Quantitative comparison of leafing, flowering, and fruiting phenology in temperate and tropical montane plant communities

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Quantitative comparison of leafing, flowering, and fruiting phenology in temperate and tropical montane plant communities

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Contents

Chapter 1: General introduction

1.1 What is phenology?

The phenology, timing of the life cycle or seasonal events, of plants is key to the reproductive success of individuals and the long-term persistence of populations (Craine *et al.* 2012; Rathcke & Lacey 1985). The phenology differs between and within species, and this fact has been known since ancient Greece (Theophrastus, "*Historia Plantarum*"). It was, however, as late as the mid-19th century that plant phenology attracted attentions of botanists. In the mid-19th century, the word "phenology", which derived from an ancient Greek word, was first used in the meaning of specifically addressing successive appearances of phenomena and putting its focus on their timing and their relationship with the Earth's environment by a Belgium botanist in his public lecture (Demarée & Rutishauser 2009). Perhaps because of this naming, phenology has attracted the attention of botanists. From late-19th century, phenological studies increased and has deepened our understanding on phenological patterns of plants, such as leafing, flowering, and fruiting.

Leafing includes bud breaks, leaf emergence, and development. Numerous comparative studies on trees in tropics (Borchert 1994; Frankie *et al.* 1974; Williams-Linera 1997) and temperate (Edwards *et al.* 2017; Nitta & Ohsawa 1997) distinguished two classes of leafing phenology: evergreen, in which individuals retain full canopy throughout the year and deciduous, in which individuals fall all leaves during the dry season or winter, and remained leafless for at least one month. Leafing on deciduous trees signals the transition from winter (or dry season) to spring (or wet season) and the onset of the growing season in temperate and seasonal tropical forests (Polgar & Primack 2011). Those phenologies are influenced by abiotic factors, including daylength (Williams *et al.*

2008), frost/temperature (Doi *et al.* 2008; Williams-Linera 1997), and water/precipitation (Williams *et al.* 2008). Similary, leafing phenologies are known to be influenced by biotic factors, such as the existence of herbivores (Nitta & Ohsawa 1997). Given the severity of seasonal drought and the physiological dependence of leafing upon water, it is advantageous for plants to expand new leaves in wet season (Williams *et al.* 2008). On the other hand, leafing in dry season may be advantageous in avoiding or minimising damage from herbivores (Aide 1992; Rivera *et al.* 2002). Those inconsistent advantages may produce various patterns of leafing phenology.

Flowering is associated with a series of events including floral bud initiation and development, blooming, and floral persistence (Borchert 1983; Rathcke & Lacey 1985). Initial comparative studies on trees in tropical forests distinguished two classes of flowering phenology (Janzen 1971): mass flowering, in which individuals flower synchronously with short durations (Augspurger 1983; Bawa 1983; Heinrich & Raven 1972) and extended flowering, in which individuals flower less synchronously with long durations (Bawa 1983; Frankie *et al.* 1974). Those flowering phenologies are known to be influenced by abiotic factors, daylength (Cortés-Flores *et al.* 2017; Elzinga *et al.* 2007), frost/temperature (Reader 1983), snowmelt (Kudo *et al.* 2008), water/precipitation (Elzinga *et al.* 2007; Vasek & Sauer 1971; Williams *et al.* 2008), and the availability of nitrogen and carbon (Miyazaki *et al.* 2014). Similary, flowering phenologies are known to be influenced by biotic factors, such as herbivore activities (Albrectsen 2000; Elzinga *et al.* 2007; Mahoro 2003), pollinator availability (Mosquin 1971; Robertson 1895; Tepedino & Stanton 1981), and pollination insurance (Pojar 1974). While studies of

flowering phenology are biased toward trees, interspecific variation in flowering phenology of herbs has also been examined since the pioneering studies of Schemske (1977) and Schemske et al. (1978). In a review of those studies, Rathcke and Lacey (1985) pointed out that large plants of annuals and of perennials including herbs and shrubs tend to produce more flowers than small plants over a longer duration and argued that flowering patterns are influenced by resource availability.

Fruiting is a process including initiation, growth, and ripening of fruits and presentation of fruits to dispersers (Rathcke & Lacey 1985). Similar to phenological patterns of flowering, there are two classes of fruiting phenology: synchronous fruiting, in which individuals set fruits synchronously with short durations (Howe & Estabrook 1977; Thompson & Willson 1979) and extended fruiting, in which individuals set fruits less synchronously with long durations (Lacey 1982). Those fruiting phenologies are known to be influenced by abiotic factors, including frost/temperature (Tukey 1952; Stephanson 1981), and water/precipitation (Janzen 1967; Karr 1976; Lieberman 1982). Similarly, fruiting phenologies are known to be influenced by biotic factors, such as frugivore activity and seed disperser availability (Kitamura *et al.* 2005a; Kitamura *et al.* 2002; Kitamura *et al.* 2005b); the latter is often associated with bird migrations (Herrera 1982, 1984; Morton 1973; Stiles 1980; Thompson & Willson 1979).

What those studies suggested in common is that the plant phenology reflects the influences of various abiotic and biotic environments and also has a large influence on the abiotic and biotic environments. Therefore, under recent climate changes at the global, regional, and local scales, how those changes affect phenology and ecosystem

functions is becoming an urgent research question (Sakai & Kitajima 2019). In mid to high latitudes, phenological shifts are already evident, especially in terms of growing season lengths (IPCC 2014). Astonishing number of studies reported phenology shifts that differ between plants and pollinators (Burkle & Alarcón 2011; Elzinga *et al.* 2007), herbivores (Inouye *et al.* 2000), or seed dispersers (Miller-Rushing *et al.* 2010). To reveal and forecast the effects of global, regional, and local climatic changes to ecosystems, it is needed to describe and compare plant phenologies, and elucidate how they are changing in various spatial scales.

1.2 Various phenologies in East and Southeast Asia

In East and Southeast Asia, diversified patterns of leafing, flowering, and fruiting phenologies are observed in tropical rain forests, tropical seasonal forests, and temperate forests (Peel *et al.* 2007). In tropical rain forests, subannual, annual, and supra-annual pattern of leafing (Ichie *et al.* 2004; Putz 1979), flowering and fruiting (Sakai *et al.* 1999, 2002) has been reported. Leafing phenology generally does not show a peak and 10–50% of species expand new leaves through the year (Ichie *et al.* 2004; Putz 1979), and the number of leafing species doubles after short-term drought induced by the El Niño southern oscillation (ENSO; Ichie *et al.* 2004). Similarly, flowering and fruiting phenology show a peak after short-term drought, called 'general flowering (mass flowering)', but the number of flowering and fruiting species is usually less than 10% (Brearley *et al.* 2007; Chen *et al.* 2018; Putz 1979; Sakai *et al.* 2006; Sakai *et al.* 1999; Ushio *et al.* 2019). Theoretical and empirical studies (Sakai *et al.* 2006; Ushio *et al.* 2019)

(Chen *et al.* 2018) supported that general flowering is triggered by both irregular droughts and low temperature associated with ENSO.

In tropical seasonal forest, leafing phenology shows a peak in dry season (November–April) that is associated with changes in daylength in some species and in precipitation in other species (Williams *et al.* 2008). Flowering phenology shows a peak at the end of the dry season (Kato *et al.* 2008) and both precipitation and temperature are considered as cues for flowering (Kurten *et al.* 2018).

In temperate forests, annual patterns of leafing phenology (Edwards *et al.* 2017; Li *et al.* 2005; Nitta & Ohsawa 1997; Zhang *et al.* 2007), and flowering phenology (Chang-Yang *et al.* 2013; Nagahama & Yahara 2019; Noma & Yumoto 1997; Shibata *et al.* 2002; Takanose & Kamitani 2003; Yumoto 1987; Zhang *et al.* 2007) are observed in both deciduous and evergreen stands. Leafing phenology generally peaks around April (Edwards *et al.* 2017; Li *et al.* 2005; Nitta & Ohsawa 1997; Zhang *et al.* 2007) and consider to be triggered by the onset of spring rains (Edwards *et al.* 2017). Flowering phenology shows a peak from spring (March) to summer (August) (Chang-Yang *et al.* 2013; Noma & Yumoto 1997; Shibata *et al.* 2002; Takanose & Kamitani 2003; Yumoto 1987) and those patterns match seasonal changes in day length, temperature, and irradiance (Chang-Yang *et al.* 2013), but deciduous species observed by Zhang et al. (2007) bloomed from autumn (October) to early spring (March).

1.3 Aims of this study

The following problems remain unresolved in phenological studies, inspite that numerous studies have been made since the 19th century as summarized above. First, most of previous studies did not distinguish mean flowering length of individuals from total flowering length of population or species in recording or comparing phenology (Nagahama & Yahara 2019). To describe and compare phenology quantitively among species, distinguishing the patterns at individual and population levels is important because total flowering length at the population level is determined not only by mean flowering length but also by variance of flowering length. Second, many studies suggested that flowering phenology differs among life forms, such as trees, perennial herbs, and annuals, but it is still unclear how patterns of flowering phenology differ among them within a temperate community. Revealing the phenological differences among life forms will advance our integrative understanding of phenology and life history strategy, both of which are influenced by resource availability and climatic factors. Third, our knowledge of the phenology of tropical forests are biased to lowland forests where most of previous studies have been made. Phenological studies in the tropical montane forests are limited inspite that many primitive angiosperms are found (Axelrod 1966; Morlay 2001), and ancestral phenological states of forests would be observed there. Fourth, despite astonishing numbers of studies have been made on phenology, few studies compared phenologies of different types of forests and elucidated similarities and differences of phenologies between them. Revealing the phenological differences among forests across climate zones will advance our integrative understanding of regional

phenology and relationship with climate factors, which is essential to forecast the effects of global, regional, and local climatic changes to ecosystems.

In this study, I addressed the following four questions regarding phenology in a plant community. (1) How can phenology be described quantitively? (2) How does flowering phenology differ among life forms? (3) What kind of phenological pattern is observed in tropical montane forests? (4) How does phenology differ among forests in East and Southeast Asia? To answer those questions, I performed two studies: one in temperate community (Chapter 2) and the other in tropical montane forest (Chapter 3). Below, I summarize the contents of two chapters.

1.4 Summary of Chapter 2

To answer the questions (1) and (2), I recorded flowering events for individuals of insect-pollinated trees, perennial herbs, and annuals from spring to summer of 2016 and 2017 in a warm-temperate forest in Japan. To compare phenological variables including mean and variance of flowering length, I standardized the number of observed individuals for each species and tested differences in variables, considering the phylogenetic relationships among species. Total flowering length in trees (9–50 d) was significantly shorter than perennial herbs (27–113 d) or annuals (22–89 d), but mean flowering length was not significantly different among them. Flowering length variance was significantly smaller and intraspecies synchrony significantly higher in trees than in perennial herbs and annuals. At the community level, flowering times largely overlapped among successively flowering species, but interspecies synchrony was positive for all life forms.

Shorter total flowering length and higher intraspecific synchrony in trees are explained by a modified pollinator attraction hypothesis suggesting that selection favors higher intraspecific synchrony because it promotes between-individual movement of pollinators. At the community level, positive interspecific synchrony for all life forms supports the hypothesis that flowering times tend to converge among species.

1.5 Summary of Chapter 3

To answer the questions (3) and (4), I observed leafing, flowering and fruiting phenologies in the tropical montane forests of Vietnam to characterize phenological patterns and reveal the correlations between meteorological factors and phenology. Leafing, flowering, and fruiting phenologies of 91 species were observed every three months in five plots located along the elevation from 1460 m to 1920 m of Bidoup-Nui Ba National Park in southern Vietnam. We examined how the number of leafing, flowering, or fruiting species varies with precipitation, temperature, or daylength using Generalized Linear Models (GLMs). As a result, leafing phenology showed a peak at the beginning of the wet season (April), and was significantly influenced by all of daylength, precipitation, and temperature. Flowering phenology did not show any distinct peak, but was influenced by daylength and precipitation. Fruiting phenology showed a low peak from the wet season (July) to the beginning of the dry season (December), but was not significantly influenced by those meteorological factors. Comparing with phenological patterns of other forests, leafing pattern in Bidoup-Nui Ba National Park was similar to those in the other tropical montane forest in Mt. Kinabalu, tropical seasonal forest, and

temperate forest, but flowering and fruiting patterns in Bidoup-Nui Ba National Park were different from all of those in the other forests. By assuming that those unique phenological patterns of tropical montane forest are ancestral to patterns of other forests, I propose a hypothetical scheme for the evolutionary processes of phenologies in forests of South East and East Asia.

Chapter 2: Quantitative comparison of flowering phenology traits among trees, perennial herbs, and annuals in a temperate plant community

The study in this chapter, conducted in collaboration with Dr. Tetsukazu Yahara, was published in *American Journal of Botany* 106(12) in 2019.

2.1 Introduction

In angiosperms, flowering phenology varies widely among species. This interspecific variation in flowering phenology has been examined in a range of tropical and temperate forests. Initial comparative studies on trees in tropical forests distinguished two classes of flowering phenology (Janzen 1971): mass flowering, in which individuals flower synchronously with short durations (Augspurger 1983; Bawa 1983; Heinrich & Raven 1972; seasonal flowering by Frankie et al. 1974; big bang by Gentry 1974) and extended flowering, in which individuals flower less synchronously with long durations (Bawa 1983; Frankie *et al*. 1974; steady-state flowering by Augspurger 1983; Gentry 1974). According to Frankie *et al.* (1974), extended flowering is common in nonseasonal environments such as tropical rain forests. Later, Rathcke and Lacey (1985) reviewed the studies on tropical rain forests and concluded that mass flowering was common among trees that flower during the dry season, whereas extended flowering was found for most understory species. These two flowering patterns were also observed in temperate forests, where mass flowering was common for canopy trees and extended flowering was found for understory species (Yumoto 1987, 1988). Further studies on tropical rain forest trees showed that these flowering patterns were two extremes of a continuous variation, and Newstrom et al. (1994) proposed three categories of annual flowering patterns: brief flowering (<1 month), intermediate flowering (1–5 months), and extended flowering (>5 months).

While studies of flowering phenology are biased toward trees, interspecific variation in flowering phenology of herbs has also been examined since the pioneering

studies of Schemske (1977) and Schemske et al. (1978). In a review of those studies, Rathcke and Lacey (1985) pointed out that large plants of annuals and of perennials including herbs and shrubs tend to produce more flowers than small plants over a longer duration and argued that flowering patterns are influenced by resource availability. Another notable finding for herbs is that the flowering phenology of herbs in tropical seasonal communities is more tightly linked to rainy seasons compared with trees (Batalha & Martins 2004; Joshi & Janarthanam 2004). Those studies suggest that patterns of flowering phenology may differ between trees and herbs within a community, reflecting differences in resource availability and in responses to climatic factors. However, few comparisons were made for patterns of flowering phenology between trees and herbs within a community, and those comparisons have been confined to tropical seasonal communities (Batalha & Martins 2004; Cortés-Flores *et al.* 2017; Joshi & Janarthanam 2004; Marques *et al.* 2004) except one study for temperate, subalpine, and alpine vegetation in Japan (Kato *et al.* 1993). Thus, it is still unclear how patterns of flowering phenology differ among trees, perennial herbs, and annuals within and among various plant communities. To fill this gap, we compared patterns of flowering phenology among trees, perennial herbs, and annuals in a plant community in a temperate climate using the following quantitative variables.

Flowering phenology is quantitatively defined as a time-series distribution of the number of flowers characterized by variables such as onset date, mean, variance, and skewness of flowering length, and synchrony of flowering among individuals (Rathcke & Lacey 1985). However, these variables were not always fully described in previous

studies. To deepen our understanding of the variability of flowering phenology and its adaptive significance, we need to compare the above quantitative variables of flowering phenology among various species. In particular, we need to distinguish mean flowering length from total flowering length because total flowering length is determined not only by mean flowering length but also by variance of flowering length. This distinction is important when considering the adaptive significance of flowering phenology because mean and variance of flowering length may evolve independently under different selection pressures. Synchrony of flowering among individuals is another key variable of flowering phenology. It can be measured by indicators describing the temporal distribution of flowering individuals including the aggregation index Morisita's $I\delta$ (Morisita 1959; Yumoto 1987), the variance of onset day, or the variance of flowering length. These quantitative variables can help explain the adaptive significance of flowering patterns.

Various hypotheses have been proposed to explain the adaptive significance of flowering patterns, and these can be summarized as follows (Rathcke & Lacey 1985). First, individuals that bloom synchronously for short durations can attract many generalist pollinators with a large floral display (Cortés-Flores *et al.* 2017; Fenner 1998; Janzen 1967; Kacelnik *et al.* 1986; Makino *et al.* 2007; Nattero *et al.* 2011; Ohashi & Yahara 2002). On the other hand, individuals that bloom less synchronously over longer durations may be advantageous for flowers pollinated by specialist pollinators that visit flowers infrequently but have high flower constancy (Heinrich *et al.* 1977). This hypothesis was supported by Yumoto (1987, 1988) who showed that flowers of tall trees

bloomed synchronously for shorter durations and attracted many generalist pollinators in the canopy, whereas flowers of understory trees bloomed less synchronously for longer durations and attracted more specialized pollinators. Hereafter, we call this the pollinator attraction hypothesis. Second, individuals of self-incompatible species are expected to flower longer than self-compatible plants (Pojar 1974) because more opportunities for pollination would be expected by flowering longer (Primack 1985; Rathcke & Lacey 1985). In self-incompatible individuals in which pollen transfer by pollinators is obligatory for reproduction, longer flowering durations are considered advantageous for ensuring pollination success under uncertain pollinator activity due to daily fluctuations in weather conditions (Schemske & Lande 1985; Yumoto 1986) or between-year climate change (Primack 1985; Rathcke & Lacey 1985). Hereafter, we call this hypothesis the pollination insurance hypothesis. Third, individuals with larger plant size can accumulate more resources and flower longer because the number of flowers is known to increase with plant size (Bazzaz *et al.* 1987; Fabbro & Körner 2004; Samson & Werk 1986) and the flowering length of individuals increases with the number of flowers in trees (Otarola *et al.* 2013), perennial herbs, and annuals (Ollerton & Lack 1998; Rathcke & Lacey 1985). Also, plants (typically annuals) growing in unpredictable habitats flower earlier and longer to ensure seed production before dying due to disturbance (Ollerton & Lack 1998; Rathcke & Lacey 1985). Hereafter, we call this the resource availability hypothesis.

To determine which hypothesis better fits our data for a temperate plant community, we derived the following predictions for trees, perennial herbs, and annuals of insect-pollinated species. We excluded wind-pollinated species from our study because

pollinator attraction and pollination insurance hypotheses hold only for insect-pollinated species. At our study site, the trees we observed are pollinated by generalist insect pollinators including hymenopterans, dipterans, lepidopterans, and coleopterans (Kuwata 2013; Appendix S2.1). According to the pollinator attraction hypothesis (Table 2.1, top), tree individuals are predicted to flower for a shorter duration and more synchronously to attract generalist pollinators (Yumoto 1987, 1988). On the other hand, individuals of perennial herbs specialized for particular pollinators such as bees are predicted to flower longer and less synchronously (Yumoto 1987, 1988). In our study, the latter prediction is the case for nonweedy perennial herbs (Appendix S2.2). For weedy perennial and annual herbs, individuals are predicted to bloom less synchronously because those species are often selfing or asexually reproducing. The pollinator attraction hypothesis does not lead to any specific predictions about the flowering period of weedy herbs. According to the pollination insurance hypothesis (Table 2.1, middle), tree individuals, which are highly outcrossing, are predicted to flower longer, and individuals of annual herbs are predicted to flower for a shorter duration (Abe 2001; Pojar 1974; Primack 1985). Perennial herbs are predicted to flower longer than annual herbs because they include more outcrossing species than annual herbs (Appendix S2.2; see also Baker, 1974). According to the resource availability hypothesis (Table 2.1, bottom), flowering period is expected to increase as plant size increases for the categories of annuals, perennial herbs, and trees, if habitats are predictable. We can also predict that variance of flowering length increases with plant size, because variation in the amount of available resource (e.g., nitrogen) among individuals will be larger in larger plants. This prediction

means that trees show larger variance of flowering length than perennial herbs and annuals. On the other hand, in unpredictable habitats, annuals should flower earlier and longer, with larger variance, to insure some seed production even when the growing season is cut short (Rathcke & Lacey 1985). These predictions can be examined using quantitative variables such as onset date, mean, variance, and skewness of flowering length, and synchrony of flowering among individuals.

On the basis of the data obtained for this study, we could also compare flowering phenology between species. Some have claimed that plant species may evolve traits that decrease phenological overlap with other species competing to attract common pollinators (van Schaik *et al.* 1993). However, Rathcke and Lacey (Rathcke & Lacey 1985) reviewed empirical studies and concluded that interspecific divergence in flowering within plant communities is rarely supported by statistical tests. Yumoto (1987, 1988) suggested that flowering phenology among canopy species is asynchronous to avoid competition for generalist pollinators. In addition, Sakai et al. (Sakai *et al.* 1999) suggested that plant species that attract specialist pollinators flower synchronously with other species. The ideas of Yumoto (1987, 1988) and Sakai et al. (Sakai *et al.* 1999) support the hypothesis that flowering phenology is more synchronous among herbaceous species than among trees.

We address the following specific questions regarding patterns of flowering phenology in a temperate plant community. (1) Do intraspecific measures of flowering phenology variables, including total, mean, and variance of flowering length, differ among trees, perennial herbs, and annuals? (2) Which predictions of the pollinator

attraction, pollination insurance, and resource availability hypotheses better explain our observations on intraspecific patterns of flowering phenology? (3) Does interspecific synchrony of flowering phenology differ among trees, perennial herbs, and annuals?

2.2 Materials and Methods

2.2.1 Observations

Plants were monitored for flowering once a week from 1 March to 31 July in 2016 and 2017 in the biodiversity reserve of Ito campus (33º35'47.5"N, 130º12'50.0"E; Fig. 2.1), Kyushu University, Fukuoka, Japan, an area of about 37 ha at an elevation from 20 to 57 m a.s.l., where monthly average temperatures fluctuated from 6.2°C in January to 27.4°C in August (a 21.2°C difference), and monthly precipitation fluctuated from 75.5 mm in March to 337 mm in June (261.5 mm difference; Kyushu University 2018; Appendix S2.3). The reserve is located in a small valley facing northeast, surrounded by two ridges running from southwest to northeast that are covered with evergreen broad-leaved forest dominated by Q*uercus glauca* Thunb., *Castanopsis sieboldii* (Makino) Hatus., and *Neolitsea sericea* (Blume) Koidz. mixed with some deciduous trees including *Mallotus japonicus* (L.f.) Müll.Arg., *Celtis sinensis* Pers., and *Aphananthe aspera* Planch. The central area of the reserve lies between a small stream and a road and is maintained as an open grassland by mowing; three small ponds are surrounded by tall grass. A forest margin along the road is covered with herbaceous vegetation composed of weedy annuals such as *Galium spurium* L. and *Corydalis incisa* Pers. and perennial herbs such as

Trifolium repens L. and *Farfugium japonicum* (L.) Kitam. Approximately 650 plant species have been recorded in the biodiversity reserve. Among them, we observed 48 insect-pollinated plant species belonging to 36 genera of 24 families, which flowered for more than two observation days along the survey route (Fig. 2.1). Each genus included up to three species, and each family included up to four genera. Our sample included 13 outcrossing species of trees, 15 perennial herbs including 12 outcrossing species and one each of selfing, agamospermus, and vegetatively reproducing species, and 20 annuals including nine outcrossing, 10 selfing, and one agamospermus species (Appendix S2.2). Perennial herbs included four species of arable weeds, six species of roadside weeds, and five nonweedy species; all were polycarpic. Annuals included 17 species of arable weeds, two species of roadside weeds, and one nonweedy species (Asai 2012, 2016).

For trees, Kuwata (Kuwata 2013) recorded insect flower visitors by taking a photograph every 10 min using programmable digital cameras (PENTAX Optio-W80 and WG-1, Ricoh Imaging Co., Tokyo, Japan) from 6 April to 30 September 2015. This method often fails to record the visits of bees including *Bombus ardens* Smith, *Xylocopa appendiculata* Smith, and *Apis mellifera* L. To record the visits of bees, we directly observed visitors to tree flowers by collecting insects on the flowers 3 h or longer per day for a total of 14 days in April, May, and June in 2018 (Appendix S2.1). For herbaceous species, we recorded insect flower visitors including bees by direct observation. For *Cirsium japonicum* DC., we also used the camera to record flower visitors (Appendix S2.1).

For trees, flowering was observed and recorded for each individual found along the survey route. For perennial herbs and annuals, flowering was observed and recorded in 50 plots of 1 × 1 m along the survey route. These small plots corresponded to one individual for large herbaceous species and multiple individuals for small herbaceous species, but for practical purposes we regarded each flowering shoot of a species in a plot as an individual because the individual small herbaceous plants in a plot were often difficult to distinguish. For each "individual", we recorded the following dates: (1) the onset date of flowering, defined as the day when the first flower opened, and (2) the end date of flowering, defined as the day when the petals of the last flower became discolored or fell off. Flowering length of an individual was determined as the time between the onset and end days for the individual, and the total flowering length of a species was determined as the time from the onset day of the first-flowering individual to the end day of the last flowering individual. The mean flowering length was determined as the arithmetic mean of flowering durations recorded for individuals of the same species.

