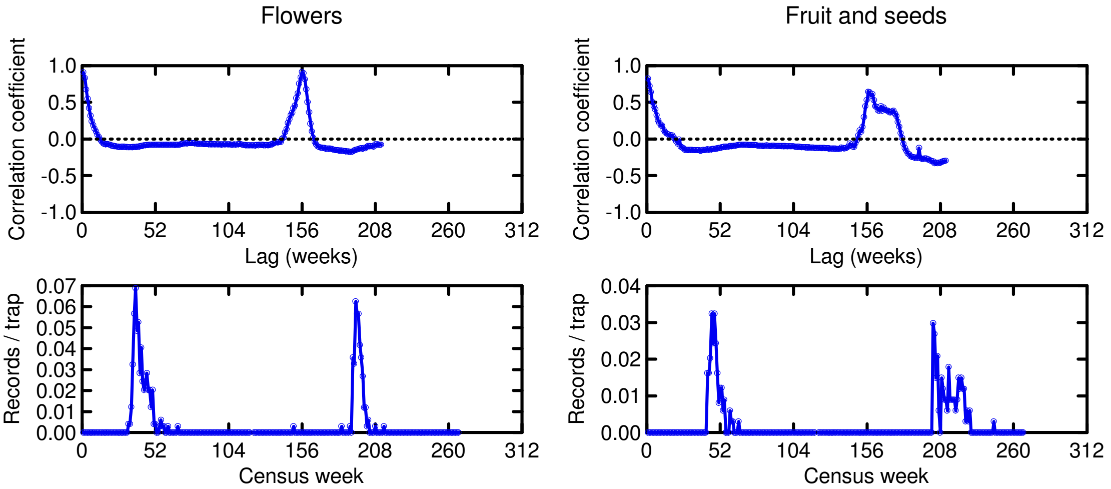
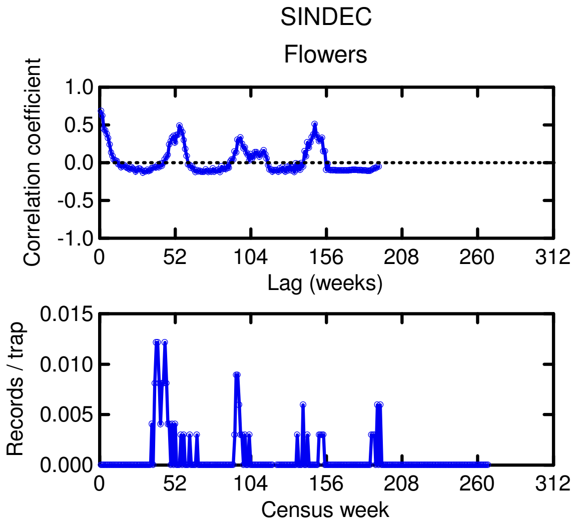
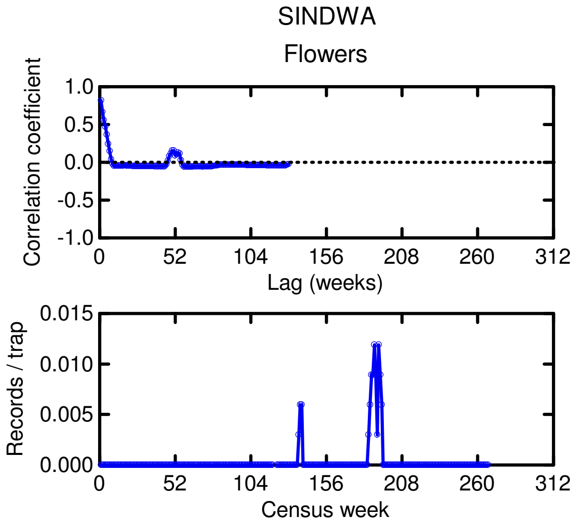
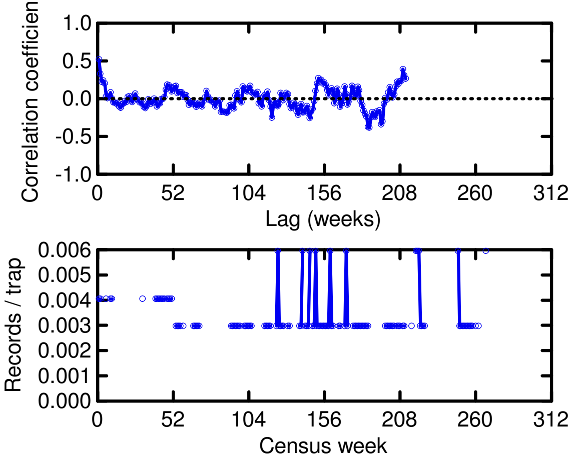