2.2.2 Phenological variables used for each species

We calculated the following phenological variables for species with five or more individuals in the study area. As a set of basic quantitative variables, we compared total flowering length of species (TFL), mean flowering length of individuals (MFL) and its variance (VFL), and skewness and kurtosis of the flowering length distribution among individuals. To display the distributions of TFL for trees, perennial herbs, and annuals, we drew violin plots using the R package ggplot2 (v.2.2.1; Wickham 2010). The VFL

describes the variation in flowering length among individuals. Skewness provides a measure of the asymmetry of the flowering length distribution; the more skewed the distribution, the more individuals flower for short durations, usually immediately after the onset day, and the fewer individuals flower near the end day. Kurtosis represents the deviation from the normal distribution and describes the weight of the distribution tail. In addition, we examined flowering synchrony among individuals using the following two measures: (1) the variance of the onset date and (2) the Morisita aggregation index ($I\delta$; Morisita 1959) . To calculate the variance of the onset date, we standardized the onset day of the first-blooming individual as 0. Smaller variance in the onset date represents higher synchrony among individuals. On the other hand, larger $I\delta$ values represent higher synchrony among individuals. $I\delta$ was calculated using the R package vegan (v.2.4.4; Oksanen et al. 2017).

2.2.3 Phenological variables used for interspecific comparison

We also tested whether the synchrony of flowering phenology varied among the life forms using the following two measures: (1) skewness of the onset dates of flowering and (2) an index of community-wide synchrony (Loreau & de Mazancourt 2008). We calculated these indices for each life form and each year. The skewness of each life form was compared by resampling the data 1000 times. The latter index was calculated using the following formula:

$$\varphi = \frac{\sigma_{x_T}^2}{\left(\sum \sigma_{x_i}\right)^2} ,$$

where σ^2 is the temporal variance of the community time series $x_T(t) = \sum^{x_T} x_i(t)$, and $\left(\sum \sigma_{x_i}\right)^2$ is the sum of the temporal standard deviation of the time series across all species. This describes the rate of increase of flowering individuals in a species relative to the increase in flowering individuals in a community (Loreau & de Mazancourt 2008). The index approaches 1 when the flowering of two species is highly synchronous. These two phenological variables were determined for the 39 species for which we observed five or more individuals. For calculating the community-wide synchrony index, the R package synchrony (v.0.2.3; Gouhier & Guichard 2014) was used.

2.2.4 Construction of a phylogenetic tree and testing for phylogenetic signal

Although flowering phenology is often constrained by phylogenetic relationships among species (CaraDonna & Inouye 2015; Cortés-Flores *et al.* 2017; Davies *et al.* 2013; Du *et al.* 2015; Pei *et al.* 2015), a study showed that flowering period is not constrained by phylogenetic relationships (CaraDonna & Inouye 2015). If the former is the case, we need to consider phylogenetic relationships in our analysis of the data (Felsenstein 1985; Harvey & Pagel 1991). If the latter is the case, we can apply standard statistical tests in which random sampling is assumed. To test which was the case for our data set, we constructed a phylogenetic tree (see below) and determined Blomberg's *K* (Blomberg *et al.* 2003). Blomberg's *K* compares the distribution of observed trait values with a distribution expected for trait evolution under Brownian motion (Ackerly 2009; Blomberg *et al.* 2003). When *K* is 1, the observed distribution is identical to the expected distribution, indicating that the trait distribution is highly

influenced by phylogenetic relationships. On the other hand, *K* values close to 0 show negligible phylogenetic signals. To test the significance of *K*, we calculated phylogenetic independent contrasts (Felsenstein 1985) of each phenological trait value and compared them with randomly shuffled trait values across the phylogeny (CaraDonna & Inouye 2015). Blomberg's *K* was determined and tested using the R package phytools (v.0.5-10; Revell 2012) for species with five or more individuals.

We constructed a phylogenetic tree of all observed species using DNA sequences of *rbcL* and *matK* and *Euryale ferox* Salisb. as the outgroup (Appendix S2.4). The DNA sequences of the observed species and the outgroup were downloaded from the National Center for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih. gov). We aligned the sequences using the program MEGA 7 (v.7.0.3). After aligning the sequences, we reconstructed phylogenetic relationships among plant species examined using the program BEAST (v. 1.8.3; Drummond et al. 2006) and the GTR (general time reversible) model (Lanave *et al.* 1984; Tavaré 1986) for nucleotide substitution, gamma distribution for site heterogeneity, the lognormal relaxed clock model (Drummond et al., 2006) for lineage-specific rate variation, the Yule process model (Yule 1925) for diversification, and UPGMA for obtaining a tree prior. With those settings, we estimated a time-measured phylogeny by running Markov chain Monte Carlo (MCMC) for 100 million generations, sampling every 10,000 trees, and discarding the first 1000 trees as a burn-in. We repeated this estimation five times independently and obtained five phylogenetic trees. We obtained the maximum credibility tree from those five

phylogenetic trees using the LogCombiner program of BEAST. Finally, we determined clade ages based on calibration with the ages estimated as described by (Bell *et al.* 2010).

2.2.5 Statistical analysis 1: tests of variables for each species

We observed phenological variables for 2 years (2016 and 2017), and the number of individuals observed per species varied from 1 to 69. To consider the possible effects of this variation on statistical tests of phenological variables, we used the following two methods. First, we tested whether each phenological variable (an average of a variable for a species for 2016 or 2017) varies with year and/or the number of observed individuals, using GLMM with an average of a phenological variable as the outcome variable, year and the number of individuals observed in 2016 or 2017 for each species as predictor variables, and genus as a random factor, using a lognormal link function and gamma distribution of errors. For skewness, which includes negative values, we tested the effects of year and the number of observed individuals using LMM with an identity link function and Gaussian distribution of errors including genus as a random factor. We used genus as a random factor because previous studies showed that phenological characteristics are phylogenetically constrained (CaraDonna & Inouye 2015; Cortés-Flores *et al.* 2017; Davis *et al.* 2010; Du *et al.* 2015; Pei *et al.* 2015). Thus, in addition to the test using Blomberg's *K*, we considered possible phylogenetic effects using genus as a random factor for GLMM or LMM. We used the R package lme4 (v.1.1.15; Bates et al. 2014) for these tests. For skewness, we tested differences between model 0 containing included only a random factor (genus) and the following two LMM models: model 1 containing

year and a random factor (genus); model 2 containing the number of observed individuals and a random factor (genus). If model 0 significantly differed from model 1 or 2, we considered the other model to be more reliable for explaining the effects of year and the number of observed individuals on skewness. For those tests, we used 43 species, including 11 species of trees, 12 perennial herbs, and 20 annuals that had five or more observed individuals in both 2016 and 2017. If there was no significant effect of year or number of observed individuals, we further tested the differences in each phenological variable among trees, perennial herbs, and annuals using data for all species, including species with fewer than five individuals in either year. To test the difference between trees and herbs or between perennial herbs and annuals, we used a GLMM with lognormal link function and Gamma distribution of errors, in which genus was included as a random factor.

Second, to adjust the number of individuals to be compared, we determined a rarefaction–extrapolation curve for each phenological variable of each species using the following bootstrap method. We carried out bootstrapping 1000 times for each phenological variable of each species for the sample size from 1 to 69. We then fitted linear, quadratic, logarithmic, and logistic models to the relationship between a phenological variable and sample size and chose a model using the Bayesian information criterion (BIC). We conducted this model selection process for each phenological variable using data obtained by pooling bootstrap samples of all species in which the maximum of a phenological variable in each species was standardized to one. Finally, the model selected for each variable was applied to data of each species to describe the change

in a phenological variable as a function of the number of observed individuals (from 1 to 69).

We tested differences in phenological variables among life forms using rarefaction–extrapolation curves as follows. First, we determined a value of each variable for 5, 7, 12, 18, or 22 individuals representing the minimum, first quartile, median, nearest integer to the average value 17.8, and third quantile in the distribution of numbers of observed individuals, respectively. Second, in each case (5, 7, 12, 18, or 22 individuals), we used t-tests if data of two groups followed a normal distribution, the Wilcoxon's rank sum test if either group did not follow a normal distribution but both groups had the same variance, or the Fligner–Policello test if either group did not follow a normal distribution and the variance of the two groups differed, using R (v.3.4.1; R core Team 2017) . In these comparisons, p-values were adjusted using the Holm–Bonferroni method for multiple comparisons (Holm 1979).

2.2.6 Statistical analysis 2: tests of variables for interspecies comparison

We tested the significance of the skewness of onset date using D'Agostino's K-squared test. For this calculation, we used the R package moments (v.0.14; Komsta & Novomestky 2015) . For testing the differences in the community-wide synchrony index (Loreau & de Mazancourt 2008) among life forms, we computed its distribution for trees, perennial herbs, and annuals using 1000 bootstraps of 11 species of trees, 12 perennial herbs, and 20 annuals, from the original data, allowing resampling of the same species.

We calculated their 95% confidence intervals using R (v.3.4.1; R core Team 2017) and compared them among life forms.

2.3 Results

2.3.1 Phenological observations

We observed the flowering phenology of 48 insect-pollinated species (13 species of trees, 15 perennial herbs, and 20 annual herbs; Fig. 2.2) during the survey period that had five or more individuals in total for both years. Among these species, 43 (11 species of trees, 12 perennial herbs, and 20 annuals) were monitored in both 2016 and 2017. Total flowering length of species (TFL) varied from 9 days in *Prunus serrulata* Lindl. to 48 days in *Albizia julibrissin* Durazz. and 79 days in *Rubus hirsutus* Thunb. in tree species (note that *R. hirsutus* is a small shrub similar to perennial herbs; Appendix S2.3). In perennial species, TFL ranged from 27 days in *Sedum bulbiferum* Makino to 113 days in Trifolium repens; the TFL in annual species ranged from 22 days in *Veronica hederifolia* L. to 89 days in *Torilis japonica* DC. (Fig. 2.2). The TFL tended to be shorter in trees than in perennial and annual herbs (see Fig. 2.2; the results of statistical tests are described later). The variance of flowering length of individuals (VFL) was also smaller in trees than in perennial herbs and annual herbs, but mean flowering length of individuals (MFL) was similar among trees, perennial herbs, and annuals. For all life forms, skewness was close to zero and kurtosis above two. Trees tended to have higher $I\delta$ values than for perennial herbs or annuals and smaller variance of onset day than for perennial herbs.

Tall trees and shrubs are pollinated by many generalist insect pollinators including hymenopterans, dipterans, lepidopterans, and coleopterans (Appendix S2.1, including observations by Kuwata 2013 and ourselves). Three perennial herbs, *Cirsium japonicum* (Asteraceae), *Lamium album* L. (Lamiaceae), and *Trifolium repens* (Fabaceae), were visited by bees (*Bombus ardens*, *Xylocopa appendiculata*, and *Apis mellifera*), while other perennial herbs and annuals were visited mostly by dipterans.

For rarefaction–extrapolation curves used to adjust the number of individuals in statistical tests, the logistic model fitted best for TFL, skewness, and kurtosis, while the logarithmic model fitted best for MFL, VFL, and variance of onset date (Appendices S5, S6). The quadratic model gave the best fit for the aggregation index (Morisita 1959). In the rarefaction-extrapolation curves, TFL, skewness, and kurtosis increased from 0 to ca. 10 individuals and then leveled off, whereas MFL, VFL, and variance of onset date were almost constant regardless of the number of observed individuals (Appendix S2.6). The $I\delta$ values (Morisita 1959) increased with the number of observed individuals (Appendix S2.6).

2.3.2 Testing for phylogenetic signal

Blomberg's K was small and not significantly different from zero for any of the phenological variables (Appendix S2.7). This result is consistent with the fact that our data for 48 species, 36 genera, and 24 families are not biased toward specific clades. Therefore, we used standard statistical tests assuming random sampling.

2.3.3 Statistical analysis 1: tests of variables for each species

For the raw data, we first examined the effects of year and the number of observed individuals using a GLMM (or LMM for skewness), in which genus was included as a random factor. The effect of year was not significant for TFL, MFL, VFL, kurtosis, or *Iδ* (Appendix S2.8). For variance of onset date and skewness, the effect of year was significant (Appendices S2.8, S2.9). The effect of the number of observed individuals was significant for TFL, MFL, and *Iδ*; TFL, MFL, and *Iδ* increased when more individuals were observed (Appendix S2.8).

Because there was no significant effect of year on TFL, MFL, VFL, kurtosis, or *Iδ*, we tested differences in those variables between trees and herbs by pooling the data for 2 years and used a GLMM in which genus was included as a random factor. TFL, MFL, and VFL were significantly smaller in trees, and *Iδ* was significantly larger in trees (Table 2.2). Kurtosis did not differ between trees and herbs. Using the data for 2 years, we also tested differences in TFL, MFL, VFL, kurtosis, and *Iδ* between annuals and perennial herbs. *Iδ* tended to be larger in annuals, but deviations were marginal (p = 0.0509; Table 2.2). TFL, MFL, VFL, and kurtosis did not differ between annuals and perennial herbs.

For the data standardized for 5, 7, 12, 18, or 22 individuals, TFL was significantly shorter in trees than in annuals, whereas there was no significant difference between perennial herbs and annuals (Table 2.3, Fig. 2.3; Appendices S2.10, S2.11). On the other hand, there were no significant differences in MFL among life forms. VFL was significantly smaller in trees than in annuals, whereas there was no significant difference

between perennial herbs and annuals. The variance of the onset dates was significantly smaller in trees than in perennial herbs when the raw data were tested but was not significantly different among life forms when standardized values were tested. There were no significant differences in skewness and kurtosis among life forms. $I\delta$ was significantly higher in trees than in perennial herbs and annual herbs in both tests using the raw data and the data standardized for 18 or 22 individuals. For the data standardized for 5, 7, and 12 individuals, $I\delta$ was not significantly higher in trees than in perennial herbs or annual herbs but deviations in the data standardized for 12 individuals were marginal ($p = 0.053$ for tree vs. perennial comparison, and $p = 0.053$ for tree vs. annual comparison; Table 2.3).

2.3.4 Statistical analysis 2: tests of variables for interspecies comparison

The onset dates varied widely from March to July in both trees and herbs, although relatively more tree species tend to flower in May, more perennial herbs flower in April, and more annuals flower from March to April (Appendix S2.12). The skewness of the distribution of onset date was positive and significant for annuals in 2016 (Appendices S2.12, S2.13), and relatively large and positive skewness values were also found for annuals in 2017 and perennial herbs in 2016. However, bootstrapped skewness distributions largely overlapped, showing that the skewness was not significantly different among life forms (Table 2.4). The community-wide synchrony index values were above zero and medians below 0.5 for all life forms; these values were larger for

annuals than for perennial herbs and trees in both 2016 and 2017, but the difference was not significant (Table 2.5, Fig. 2.4).

2.4 Discussion

2.4.1 Differences in flowering patterns among trees, perennial herbs, and annuals

This study revealed two significant differences in characteristics of flowering phenology between trees and perennial or annual herbs in a temperate, evergreen–broad-leaved forest. First, trees have shorter TFL (total flowering length of species) than annual and perennial herbs. However, MFL (mean flowering length of individuals) did not differ significantly among life forms. Second, synchronization of flowering was greater among individual trees than among perennial herbs or annual herbs (larger Morisita's $I\delta$ and smaller variance of flowering length of individuals [VFL]). Those results showed that differences of TFL among life forms were derived from differences in VFL and intraspecific synchrony rather than differences in MFL.

While our study in a temperate, evergreen–broad-leaved forest demonstrated that VFL are smaller and intraspecific synchrony is greater for trees than herbs, another study (Kato *et al.* 1993) reported that trees flowered for shorter periods than herbs in cool-temperate deciduous forests, subalpine coniferous forests, and alpine meadows in Japan. However, Kato et al. (Kato *et al.* 1993) only described TFL, and it is uncertain whether the difference of TFL stems from the difference in VFL, intraspecific synchrony, and/or MFL. In a tropical dry forest, Cortés-Flores et al. (Cortés-Flores *et al.* 2017) compared TFL between trees and herbs and showed that flowering period was greater for trees than

herbs. Descriptions of MFL, VFL, and intraspecific synchrony would be helpful for interpreting this difference from our study. In their seminal review on phenological patterns of terrestrial plants, Rathcke and Lacey (Rathcke & Lacey 1985) suggested that the phenological pattern is quantitatively described at the levels of individuals, species, and communities by such variables as time of occurrence (onset, mean, mode), duration (range), synchrony (variance), and skewness. Despite this reasonable suggestion, these variables have not been described quantitatively at the levels of individuals, species, and communities until the present study. Here, we established a method to record flowering events at the level of individuals that allows the variables to be calculated at the species and community levels. Below, we compare our observations using the variables with predictions for individual flowering behavior, although further studies using this method are needed to confirm the generality of our findings.

The three hypotheses to explain the differences in flowering phenology among species (Rathcke & Lacey 1985)—the pollinator attraction hypothesis (Cortés-Flores et al. 2017; Heinrich et al. 1977; Janzen 1967; Yumoto 1987, 1988), the pollination insurance hypothesis (Pojar 1974), and the resource availability hypothesis (Frankie *et al.* 1974)—lead to different predictions regarding the relationship between flowering duration and life form (Table 2.1). We thus next consider which hypothesis better fits the results of our study.

First, the pollinator attraction hypothesis is unlikely to be supported by our observations, given that there was no significant difference in MFL among life forms (Table 2.6), although intraspecific synchrony was marginally higher in trees as predicted.

According to the pollinator attraction hypothesis (Table 2.1, top), tree individuals are predicted to flower for a shorter duration with greater synchrony to attract more generalist pollinators (Cortés-Flores *et al*. 2017; Janzen 1967; Yumoto 1987, 1988). This prediction is also derived from an optimization model for the evolution of flowering duration developed by Schoen and Ashman (Schoen & Ashman 1995), who suggested that optimal flower longevity is determined by the trade-off between increasing pollination success by flowering longer and the increasing cost of maintaining flowers. Under this trade-off, shorter flower longevity will be favored if the return on pollination success is larger but decelerating and the maintenance cost is high. Using the same framework of the optimization model, we predicted that MFL would be shorter in trees than in herbs because trees attract many generalist pollinators (as is the case in temperate forest trees; Yumoto 1987, 1988) by flowering more abundantly than herbs. Our observations did not agree with this prediction.

Second, the pollination insurance hypothesis does not appear to be supported by our observations for MFL (Table 2.6). According to the pollination insurance hypothesis (Table 2.1 middle), selfing annuals are expected to flower for shorter durations because fertilization is ensured by selfing. While annual species do not necessarily self-fertilize (Aarssen 2000), most annual weeds are able to set seeds by autogamy (Baker 1974). In colonizers such as annual weeds, an ability to self-fertilize ovules is more advantageous than outcrossing because colonizers often lack compatible mates and fewer pollinators are present (Pannell 2015). In this study, although most of annuals we observed were colonizing weeds, MFL did not differ between annuals and other life forms.

Third, our observations provided mixed support for the resource availability hypothesis (Table 2.6). According to the resource availability hypothesis (Table 2.1, below), (1) in unpredictable habitats, annuals should flower earlier and longer, with larger variance (Grime 1977; Harper & White 1974; Klimesova *et al.* 2016; Masuda & Yahara 1994; Sakai & Harada 1993), and (2) in predictable habitats, larger plants flower longer for all life forms (Bazzaz *et al.* 1987; Fabbro & Körner 2004; Samson & Werk 1986), and consequently trees should show larger MFL and VFL than perennial and annual herbs. Among these possibilities, the prediction for plants in unpredictable habitats was supported by our observation that VFL was larger in annuals. The prediction for reduced MFL and greater VFL for plants of predictable habitats, however, did not agree with our observations that MFL did not differ among life forms and VFL was smaller in trees than herbs.

We suggest that the smaller VFL of trees relative to perennial and annual herbs may be a mechanism to increase outcrossing by promoting between-tree movement of pollinators. Because individual trees have many flowers, there is a higher risk of geitonogamy if pollinators stay longer in one tree. According to the theoretical and empirical study of Ohashi and Yahara (Ohashi & Yahara 2002), a higher density of simultaneously flowering plants promotes between-individual movement of pollinators because the energetic costs of between-individual movement relative to within-individual movement is lower under a higher density of flowering individuals. Therefore, natural selection would favor more accurate detection of cues that enable individual trees to synchronize flowering among conspecific individuals within a population to promote

between-individual movement of pollinators. This hypothesis, here designated as a modified pollinator attraction hypothesis, explains our finding that VFL is smaller in trees than in herbs. Yumoto (1987) also showed that flowering canopy tree species showed higher intraspecific synchrony (larger Morisita's $I\delta$) than did flowering understory-tree species. This finding is consistent with our view because canopy tree species have more flowers and a higher risk of geitonogamy than do understory tree species.

2.4.2 Community-wide flowering patterns

There were no significant differences in the variance of onset date and community-wide interspecific synchrony between trees, perennial herbs, and annuals. Interspecific synchrony, however, was greater than zero in all life forms (Fig. 2.4), indicating that flowering events are weakly synchronized. In another comparison of flowering patterns between trees and herbs (Kato *et al.* 1993), flowering durations in both trees and herbs largely overlapped among successively flowering species, but community-wide interspecific synchrony was not determined.

Community-wide interspecific synchrony has been reported also for tropical forest where rainfall varies seasonally: more trees flowered during late dry and early wet seasons, whereas more herbs flowered during late wet season (Batalha & Martins 2004 , in tropical wet forest; Joshi & Janarthanam 2004, in plateaus, moist deciduous forest, semi-evergreen forest, evergreen forest, and mangroves; Monasterio & Sarmiento 1976, in tropical savanna and the semi-deciduous forest). On the other hand, the weak flowering synchrony in all life forms of temperate forests may be explained by the existence of

winter, a period not suitable for growth and flowering (see Doi *et al.* 2008; Forrest 2015; Inouye 2008).

2.5 Conclusion

In conclusion, the differences in flowering phenology variables (TFL, VFL and intraspecies synchrony) among trees, perennial herbs, and annuals are likely to be explained by the modified pollinator attraction hypothesis for trees, and the resource availability hypothesis in unpredictable habitats for annuals. On the other hand, weak but positive interspecific synchrony supports that flowering times tend to converge rather than diverge between species. These conclusions are derived from quantitative observations of the flowering phenology of individual plants, enabling comparisons of TFL, MFL, VFL, and interspecies synchrony among trees, perennial herbs, and annual herbs. Further quantitative studies using this protocol are needed to determine whether similar patterns are observed in plant communities under different climatic conditions. We showed that TFL and VFL varied among life forms but MFL did not. This result suggests that phenological responses to environmental changes, such as earlier emergence of pollinators due to global warming (Elzinga *et al.* 2007), would occur through changes in TFL and VFL rather than changes in MFL, and those responses would differ among life forms. In recent years, possibly reflecting environmental fluctuations due to climate change, phenological fluctuations associated with pollinator–plant interactions (Hegland *et al.* 2009; Parmesan 2006) and plant–plant interactions have been reported (CaraDonna *et al.* 2014; Dunne *et al.* 2003; Forrest *et al.* 2010; Heberling *et al.* 2019; Miller-Rushing

et al. 2006; Sparks *et al.* 2000). To deepen our understanding of those phenological responses to climate change, we need additional detailed studies of phenology to determine TFL, MFL, and VFL and interspecific synchrony for different life forms.

2.6 Tables

Table 2.1 Predictions based on three hypotheses for trees, perennial herbs, and annuals.

Hypothesis	Trees	Perennial herbs	Annuals
Pollinator attraction	Individuals flower for a shorter period and higher synchronously than herbs.	In nonweedy (more outcrossing) species adapted to specialized pollinators, individuals flower longer and less synchrously than trees. In weedy (selfing) species, individuals flower less synchronously; no specific prediction for flowering period.	Individuals flower less synchronously than trees; no specific prediction for flowering period.
Pollination insurance	Individuals flower longer than perennial herbs.	Individuals flower for shorter periods than trees and longer than annuals.	Individuals flower for shorter periods than perennial herbs.
Resource availability	Tree individuals flower longer than herbs, with larger variance.	Flowering length and its variance intermediate between trees and annuals.	In predictable habitats, annuals smaller than perennials flower shorter, with smaller variance. In unpredictable habitats, annuals flower earlier and longer, with larger variance.

Table 2.2 GLMMs examining the effects of life forms on phenological variables. * $P < 0.05$, *** $P < 0.005$.

Phenological variables	Explanatory variables	Intercept	Slope	*P*	
TFL	Tree - Herb	4.07	−0.52	0.00	***
	Perennial - Annual	4.12	−0.06	0.64	
MFL	Tree - Herb	3.18	−0.31	0.03	*
	Perennial - Annual	3.30	−0.20	0.14	
VFL	Tree - Herb	5.31	−1.39	0.00	***
	Perennial - Annual	5.52	−0.29	0.33	
Kurtosis	Tree - Herb	0.95	−0.01	0.95	
	Perennial - Annual	0.94	0.01	0.92	
Iδ	Tree - Herb	1.35	0.41	0.02	*
	Perennial - Annual	1.18	0.32	0.05	

Table 2.3 Tests among life forms for each phenological variable for 12 individuals, and the raw data. Student's *t* test, Wilcoxon rank sum test, and Fligner-Policello test were used depending on normality and variance of groups. *P*-values were adjusted using the Holm method. * $P < 0.05$, *** $P < 0.005$. Similar trends were observed in the case of 5, 7, 18, and 22 individuals (Appendix S13).