SINDEC
Flowers


SINDWA
Flowers

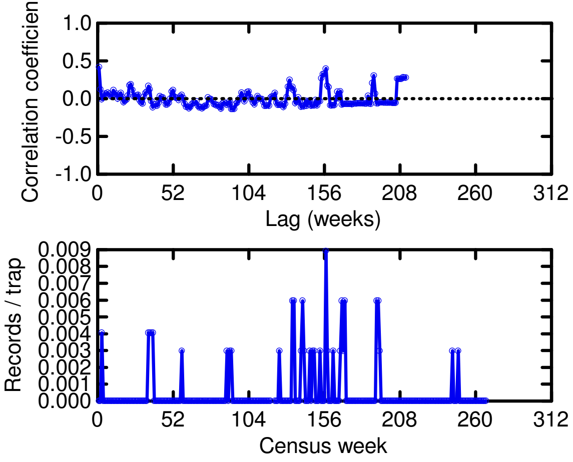
STERPA

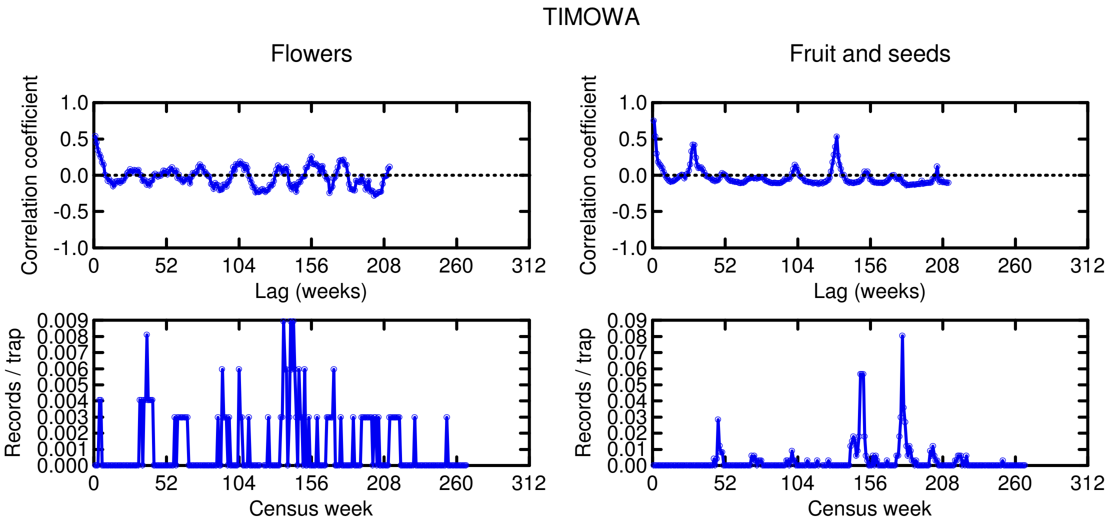
Flowers

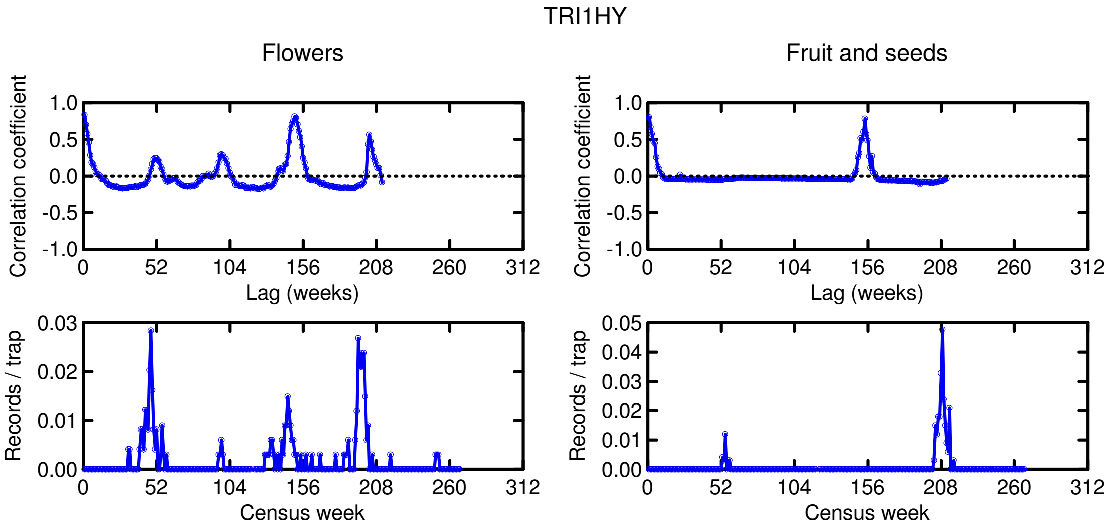


STYRBE

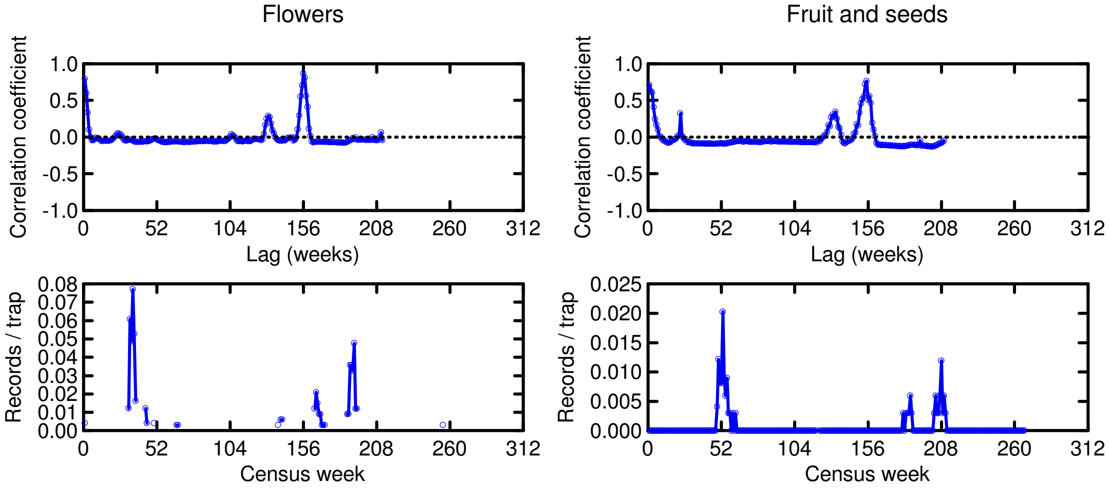
Flowers



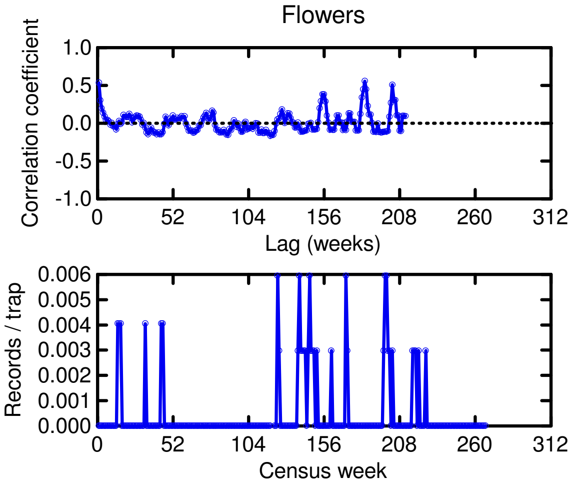

TIMOWA
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

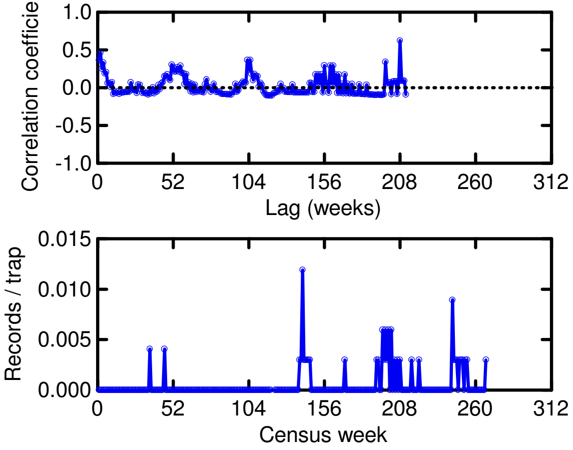

TRI1HY
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.03
0.02
0.01
0.00
0.05
0.04
0.03
0.02
0.01
0.00
Census week

TRIOMA



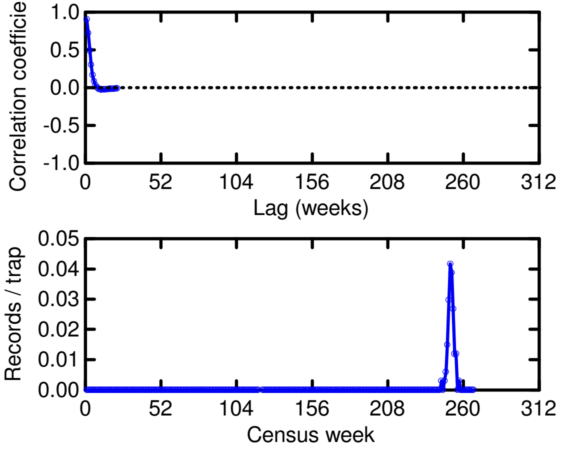
UNK060





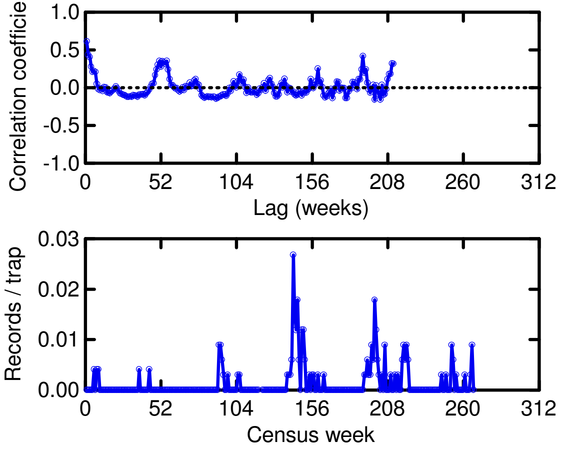
UNK200

Flowers

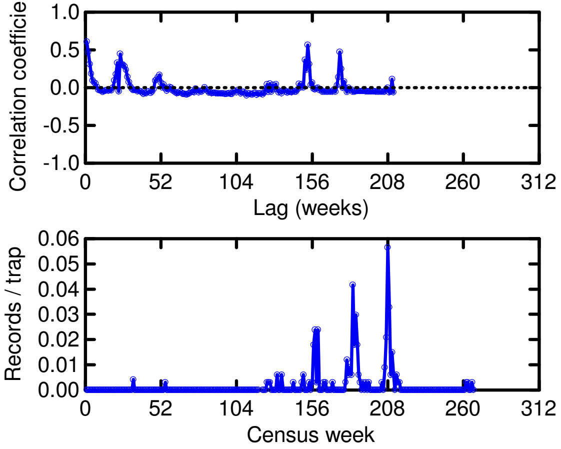


UNK1521

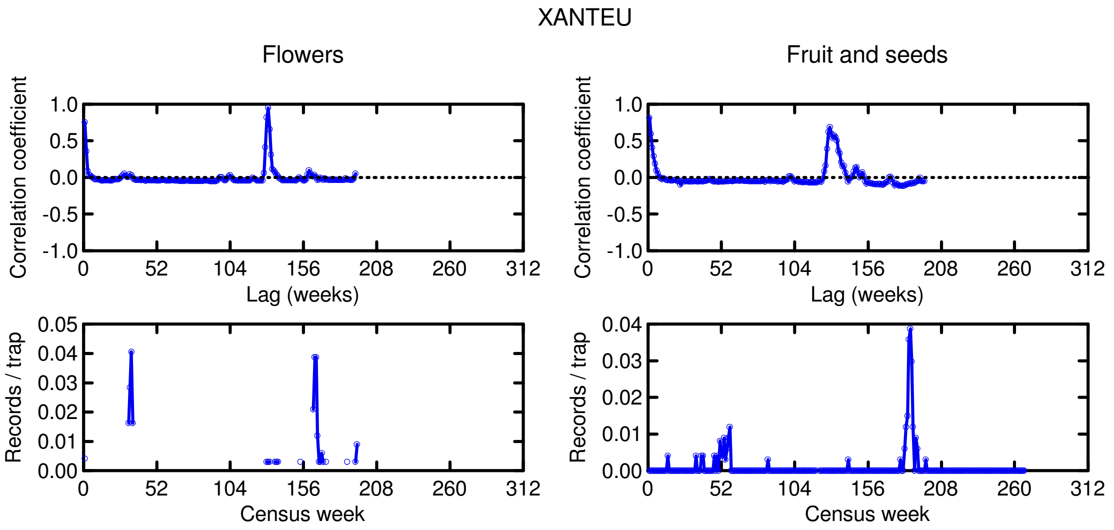
Flowers

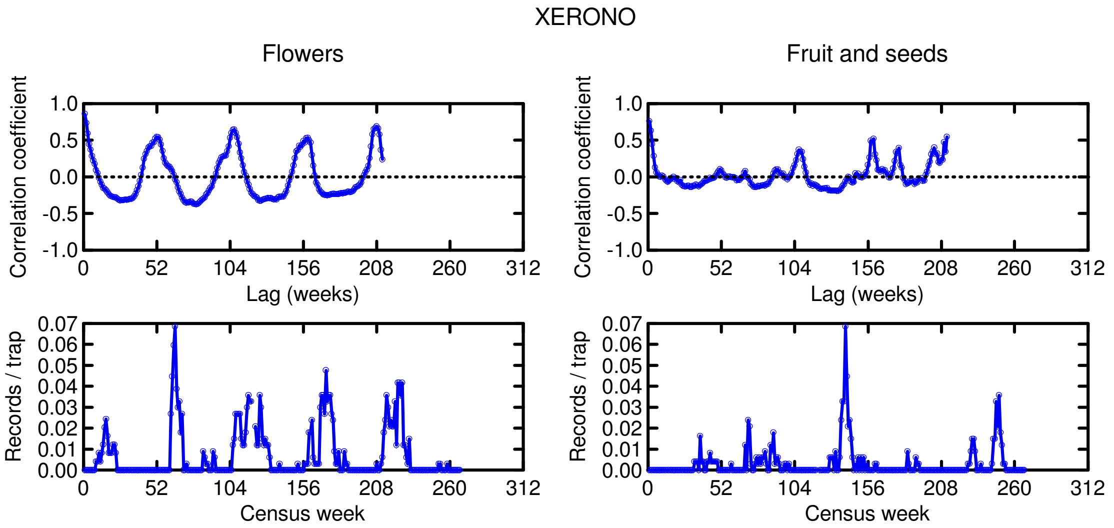

VATIBE

Flowers

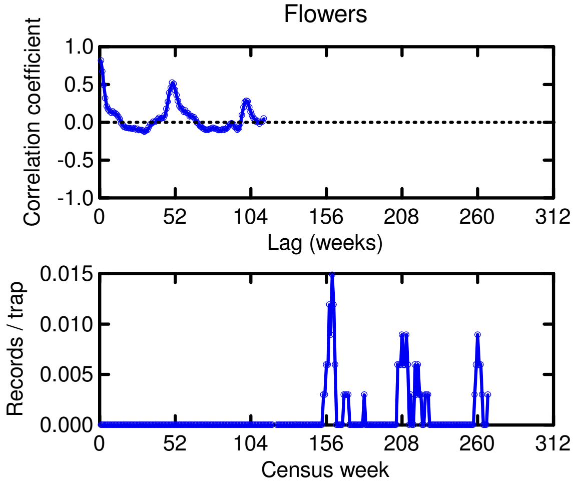

VERNAR

Fruit and seeds

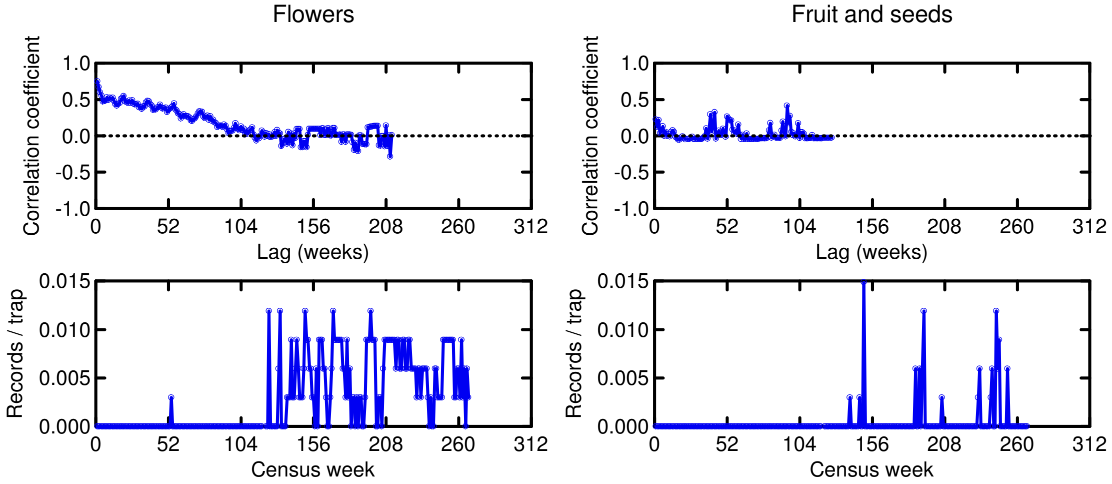

XANTEU
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.05
0.04
0.03
0.02
0.01
0.00
Census week


XERONO
Flowers
Fruit and seeds
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
52
104
156
208
260
312
Lag (weeks)
Records / trap
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Census week

XYLOCA



XYLOFE



Appendix B Assignment of phenological patterns and ecological functional traits. We have excluded 21 species from appendix A and included 162 species over which we were confident in the accuracy of species identification. Periodicity assignments were based on ACF plots while assignments on GF feature were based on D metric tests. In periodicity assignments, we assigned species into continuous, biannual, annual, or supra annual (“supra” in the table) species. In GF feature assignments, species that showed significant synchrony with species in the genus Shorea section mutica were assigned as GF species while species lack of synchrony with the mutica species were the nonGF species. Dispersal modes and reward types were assigned based on fruit types and our knowledge from literatures and from the field. Dispersal modes includes animal, wind, and ballistic dispersal. Reward types includes endozoochorous (e.g. berries and drupes), dyszoochorous (e.g. nuts and legumes), and nonzoochorous (e.g. samaras and achenes). Growth forms included three layers of tree canopy: emergent (T), canopy (M), sub-canopy (U), and liana (L) layer. Tree canopy categorization was suggested by the Forest Research Institute Malaysia. In all fields, NA indicated that a particular type of information was not available for the species.