Data set		Raw data			*n* = 12		
Phenological variables	**Pairs**	**Statistic**	***P***		**Statistic**	***P***	
TFL	Tree–Perennial	−2.765	0.021	*	65.00	0.285	
	Perennial–Annual	−0.697	0.491		113.00	0.285	
	Annual–Tree	4.470	0.000	***	3.06	0.013	*
MFL	Tree–Perennial	−2.215	0.107		−1.57	0.258	
	Perennial–Annual	0.864	0.394		0.07	0.944	
	Annual–Tree	1.984	0.112		2.19	0.109	
VFL	Tree–Perennial	−4.154	0.000	***	−1.89	0.117	
	Perennial–Annual	0.497	0.497		−0.71	0.479	
	Annual–Tree	4.281	0.000	***	199.00	0.030	*
Variance of onset date	Tree–Perennial	−3.992	0.000	*	−1.73	0.250	
	Perennial–Annual	1.861	0.126		0.44	0.661	
	Annual–Tree	1.829	0.126		1.18	0.479	
Skewness	Tree–Perennial	101.000	0.883		85.00	1.000	
	Perennial–Annual	−1.26	0.437		−0.46	1.000	
	Annual–Tree	176.000	0.277		170.00	0.442	
Kurtosis	Tree–Perennial	−0.690	0.490		−1.27	0.283	
	Perennial–Annual	−1.795	0.145		−1.51	0.283	
	Annual–Tree	187.000	0.108		2.06	0.119	
Iδ	Tree–Perennial	5.063	0.000	***	147.00	0.053	
	Perennial–Annual	−1.07	0.286		135.00	0.633	
	Annual–Tree	−3.908	0.000	***	66.00	0.053	

Table 2.4 Differences in skewness among life forms.

	2016		2017	
Form	**2.50%**	**97.50%**	**2.50%**	**97.50%**
Tree	−0.69	0.85	−1.02	0.52
Perennial	−0.61	1.01	−0.61	1.02
Annual	0.5	3.1	−0.12	2.38

Table 2.5 Differences in the community-wide synchrony index among life forms.

Form	**2.50%**	**97.50%**
Tree	0.12	0.426
Perennial	0.15	0.456
Annual	0.219	0.696

Table 2.6 Results of each phenological variable for each life form.

Phenological variables	Trees	Perennial herbs	Annuals	Support for hypotheses
TFL	Shorter	Intermediate (ns)	Longer	The three hypotheses are not relevant because they make predictions for individuals.
MFL	(ns)	(ns)	(ns)	None of the hypotheses were supported.
VFL	Smaller	Intermediate (ns)	Larger	Resource availability hypothesis was supported only for annuals.
Synchronicity ($I\delta$)	Higher (ns)	Lower (ns)	Lower (ns)	Pollinator attraction hypothesis was supported only marginally.

2.7 Figures

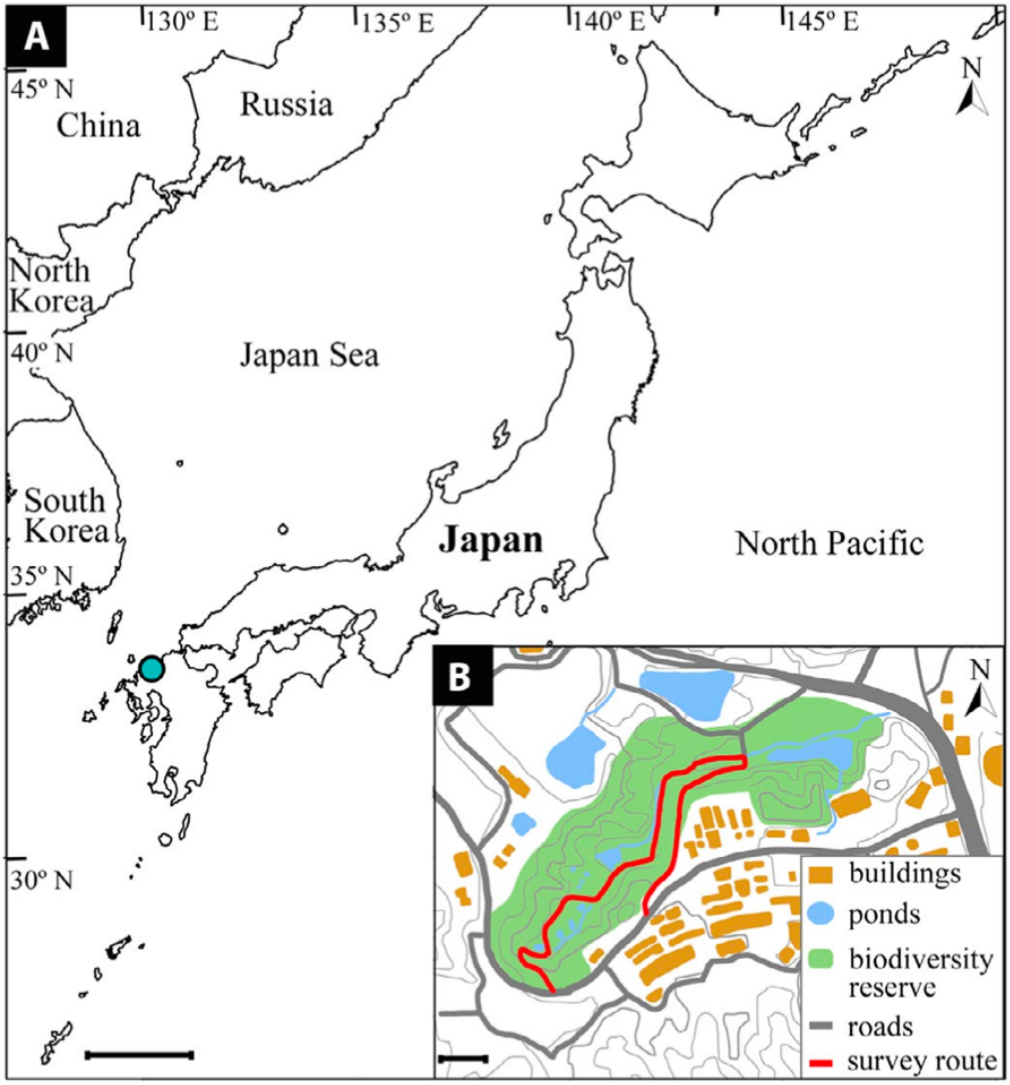


Figure 2.1 Map of study site and survey route. (A) Blue dot marks Fukuoka, Japan. Scale bar = 200 km. (B) Close up of study site showing survey route. Scale bar = 100 m.

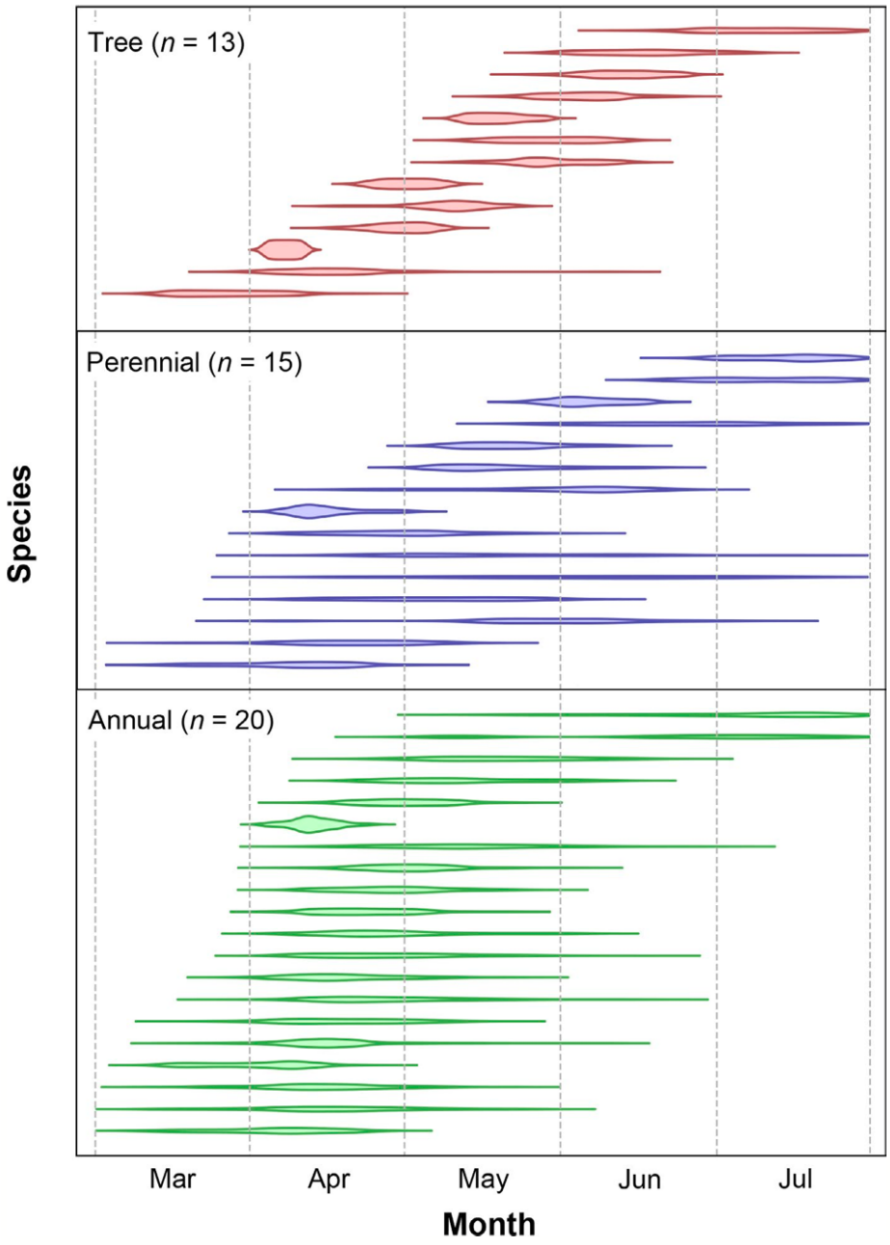


Figure 2.2 Flowering phenology of insect-pollinated species. Each line shows the total flowering duration for each species. The tree species (in order of earlier to later flowering): *Eurya japonica* Thunb., *Rubus hirsutus*, *Prunus serrulata*, *Viburnum japonicum* Spreng., *Castanopsis sieboldii*, *Euonymus alatus* (Thunb.) Siebold, *Toxicodendron succedaneum* (L.) Kuntze, *Premna microphylla* Turcz., *Rosa multiflora* Thunb., *Ligustrum japonicum* Thunb., *Cornus macrophylla* Wall., *Trachelospermum*

asiaticum Nakai, *Albizia julibrissin*; perennial herbs: *Semiaquilegia adoxoides* Makino, *Lamium album*, *Ranunculus silerifolius* H.Lév. var. *glaber* (H.Boissieu) Tamura, *Cirsium japonicum*, *Trifolium repens*, *Oxalis corniculata* L., *Ranunculus japonicus* Thunb., *Glechoma grandis* (A.Gray) Kprian., *Houttuynia cordata* Thunb., *Clinopodium gracile* (Benth.) Kuntze, *Sisyrinchium rosulatum* E.P.Bicknell, *Erigeron philadelphicus* L., *Sedum bulbiferum*, *Cryptotaenia japonica* Hassk., *Cayratia japonica* Gagnep.; annuals: *Lamium purpureum* L., *Veronica persica* Poir., *Stellaria neglecta* (Lej.) Weihe, *Lamium amplexicaule* L., *Cerastium glomeratum* Thuill., *Stellaria media* (L.) Vill., *Ranunculus muricatus* L., *Corydalis incisa*, *Veronica arvensis* L., *Trigonotis peduncularis* Benth. ex S.Moore & Baker, *Vicia sativa* L. subsp. *nigra* (L.) Ehrh., *Vicia hirsuta* (L.) Gray, *Vicia tetrasperma* (L.) Schreb., *Stellaria aquatica* Scop., *Veronica hederifolia*, *Youngia japonica* (L.) DC., *Geranium carolinianum* L., *Trifolium dubium* Sibth., *Torilis japonica*, *Erigeron annuus* (L.) Pers.

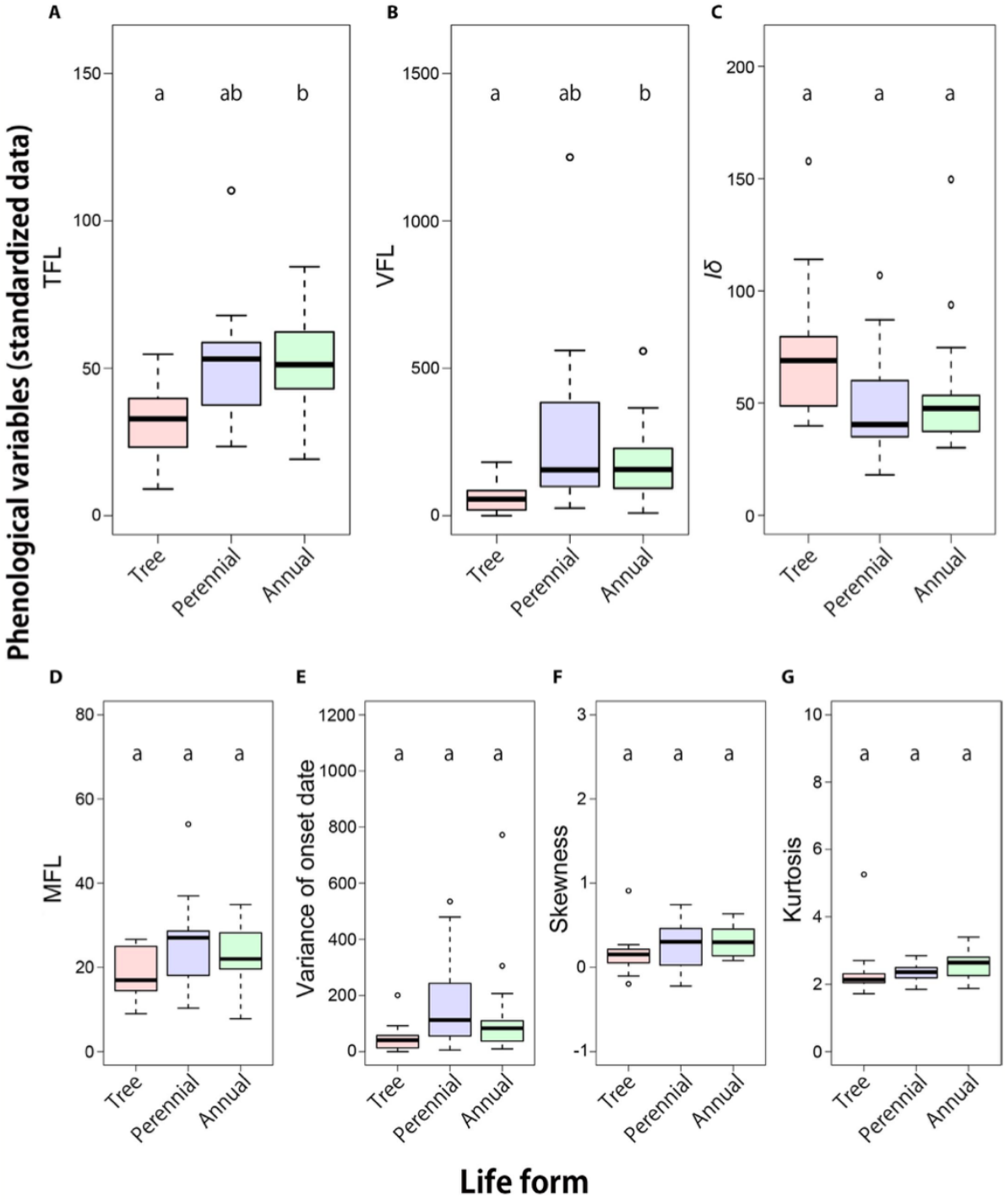


Figure 2.3 Phenological variables of tree, perennial, and annual species for 12 individuals. (A) TFL: total flowering length, (B) VFL: variance of flowering length, (C) *Iδ*, (D) MFL: mean flowering length, (E) variance of onset dates, (F) skewness, and (G) kurtosis of tree (red box; n = 13), perennial herbs (blue box; n = 15), and annual herbs (green box; n =

20) are shown. The black line inside the box shows the median, the box shows the first quartile to the third quartile, the upper and lower lines show the maximum and minimum values in the range of 1.5 times the length of the box, and the white circles show the outliers. The letters above the boxes indicate their significance; different letters indicate a significant difference. Similar trends were observed in the case of 5, 7, 18, and 22 individuals.

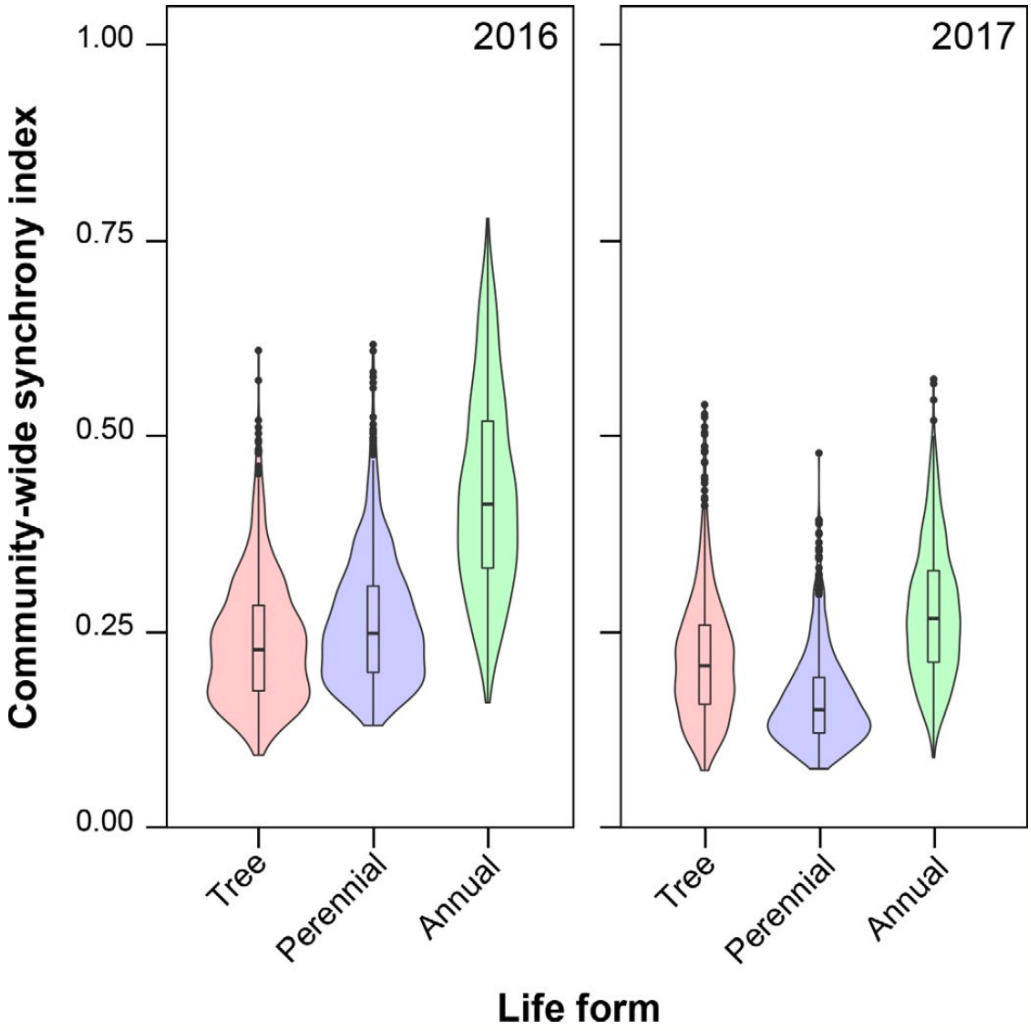


Figure 2.4 Distributions of the community-wide synchrony index in trees (red), perennial herbs (blue), and annual herbs (green) in 2016 (left), and in 2017 (right). The black line inside the box shows the median, the box shows the first quartile to the third quartile, the upper and lower lines show the maximum and minimum values in the range of 1.5 times the length of the box, and the black circles show the outliers.

2.8 Appendices

Appendix S2.1 Details on pollinators observed in trees. Insect flower visitors were monitored by taking a photograph every10 min using programmable digital cameras for trees (Camera; Kuwata 2013) or direct visual observation (Direct).

Family	Observed species	Life form	Method	Hymenoptera	Diptera	Lepidoptera	Coleoptera	Total
Adoxaceae	*Viburnum japonicum* Spreng.	Shrub	Camera	1	33	0	181	220
Apocynaceae	*Trachelospermum asiaticum* Nakai	Woody vine	Camera	0	1	6	0	7
Celastraceae	*Euonymus alatus* (Thunb.) Siebold	Shrub	Camera	2	5	0	0	8
			Direct	22	30	0	14	78
Rosaceae	*Rosa multiflora* Thunb.	Shrub	Camera	1	4	0	5	13
			Direct	63	8	0	1	72
Rosaceae	*Rubus hirsutus* Thunb.	Shrub	Camera	6	7	7	4	25
Ternstroemiaceae	*Eurya japonica* Thunb.	Shrub	Camera	0	18	7	4	29
Asteraceae	*Cirsium japonicum* DC.	Perenial herb	Direct	36	10	15	18	85
Anacardiaceae	*Toxicodendron succedaneum* (L.) Kuntze	Tall tree	Camera	0	14	7	11	32
			Direct	11	22	1	15	49
Cornaceae	*Cornus macrophylla* Wall.	Tall tree	Camera	0	1	1	16	24
			Direct	21	25	2	13	73
Fabaceae	*Albizia julibrissin* Durazz.	Tall tree	Camera	1	0	4	5	11
Fagaceae	*Castanopsis sieboldii* (Makino) Hatus.	Tall tree	Camera	2	16	0	68	95
Oleaceae	*Ligustrum japonicum* Thunb.	Tall tree	Camera	9	5	7	5	35
			Direct	47	11	10	0	71
Rosaceae	*Prunus serrulata* Lindl.	Tall tree	Camera	0	11	0	7	20

Appendix S2.2 Details on plant species monitored.

Family	Species	Life form	Weediness	Reproductive system
Adoxaceae	*Viburnum japonicum* Spreng.	Tree	0	Outcrossing (Kuwata 2013)
Anacardiaceae	*Toxicodendron succedaneum* (L.) Kuntze	Tree	0	Outcrossing (Kuwata 2013)
Apocynaceae	*Trachelospermum asiaticum* Nakai	Tree	0	Outcrossing (Kuwata 2013)
Celastraceae	*Euonymus alatus* (Thunb.) Siebold	Tree	0	Insect (Kuwata 2013)
Cornaceae	*Cornus macrophylla* Wall.	Tree	0	Insect (Kuwata 2013)
Fabaceae	*Albizia julibrissin* Durazz.	Tree	0	Insect (Kuwata 2013)
Fagaceae	*Castanopsis sieboldii* (Makino) Hatus.	Tree	0	Insect (Kuwata 2013)
Lamiaceae	*Premna microphylla* Turcz.	Tree	0	Insect (Kuwata 2013)
Oleaceae	*Ligustrum japonicum* Thunb.	Tree	0	Insect (Kuwata 2013)
Pentaphylacaceae	*Eurya japonica* Thunb.	Tree	0	Insect (Kuwata 2013)
Rosaceae	*Prunus serrulata* Lindl.	Tree	0	Insect (Kuwata 2013)
Rosaceae	*Rosa multiflora* Thunb.	Tree	0	Insect (Kuwata 2013)
Rosaceae	*Rubus hirsutus* Thunb.	Tree*	0	Insect (Kuwata 2013)
Apiaceae	*Cryptotaenia japonica* Hassk.	Perennial	0	Insect**
Asteraceae	*Cirsium japonicum* DC.	Perennial	Roadside (Asai 2016)	Insect**
Asteraceae	*Erigeron philadelphicus* L.	Perennial	Arable (Asai 2012)	Insect**
Crassulaceae	*Sedum bulbiferum* Makino	Perennial	Roadside (Asai 2016)	Vegetable reproduction**
Fabaceae	*Trifolium repens* L.	Perennial	Arable (Asai 2012)	Insect**
Iridaceae	*Sisyrinchium rosulatum* E.P.Bicknell	Perennial	Arable (Asai 2012)	Insect**
Lamiaceae	*Clinopodium gracile* (Benth.) Kuntze	Perennial	Roadside (Asai 2016)	Insect**
Lamiaceae	*Glechoma grandis* (A.Gray) Kuprian	Perennial	Roadside (Asai 2016)	Insect**
Lamiaceae	*Lamium album* L.	Perennial	0	Insect**
Oxalidaceae	*Oxalis corniculata* L.	Perennial	Arable (Asai 2012)	Insect**
Ranunculaceae	*Ranunculus japonicus* Thunb.	Perennial	0	Insect**

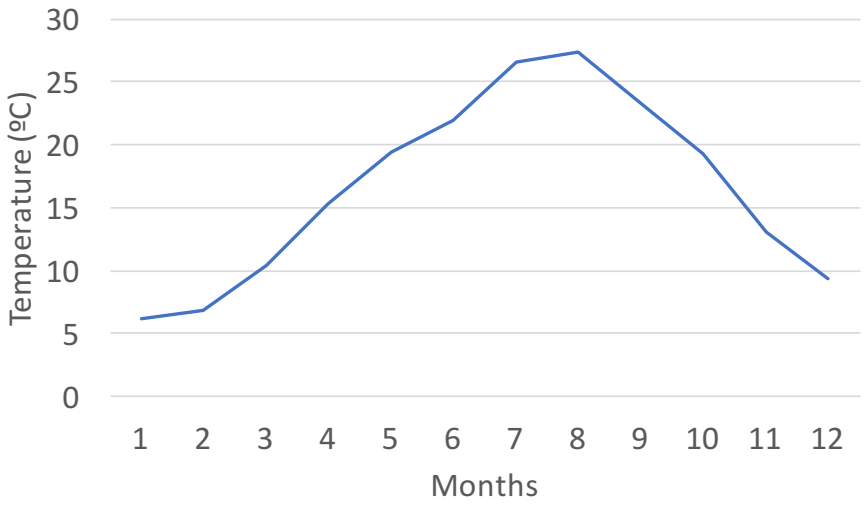
Ranunculaceae	*Ranunculus silerifolius* H.Lév. var. *glaber* (H.Boissieu) Tamura	Perennial	0	Insect**
Ranunculaceae	*Semiaquilegia adoxoides* Makino	Perennial	0	Selfing**
Saururaceae	*Houttuynia cordata* Thunb.	Perennial	Roadside (Asai 2016)	Agamospermy **
Vitaceae	*Cayratia japonica* Gagnep.	Perennial	Roadside (Asai 2016)	Insect**
Apiaceae	*Torilis japonica* DC.	Annual	Arable (Asai 2012)	Insect**
Asteraceae	*Erigeron annuus* (L.) Pers.	Annual	Arable (Asai 2012)	Agamospermy **
Asteraceae	*Youngia japonica* (L.) DC.	Annual	Arable (Asai 2012)	Insect**
Boraginaceae	*Trigonotis peduncularis* Benth. ex S.Moore & Baker	Annual	Arable (Asai 2012)	Selfing**
Caryophyllaceae	*Cerastium glomeratum* Thuill.	Annual	Arable (Asai 2012)	Selfing**
Caryophyllaceae	*Stellaria aquatica* Scop.	Annual	Arable (Asai 2012)	Insect/selfing**
Caryophyllaceae	*Stellaria media* (L.) Vill.	Annual	Arable (Asai 2012)	Selfing**
Caryophyllaceae	*Stellaria neglecta* (Lej.) Weihe	Annual	Roadside (Asai 2016)	Insect/selfing**
Fabaceae	*Trifolium dubium* Sibth.	Annual	Arable (Asai 2012)	Insect**
Fabaceae	*Vicia hirsute* (L.) Gray	Annual	Arable (Asai 2012)	Selfing**
Fabaceae	*Vicia sativa* L. subsp. *nigra* (L.) Ehrh.	Annual	Arable (Asai 2012)	Insect**
Fabaceae	*Vicia tetrasperma* (L.) Schreb.	Annual	Arable (Asai 2012)	Insect**
Geraniaceae	*Geranium carolinianum* L.	Annual	Arable (Asai 2012)	Selfing**
Lamiaceae	*Lamium amplexicaule* L.	Annual	Arable (Asai 2012)	Insect**
Lamiaceae	*Lamium purpureum* L.	Annual	Arable (Asai 2012)	Selfing**
Papaveraceae	*Corydalis incisa* Pers.	Annual	0	Insect**
Plantaginaceae	*Veronica arvensis* L.	Annual	Arable (Asai 2012)	Selfing**
Plantaginaceae	*Veronica hederifolia* L.	Annual	Arable (Asai 2012)	Insect/selfing (Tsuruuchi 1994)
Plantaginaceae	*Veronica persica* Poir.	Annual	Arable (Asai 2012)	Insect/selfing (Tsuruuchi 1994)
Ranunculaceae	*Ranunculus muricatus* L.	Annual	Roadside (Asai 2016)	Insect**

*For the life form of *Rubus hirsutus*, we used the classification of Naruhashi and Terao (1978), who described it as suffruticose or a small shrub. It is intermediate between a tree

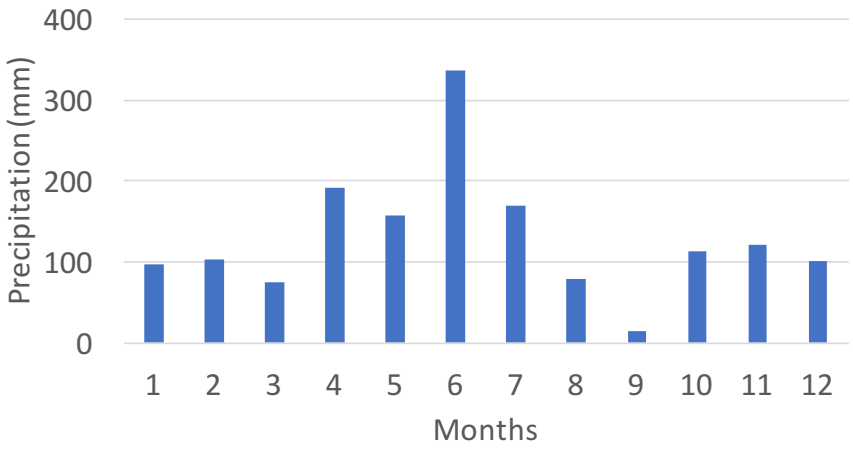
and herb in that stem longevity is from 1 to 1.5 years. Also, its flowering duration is the longest among tree species (Fig. 2.2). Including *R. hirsutus* as a perennial herbs was more advantageous for our conclusion, so to be conservative, we included it as a tree.

** Nagahama & Yahara, unpublished.

(a)



(b)



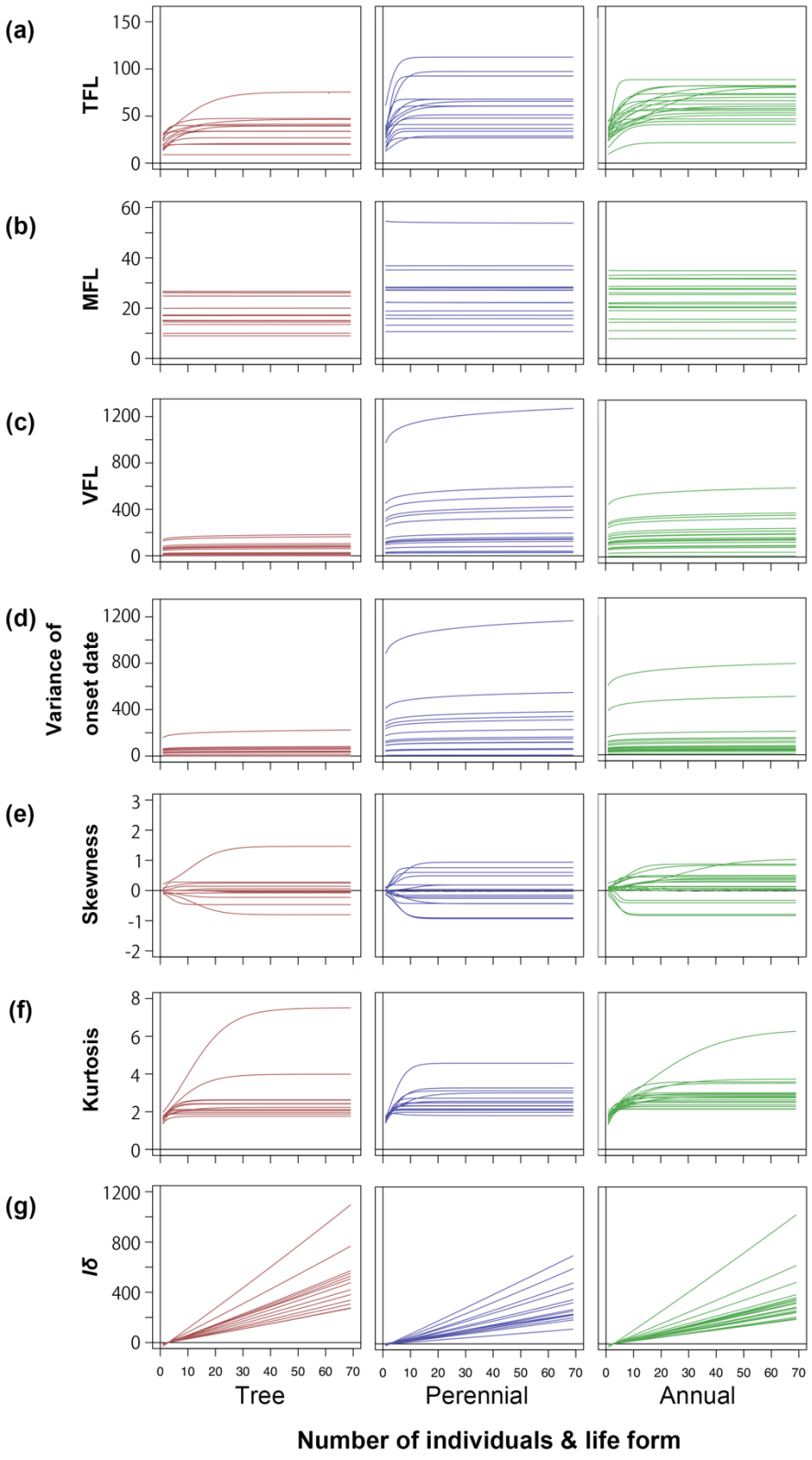
Appendix S2.3 Monthly mean temperature (a) and precipitation (b) in 2016 in the biodiversity reserve of Ito campus, Kyushu University, Fukuoka, Japan. Monthly average temperature ranged from 6.2°C in January to 27.4°C in August (range: 21.2°C) and monthly precipitation ranged from 75.5 mm in March to 337 mm in June (range: 261.5 mm). We removed the precipitation data in September 2016 because of equipment failure. Data were recorded by Kyushu University (2018).

Appendix S2.4 DNA sequences used to construct phylogenetic trees. Species in bold were used for all analyses.

Family	Species	Accession	
		rbcL	***matK***
Adoxaceae	*Sambucus racemosa* L. subsp. *sieboldiana* Blume ex Miq.	AB586169	HQ714381
	Viburnum japonicum Spreng.	HQ591733	HQ591592
	Viburnum awabuki K.Koch	HQ591704	JF95680
Anacardiaceae	*Rhus chinensis* Mill.	GQ436548	KP093558
	Toxicodendron succedaneum (L.) Kuntze	AB983117	KP093670
Apiaceae	*Chamaele decumbens* Makino	D44560	-
	Cryptotaenia japonica Hassk.	DQ006050	HQ593258
	Osmorhiza aristata (Thunb.) Rydb.	D44578	JF954794
	Torilis japonica DC.	D44590	JN895299
Apocynaceae	***Trachelospermum asiaticum*** Nakai	GQ436400	EF456324
Aquifoliaceae	*Ilex integra* Thunb.	FJ394619	KJ687631
	Ilex rotunda Thunb.	JN407236	HQ415255
Araceae	*Arisaema ringens* Schott	KT025754	KT025804
Araliaceae	*Aralia elata* (Miq.) Seem.	KF412439	KF412425
Asparagaceae	*Liriope muscari* L.H.Bailey	KC704932	AB029784
Asteraceae	***Cirsium japonicum*** DC.	GQ436443	HM989744
Asteraceae	***Erigeron annuus*** (L.) Pers.	AB851488	HM989796
	Erigeron philadelphicus L.	JX848412	HQ593287
	Gamochaeta pensylvanica (Willd.) Cabrera	EU384977	EU385354
	Ixeris japonica Nakai	KX527023	KX526560
	Sonchus oleraceus L.	KF196024	KF195980
	Taraxacum officinale F.H.Wigg.	KM361005	AJ633157
	Youngia japonica (L.) DC.	HQ644085	HM989752
Betulaceae	*Alnus sieboldiana* Matsum.	AB060562	AB060053
Boraginaceae	***Trigonotis peduncularis*** Benth. ex S.Moore & Baker	AB744074	-
Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.	D88904	KF923122
	Cardamine scutata Thunb.	JF941125	JF953420
	Lepidium virginicum L.	D88906	HM850737
	Rorippa indica (L.) Hiern	D88907	AF144355
Campanulaceae	*Triodanis perfoliata* (L.) Nieuwl.	EU713363	EU713256
Cannabaceae	*Celtis sinensis* Pers.	LC050727	AF345316
Caprifoliaceae	*Lonicera japonica* Thunb.	HM228498	HM228455
Caryophyllaceae	*Arenaria serpyllifolia* L.	KM360648	AY936304
	Cerastium fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet	KM360705	JN893959
	Cerastium glomeratum Thuill.	HM849882	JN895359
	Stellaria aquatica Scop.	KM360890	FJ404855
	Stellaria media (L.) Vill.	M62570	KP642870
	Stellaria neglecta (Lej.) Weihe	JN892188	JN893860
	Stellaria alsine Hoffm. subsp. *undulata* (Thunb.) Vorosch.	KC484153	HM850778
Celastraceae	*Celastrus orbiculatus* Thunb.	LC006125	LC006126
	Euonymus alatus (Thunb.) Siebold	AB233942 AF530905	EF135537
Commelinaceae	*Commelina communis* L.	JX903248	GQ434279
	Pollia japonica Thunb.	KM895510	FR832815
Cornaceae	***Cornus macrophylla*** Wall.	AF190433	DQ340461
Crassulaceae	***Sedum bulbiferum*** Makino	GQ436423	AF115652
Euphorbiaceae	*Mallotus japonicus* (L.f.) Müll.Arg.	AB267923 AF530857	EF582649
Fabaceae	***Albizia julibrissin*** Durazz.	Z70147	AY386855

	Astragalus sinicus L.	LN873177	AY920450
	Lotus japonicus (Regel) K.Larsen	KM372981	KM372671
	Medicago polymorpha L.	KJ773677	JX505826
	Robinia pseudoacacia L.	U74220	HM049518
	Trifolium dubium Sibth.	HM850412	AF522121
	Trifolium repens L.	GQ436346	AF522131
	Vicia hirsuta (L.) Gray	KP896752	AF522157
	Vicia sativa L. subsp. ***nigra*** (L.) Ehrh.	AB517630	JX505840
	Vicia tetrasperma (L.) Schreb.	KP896751	HM026384
	Wisteria brachybotrys Siebold & Zucc	AB729100	EU424078
Fagaceae	***Castanopsis sieboldii*** (Makino) Hatus.	AB060564	AB060055
	Lithocarpus edulis Nakai	AB060569	AB060060
	Quercus acutissima Carruth.	AB060578	AB060069
	Quercus glauca Thunb.	AB060571	AB060062
	Quercus serrata Murray	AB060576	AB060067
	Quercus variabilis Blume	AB060574	AB060065
Garryaceae	*Aucuba japonica* Thunb.	AY725858	AJ429318
Geraniaceae	***Geranium carolinianum*** L.	JF941753	EU922172
	Geranium thunbergii Siebold ex Lindl. & Paxton	JF941758	JF953875
Hydrangeaceae	*Deutzia crenata* Siebold & Zucc.	JF308656	KP120222
Iridaceae	*Sisyrinchium angustifolium* Mill.	JQ670565	JQ670487
	Sisyrinchium rosulatum E.P.Bicknell	AB744223	HQ606747
Lamiaceae	*Ajuga decumbens* Thunb.	JQ322527	AF315299
	Callicarpa japonica Thunb.	JQ618479	FM163257
	Callicarpa mollis Siebold & Zucc.	HQ384868	HQ384498
	Clinopodium gracile (Benth.) Kuntze	KX527227	KX526669
	Glechoma grandis (A.Gray) Kprian.	AB266226	HQ593314
	Lamium album L.	KM360840	AJ429332
	Lamium amplexicaule L.	AB266225	JN894206
	Lamium purpureum L.	AB266224	HQ384493
	Premna microphylla Turcz.	U28883	HQ427331
	Salvia plebeia R.Br.	AB295077	JQ934085
Lardizabalaceae	*Akebia quinata* (Thunb. ex Houtt.) Decne.	GQ436540	AF542587
Lardizabalaceae	*Stauntonia hexaphylla* Decne.	D85694	FJ626517
Lauraceae	*Cinnamomum yabunikkei* H.Ohba	HM019460	KF740405
Liliaceae	*Cardiocrinum cordatum* Makino	AB034918	AB049523
Menispermaceae	*Cocculus trilobus* DC.	D85696	DQ478611
Moraceae	*Morus alba* L.	KC584883	AY257531
Myricaceae	*Morella rubra* Lour.	KF418924	KF419021
Oleaceae	*Forsythia suspensa* Vahl	GQ436541	FJ263956
	Ligustrum japonicum Thunb.	JF830477	JF830553
Onagraceae	*Oenothera laciniata* Hill.	KJ773700	KJ772960
Orchidaceae	*Spiranthes sinensis* (Pers.) Ames	JF972913	JF972946
Orobanchaceae	*Bellardia viscosa* (L.) Fisch. & C.A.Mey	KM360915	AY849606
Oxalidaceae	***Oxalis corniculata*** L.	AB233943_AF530906	AB233839
	Oxalis debilis Kunth subsp. *corymbosa* (DC.) O.Bolòs & Vigo	KJ773708	HM851018
	Oxalis dillenii Jacq.	L01938	KT456915
Papaveraceae	***Corydalis incisa*** Pers.	KX272421	KU362910
Phrymaceae	*Mazus miquelii* Makino	HQ384872	HQ384502
	Mazus pumilus (Burm.f.) Steenis	FJ172728	HM850959
Pittosporaceae	*Pittosporum tobira* W.T.Aiton	D44582	HQ619824
Plantaginaceae	*Nuttallanthus canadensis* (L.) D.A.Sutton	KJ773632	KJ772895
	Plantago asiatica L.	GQ436317	GQ434075
	Plantago virginica L.	KJ773757	KJ773014
	Veronica arvensis L.	HM850447	AF052003

	Veronica hederifolia L.	KP402621	JN894703
	Veronica persica Poir.	HM850452	HQ384536
Polygonaceae	*Fallopia japonica* (Houtt.) Ronse Decr.	JF950004	EU024772
	Persicaria longiseta (Bruijn) Kitag.	FM883631	EU196943
	Persicaria sagittata (L.) H.Gross	EF653773	KJ840962
	Persicaria thunbergii (Siebold & Zucc.) H.Gross	HQ435356	EF653719
	Rumex acetosa L.	KX095189	KX095187
	Rumex japonicus Houtt.	AB744072	GQ434138
Primulaceae	*Lysimachia japonica* Thunb.	KJ841403	JN895201
Ranunculaceae	***Ranunculus japonicus*** Thunb.	FJ449862	AY954200
	Ranunculus muricatus L.	HM850296	AY954191
	Ranunculus sceleratus L.	AB517148	GU257993
	Ranunculus silerifolius H.Lév. var. ***glaber*** (H.Boissieu) Tamura	FJ449861	HQ338367
	Semiaquilegia adoxoides Makino	EF437147	EF437137
Rosaceae	***Prunus serrulata*** Lindl.	AB729085	KP760073
	Potentilla anemonifolia Lehm.	GQ436578	GQ434187
	Potentilla indica (Andrews) Th.Wolf	KX527251	KT808472
	Rhaphiolepis indica (L.) Lindl. var. *umbellata* (Thunb. ex Murray) H.Ohashi	AB936040	AB936041
	Rosa multiflora Thunb.	KP402729	FJ472524
	Rosa multiflora Thunb. var. *adenochaeta* (Koidz.) Ohwi ex H.Ohba	-	AB039305
	Rosa sambucina Koidz.	KP095034	AB039306
	Rubus hirsutus Thunb.	GU363792	JN566120
	Rubus parvifolius L.	GU363802	AB073699
Rubiaceae	*Galium kikumugura* Ohwi	JX848534	HQ593306
	Galium spurium L.	KM980627	KJ204484
	Paederia foetida L.	KC305913	AY538409
Salicaceae	*Salix triandra* L.	FJ788587	EU790687
Saururaceae	***Houttuynia cordata*** Thunb.	AB205610	AF543737
	Saururus chinensis Hort. ex Loudon	AF332101	GQ434225
Schisandraceae	*Kadsura japonica* (L.) Dunal	KP689922	AF542565
Smilacaceae	*Smilax china* L.	D28333	AB040204
Staphyleaceae	*Euscaphis japonica* (Thunb.) Kanitz	DQ307099	DQ663628
Styracaceae	*Styrax japonica* Siebold & Zucc.	Z80189	-
Symplocaceae	*Symplocos kuroki* Nagam.	AB729084	AB925051
Ternstroemiaceae	***Eurya japonica*** Thunb.	AF380039	AF380081
Theaceae	*Camellia japonica* L.	AF380035	KU054403
Urticaceae	*Boehmeria nivea* (L.) Gaudich.	AB125345	KP093304
Verbenaceae	*Verbena brasiliensis* Vell.	HQ644080	GQ434146
Violaceae	*Viola japonica* Langsd. ex Ging.	JQ950626	DQ842592
	Viola verecunda A.Gray	JQ950629	DQ842580
Vitaceae	*Ampelopsis glandulosa* (Wall.) Momiy. var. *heterophylla* (Thunb.) Momiy.	KT006333	KX526800
	Cayratia japonica Gagnep.	AB851492	KX526802


(a)
TFL
150
100
50
0
(b)
MFL
60
40
20
0
(c)
VFL
1200
800
400
0
(d)
Variance of onset date
1200
800
400
0
(e)
Skewness
3
2
1
0
-1
-2
(f)
Kurtosis
8
6
4
2
0
(g)
Iδ
1200
800
400
0
0 10 20 30 40 50 60 70
Tree
0 10 20 30 40 50 60 70
Perennial
0 10 20 30 40 50 60 70
Annual
Number of individuals & life form

Appendix S2.5 Rarefaction–extrapolation curves for seven phenological variables for 13 species of trees, 15 perennial herbs, and 20 annuals. (a) TFL: total flowering length, (b) MFL: mean flowering length, (c) VFL: variance of flowering length, (d) variance of onset dates, (e) skewness, (f) kurtosis (the deviation from normal distribution and describes the weight of the distribution tail), (g) Morisita aggregation index ($I\delta$; larger values represent higher synchrony among individuals).

Appendix S2.6 Model selection using Bayesian information criterion (BIC). Bold numbers are the smallest values for each phenological variable. Total flowering length of species (TFL), mean flowering length of individuals (MFL) and its variance (VFL).

Phenological variables	**Linear**		**Quadratic**		**Logarithmic**		**Logistic**	
	Df	**BIC**	**Df**	**BIC**	**Df**	**BIC**	**Df**	**BIC**
TFL	3	-1312.1	4	-1498.7	3	-1765.8	4	**-2078.1**
MFL	3	-5964.1	4	-5962.8	3	**-5969.1**	4	-5965.9
VFL	3	-3866.0	4	-3866.2	3	**-3867.0**	4	-3861.5
Variance of onset date	3	-3843.5	4	-3836.7	3	**-3843.8**	4	-3836.7
Skewness	3	1642.0	4	1585.4	3	1569.5	4	**1562.8**
Kurtosis	3	-1735.0	4	-1890.7	3	-2083.1	4	**-2263.5**
$I\delta$	3	-23499.2	4	**-24245.2**	3	-4053.4	4	-14300.2

Appendix S2.7 Tests of phylogenetic signals.

Dataset	Raw data		n = 5		n = 7		n = 12		n = 18		n = 22	
Phenological variables	*K*	*P*-value	*K*	*P*-value	*K*	*P*-value	*K*	*P*-value	*K*	*P*-value	*K*	*P*-value
TFL	0.242	0.155	0.238	0.174	0.236	0.176	0.235	0.219	0.229	0.217	0.229	0.201
MFL	0.114	0.903	0.204	0.352	0.204	0.358	0.204	0.334	0.204	0.366	0.204	0.331
VFL	0.159	0.553	0.232	0.335	0.231	0.372	0.229	0.393	0.228	0.388	0.227	0.429
Variance of onset date	0.140	0.640	0.238	0.315	0.238	0.300	0.239	0.311	0.239	0.319	0.240	0.282
Skewness	0.163	0.557	0.276	0.086	0.223	0.190	0.219	0.246	0.209	0.317	0.206	0.298
Kurtosis	0.191	0.413	0.179	0.486	0.179	0.541	0.163	0.625	0.185	0.561	0.175	0.601
$I\delta$	0.362	0.106	0.239	0.236	0.248	0.216	0.256	0.185	0.259	0.175	0.229	0.234

Appendix S2.8 GLMMs examining the effects of year and the number of observed individuals on phenological variables. GLMMs examining the effects of year and the number of observed individuals on phenological variables including total flowering length of species (TFL), mean flowering length of individuals (MFL) and its variance (VFL). * $p < 0.05$, *** $p < 0.005$.