Species code	Family	Species	periodicity of flowers	periodicity of fruits	GF of flowers	GF of fruits	Flower records	Fruit records	Dispersal mode	Reward type	Growth form
ADENBI	LEGUMINOSAE	*Adenanthera bicolor*	biannual	biannual	GF	GF	234	190	animal	dyszoochorous	M
AGLARB	MELIACEAE	*Aglaia rubescens*	excluded	annual	excluded	nonGF	<30	34	animal	endozoochorous	T
AIDIWA	RUBIACEAE	*Aidia wallichiana*	annual	annual	nonGF	GF	270	147	animal	endozoochorous	U
ALANEB	ALANGIACEAE	*Alangium ebenaceum*	supra	supra	GF	nonGF	210	74	animal	endozoochorous	M
ALPHMA	ANNONACEAE	*Alphonsea maingayi*	supra	excluded	GF	excluded	64	<30	animal	endozoochorous	M
ANAXJA	ANNONACEAE	*Anaxagorea javanica*	inconclusive	supra	nonGF	GF	40	55	blastic	nonzoochorous	U
ANI1LA	DIPTEROCARPACEAE	*Anisoptera laevis*	inconclusive	excluded	nonGF	excluded	33	<30	wind	dyszoochorous	T
ANT1CU	EUPHORBIACEAE	*Antidesma cuspidatum*	excluded	biannual	excluded	GF	<30	84	animal	endozoochorous	U
APORM1	EUPHORBIACEAE	*Aporusa microstachya*	supra	supra	GF	GF	40	113	animal	endozoochorous	U
APORN2	EUPHORBIACEAE	*Aporusa nigropunctata*	supra	excluded	excluded	GF	<30	63	animal	endozoochorous	U
APORNE	EUPHORBIACEAE	*Aporusa nervosa*	excluded	supra	excluded	nonGF	<30	50	animal	endozoochorous	M
APORPR	EUPHORBIACEAE	*Aporusa prainiana*	excluded	supra	excluded	GF	<30	93	animal	endozoochorous	U
ARCHBU	LEGUMINOSAE	*Archidendron bubalinum*	annual	supra	nonGF	GF	102	138	animal	dyszoochorous	U
ARDICR	MYRSINACEAE	*Ardisia crassa*	biannual	supra	GF	GF	94	122	animal	endozoochorous	U
BARRMA	LECYTHIDACEAE	*Barringtonia macrostachya*	annual	excluded	nonGF	excluded	40	<30	animal	endozoochorous	U
BUCHSE	ANACARDIACEAE	*Buchanania sessifolia*	annual	annual	GF	nonGF	70	61	animal	endozoochorous	U
CALLMA	VERBENACEAE	*Callicarpa maingayi*	biannual	biannual	GF	GF	65	74	animal	endozoochorous	U
CANAAP	BURSERACEAE	*Canarium apertum*	annual	excluded	GF	excluded	49	<30	animal	endozoochorous	T
CANALR	BURSERACEAE	*Canarium littorale_var._rufum*	continuous	excluded	GF	excluded	135	<30	animal	endozoochorous	M
CARABR	RHIZOPHORACEAE	*Carallia brachiata*	excluded	biannual	excluded	GF	<30	87	animal	endozoochorous	M
CASTSC	FAGACEAE	*Castanopsis schefferiana*	inconclusive	excluded	nonGF	excluded	45	<30	animal	dyszoochorous	M
CLM001	NA	*NA*	supra	excluded	GF	excluded	302	<30	wind	nonzoochorous	L
CLM002	NA	*NA*	supra	supra	GF	GF	1005	260	wind	nonzoochorous	L
CLM006	ANNONACEAE	*NA*	inconclusive	excluded	nonGF	excluded	82	<30	animal	endozoochorous	L

CLM007	RHAMNACEAE	*NA*	supra	supra	nonGF	GF	106	210	wind	dyszoochorous	L
CLM009	NA	*NA*	supra	supra	GF	GF	45	120	NA	NA	L
CLM011	NA	*NA*	continuous	annual	nonGF	nonGF	73	239	wind	nonzoochorous	L
CLM015	STERCULIACEAE	*Byttneria maingayi*	supra	supra	GF	GF	488	241	gravity	dyszoochorous	L
CLM016	NA	*NA*	supra	excluded	GF	excluded	228	<30	NA	NA	L
CLM018	NA	*NA*	supra	excluded	GF	excluded	318	<30	NA	NA	L
CLM022	NA	*NA*	supra	supra	GF	GF	70	33	NA	NA	L
CLM024	CONNARACEAE	*Connarus paniculatus*	excluded	annual	excluded	GF	<30	33	animal	endozoochorous	L
CLM025	LEGUMINOSAE	*Caesalpinia parvifolia*	supra	supra	GF	GF	883	911	animal	dyszoochorous	L
CLM026	LEGUMINOSAE	*Bauhinia bidentata*	supra	supra	GF	GF	1053	151	animal	dyszoochorous	L
CLM027	LEGUMINOSAE	*Derris ferrugineus*	supra	supra	GF	GF	114	92	animal	dyszoochorous	L
CLM030	LEGUMINOSAE	*NA*	supra	supra	GF	GF	88	166	animal	dyszoochorous	L
CLM033	LEGUMINOSAE	*NA*	annual	excluded	GF	excluded	299	<30	animal	dyszoochorous	L
CLM034	APOCYNACEAE	*NA*	excluded	annual	excluded	GF	<30	349	wind	nonzoochorous	L
CLM040	ANNONACEAE	*NA*	annual	annual	nonGF	nonGF	640	397	animal	endozoochorous	L
CLM041	COMBRETACEAE	*NA*	supra	supra	GF	nonGF	181	70	wind	nonzoochorous	L
CLM042	EUPHORBIACEAE	*NA*	annual	annual	GF	GF	71	102	blastic	dyszoochorous	L
CLM044	NA	*NA*	supra	supra	GF	nonGF	95	63	NA	NA	L
CLM049	NA	*NA*	supra	excluded	GF	excluded	38	<30	NA	NA	L
CLM054	NA	*NA*	annual	excluded	nonGF	excluded	154	<30	NA	NA	L
CLM057	NA	*NA*	inconclusive	excluded	nonGF	excluded	35	<30	NA	NA	L
CLM058	NA	*NA*	annual	excluded	GF	nonGF	225	505	NA	NA	L
CLM059	COMBRETACEAE	*NA*	supra	excluded	excluded	GF	<30	121	wind	nonzoochorous	L
CLM060	APOCYNACEAE	*NA*	inconclusive	excluded	nonGF	excluded	76	<30	NA	NA	L
CLM067	NA	*NA*	annual	excluded	nonGF	excluded	69	<30	NA	NA	L
CLM069	NA	*NA*	supra	supra	GF	nonGF	46	31	NA	NA	L

CLM070	ANNONACEAE	*NA*	biannual	continuous	GF	GF	258	94	animal	endozoochorous	L
CLM074	NA	*NA*	supra	excluded	GF	excluded	46	<30	NA	NA	L
CLM079	NA	*NA*	annual	excluded	GF	excluded	140	<30	NA	NA	L
CLM104	NA	*NA*	excluded	supra	excluded	nonGF	<30	39	NA	NA	L
CLM110	NA	*NA*	supra	supra	GF	nonGF	119	97	NA	NA	L
CLM113	NA	*NA*	biannual	excluded	nonGF	excluded	81	<30	NA	NA	L
CRATMA	HYPERICACEAE	*Cratoxylum maingayi*	annual	annual	GF	nonGF	32	373	wind	nonzoochorous	M
CROTAR	EUPHORBIACEAE	*Croton argyratus*	annual	annual	GF	GF	121	206	blastic	dyszoochorous	U
CROTLA	EUPHORBIACEAE	*Croton laevifolius*	supra	excluded	GF	nonGF	70	89	blastic	dyszoochorous	U
DACRLA	BURSERACEAE	*Dacryodes laxa*	supra	excluded	GF	excluded	31	<30	animal	endozoochorous	T
DACRR1	BURSERACEAE	*Dacryodes rugosa*	supra	supra	GF	GF	44	189	animal	endozoochorous	M
DIALPL	LEGUMINOSAE	*Dialium platysepalum*	supra	supra	GF	GF	173	50	animal	dyszoochorous	T
DIOSAP	EBENACEAE	*Diospyros apiculata*	biannual	excluded	GF	excluded	85	<30	animal	endozoochorous	U
DIOSMA	EBENACEAE	*Diospyros maingayi*	excluded	supra	excluded	nonGF	<30	41	animal	endozoochorous	T
DIPLMA	RUBIACEAE	*Diplospora malaccensis*	annual	excluded	GF	excluded	51	<30	animal	endozoochorous	U
DIPTC1	DIPTEROCARPACEAE	*Dipterocarpus cornutus*	supra	supra	GF	GF	225	86	wind	dyszoochorous	T
DIPTC2	DIPTEROCARPACEAE	*Dipterocarpus costulatus*	supra	excluded	GF	excluded	220	<30	wind	dyszoochorous	T
DIPTCR	DIPTEROCARPACEAE	*Dipterocarpus crinitus*	supra	supra	GF	GF	151	42	wind	dyszoochorous	T
DRYPLO	EUPHORBIACEAE	*Drypetes longifolia*	excluded	supra	excluded	GF	<30	35	animal	endozoochorous	M
DURIGR	BOMBACACEAE	*Durio griffithii*	biannual	supra	GF	GF	313	52	animal	endozoochorous	M
DYERCO	APOCYNACEAE	*Dyera costulata*	continuous	continuous	nonGF	nonGF	514	54	wind	nonzoochorous	T
ELAEP3	ELAEOCARPACEAE	*Elaeocarpus palembanicus*	excluded	supra	excluded	nonGF	<30	52	animal	endozoochorous	T
ELATTA	EUPHORBIACEAE	*Elateriospermum tapos*	annual	excluded	GF	excluded	59	<30	animal	endozoochorous	M
EPIPMA	EUPHORBIACEAE	*Epiprinus malayanus*	supra	excluded	GF	excluded	53	<30	blastic	nonzoochorous	U
EUGENI	MYRTACEAE	*Eugenia nigricans*	excluded	annual	excluded	GF	<30	51	animal	endozoochorous	M
EURYLO	SIMAROUBACEAE	*Eurycoma longifolia*	excluded	supra	excluded	GF	<30	32	animal	endozoochorous	S