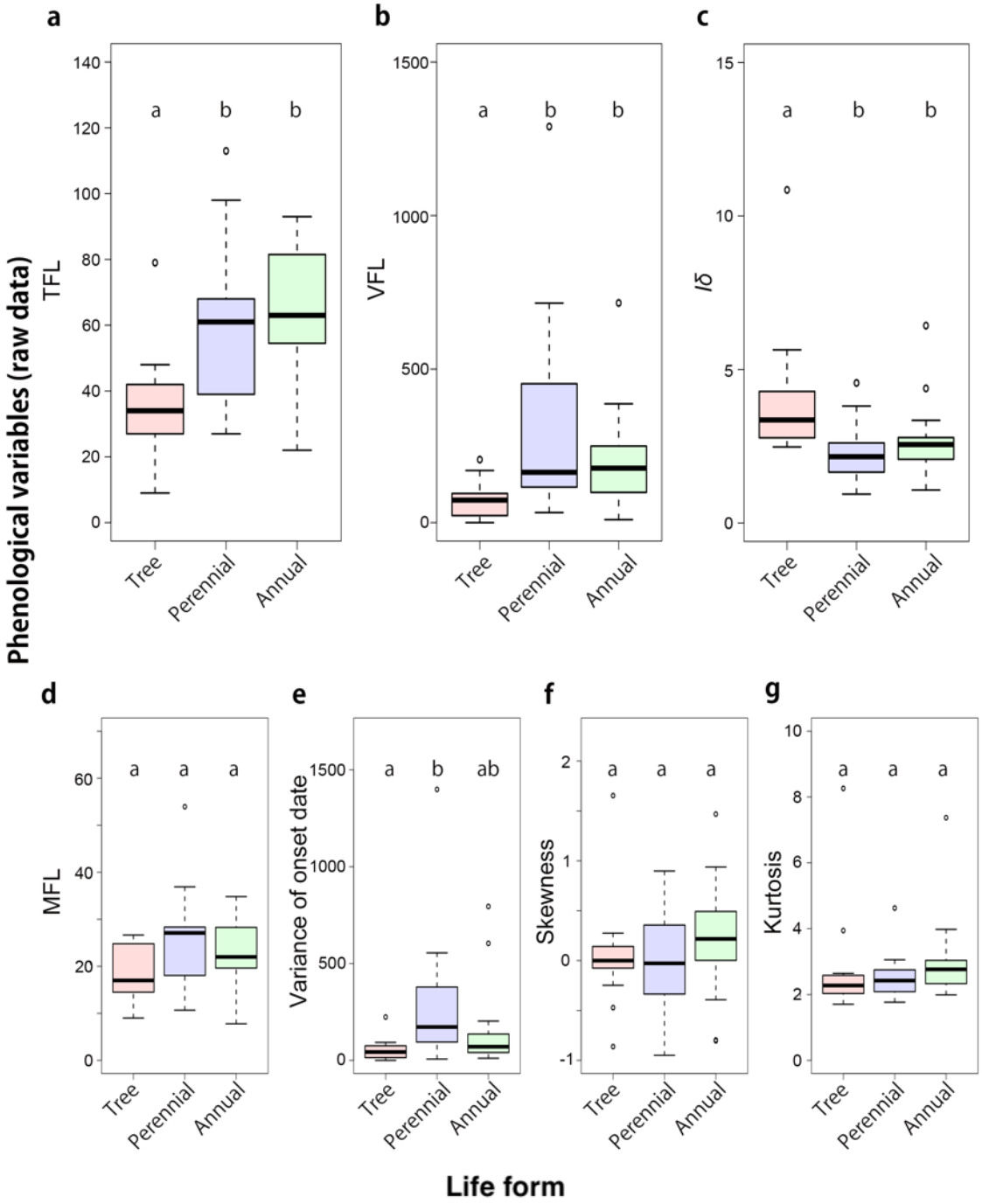
Phenological variables	**Explanatory variables**						
	Intercept	**Year**			**Number of observed individuals**		
		Slope	***P*-value**		**Slope**	***P*-value**	
TFL	3.50	-0.02	0.75		0.02	0.00	***
MFL	2.81	-0.12	0.20		0.01	0.03	*
VFL	4.42	-0.38	0.10		0.02	0.11	
Variance of onset date	3.71	0.70	0.02	*	0.00	1.00	
Skewness	-	-	-		-	-	
Kurtosis	1.01	-0.17	0.06		0.00	0.50	
$I\delta$	1.86	0.08	0.40		-0.02	0.04	*

Appendix S2.9 LMM examining the effects of year and the number of observed individuals on skewness. ** $P < 0.01$.

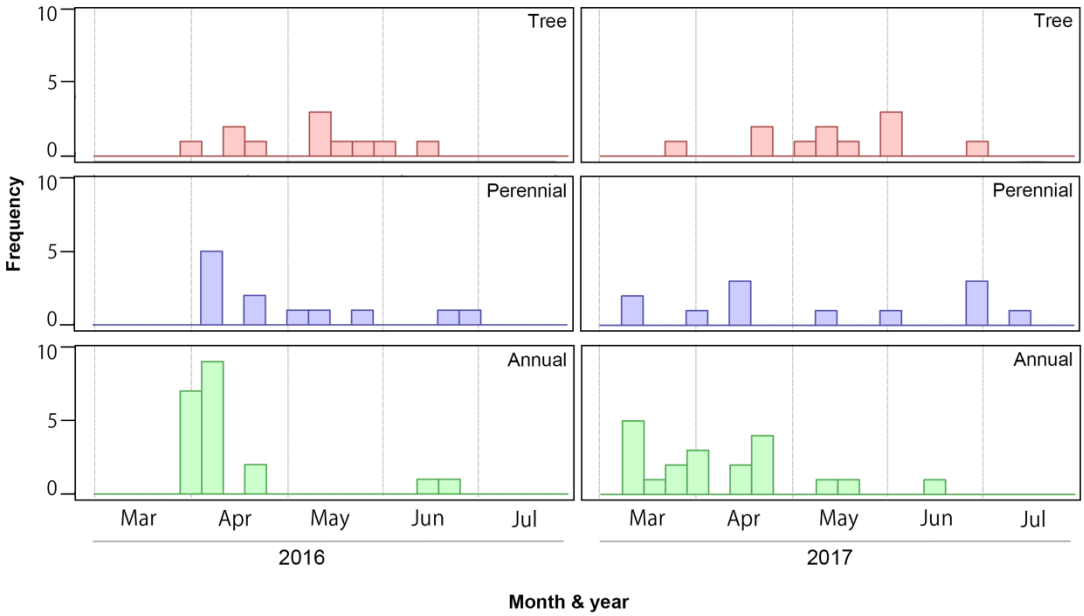
Model	χ^2	**df**	***P***	
1	9.34	1	0.00	**
2	0.00	0	1.00	

Appendix S2.10 Tests among life forms for each phenological variable for 5, 7, 18, and 22 individuals, and the raw data. Student's *t* test, Wilcoxon rank sum test, or Fligner-Policello test was used depending on normality and variance of groups. *P*-values were adjusted using the Holm method. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

Dataset		***n* = 5**			***n* = 7**			***n* = 18**			***n* = 22**		
Variable	**Pairs**	**Test statistic**	***P***		**Test statistic**	***P***		**Test statistic**	***P***		**Test statistic**	***P***	
TFL	Tree–Perennial	60.00	0.177		63.00	0.237		66.00	0.311		66.00	0.311	
	Perennial–Annual	121.00	0.347		120.00	0.330		112.00	0.311		111.00	0.311	
	Annual–Tree	2.86	0.022	*	2.97	0.017	*	3.03	0.015	*	3.06	0.013	*
MFL	Tree–Perennial	-1.58	0.251		-1.58	0.253		-1.56	0.262		-1.56	0.264	
	Perennial–Annual	0.07	0.948		0.07	0.946		0.07	0.943		0.07	0.942	
	Annual–Tree	2.21	0.105		2.20	0.106		2.18	0.111		2.18	0.112	
VFL	Tree–Perennial	-1.89	0.117		-1.89	0.117		-1.89	0.117		-1.84	0.131	
	Perennial–Annual	-0.71	0.481		-0.67	0.500		-0.71	0.479		-0.71	0.479	
	Annual–Tree	200.00	0.027	*	200.00	0.027	*	199.00	0.030	*	199.00	0.030	*
Variance of onset date	Tree–Perennial	-1.73	0.250		-1.73	0.250		-1.73	0.250		-1.73	0.250	
	Perennial–Annual	0.41	0.683		0.44	0.661		0.44	0.661		0.44	0.661	
	Annual–Tree	1.06	0.581		1.10	0.547		1.22	0.448		1.30	0.390	
Skewness	Tree–Perennial	-0.26	1.000		-0.71	0.971		87.00	0.988		87.00	1.000	
	Perennial–Annual	-0.30	1.000		-0.19	0.971		-0.69	0.988		-0.66	1.000	
	Annual–Tree	0.94	1.000		1.27	0.640		174.00	0.329		177.00	0.260	
Kurtosis	Tree–Perennial	-0.90	0.752		69.00	0.401		-1.33	0.367		-1.28	0.400	
	Perennial–Annual	-0.17	0.868		-0.51	0.615		-1.05	0.367		-1.18	0.400	
	Annual–Tree	1.22	0.691		179.00	0.221		2.01	0.135		1.95	0.153	
Iδ	Tree–Perennial	1.92	0.132		146.00	0.066		149.00	0.048	*	150.00	0.043	*
	Perennial–Annual	146.00	0.908		141.00	0.780		132.00	0.564		132.00	0.564	
	Annual–Tree	73.00	0.108		68.00	0.066		65.00	0.048	*	64.00	0.043	*


a
b
c
d
e
f
g
Phenological variables (raw data)
TFL
VFL
Iδ
MFL
Variance of onset date
Skewness
Kurtosis
Tree
Perennial
Annual
Life form

Appendix S2.11 The results of comparing raw data for each phenological variable for the species among life forms. (a) TFL: total flowering length, (b) VFL: variance of mean flowering length, (c) Iδ, (d) MFL: mean flowering length, (e) variance of onset dates, (f) skewness, and (g) kurtosis of tree (red box; n = 13), perennial herbs (blue box; n = 15), and annual herbs (green box; n = 20) are shown. The black line inside the box shows the median, the box shows the first quartile to the third quartile, the upper and lower lines show the maximum and minimum values in the range of 1.5 times the length of the box, and the white circles show the outliers. The letters above the boxes indicate significance; different letters indicate a significant difference.



Appendix S2.12 Distributions of flowering onset date for trees (red), perennial herbs (blue), and annual herbs in 2016 (left), and in 2017 (right). Vertical axis shows number of species that started to flower.

Appendix S2.13 Differences in the distributions of onset date from normal.

	2016			2017		
Life form	Skewness	*z*	*P*	Skewness	*z*	*P*
Tree	-0.06	-0.11	0.910	-0.27	-0.50	0.615
Perennial	0.91	1.65	0.098	0.14	0.26	0.798
Annual	2.45	4.04	0.000	0.80	1.71	0.088

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Chapter 3: Phenology of tropical montane forests in Southern Vietnam: Leafing is associated with precipitation but flowering is not

3.1 Introduction

In East and Southeast Asia, forests have been classified to temperate forests, tropical seasonal forests, and tropical rain forests (Peel *et al.* 2007), where specific phenological patterns are observed (Kira 1991). In the temperate forests, environmental factors such as day length, temperature, and precipitation change predictably throughout the year, providing reliable signals for plants to sense seasonal progress (Borchert *et al.* 2005; Lechowicz 1984; Rathcke & Lacey 1985; Sakai & Kitajima 2019). Consequently, species in temperate forests mainly develop new leaves in spring, bloom from spring to summer, and bear fruits mainly in autumn (Edwards *et al.* 2017; Nagahama & Yahara 2019; Zhang *et al.* 2007). Similarly, in tropical seasonal forests, precipitation changes predictably through the year, forming rainy and dry seasons, and plants can sense seasonal progress by monitoring water availability (Rathcke & Lacey 1985). Consequently, in tropical seasonal forests, plants have a peak of leafing in either wet or dry season depending on the accessibility to deeper water (Wright & van Schaik 1994), a peak of flowering at the end of the dry season, and a peak of fruiting early in the wet season (Kurten *et al.* 2018). In contrast, in the tropical rain forests, annual fluctuations in temperature and precipitation are much lower and unpredictable than in temperate or tropical seasonal forests. Consequently, species in the tropical rain forests bloom through the year, or only in years with exceptionally low rainfall and low temperature (Ichie *et al.* 2004; Nakagawa *et al.* 2019; Sakai *et al.* 1999). The latter is called supra-annual flowering or general flowering (Sakai 2002). It is notable that species common to the tropical seasonal and rain forests usually bloom each year in the former but every few years in the latter (Kurten *et al.* 2018).

These generalizations on the phenology of tropical forests are, however, based on observations in lowland forests where most of previous studies have been made. The phenology in the tropical montane forests, that develop above alt. 1000 m and have species composition different from lowland forests (Kira 1991), is still poorly understood in Asia. Phenological studies in the tropical montane forests are important particularly in Asia because many primitive angiosperms are found there (Axelrod 1966; Morlay 2001) and phenological patterns in the tropical montane forests may provide clues in inferring ancestral phenological states of forests in Asia. According to Axelrod (Axelrod 1966), angiosperms evolved in the tropical mountains during the Cretaceous period. In the process of expanding the distribution of angiosperms after Cretaceous, deciduousness evolved as an adaptation to dry climates in the northern hemisphere, while evergreenness have been maintained as an adaptation to climates without dry season in the southern hemisphere. According to this hypothesis, the phenology of species growing in the tropical montane forests in Southeast Asia is regarded as an ancestral state in angiosperms. Therefore, our understanding on the relationship between phenology and meteorological factors in the tropical montane forests of Southeast Asia will help reconstruct the history of phenological divergence from tropical montane forests to tropical lowland and temperate forests.

In the tropical montane forests of Southeast Asia, the relationship between phenology and meteorological factors has been studied only in Mt. Kinabalu, Malaysia (Nomura *et al.* 2003 for leafing; Kimura *et al.* 2009 for flowering and fruiting). The average annual temperature and average annual precipitation of 1560 m at Mt. Kinabalu are 18.9 ºC and 2,714 mm, respectively, but the precipitation will decrease significantly in the year when El Niño occurs. The average monthly temperature changes from 16.5 ºC

(January) to 19.5 ºC (September), and the average monthly precipitation changes from 100 mm (June) to 550 mm (November). Annual changes in precipitation have negative correlation with solar radiation. According to a study of leafing phenology (Nomura *et al.* 2003), tree species in the lower mountain forests (elev. 1560 m) developed new leaves after the dry period caused by El Niño, while tree species in the upper mountain forests (elev. 2590 m) developed new leaves during and after the dry period caused by El Niño. In contrast, tree species in subalpine zone (elev. 3081 m) developed new leaves through the year. Those results show that the meteorological factors affecting the leaf phenology varied by altitude. According to a study of flowering and fruiting phenology observed at elev. 1600–1800 m (Kimura *et al.* 2009), flowering was observed twice per year, in June (a season when temperature rises) and January (a season when temperature drops) and was correlated only with temperature, but fruiting was observed once a year for most species and was correlated with both temperature and solar radiation. This study, however, examined only 8 species of *Medinilla* (Melastomataceae) and it remains uncertain whether the observed patterns are common to many other plant groups native in Mt. Kinabalu.

Although these studies provide valuable data for a preliminary understanding of the phenology of tropical mountain forests in Asia, it is difficult to generalize the relationships between meteorological factors and phenologies shown by Nomura *et al.* (2003) and Kimura *et al.* (2009) at Mt. Kinabalu to all tropical montane forests in Southeast Asia. This is because the climate conditions are not uniform throughout Southeast Asia. For precipitation frequently used as a cue of phenological changes by plants, annual change is not significant in Mt. Kinabalu, but significant in Mainland Southeast Asia, creating a difference between the dry and rainy seasons (Kumagai *et al.*

2005). In addition, annual precipitation is higher in Mt. Kinabalu (2510–5000 mm) than in southern Vietnam (2000 mm), which is the most rainy region in Mainland Southeast Asia (Hijmans *et al.* 2005). Thus, the relationship between meteorological factors and phenology in the tropical montane forests of Mainland Southeast Asia is expected to be different from that of Mt. Kinabalu.

In this study, we observed leafing, flowering, and fruiting phenology every three months in five plots located between 1460m and 1920 m of Bidoup-Nui Ba National Park, Vietnam, in Mainland Southeast Asia. In Bidoup-Nui Ba National Park, the monthly average temperature changes by only 3.6°C per year and the annual average is 18.7ºC, but the average monthly precipitation varies from 10 mm in January to 281 mm in September, with an average annual precipitation of 1678 mm (Fick & Hijmans 2017). Under those annual changes in precipitation, there is a distinct dry season (December-March) and rainy season (April-November). The forest of Bidoup-Nui Ba National Park is mainly composed of broadleaved evergreen trees of Fagaceae, Lauraceae, and others, and some deciduous tree species such as Acer (Sapindaceae) are also common (Nagahama *et al.* 2019). To characterize patterns of leafing, flowering, and fruiting phenology in the tropical montane forests of Bidoup-Nui Ba National Park, we addressed the following two questions.

(1) What kind of leafing, flowering, and fruiting patterns is observed in tropical montane forests in Vietnam?

(2) Which meteorological factors correlate with leafing, flowering and fruiting patterns in tropical montane forests in Vietnam?

3.2 Material and Methods

3.2.1 Study site

Leafing, flowering, and fruiting phenology was observed in five plots located along the elevation from 1460 m to 1920 m in Bidoup-Nui Ba National Park in southern Vietnam (Table 3.1; Fig. 3.1), Lam Dong Province, southern Vietnam. In this area, monthly average temperature varies from 16.7°C in January to 20.3°C in May (3.6°C difference), and monthly precipitation varies from 10 mm in January to 281 mm in September (271 mm difference; Fick & Hijmans 2017; Appendix S3.1). Dry season is from April to November and rainy season is from December to March.

3.2.2 Observations

Five plots for phenological observations were located at Giang Ly (GL), Hon Giao (HG), Dung Iar Reing (DIG), Cong Troi (CT), and Langbian (LB; Table 3.1; Fig. 3.1). The size of plots varied from 1000 m2 (10 m x 100 m; HG) to 2500 m2 (50 m x 50 m; DIG). The distance between the westernmost plot (CT) and the easternmost plot (HG) was 45 km. The elevation of five plots was from 1460 m (GL) to 1920 m (LB). In June 2018, we recorded girth and height for all tree individuals 4 m or taller in each plot and attached a number tag to the trunk of each individual. We distinguished species in the field and collected a voucher specimen of each species for identification and small pieces of leaves for DNA analysis. We identified species based on molecular phylogeny and morphology using taxonomic literature and type specimen images (Nagahama *et al.* 2019). For Fagaceae and Lauraceae with many similar species difficult to be distinguished in the fields, we collected a specimen for each tree. Based on the abundance record of each species, 20 dominant tree species were selected in each plot and, and for each of the

selected dominant species, five individuals with larger girth were selected for phenological observations. Among 100 species for which we recorded phenological states, seven species had one or two individuals due to misidentification in the first records of June 2018. Then, we removed these seven species from the following analysis.

We recorded phenological states as binary values: presence/absence of new leaves, flowers, and fruits. We recorded leafing, flowering, and fruiting events in a total of 91 species (17 spp. in CT, 18 spp. in DIG and HG plot, 19 spp. in LB and GL plots) in the plots in June, September, and December of 2018, April, July, and October of 2019, and January 2020 (only one individual was observed for each species in June 2018). In some species, flowers and fruits were rare, often only in very large trees. For those species, we also searched for flowering and fruiting trees around the plots, and when found, recorded flowering and fruiting events.

3.2.3 Meteorological data collection

Data of precipitation and temperature were obtained from the weather database WorldClim (Fick & Hijmans 2017). Data of day length was obtained from Worldwide Elevation Map Finder (https://elevation.maplogs.com/).

3.2.4 Categorizing phenological patterns

Considering sample size, we pooled data from five plots in the following analyses. For 91 species that we observed in five plots, we calculated the proportions of leafing, flowering, and fruiting species in each observation using Excel for Mac (16.16.12). We summarized phenological variation of 91 species by principal component analysis (PCA) and classified phenological patterns by clustering analysis, using presence/absence data

of new leaves, flowers, or fruits in seven observations. We performed PCA using the function "prcomp" in R (3.4.3; R core Team 2017). We calculated phenological similarity among species and meteorological similarity among observed months by squared Euclidean distance using the function "dist" in R (3.4.3) and constructed dendrograms using UPGMA method. Before performing PCA and clustering analysis, we confirmed that there is no large multicollinearity between the explanatory variables using Variance Inflation Factor (VIF).

3.2.5 Relationship between phenology and meteorological factors

We examined how the number of leafing, flowering, or fruiting species varies with precipitation, temperature, or daylength using Generalized Linear Models (GLMs) with logit link function and binomial distribution of errors. Three meteorological factors were strongly correlated with each other (Appendix S3.2). Thus, we summarized these correlations by the following methods. First, we performed PCA for six variables including temperatures, precipitations, and daylengths of current and previous months, and we tested the relationship between phenology and meteorological factors using GLMs with PC1 and PC2 as explanatory variables. Second, we performed two regression analyses, one between daylength and precipitation, and another between daylength and temperature, and determined residuals in each regression. Then, we tested the relationship using GLMs with daylength, residual precipitation, and residual temperature as explanatory variables. All calculations were performed by R (3.4.3).

3.2.6 Comparison of phenological patterns among forests in East and Southeast Asia

Based on previous studies, we compared phenological patterns of leafing, flowering, and fruiting in well-studied locations of aseasonal tropical, seasonal tropical, subtropical, and temperate zones (Table 3.2). Each phenological record was averaged into annual (twelve months) records and calculated into percentage data (Appendix S3.3).

Because there is no annual resting season throughout the tropics, the year should be considered as a circular continuum to interpret plant phenology (Morellato *et al.* 2010). Therefore, we transformed the datasets onto a circular scale and confirmed their modality by Kuiper's test (null hypothesis: circular uniform distribution; Kuiper 1960; Mardia & Jupp 2000) using R package 'circular' (Lund *et al.* 2017).

We calculated variances of the number of leafing, flowering, and fruiting species at nine locations, and used them to categorize their patterns. If the variance was less than 0.5, the pattern was considered highly peaked; otherwise the pattern was considered low peaked (extended pattern). Using highly/low peaked data of leafing, flowering, and fruiting and climate zone categories (Table 3.2), we constructed a maximum parsimony tree to examine the similarity of phenological patterns between locations. In this construction, Mt. Kinabalu was set as the root. We used PHYLIP (Felsenstein 1989) for this construction.

We also calculated meteorological similarity and classified annual patterns of daylength, temperature, precipitation of nine locations by clustering analysis with squared Euclidean distance, using 30 years historical climate data from WorldClim database (Fick & Hijmans 2017).

3.3 Results

3.3.1 Species composition

In five plots, we recorded 3,859 tree individuals. These trees belonged to 56 families (Fig. 3.2). Fagaceae was the most common family (448 individuals; 11.6%) followed by Lauraceae (412 individuals; 10.7%), Rubiaceae (370 individuals; 9.6%), Symplocaceae (311 individuals; 8.1%), and Rosaceae (185 individuals; 4.8%). The rest 2,133 individuals (55.3 %) belonged to the other 57 families or unknwon families. Fifteen families were represented only by a single individual.

Among the 19 dominant tree species in LB plot (Appendix S3.4; one among 20 species was excluded because of limited sample size), *Claoxylon langbiangense* A.Nagah. & Tagane (Euphorbiaceae; Nagahama et al. *in press*) was the most common species (43 individuals; 11.6%), which appeared almost twice as often as the second common species, *Prunus wallichii* Steud. (Rosaceae; 27 individuals; 7.3%). In CT plot, *Quercus bidoupensis* H.T.Binh & Ngoc was the most common species (61 individuals; 10.7%), which appeared nearly three times as often as the second common species, *Melicope pteleifolia* (Champ. ex Benth.) T. Hart. (Rutaceae; 22 individuals; 3.9%). In HG plot, two species of Rubiaceae, *Diplospora* sp. (119 individuals; 7.7%) and *Urophyllum* sp. (109 individuals; 7.1%), had more than 100 individuals within a plot. In DIG plot, *Quercus* sp. (Fagaceae) was the most common species (63 individuals; 7.9%) followed by *Symplocos acuminata* (Fagaceae; 55 individuals; 6.9%) and *Litsea* sp. (Lauraceae; 41 individuals; 5.2%). In GL plot, *Adinandra donnaiensis* Gagnep. ex Kobuski (Pentaphylacaceae) was the most common species (48 individuals; 7.5%) followed by *Melicope pteleifolia* (Rutaceae; 43 individuals; 6.8%) and *Symplocos hayatae* K. Mori (Symplocaceae; 34 individuals; 5.3%). Among monitored tree species, only four species, *Meliosma pinnata*

(Roxb.) Maxim. (Sabiaceae) in GL plot, and *Acer erythranthum* Gagnep., *A. flabellatum* Rehder (Sapindaceae) and *Engelhardia serrata* Blume (Juglandaceae) in LB plot, were deciduous species and others were evergreen species.

3.3.2 Phenological pattern

Among 91 monitored species, we recorded leafing, flowering, and fruiting events for 91 spp. (100.0 %), 65 spp. (71.4%), and 54 spp. (59.3 %), respectively. The number of leafing species varied 4.6 times, from 20 spp. (22.0%) in June to 91 spp. (100%) in April (Fig. 3.3a). The number of flowering species varied 2.2 times, from 15 spp. (16.5%) in September to 33 spp. (36.3%) in December (Fig. 3.3b). The number of fruiting species varied 2.3 times, from 12 spp. (13.2%) in January to 27 spp. (29.7%) in July (Fig. 3.3c).

The phenological variations of leafing, flowering, and fruiting events were summarized into four principal components (Table 3.3; PC1 to PC4): 77.6%, 77.8%, and 80.2% of the total variance, respectively. In all of leafing, flowering, and fruiting data, all of presence records in seven observation months positively contributed to PC1. In contrast, presence records positively or negatively contributed to PC2, PC3, and PC4 (Table 3.3).

3.3.3 Leafing phenology

In leafing phenology, the first, second, third, and fourth principal components accounted for 27.5%, 19.8%, 16.3%, and 14.0% of the total variance (Table 3.3). A group of 8 species characterized by leafing only in January and April had the highest PC1 score (Fig. 3.4a). Conversely, *Maesa perlaria* (Lour.) Merr., *Urophyllum* sp. 1, and *Saurauia napaulensis* DC. had new leaves in all 7 times and had the lowest PC1 scores.