GARCBA	CLUSIACEAE	*Garcinia bancana*	inconclusive	excluded	nonGF	excluded	33	<30	animal	endozoochorous	M
GARCMA	CLUSIACEAE	*Garcinia malaccensis*	supra	excluded	GF	excluded	46	<30	animal	endozoochorous	M
GIRONE	ULMACEAE	*Gironniera nervosa*	excluded	supra	excluded	nonGF	<30	112	animal	endozoochorous	M
GIROPA	ULMACEAE	*Gironniera parvifolia*	biannual	continuous	GF	GF	191	565	animal	endozoochorous	U
GOM1SE	OCHNACEAE	*Gomphia serrata*	annual	inconclusive	GF	GF	102	69	animal	endozoochorous	U
GREWMI	TILIACEAE	*Grewia miqueliana*	annual	supra	nonGF	nonGF	55	32	animal	endozoochorous	S
GYNOAX	RHIZOPHORACEAE	*Gynotroches axillaris*	biannual	biannual	GF	nonGF	210	124	animal	endozoochorous	U
HOPEDR	DIPTEROCARPACEAE	*Hopea dryobalanoides*	supra	supra	GF	nonGF	73	97	wind	dyszoochorous	T
HOPEME	DIPTEROCARPACEAE	*Hopea mengerawan*	annual	annual	nonGF	nonGF	49	96	wind	dyszoochorous	T
INTSPA	LEGUMINOSAE	*Intsia palembanica*	supra	supra	GF	GF	78	39	animal	dyszoochorous	T
IXONIC	IXONANTHACEAE	*Ixonanthes icosandra*	biannual	biannual	nonGF	GF	2121	2198	wind	nonzoochorous	M
KNEMCO	MYRISTICACEAE	*Knema conferta*	continuous	excluded	nonGF	excluded	147	<30	animal	endozoochorous	M
KNEMPA	MYRISTICACEAE	*Knema patentinervia*	annual	excluded	nonGF	excluded	48	<30	animal	endozoochorous	M
KOOMMA	LEGUMINOSAE	*Koompassia malaccensis*	supra	supra	GF	GF	266	407	animal	dyszoochorous	T
LICASP	CHRYSOBALANACEAE	*Licania splendens*	annual	annual	GF	GF	83	152	animal	endozoochorous	U
LITHCU	FAGACEAE	*Lithocarpus curtisii*	annual	excluded	nonGF	excluded	190	<30	animal	dyszoochorous	M
LITHRA	FAGACEAE	*Lithocarpus rassa*	annual	annual	nonGF	GF	113	40	animal	dyszoochorous	U
LITHWA	FAGACEAE	*Lithocarpus wallichianus*	annual	excluded	nonGF	excluded	37	<30	animal	dyszoochorous	T
LITHWR	FAGACEAE	*Lithocarpus wrayi*	inconclusive	supra	GF	GF	36	51	animal	dyszoochorous	M
LITSCA	LAURACEAE	*Litsea castanea*	supra	excluded	nonGF	excluded	43	<30	animal	endozoochorous	T
MACALO	EUPHORBIACEAE	*Macaranga lowii*	supra	supra	GF	nonGF	99	303	blastic	nonzoochorous	U
MACARE	EUPHORBIACEAE	*Macaranga recurvata*	excluded	inconclusive	excluded	nonGF	<30	33	blastic	nonzoochorous	M
MALLLE	EUPHORBIACEAE	*Mallotus leocodermis*	excluded	supra	excluded	nonGF	<30	139	blastic	nonzoochorous	M
MALLPE	EUPHORBIACEAE	*Mallotus penangensis*	excluded	supra	excluded	GF	<30	125	blastic	nonzoochorous	U
MESUFE	CLUSIACEAE	*Mesua ferrea*	supra	supra	GF	GF	118	77	blastic	nonzoochorous	M
MIC1CA	PANDACEAE	*Microdesmis casearifolia*	inconclusive	excluded	nonGF	excluded	52	<30	NA	NA	S

MILLAT	LEGUMINOSAE	*Millettia atropurpurea*	supra	supra	GF	GF	145	48	animal	dyszoochorous	M
MONOMA	ANNONACEAE	*Monocarpia marginalis*	biannual	biannual	GF	nonGF	713	93	animal	endozoochorous	M
MYRICI	MYRISTICACEAE	*Myristica cinnamomea*	inconclusive	excluded	GF	excluded	48	<30	animal	endozoochorous	M
NEOBHE	DIPTEROCARPACEAE	*Neobalanocarpus heimii*	supra	supra	GF	nonGF	282	536	gravity	dyszoochorous	T
NEOSKI	EUPHORBIACEAE	*Neoscortechinia kingii*	supra	supra	GF	GF	48	188	animal	endozoochorous	M
NEOSNI	EUPHORBIACEAE	*Neoscortechinia nicobarica*	excluded	supra	excluded	nonGF	<30	58	animal	endozoochorous	M
NEPHCO	SAPINDACEAE	*Nephelium costatum*	supra	supra	GF	nonGF	59	30	animal	endozoochorous	M
OCHAAM	OLACACEAE	*Ochanostachys amentacea*	supra	supra	GF	nonGF	48	45	animal	endozoochorous	M
ORANSY	ARECACEAE	*Orania sylvicola*	continuous	excluded	GF	excluded	108	<30	animal	endozoochorous	U
PALAGU	SAPOTACEAE	*Palaquium gutta*	supra	excluded	GF	excluded	30	<30	animal	endozoochorous	M
PALAHE	SAPOTACEAE	*Palaquium hexandrum*	supra	excluded	GF	excluded	148	<30	animal	endozoochorous	T
PALAMA	SAPOTACEAE	*Palaquium maingayi*	supra	supra	GF	GF	109	41	animal	endozoochorous	T
PARKSP	LEGUMINOSAE	*Parkia speciosa*	biannual	excluded	nonGF	excluded	93	<30	animal	dyszoochorous	T
PAROVA	FLACOURTIACEAE	*Paropsia vareciformis*	annual	supra	GF	GF	274	615	animal	endozoochorous	S
PAYELU	SAPOTACEAE	*Payena lucida*	annual	annual	GF	GF	319	181	animal	endozoochorous	M
PAYEMA	SAPOTACEAE	*Payena maingayi*	supra	excluded	GF	excluded	32	<30	animal	endozoochorous	M
PEN1MO	ANACARDIACEAE	*Pentaspadon motleyi*	supra	supra	GF	GF	338	60	gravity	nonzoochorous	T
PIMEGR	EUPHORBIACEAE	*Pimelodendron griffithianum*	supra	excluded	GF	excluded	38	<30	animal	endozoochorous	M
POL1GL	ANNONACEAE	*Polyalthia glauca*	annual	annual	nonGF	nonGF	37	33	animal	endozoochorous	M
POL1RU	ANNONACEAE	*Polyalthia rumphii*	biannual	annual	GF	GF	71	266	animal	endozoochorous	M
POMEPA	SAPINDACEAE	*Pometia pinnata_var._alnifolia*	supra	excluded	GF	excluded	63	<30	animal	endozoochorous	T
POPOPI	ANNONACEAE	*Popowia pisocarpa*	inconclusive	excluded	GF	excluded	51	<30	animal	endozoochorous	U
PORTAN	RUBIACEAE	*Porterandia anisophylla*	annual	annual	GF	nonGF	656	148	animal	endozoochorous	U
PTE1CO	MELASTOMATACEAE	*Pternandra coerulescens*	biannual	biannual	GF	GF	229	31	animal	endozoochorous	U
PTE1EC	MELASTOMATACEAE	*Pternandra echinata*	continuous	continuous	GF	nonGF	150	37	animal	endozoochorous	U
PTE2TU	STERCULIACEAE	*Pterocymbium tubulatum*	excluded	supra	excluded	GF	<30	41	wind	dyszoochorous	M