By a clustering analysis, 91 species can be classified to three groups, designated as Group 1–3 in Fig. 3.5. Species of Group1 showed new leaves at low frequency, had high PC1 scores, and expanded new leaves in April but rarely in June, September, and October. Group 1 included one deciduous species (*Meliosma pinnata*) and 40 evergreen species. Species of Group 2 showed new leaves at high frequency, had low PC1 scores, and expanded new leaves in most observed months. Group 2 included two deciduous species (*Acer flabellatum* and *Engelhaldia serrata*) and 44 evergreen species. Species of Group 3 showed new leaves at low frequency, had low PC1 scores, and expanded new leaves usually in April and June, not in July, October, and September. Group 3 included one deciduous species (*Acer erythranthum*) and three evergreen species.

By another clustering analysis, observed months can be classified to two groups (Fig. 3.5): January, April, July, and December when many species expanded new leaves, and June, September, and October when some species of Group 2 expanded new leaves.

3.3.4 Flowering phenology

In flowering phenology, the first, second, third, and fourth principal components accounted for 32.0%, 19.2%, 15.5%, and 11.0% of the total variance (Table 3.3). A group of 26 species characterized by no flowering events had the lowest PC1 scores. Conversely, three species, *Melicope pteleifolia* in plot GL, *Diplospora hongiaoensis*, and *Maesa* sp. flowered five or six times and had high PC1 scores.

By a clustering analysis, 91 species can be classified to three groups designated as Group 1–4 in Fig. 3.6. Species in Group 1 flowered frequently in dry season (December and January) and had high PC1 scores. Group 1 included 15 evergreen species. Species of Group 2 flowered at low frequently, or did not bloom in our observation periods, and

had low PC1 scores. Group 2 included four deciduous species and 56 evergreen species. Species of Group 3 flowered frequently in late wet season (September, and October), and had intermediate PC1 scores. Group 3 included seven evergreen species. Species of Group 4 flowered frequently in the beginning of wet season (April, June, and July), and had intermediate PC1 scores. Group 4 included nine evergreen species.

By another clustering analysis, observed months can be divided into three groups: (1) April and July when Group 4 species frequently flowered, (2) June, September, and October when Group 3 species frequently flowered, and (3) January and December when Group 1 species frequently flowered.

3.3.5 Fruiting phenology

In fruiting phenology, the first, second, third, and fourth principal components accounted for 42.2%, 16.4%, 11.8%, and 9.9% of the total variance (Table 3.3). A group of 37 species characterized by no fruiting events had the highest PC1 score. Conversely, *Maesa* sp., *Illicium* sp., and *Litsea* sp. set fruits all observation months except January and had high PC1 scores.

By another clustering analysis, 91 species can be classified to two groups designated as Group 1 and 2 in Fig. 3.7. Species of Group 1 set fruits at high frequency and had high PC1 scores. Species of Group 2 set fruits at low frequency or did not fruit and got low PC1 scoress.

By another clustering analysis, observed months can be divided into two groups: (1) June, July, and September (middle of wet season), (2) January, April, October, and December (the beginning and end of wet season, and dry season).

3.3.6 Relationship between phenology and meteorological factors

Both temperature and precipitation were highly correlated with daylength (Fig. 3.8); correlation coefficients between temperature vs. daylength and precipitation vs. daylength were 0.89 and 0.83, respectively. It is notable that correlation between temperatures of current and previous months was weaker (0.78); similarly, correlation between precipitations of current and previous months was 0.74. Those are smaller than the correlation between day lengths of current and previous months (0.87). Summary statistics of these six meteorological factors were obtained by a principal component analysis, and PC1 and PC2 accounted for 81.5% and 11.8% of total the variance, respectively. PC1 reflected whether six correlated variables showed higher or lower scores, and was positive in wet season and negative in dry season (Fig. 3.9d). PC2 reflected a proportion of current month temperature and previous month precipitation, and was the lowest in April, a turning point from dry to wet season, and the highest in October and November, a turning point from wet to dry season. All variables increased in the former turning point, and decreased in the latter (Fig. 3.9e). The annual change of the residual precipitation of previous month relative to daylength of that month and was similar to the annual change of PC2 (Fig. 3.9f). As a result of statistical tests using GLM with PC1 and PC2 as explanatory variables, the number of leafing species showed significant negative correlation with both PC1 and PC2 ($p < 0.001$ for both PC1, and PC2), the number of flowering species showed significant negative correlation with PC1 ($p < 0.001$ for PC1, $p = 0.231$ for PC2), and the number of fruiting species showed significant correlation with neither PC1 nor PC2 ($p = 0.373$, $p = 0.097$ for PC1, and PC2, respectively).

Based on the result of the statistical tests using GLM with daylength, residual precipitation, and residual temperature as explanatory variables, the number of leafing species showed significant negative correlation with daylength and residual precipitation, and significant positive correlation with residual temperature ($p < 0.001$ for daylength and residual precipitation, and $p < 0.01$ for residual temperature). The number of flowering species showed significant negative correlation with daylength and residual precipitation, and did not show significant correlation with residual temperature ($p < 0.01$ for daylength, $p < 0.05$ for residual precipitation, $p = 0.586$ for residual temperature). The number of fruiting species did not show significant correlation with any explanatory variables ($p = 0.918$, 0.165, 0.504 for daylength, residual precipitation, and residual temperature, respectively).

3.3.7 Comparison of phenological patterns among forests in East and Southeast Asia

Based on the results of Kuiper's test, all phenological patterns were significantly different from the circular uniform distribution (Appendix S3.5). In the constructed maximum parsimony tree, patterns were divided into two groups designated as Group 1 and 2 in Fig. 3.10. Group 1, consinsting of three locations of Malaysia and Bidoup-Nui Ba, showed extended patterns in all leafing, flowering, and fruiting. Group 2, consisting of Thailand, China, Taiwan, and Japan, highly peaked in leafing. Thailand and Bidoup-Nui Ba were geographically close, but belonged to different groups in terms of phenological patterns (Fig. 3.10).

Based on the result of a clustering analysis of annual meteorological change, nine locations can be classified to two groups designated as Group 1 and 2 (Fig. 3.11). Group 1, including Malaysia, Thailand, Bidoup-Nui Ba NP, and China, showed

consistently high levels of solar radiation and temperature. In contrast, Group 2, including Taiwan and Japan, had a peak for both solar radiation and temperature. The topology of nine locations in this clustering analysis was not perfectly matched to that in the maximum parsimony tree.

3.4 Discussion

3.4.1 Summary of results

Based on the results described above, we can characterize phenological patterns in the tropical montane forest of Bidoup-Nui Ba, Vietnam as follows. First, leafing phenology had a peak at the beginning of the wet season (April), and was significantly influenced by daylength, precipitation, and temperature. Second, flowering phenology did not show any distinct peak, and was influenced by daylength and precipitation. Third, fruiting phenology showed a low peak from wet season (July) to early dry season (December), and was not significantly influenced by any meteorological factor. Fourth, all species expanded new leaves at least once a year, but more than one quarter of monitored species had neither flowers nor fruits nearly two years. Based on a principal component analysis of meteorological factors, we characterized seasons in the tropical montane forest of Bidoup-Nui Ba, Vietnam as dry and wet season, and two transition stages; one from dry to wet season around April and another from wet to dry season around October. These two transition stages appear to correspond to “spring” and “autumn” in the temperate climate.

This is the third phenological study in the tropical montane forest of Southeast Asia, following the first and second studies at Mt. Kinabalu (Nomura et al. 2003; Kimura et al. 2009). By comparing the phenological patterns observed in two montane forests

with patterns observed in diversified forests of East and Southeast Asia, we could deepen our understanding of the relationship between different phenological patterns. According to the clustering analysis of phenologies recorded at nine area (Fig. 3.10), phenologies of tropical montane forests of Mt. Kinabalu (leafing, Nomura et al. 2003; flowering and fruiting, Kimura et al. 2009) and Bidoup-Nui Ba were similar to lowland Dipterocarp forests of Lambir and Pasoh, Malaysia, and did not form a particular cluster of 'tropical montane forest'.

3.4.2 Comparison of phenological patterns among forests in East and Southeast Asia

In the following discussion, we will first compare our results with the previous studies on Mt. Kinabalu to clarify the similarities and differences. Second, we will compare the phenological pattens of tropical montane forest and lowland Dipterocarp forest, which are basal in the clustering tree. Third, we will compare the phenological patterns of tropical montane forest with tropical seasonal, subtropical, and temperate forest, which clustered in a different group in the clustering tree. Then, we infer how the phenologies of the tropical montane forests, lowland Dipterocarp forests, and seasonal forests were diverged.

Among community-wide phenological patterns observed in tropical montane forests of Mt. Kinabalu and Bidoup-Nui Ba (Fig. 3.10), leafing phenology of Mt. Kinabalu showed peaks associated with irregular droughts caused by El Niño (Nomura *et al.* 2003), while that of Bidoup-Nui Ba showed a predictable peak in April which was influenced by daylength, precipitation, and temperature. On the other hand, flowering phenology of Mt. Kinabalu regularly showed two low peaks in April and September, while that of Bidoup-Nui Ba did not show any noticeable peak. Those differences imply

that phenological patterns of ‘tropical montane forest’ are not uniform but diverged between Borneo Island and Mainland Southeast Asia.

The leafing phenology of Mt. Kinabalu and the flowering phenology of Bidoup-Nui Ba are similar to community-wide phenological patterns of lowland Dipterocarp forests in Lambir and Pasoh, characterized by supra-annual patterns of leafing (Ichie *et al.* 2004; Putz 1979), flowering and fruiting (Brearley *et al.* 2007; Chen *et al.* 2018; Putz 1979; Sakai *et al.* 1999; Ushio *et al.* 2019). However, the community-wide phenology of lowland Dipterocarp forests is different from that of the montane forests in the pattern known as 'general flowering (mass flowering)' (Sakai *et al.* 2006; Ushio *et al.* 2019) and lower proportions of leafing and flowering species except in the year of general flowering (Ichie *et al.* 2004; Putz 1979). During general flowering, which occurs at irregular intervals of 3–10 year after short-term drought induced by the El Niño southern oscillation (ENSO; Ichie *et al.* 2004), nearly all dipterocarp species, together with species of other families, come heavily into flower (Sakai *et al.* 1999). This general flowering might be also the case in Bidoup-Nui Ba: the fact that 26 of 91 monitored species did not flower nearly two years could be explained by a hypothesis that the observation period was an interval of general flowering. However, the effect of ENSO in Bidoup-Nui Ba is smaller than those in Lambir, and Pasoh, Malaysia (Nguyen *et al.* 2016), where general flowering was often observed. Also, those two sites in Malaysia showed similar aseasonal climate patterns of daylength, precipitation, and temperature, which differed from the seasonal climate pattern of Bidoup-Nui Ba (Fig. 3.11). Thus, the hypothesis assuming general flowering is unlikely to be supported in Bidoup-Nui Ba where seasonality is clear, although further long-term observations of phenologies are needed to test the hypothesis.

The leafing phenology of Bidoup-Nui Ba is similar to that of the tropical seasonal forest, where leafing phenology shows a peak in dry season (November–April) and is associated with changes in daylength in some species and in precipitation in other species, but different in the higher proportions of leafing species in other seasons (Williams *et al.* 2008). Also, flowering phenology in the tropical seasonal forest differed from that of Bidoup-Nui Ba in having a prominent peak at the end of the dry season (from February to April in Mountgsrimuangdee et al. 2017; March in Kato et al. 2008; April in Kurten et al. 2018) and the effects of precipitation and temperature as cues for flowering (Kurten *et al.* 2018).

Similarly, the leafing phenology of Bidoup-Nui Ba is similar to that of the subtropical forest, where leafing phenology shows a peak around April, but different in the higher proportions of leafing species in other seasons (Edwards *et al.* 2017). Also, flowering phenology in the subtropical seasonal forest differed from that of Bidoup-Nui Ba in having a peak in the late dry season and fruiting peaked in the late wet season (Mohandass *et al.* 2018) and those patterns matched seasonal changes in day length, temperature, and irradiance (Chang-Yang *et al.* 2013).

Also, the leafing phenology of Bidoup-Nui Ba is similar to leafing phenology in the temperate forests (deciduous forest, Edwards et al. 2017; evergreen forest, Nitta & Ohsawa 1997) that is generally peaked around April and consider to be triggered by the onset of spring rains (Edwards *et al.* 2017). However, flowering phenology in the temperate forests showed a peak from March in spring to August in summer (Nagahama & Yahara 2019; Noma & Yumoto 1997; Shibata *et al.* 2002; Takanose & Kamitani 2003; Yumoto 1987).

Despite this difference in flowering phenology between the temperate forest and the tropical montane forest of Bidoup-Nui Ba, masting is common to these two types of forests. In temperate forests, masting is known as non-annual flowering and fruiting pattern in some temperate species, such as Fagaceae (Miyazaki *et al.* 2014; Shibata *et al.* 2002), and is characterized by highly variable, synchronous flowering and seed production across years (Kelly & Sork 2002; Miyazaki *et al.* 2014). Masting is expected to occur in Bidoup-Nui Ba because 26 of 91 monitored species did not flower nearly two years. Compared to the hypothesis assuming general flowering, this hypothesis is more likely in Bidoup-Nui Ba, because the climate there shows clear seasonality as in the temperate regions.

As a proximate factor for masting, much recent attention has been directed to the internal resource dynamics (Crone *et al.* 2009; Smaill *et al.* 2011; Tanentzap *et al.* 2012) partly because the dynamics can be described quantitatively by the resource budget model (Isagi *et al.* 1997; Satake & Iwasa 2000). This model assumes that a tree gains a constant energy income every year from its photosynthetic activity, and that the tree may not reproduce while the energy reserve level stays below a threshold. Once the energy reserve exceeds the threshold, the tree blooms and may have ovules fertilized by outcrossed pollen (Isagi *et al.* 1997; Satake & Iwasa 2000). According to a theoretical study (Satake & Iwasa 2000), the pollen limitation is also a key factor inducing masting, and when the energy reserve exceeds the threshold and pollen limitation is high, all the trees in the forest are expected to show synchronized and fluctuating reproduction. The pollen limitation occurs in animal-pollinated plants, when pollinator visits or pollen grains delivered per visit are limited, or pollen quality is reduced under selfing or incompatible pollination (Ashman *et al.* 2004).

Among 26 species in which flowering was not observed, 23 species were animal-pollinated, and are likely to face pollen limitation. In addition, the resource availability for reproduction in tropical montane forest might be low, because the soil condition under hot and humid environment is poor of nutrients, including carbon, nitrogen, and phosphorus (Sanchez 1977; Tsujii *et al.* 2017).While tropical trees show high nutrients-use efficiency under nutrients-poor soil condition (Tsujii *et al.* 2017), they may still face nutrient limitation because tropical trees need larger amounts of resources than the amounts earned by a year to show large floral display to attract generalist pollinators (Cortés-Flores *et al.* 2017; Janzen 1967). This is supported by a study of pollination network in a subtropical montane forest in Laos (Kato et al., *in press*), where flowers of many tree species were visited by various generalist pollinators. Thus, both of two key factors favoring masting, pollinator limitation and resource limitation, seem to apply to the tropical montane forest in Bidoup-Nui Ba.

Given the above similarities and differences of phenologies found in representative forest types, here we propose a framework for the process of phenological diversification in forests of East and Southeast Asia. This framework explains how and why various phenological patterns evolved as a result of adaptive evolution of angiosperms in East and Southeast Asia.

Angiosperms in tropical and temperate regions of Asia occurred in low-latitude regions in the early Cretaceous, and extended their distribution to northern and southern regions (Axelrod 1966; Morlay 2001). It is also suggested that, prior to the entry of angiosperms into the lowland Cretaceous record, they evolved chiefly in moist tropical to warm temperate upland regions (Axelrod 1966). Based on these paleobotanical studies, we assume that the phenology of the tropical montane forest is an ancestral state of other

forests, and infer how the phenologies of various forest types diverged (Fig. 3.12). This assumption does not preclude reverse changes, but rather helps in considering reverse changes. First, in the process of extending distribution from tropical montane forest to tropical Dipterocarp forest (process 1 of Fig. 3.12), some plants lost their seasonal patterns due to the loss of seasonal climate change, resulting the aseasonal pattern of expanding new leaves, blooming, and setting fruits through the year. In contrast, other plants including masting species in tropical montane forest preserved their abilities to respond to changes in temperature and precipitation, which had originally adapted to the moderate dry season of tropical montane forest, resulting the general flowering pattern in response to irregular drought and low temperature.

Second, in the process of extending distribution from tropical montane forest to tropical seasonal forest (process 2 of Fig. 3.12), plants adapted to severe drought, resulting annual patterns of leafing and flowering in dry season, and fruiting in wet season. In this process, some plants evolved deciduousness for adaptation to severe drought (Axelrod 1966). This evolution probably occurred in the processes of horizontal migration from tropical rain forest to tropical seasonal forest, and vertical migration from sub-tropical seasonal forest to sub-tropical montane forest.

Third, in the processes of horizontal migration from tropical seasonal forest to sub-tropical seasonal forest and from sub-tropical seasonal forest to warm-temperate forest (process 3 of Fig. 3.12), plants adapted to low temperature of winter and deciduous species became dominant in some areas (Edwards *et al.* 2017), where annual patterns of leafing and flowering in spring, and fruiting in autumn emerged. In this process, only some groups, including Fagaceae, are considered to conserve masting habits.

Fourth, in the process of vertical migration from warm-temperate forest to warm-temperate montane forest (process 4 of Fig. 3.12), plants adapted to freezing in winter and deciduous species became more dominant (Edwards *et al.* 2017).

This hypothetical framework explains that longer and scattered patterns of leafing and flowering phenology are found at the low latitude area, and shorter and concentrated patterns of leafing and flowering phenology are found at the low latitude area (Fig. 3.10). The framework also suggests that phenological traits will change sensitively in response to each climate condition, implying that future climate change may significantly change the community-wide patterns of phenology throughout East and Southeast Asia. However, it should be noted that the framework of Fig. 3.12 is a simplification of the complicated changes in tree phenology actually observed in various forest types. To assess the reliability of the hypothesized framework and revise it to a more realistic framework, we need to describe and compare community-wide phenological patterns in more forests of East and Southeast Asia.

3.5 Conclusion

In conclusion, the community-wide phenological patterns of leafing, flowering, and fruiting in tropical montane forest of Bidoup-Nui Ba are unique among tropical forests of East and Southeast Asia. Particularly, our observation suggests the occurrence of a supra-annual pattern of flowering and fruiting known as masting, and masting of tropical montane forest can be an ancestral trait of both general flowering in tropical rain forest and masting of temperate forest in East and Southeast Asia. These considerations are derived from the first quantitative observations of the leafing, flowering, and fruiting phenology in the tropical montane forest of continental Asia, and comparisons of

community-wide phenological patterns among various forest types observed in East and Southeast Asia. Further quantitative studies describing community-wide phenological patterns are needed to determine whether similar patterns are observed in plant communities under similar climatic conditions or not. Also, it is needed to be consider the phylogenetic constraint among species in phenological patterns to evaluate and compare more precisely. In recent years, community level phenological shifts have been reported in several areas (Chen *et al.* 2017), suggesting that significant change will occur in synchronized ecosystems in responses to future climate change. To deepen our understanding of phenological responses to climate change, we need additional detailed studies of phenology throughout Asia.

3.6 Tables

Table 3.1 Details of study plots.

Plot	Latitude (°)	Longitude (°)	Elevation (m)	Plot size (m2)	No. of tree individuals
LB	N12.0478056	E108.438583	1920	1500 (30 m x 50 m)	370
CT	N12.0936944	E108.377444	1860	1500 (30 m x 50 m)	571
HG	N12.1875418	E108.713822	1666	1000 (10 m x 100 m)	1543
DIG	N12.1514333	E108.536289	1660	2500 (50 m x 50 m)	794
GL	N12.1852344	E108.678394	1460	1500 (30 m x 50 m)	636

Table 3.2 Nine well-studied area of previous studies.

Forest	Country	Study area	Phenology	Studies
Temperate forest	**Japan**	Nothern part of Japan	Leafing	Nitta & Ohsawa 1997
			Flowering	Takanose & Kamitani 2003
			Fruiting	
		Southern part of Japan	Leafing	Edwards et al. 2017 Yahara, unpublished
			Flowering	Nagahama & Yahara 2019 Yahara unpublished
			Fruiting	Yahara, unpublished
Subtropical forest	**Taiwan**	Nothern part of Taiwan	Leafing	Edwards et al. 2017
			Flowering	Chang-Yang et al. 2013
			Fruiting	
	China	Xishuangbanna	Leafing	Zhang et al. 2007 Zhai et al. 2019
			Flowering	Mohandass et al. 2018 Zhang et al. 2007
			Fruiting	Mohandass et al. 2018 Zhang et al. 2007
Tropical seasonal forest	**Vietnam**	Bidoup-Nui Ba	Leafing	This study
			Flowering	
			Fruiting	
	Thailand	Central part of Thailand	Leafing	Williams et al. 2008
			Flowering	Mountgsrimuangdee et al. 2017
			Fruiting	
Tropical rain forest	**Malaysia**	Pasoh	Leafing	Intachat et al. 2001
			Flowering	Intachat et al. 2001 Yamaguchi in preparing
			Fruiting	Intachat et al. 2001 Yamaguchi in preparing
		Lambir	Leafing	Ichie et al. 2004
			Flowering	Ushio et al. 2020 Sakai et al. 1999
			Fruiting	Sakai et al. 1999
		Mt. Kinabalu	Leafing	Nomura et al. 2003
			Flowering	Kimura et al. 2009
			Fruiting	

Table 3.3 Eigenvector scores of observed months in four main PCA axes, obtained from a matrix of seven months x 91 species. The three highest eigenvector scores for each PCA axis are indicated in bold.

Months	Leafing				Flowering				Fruiting			
	PC1	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**
	(27.5%)	(19.8%)	(16.3%)	(14.0%)	(32.0%)	(19.2%)	(15.5%)	(11.0%)	(42.2%)	(16.4%)	(11.8%)	(9.9%)
Jan.	0.137	**-0.611**	**0.473**	-0.235	0.316	0.220	**-0.622**	0.324	0.337	**-0.577**	0.272	**-0.216**
Apr.	-	-	-	-	0.365	**0.550**	0.025	-0.259	0.380	**-0.401**	**-0.486**	0.151
Jun.	0.228	**0.656**	0.062	0.189	0.320	0.266	**0.530**	**0.601**	0.359	0.364	0.116	**-0.747**
Jul.	0.208	**-0.381**	**-0.770**	**0.325**	**0.468**	0.256	0.048	**-0.444**	**0.400**	0.166	0.348	**0.572**
Sept.	**0.618**	-0.106	-0.038	-0.087	0.348	**-0.405**	**0.449**	**0.044**	**0.383**	**0.569**	-0.144	0.199
Oct.	**0.483**	-0.047	**0.389**	**0.630**	**0.420**	**-0.477**	-0.061	-0.360	0.361	-0.145	**0.514**	0.023
Dec.	**0.521**	0.195	-0.161	**-0.632**	**0.386**	-0.348	-0.351	0.371	**0.420**	-0.037	**-0.519**	-0.070

Figures

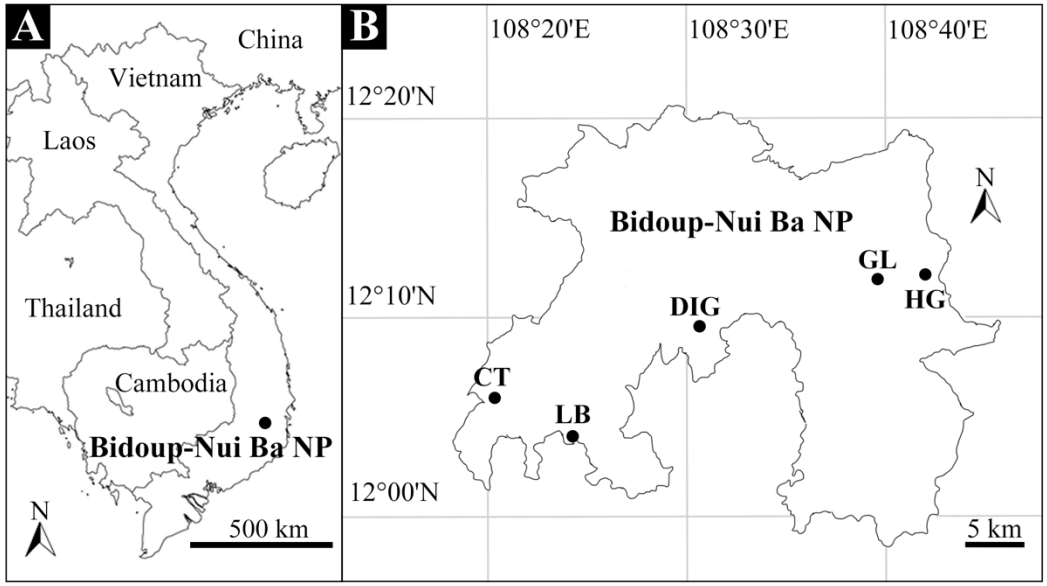


Figure 3.1 Locality of Bidoup-Nui Ba National Park (A) and survey plots in the NP (B).