QUERAR	FAGACEAE	*Quercus argentata*	biannual	biannual	GF	nonGF	414	43	animal	dyszoochorous	T
RINOAN	VIOLACEAE	*Rinorea anguifera*	supra	supra	GF	GF	223	291	blastic	dyszoochorous	U
RYPAKU	FLACOURTIACEAE	*Ryparosa kunstleri*	annual	excluded	nonGF	excluded	46	<30	animal	endozoochorous	M
SANTAP	BURSERACEAE	*Santiria apiculata*	supra	supra	GF	GF	38	98	animal	endozoochorous	U
SANTLA	BURSERACEAE	*Santiria laevigata*	excluded	supra	excluded	nonGF	<30	39	animal	endozoochorous	T
SAR1MO	OXALIDACEAE	*Sarcotheca monophylla*	biannual	biannual	nonGF	nonGF	277	67	animal	endozoochorous	U
SCA2MA	STERCULIACEAE	*Scaphium macropodum*	supra	excluded	nonGF	excluded	206	<30	wind	dyszoochorous	T
SCHOAC	TILIACEAE	*Schoutenia accrescens*	supra	supra	GF	GF	252	159	wind	dyszoochorous	M
SHORAC	DIPTEROCARPACEAE	*Shorea acuminata*	supra	supra	GF	GF	836	469	wind	dyszoochorous	T
SHORBR	DIPTEROCARPACEAE	*Shorea bracteolata*	supra	excluded	GF	excluded	51	<30	wind	dyszoochorous	T
SHORL1	DIPTEROCARPACEAE	*Shorea leprosula*	supra	supra	GF	GF	1810	1137	wind	dyszoochorous	T
SHORL2	DIPTEROCARPACEAE	*Shorea lepidota*	supra	supra	GF	GF	332	174	wind	dyszoochorous	T
SHORM1	DIPTEROCARPACEAE	*Shorea macroptera*	supra	supra	GF	GF	253	143	wind	dyszoochorous	T
SHORM2	DIPTEROCARPACEAE	*Shorea maxwelliana*	supra	supra	GF	GF	432	442	wind	dyszoochorous	T
SHOROC	DIPTEROCARPACEAE	*Shorea ochrophloia*	supra	supra	GF	GF	124	40	wind	dyszoochorous	T
SHOROV	DIPTEROCARPACEAE	*Shorea ovalis*	supra	excluded	nonGF	excluded	30	<30	wind	dyszoochorous	T
SHORP1	DIPTEROCARPACEAE	*Shorea parvifolia*	supra	supra	GF	GF	542	274	wind	dyszoochorous	T
SHORP2	DIPTEROCARPACEAE	*Shorea pauciflora*	supra	supra	GF	GF	308	93	wind	dyszoochorous	T
SINDCO	LEGUMINOSAE	*Sindora coriacea*	supra	supra	GF	nonGF	270	165	animal	dyszoochorous	T
SINDEC	LEGUMINOSAE	*Sindora echinocalyx*	annual	excluded	GF	excluded	57	<30	animal	dyszoochorous	T
SINDWA	LEGUMINOSAE	*Sindora wallichii*	annual	excluded	nonGF	excluded	31	<30	animal	dyszoochorous	T
STERPA	STERCULIACEAE	*Sterculia parviflora*	continuous	excluded	GF	excluded	136	<30	animal	dyszoochorous	T
STYRBE	STYRACACEAE	*Styrax benzoin*	inconclusive	excluded	GF	excluded	40	<30	animal	endozoochorous	M
TIMOWA	RUBIACEAE	*Timonius wallichianus*	biannual	biannual	nonGF	nonGF	93	246	animal	endozoochorous	S
TRI1HY	TRIGONIACEAE	*Trigoniastrum hypoleucum*	annual	supra	nonGF	GF	156	83	wind	dyszoochorous	M
TRIOMA	BURSERACEAE	*Triomma malaccensis*	supra	supra	GF	GF	170	47	wind	nonzoochorous	T

UNK060	NA	*NA*	inconclusive	excluded	nonGF	excluded	40	<30	NA	NA	NA
UNK200	NA	*NA*	annual	excluded	nonGF	excluded	43	<30	NA	NA	NA
VATIBE	DIPTEROCARPACEAE	*Vatica bella*	annual	excluded	nonGF	excluded	119	<30	wind	dyszoochorous	T
VERNAR	ASTERACEAE	*Vernonia arborea*	biannual	excluded	excluded	nonGF	<30	152	NA	NA	M
XANTEU	POLYGALACEAE	*Xanthophyllum eurhynchum*	supra	supra	GF	nonGF	81	82	animal	endozoochorous	U
XERONO	SAPINDACEAE	*Xerospermum noronhianum*	annual	annual	nonGF	nonGF	649	267	animal	endozoochorous	M
XYLOCA	ANNONACEAE	*Xylopia caudata*	annual	excluded	GF	excluded	70	<30	animal	endozoochorous	M
XYLOFE	ANNONACEAE	*Xylopia ferruginea_var._ferruginea*	annual	excluded	nonGF	nonGF	255	35	blastic	nonzoochorous	M