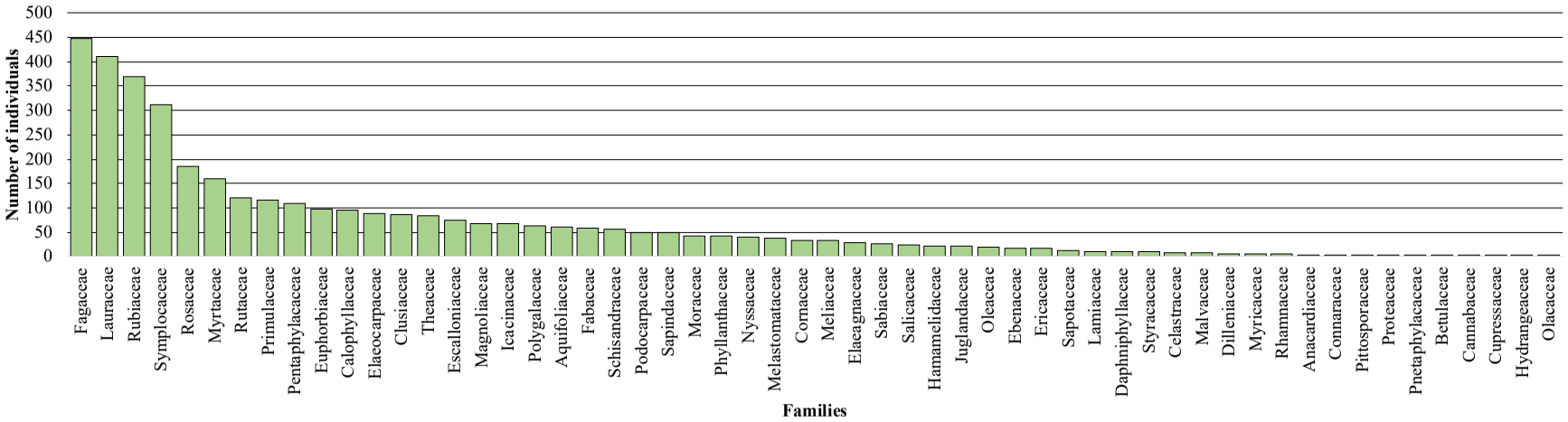


Figure 3.2 The number of individuals of each family in the study plots.

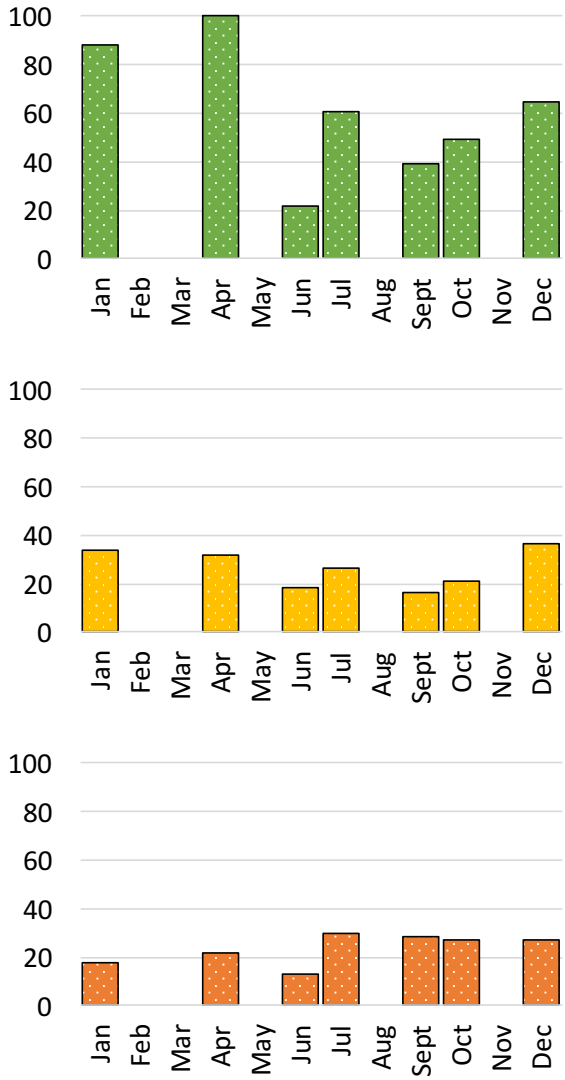


Figure 3.3 Proportions of the number of leafing (a), flowering (b), and fruiting (c) species. We did not observe in February, March, May, August, and November.

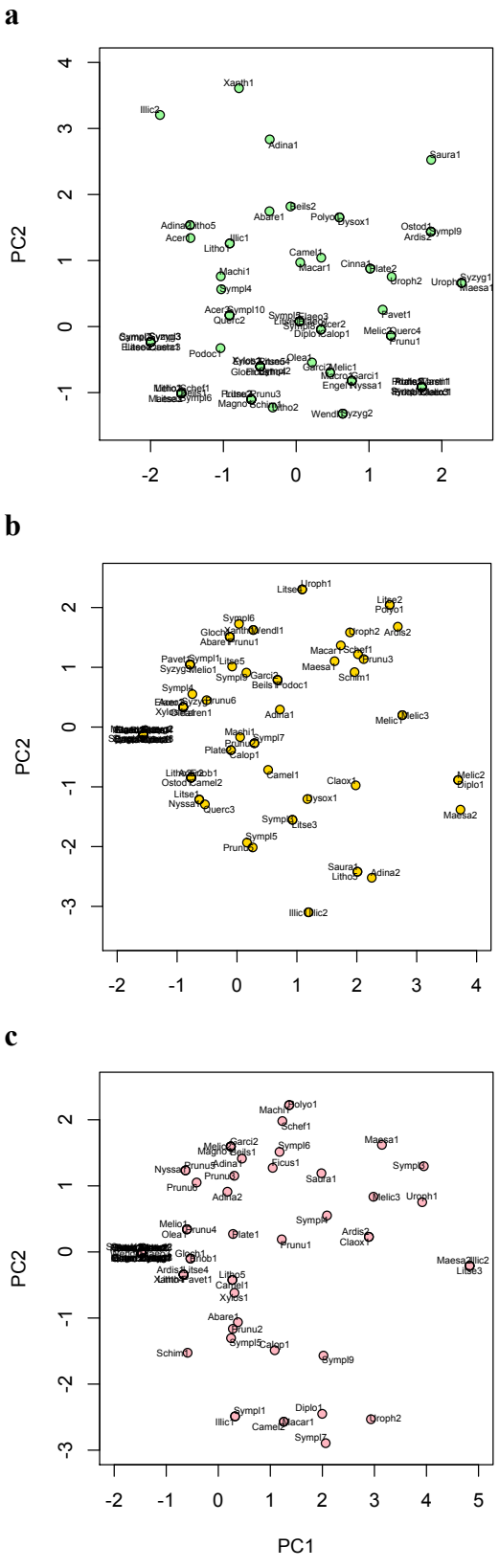


Figure 3.4 Results of PCA for leafing (a), flowering (b), and fruiting phenology (c). In all of leafing, flowering, and fruiting data, all of presence records in seven observation

months positively contributed to PC1. In contrast, some presence records positively and others negatively contributed to PC2 (See Table 3.2).

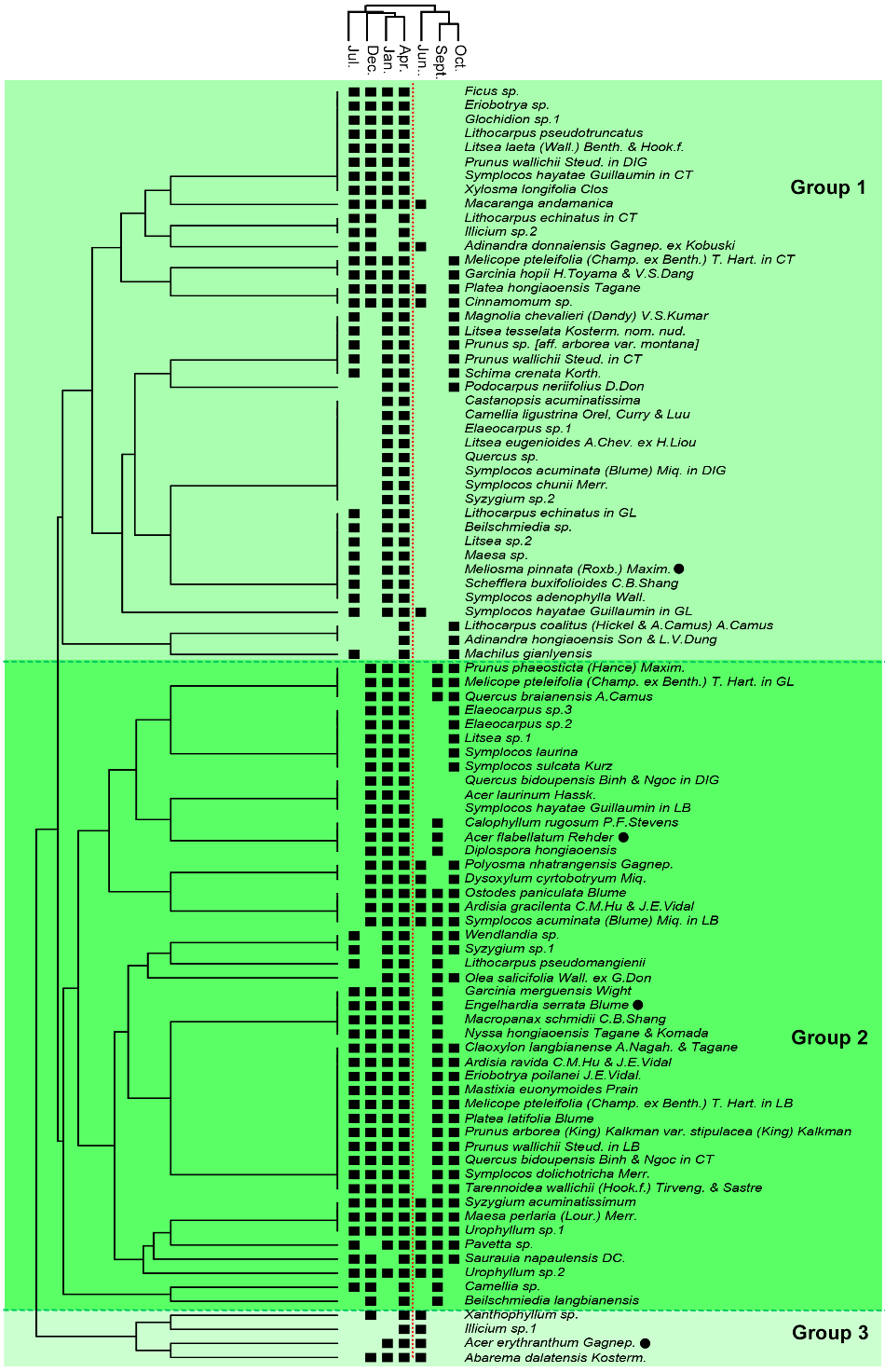


Figure 3.5 Results of clustering analysis for leafing patterns. Black squares show presence of new leaves, flowers, or fruits. Deciduous species are marked with black circles next to their names.

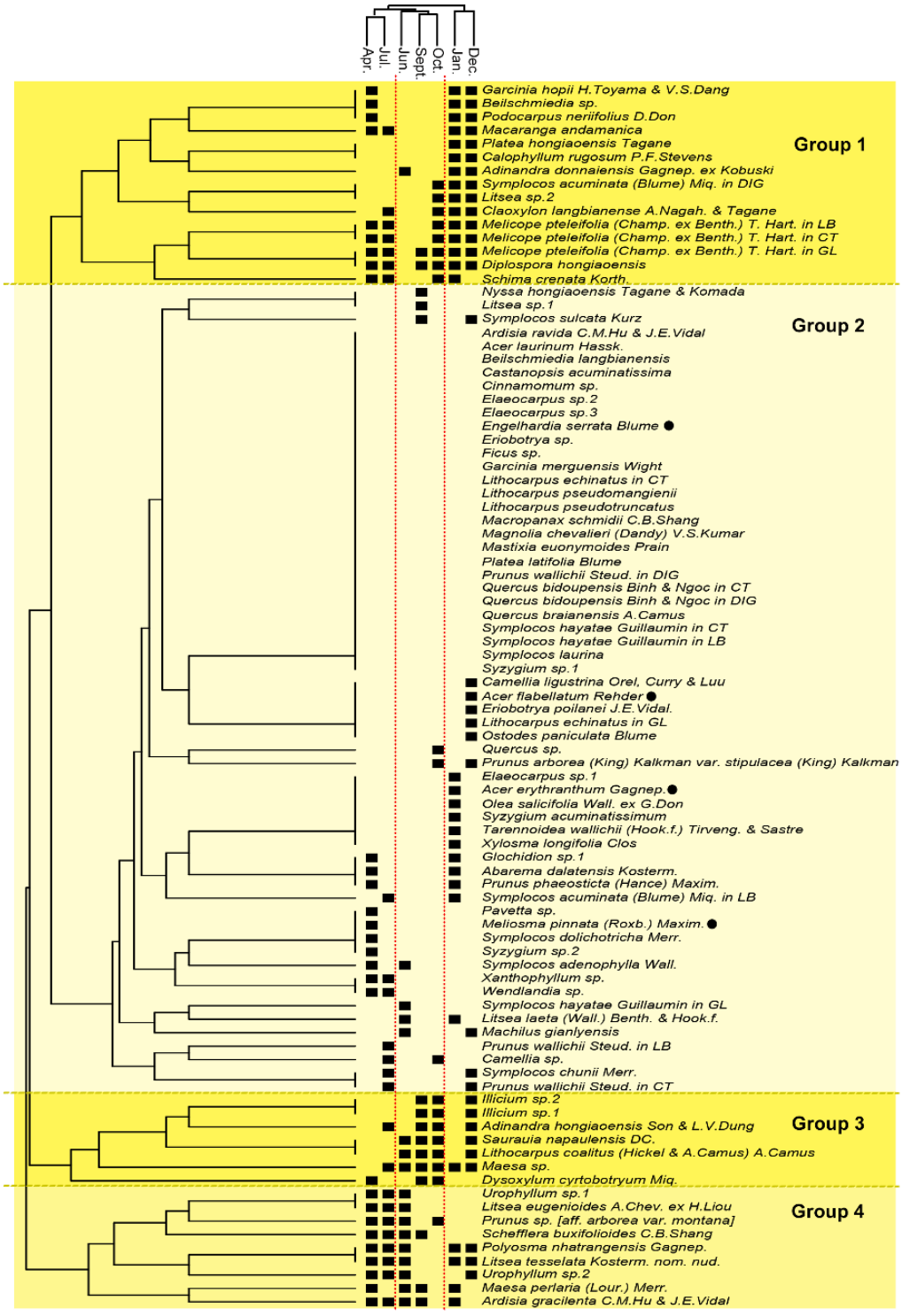


Figure 3.6 Results of clustering analysis for flowering patterns. Black squares show presence of new leaves, flowers, or fruits. Deciduous species are marked with black circles next to their names.

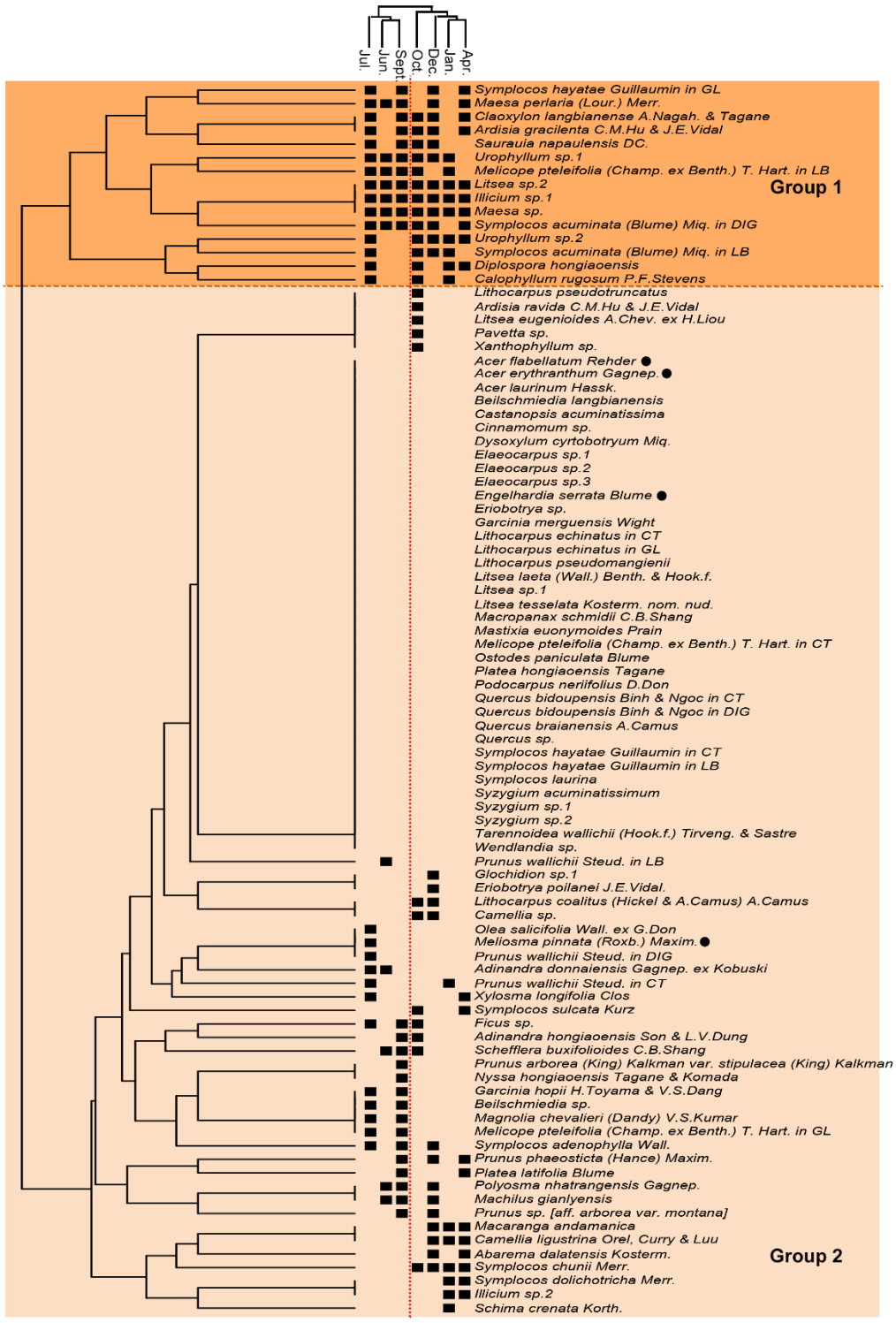


Figure 3.7 Results of clustering analysis for fruiting patterns. Black squares show presence of new leaves, flowers, or fruits. Deciduous species are marked with black circles next to their names.

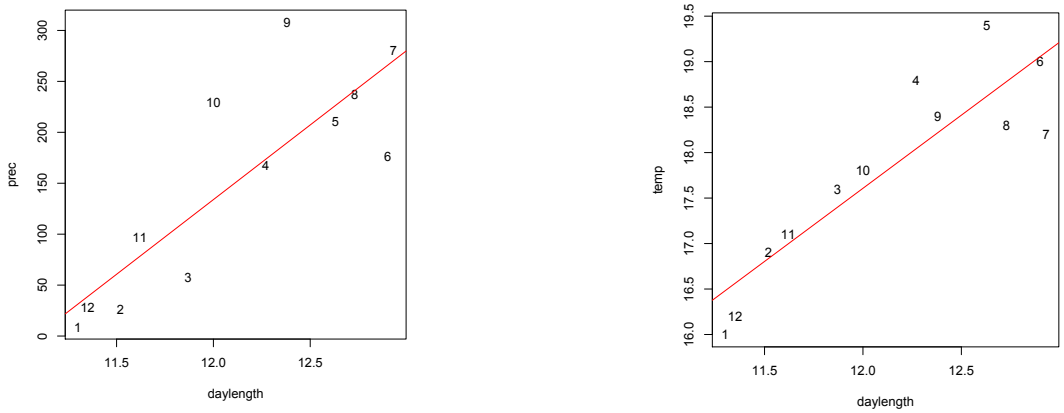


Figure 3.8 Correlations between daylength and precipitation (a), and between daylength and temperature (b).

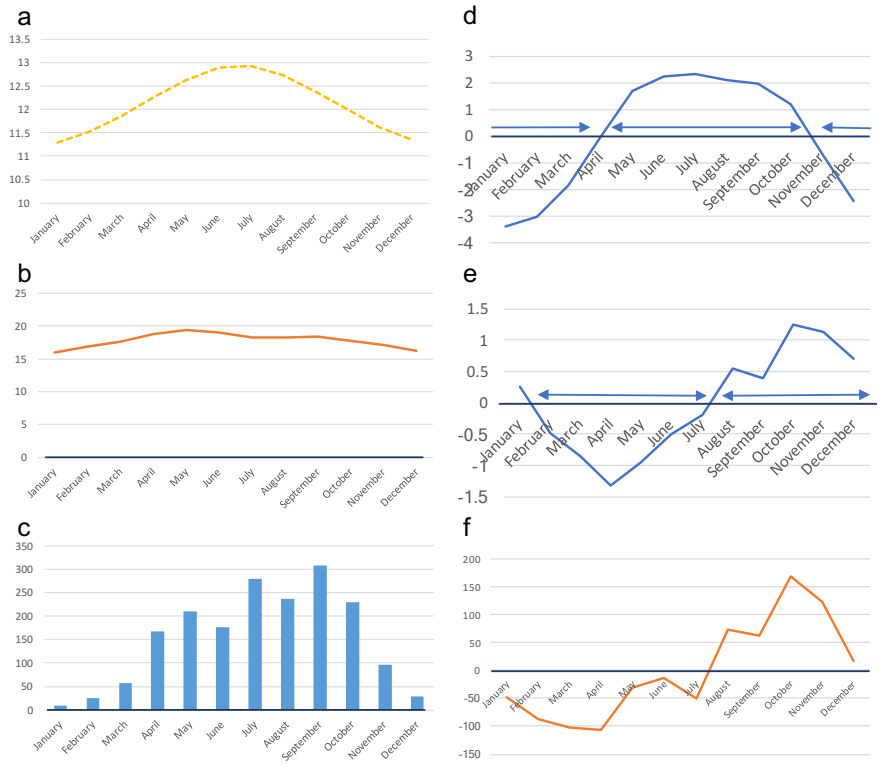


Figure 3.9 Seasonal changes of daylength (a), temperature (b), precipitation (c), summary statistics of six meteorological factors obtained by a principal component analysis (d, PC1; e, PC2), and the residual error between daylength of that month and precipitation of previous month (f). Positive and negative value of PC1 corresponds to dry season and rainy season. Similarly, positive and negative values of PC2 correspond to seasons like 'spring' and 'autumn'.

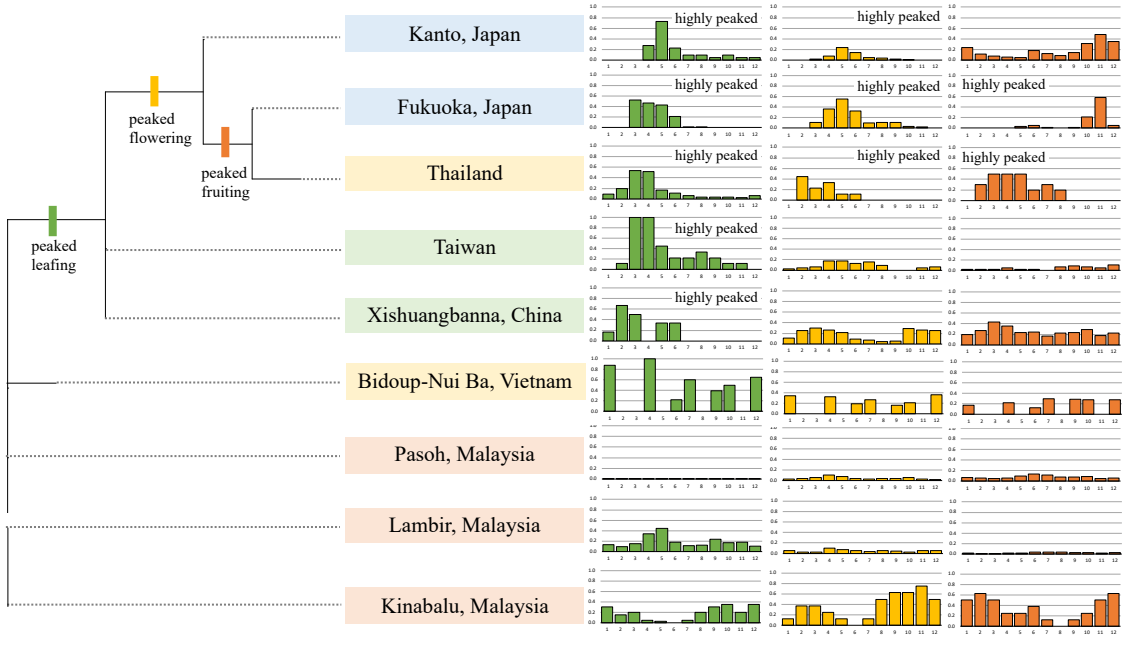


Figure 3.10 Nine locations clustered by leafing, flowering, and fruiting patterns. The patterns marked as 'highly peaked' showed the variance less than 0.5.

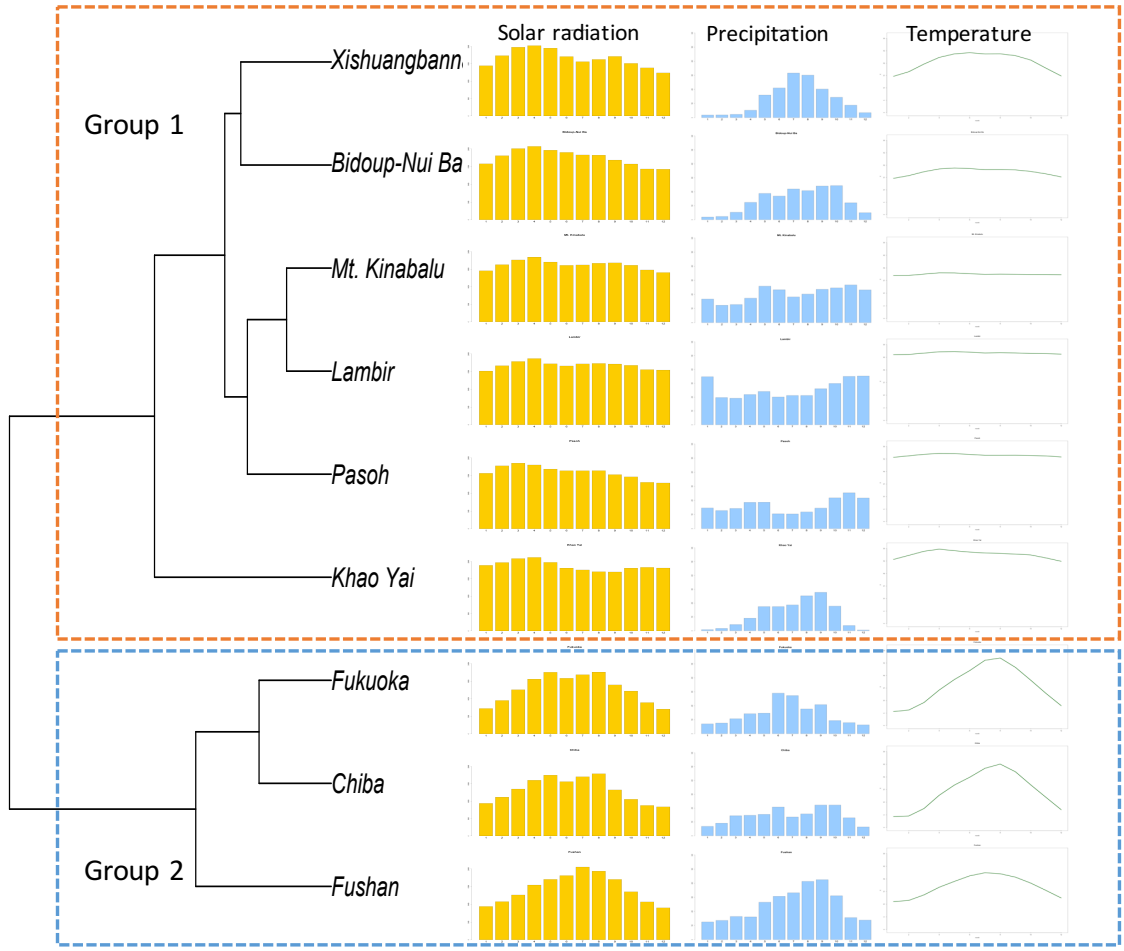


Figure 3.11 Nine forests clustered by seasonality of solar radiation, precipitation, temperature.

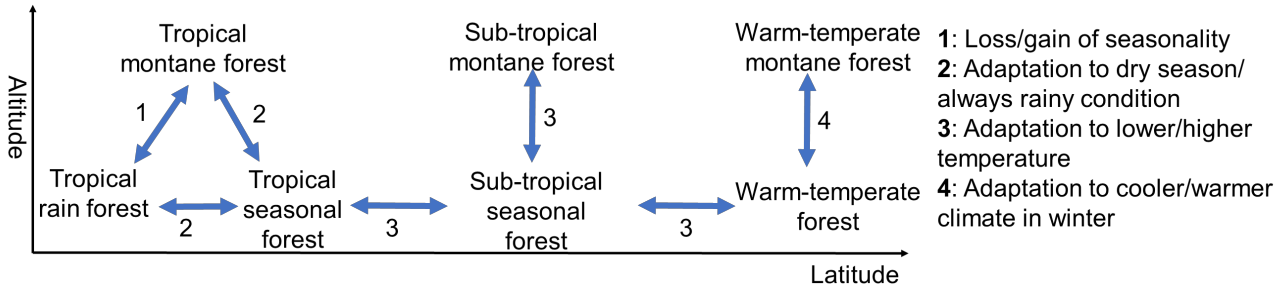
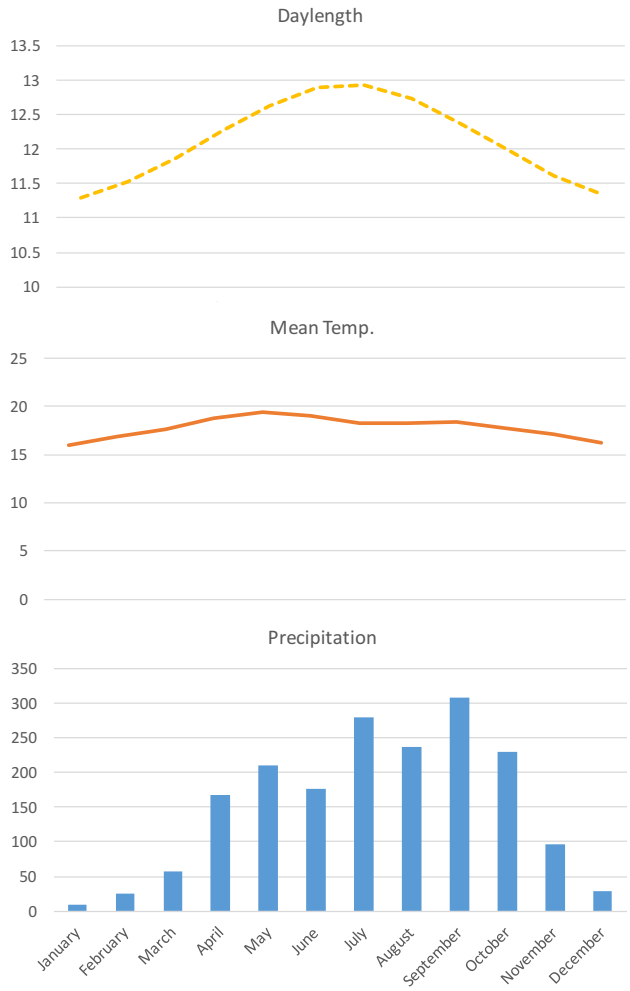


Figure 3.12 Hypothesis of expanding distribution of angiosperms.

3.8 Appendices



Appendix S3.1 Annual change of day length, temperature, precipitation in Bidoup-Nui Ba National Park. Those records were obtained from Fick et al. (2017).

Appendix S3.2 Correlation coefficient among meteorological factors.

	Daylength	**Mean temperature**	**Precipitation**
Daylength	1	-	-
Mean temperature	0.888	1	-
Precipitation	0.834	0.760	1

Appendix S3.3 The data used for comparison of phenological patterns among forests in East and Southeast Asia.

Country	Area	Phenology	January	February	March	April	May	June	July	August	September	October	November	December
Japan	Nothern part of Japan	Leafing	0.000	0.000	0.000	0.273	0.727	0.227	0.091	0.091	0.045	0.091	0.045	0.045
		Flowering	0.000	0.000	0.020	0.078	0.235	0.137	0.049	0.039	0.020	0.010	0.000	0.000
		Fruiting	0.235	0.108	0.078	0.059	0.049	0.176	0.118	0.088	0.137	0.314	0.480	0.353
	Southern part of Japan	Leafing	0.000	0.000	0.525	0.472	0.428	0.214	0.017	0.017	0.000	0.000	0.000	0.000
		Flowering	0.000	0.000	0.102	0.364	0.551	0.321	0.100	0.108	0.108	0.033	0.017	0.000
		Fruiting	0.000	0.000	0.000	0.000	0.033	0.050	0.017	0.000	0.017	0.217	0.583	0.050
Taiwan	Nothern part of Taiwan	Leafing	0.000	0.111	1.000	1.000	0.444	0.222	0.222	0.333	0.222	0.111	0.111	0.000
		Flowering	0.022	0.043	0.065	0.174	0.174	0.130	0.152	0.087	0.000	0.000	0.043	0.065
		Fruiting	0.022	0.022	0.022	0.043	0.022	0.022	0.000	0.065	0.087	0.065	0.043	0.109
China	Xishuangbanna	Leafing	0.167	0.667	0.500	0.000	0.333	0.333	0.000	0.000	0.000	0.000	0.000	0.000
		Flowering	0.106	0.249	0.302	0.264	0.212	0.092	0.072	0.046	0.053	0.286	0.263	0.257
		Fruiting	0.196	0.270	0.430	0.353	0.232	0.239	0.162	0.228	0.238	0.288	0.179	0.219
Thailand	Central part of Thailand	Leafing	0.094	0.200	0.541	0.518	0.165	0.106	0.059	0.035	0.035	0.035	0.024	0.059
		Flowering	0.000	0.444	0.222	0.333	0.111	0.111	0.000	0.000	0.000	0.000	0.000	0.000
		Fruiting	0.000	0.300	0.500	0.500	0.500	0.200	0.300	0.200	0.000	0.000	0.000	0.000
Vietnam	Bidoup-Nui Ba	Leafing	0.879	0.000	0.000	1.000	0.000	0.220	0.604	0.000	0.396	0.495	0.000	0.648
		Flowering	0.341	0.000	0.000	0.319	0.000	0.187	0.264	0.000	0.165	0.209	0.000	0.363
		Fruiting	0.176	0.000	0.000	0.220	0.000	0.132	0.297	0.000	0.286	0.275	0.000	0.275

Malaysia	Pasoh	Leafing	0.003	0.003	0.007	0.003	0.006	0.001	0.002	0.003	0.005	0.013	0.004	0.007
		Flowering	0.027	0.035	0.059	0.101	0.079	0.039	0.029	0.037	0.040	0.061	0.034	0.022
		Fruiting	0.071	0.054	0.050	0.058	0.097	0.132	0.114	0.081	0.079	0.082	0.053	0.062
	Lambir	Leafing	0.130	0.090	0.150	0.340	0.440	0.175	0.115	0.125	0.235	0.170	0.175	0.100
		Flowering	0.056	0.022	0.028	0.095	0.070	0.054	0.036	0.049	0.045	0.026	0.056	0.048
		Fruiting	0.014	0.011	0.009	0.014	0.021	0.032	0.036	0.033	0.031	0.024	0.021	0.023
Taiwan	Kinabalu	Leafing	0.300	0.150	0.200	0.050	0.030	0.000	0.050	0.200	0.300	0.350	0.200	0.350
		Flowering	0.125	0.375	0.375	0.250	0.125	0.000	0.125	0.500	0.625	0.625	0.750	0.500
		Fruiting	0.500	0.625	0.500	0.250	0.250	0.375	0.125	0.000	0.125	0.250	0.500	0.625

Appendix S3.4 Twenty dominant species of each plot.

Plot	Family	Species
CT	Elaeocarpaceae	*Elaeocarpus* sp.3
	Fagaceae	*Lithocarpus echinatus*
	Fagaceae	Lithocarpus pseudomangienii
	Fagaceae	Quercus bidoupensis Binh & Ngoc in CT
	Lauraceae	Litsea sp.1
	Lauraceae	Litsea tesselata Kosterm. nom. nud.
	Myrtaceae	Syzygium acuminatissimum
	Primulaceae	Ardisia ravida C.M.Hu & J.E.Vidal
	Rosaceae	Eriobotrya poilanei J.E.Vidal.
	Rosaceae	Prunus phaeosticta (Hance) Maxim.
	Rosaceae	Prunus wallichii Steud. in CT
	Rubiaceae	Pavetta sp.
	Rubiaceae	Tarennoidea wallichii (Hook.f.) Tirveng. & Sastre
	Rutaceae	Melicope pteleifolia (Champ. ex Benth.) T. Hart. in CT
	Schisandraceae	Illicium sp.2
	Symplocaceae	Symplocos dolichotricha Merr.
	Symplocaceae	Symplocos hayatae Guillaumin in CT
DIG	Elaeocarpaceae	Elaeocarpus sp.1
	Euphrobiaceae	Macaranga andamanica
	Fagaceae	Castanopsis acuminatissima
	Fagaceae	Quercus bidoupensis Binh & Ngoc in DIG
	Fagaceae	Quercus sp.
	Icacinaceae	Platea latifolia Blume
	Lauraceae	Beilschmiedia sp.
	Lauraceae	Cinnamomum sp.
	Lauraceae	Litsea sp.2
	Meliaceae	Dysoxylum cyrtobotryum Miq.
	Oleaceae	Olea salicifolia Wall. ex G.Don
	Primulaceae	Ardisia gracilenta C.M.Hu & J.E.Vidal
	Rosaceae	Eriobotrya sp.
	Rosaceae	Prunus sp. [aff. arborea var. montana]
	Rosaceae	Prunus wallichii Steud. in DIG
	Rubiaceae	Urophyllum sp.1

	Schisandraceae	Illicium sp.1
	Symplocaceae	Symplocos acuminata (Blume) Miq. in DIG
GL	Actinidiaceae	Saurauia napaulensis DC.
	Clusiaceae	Garcinia merguensis Wight
	Fagaceae	Lithocarpus echinophorus
	Fagaceae	Lithocarpus pseudotruncatus
	Lauraceae	Machilus gianlyensis
	Magnoliaceae	Magnolia chevalieri (Dandy) V.S.Kumar
	Moraceae	Ficus sp.
	Myrtaceae	Syzygium sp.1
	Pentaphylacaceae	Adinandra donnaiensis Gagnep. ex Kobuski
	Phyllanthaceae	Glochidion sp.1
	Primulaceae	Maesa perlaria (Lour.) Merr.
	Primulaceae	Maesa sp.
	Rubiaceae	Wendlandia sp.
	Rutaceae	Melicope pteleifolia (Champ. ex Benth.) T. Hart. in GL
	Sabiaceae	Meliosma pinnata (Roxb.) Maxim.
	Salicaceae	Xylosma longifolia Clos
	Symplocaceae	Symplocos hayatae Guillaumin in GL
	Symplocaceae	Symplocos sulcata Kurz
	Theaceae	Camellia sp.
HG	Araliaceae	Schefflera buxifolioides C.B.Shang
	Calophyllaceae	Calophyllum rugosum P.F.Stevens
	Clusiaceae	Garcinia hopii H.Toyama & V.S.Dang
	Escalloniaceae	Polyosma nhatrangensis Gagnep.
	Fabaceae	Abarema dalatensis Kosterm.
	Fagaceae	Lithocarpus coalitus (Hickel & A.Camus) A.Camus
	Fagaceae	Quercus poilanei
	Icacinaceae	Platea hongiaoensis Tagane
	Lauraceae	Litsea eugenioides A.Chev. ex H.Liou
	Myrtaceae	Syzygium sp.2
	Nyssaceae	Nyssa hongiaoensis Tagane & Komada
	Pentaphylacaceae	Adinandra hongiaoensis Son & L.V.Dung
	Podocarpaceae	Podocarpus neriifolius D.Don
	Polygalaceae	*Xanthophyllum* sp.

	Rubiaceae	*Diplospora hongiaoensis*
	Rubiaceae	*Urophyllum* sp.2
	Symplocaceae	*Symplocos adenophylla* Wall.
	Symplocaceae	*Symplocos chunii* Merr.
	Symplocaceae	*Symplocos laurina*
	Araliaceae	*Macropanax schmidii* C.B.Shang
	Cornaceae	*Mastixia euonymoides* Prain
	Elaeocarpaceae	*Elaeocarpus* sp.2
	Euphorbiaceae	*Claoxylon langbiangense* A.Nagah. & Tagane
	Euphorbiaceae	*Ostodes paniculata* Blume
	Fagaceae	*Quercus braianensis* A.Camus
	Juglandraceae	*Engelhardia serrata* Blume
	Lauraceae	*Beilschmiedia langbianensis* Yahara
	Lauraceae	*Litsea laeta* (Wall.) Benth. & Hook.f.
LB	Rosaceae	*Prunus arborea* (King) Kalkman var. stipulacea (King) Kalkman
	Rosaceae	*Prunus wallichii* Steud. in LB
	Rutaceae	*Melicope pteleifolia* (Champ. ex Benth.) T. Hart. in LB
	Sapindaceaae	*Acer erythranthum* Gagnep.
	Sapindaceae	*Acer flabellatum* Rehder
	Sapindaceae	*Acer laurinum* Hassk.
	Symplocaceae	*Symplocos acuminata* (Blume) Miq. in LB
	Symplocaceae	*Symplocos hayatae* Guillaumin in LB
	Theaceae	*Camellia ligustrina* Orel, Curry & Luu
	Theaceae	*Schima crenata* Korth.

Appendix S3.5 The statistics obtained by Kuiper's test. If the statistic value was larger than 1.747, the null hypothesis was rejected, suggesting the pattern was significantly different from the circular uniform distribution.

Country	Area	Phenology	Statistics
Japan	Nothern part of Japan	Leafing	23.70
		Flowering	14.61
		Fruiting	17.85
	Southern part of Japan	Leafing	29.96
		Flowering	23.15
		Fruiting	23.26
Taiwan	Nothern part of Taiwan	Leafing	29.61
		Flowering	12.97
		Fruiting	8.60
China	Xishuangbanna	Leafing	26.18
		Flowering	14.00
		Fruiting	9.97
Thailand	Central part of Thailand	Leafing	22.19
		Flowering	23.40
		Fruiting	25.25
Vietnam	Bidoup-Nui Ba	Leafing	18.06
		Flowering	12.84
		Fruiting	11.79
Malaysia	Pasoh	Leafing	2.00
		Flowering	6.16
		Fruiting	6.46
	Lambir	Leafing	12.56
		Flowering	5.06
		Fruiting	4.09
	Kinabalu	Leafing	17.01
		Flowering	23.36
		Fruiting	21.46

Chapter 4: General conclusion

4.1 What was revealed

In this study, I addressed the following four questions: (1) How can phenological changes be described quantitively? (2) How does flowering phenology differ between life forms? (3) What kind of phenological patterns are observed in tropical montane forests? (4) How do the leafing, flowering and fruiting phenologies differ between forests in East and Southeast Asia? Based on empirical evidence, I considered the questions (1) and (2) in Chapter 2, and the questions (3) and (4) in Chapter 3.

Regarding the question (1), I described the changes in flowering phenology using the following seven variables: total flowering length of species, mean flowering length of individuals and its variance, skewness and kurtosis of the flowering length distribution among individuals, the variance of the onset date, and the Morisita aggregation index ($I\delta$) (Morisita 1959). These variables have proven useful in describing the differences in flowering phenology between species and individuals with different life forms.

Regarding the question (2), I have found two significant differences in the characteristics of flowering phenology between trees and perennial or annual herbs in a temperate, evergreen broad-leaved forest. First, tree species have shorter total flowering length than annual and perennial herbaceous species. However, the mean flowering length of individuals was not significantly different between life forms. Second, individual trees of the same species have greater flowering synchronization than conspecific individuals of perennial herbs or annual herbs. Those results showed that the difference in the total flowering length of species between life forms was derived from differences in the variance of flowering length between individuals and the degree of

intraspecific synchrony rather than the differences in the mean flowering length of individuals.

Regarding the question (3), phenological patterns in the tropical montane forest of Bidoup-Nui Ba, Vietnam are characterized as follows. First, leafing phenology had a peak at the beginning of the wet season (April), and was significantly influenced by daylength, precipitation, and temperature. Second, flowering phenology did not show any distinct peak, and was influenced by daylength and precipitation, but not by temperature. Third, fruiting phenology showed a low peak from the wet season (July) to the beginning of the dry season (December), and was not significantly influenced by any meteorological factor. Fourth, all species expanded new leaves at least once a year, but more than one quarter of monitored species had neither flowers nor fruits nearly two years.

Regarding the question (4), the tropical montane forests in southern Vietnam showed an intermediate phenological pattern between lowland Dipterocarp forest and seasonal tropical forest, or temperate forest. Based on inferences using similarities and differences in phenologies between these forests, a schematic diagram (Fig. 3.12) was derived to explain how phenologies in deciduous and evergreen forests evolved in East and Southeast Asia.

Throughout this study, I was able to develop a method for quantitatively describing leafing, flowering, and fruiting phenologies found in forests in East and Southeast Asia, and to depict their evolutionary relationships that reflect the geographical differences of environmental conditions.

4.2 Implications

This study has allowed the quantitative comparison of phenology between different locations, bridging the following three gaps in previous studies. First, previous studies used different sample sizes and different observation periods in different locations and it was often uneasy to compare the results between locations. As reviewed in the first chapter, since 20th century, phenological observations have been continued over 30 years in several locations (Bush *et al.* 2018). Also, there are many locations, where phenological observations have been continued over ten years since around the end of the 20th century (Chen *et al.* 2018; Nakagawa *et al.* 2019; Ushio *et al.* 2019), when the impact of global warming was widely recognized. Needless to say, those records are valuable for phenological studies, but it had been difficult to compare with each other due to different sample sizes and different observation periods. Whereas some study recorded phenological data for 55 tree species including 5–20 individuals per species for two years (Cortés-Flores *et al.* 2017), other study observed 133 tree species including at least one individual per species (in total 204 individuals) for 18 years (Ushio *et al.* 2019). This study presented a method for comparing data with different sample sizes and observation periods as described above. The difference of sample size can be adjusted with determining a rarefaction–extrapolation curve for each total flowering length of each species, and the difference of observation periods can be tested with GLMM, using the method of subsection 2.2.5. Further studies using these methods will allow a broader comparison of datasets observed in different locations and provide new insights into biological phenology.

Second, previous studies of flowering phenology have been tree-biased, but patterns of flowering phenology may differ between trees and herbs within a community,

reflecting differences in resource availability and responses to climatic factors (Rathcke & Lacey 1985; Schemske 1977; Schemske *et al.* 1978). In two studies comparing flowering phenology between trees and herbs within a community showed that herbs showed high interspecific synchronization compared to trees in tropical seasonal communities of India (Joshi & Janarthanam 2004) and Mexico (Cortés-Flores *et al.* 2017). These results were inconsistent with the results of this study, implying that the same life forms exhibit different phenological responses to resource availability and climatic factors in different locations. Therefore, when predicting the phenological responses of different communities to global climatic changes, it is necessary to consider the variability of responses among life forms within the community.

Third, previous phenological studies have been biased towards Africa, South and Central America, and South Africa (Deb *et al.* 2018) and towards temperate forests and tropical lowland forests (Morellato *et al.* 2013), but this study have filled a gap in the tropical montane forest of Mainland Southeast Asia. Phenological studies in the tropical montane forests are important particularly in Asia because many primitive angiosperms are found there (Axelrod 1966; Morlay 2001) and phenological patterns in the tropical montane forests may provide clues in inferring ancestral phenological states of forests in Asia. In this study, I was able to compare leafing, flowering, and fruiting phenologies in a tropical montane forest in southern Vietnam with previous studies in tropical rain forest (Sakai *et al.* 1999), tropical montane forests in Borneo Island (Kimura *et al.* 2009; Nomura *et al.* 2003) and Mainland Southeast Asia, seasonal tropical forest (Kurten *et al.* 2018), temperate forest (Yumoto 1987, 1988), and temperate montane forest (Kudo *et al.* 2008). This comparison led to a schematic diagram (Fig. 3.12)

explaining how various phenological patterns evolved in forests of East and Southeast Asia.

4.3 Limitations

Despite the above contributions of this study to phenological studies, several problems remain unsolved. Chapter 2 has concluded that flowering phenology variables (TFL, VFL and intraspecies synchrony) differ between trees, perennial herbs, and annuals and has suggested that this difference is likely to be explained by the modified pollinator attraction hypothesis for trees, and the resource availability hypothesis in unpredictable habitats for annuals. Further comparative and experimental studies are needed to test these suggested hypotheses.

Chapter 3 has documented the similarities and the differences of leafing, flowering, and fruiting phenology of tropical montane forest in Vietnam compared to tropical rain forest, seasonal tropical forest, and temperate forest. The observations in Vietnam were, however, conducted in less than two years because of the difficulty of travelling under the COVID-19 pandemic. This observation period is shorter than previous phonological studies (Bush *et al.* 2018; Sakai *et al.* 1999; Ushio *et al.* 2019). This study recorded neither flowering nor fruiting for more than one quarter of monitored dominant species, and further studies are needed to describe the phenological patterns of these species.

4.4 Perspectives

How global, regional and local climate changes affect phenology and ecosystem functions, is an emergent research question (Sakai & Kitajima 2019). Recent studies on this question

revealed phenological disjunctions between interacting organisms: for instance, between plants and their pollinators (Hegland *et al.* 2009; Stenseth & Mysterud 2002; Visser & Both 2005) or their herbivores (Inouye *et al.* 2000). These findings suggest the significant impact of plant phenological changes on other organisms. Therefore, a comprehensive understanding of the bio-phenological response to climate change requires the development of predictable models of plant phenological changes. This study developed a quantitative method of plant phenological observation, showed differences in phenological characteristics between plant life forms, and explained the relationship between climatic variables and phenological changes in a tropical mountain forest. Consequently, this study provided useful methods and data for predicting phenological changes in plants with various life forms distributed under different climates.

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