

Phenology of tropical lower montane forests in southern highlands of Vietnam: leafing is associated with precipitation but flowering is not

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Abstract

The premise of the study Though phenological studies in montane forests are important, particularly in tropical Asia where primitive angiosperms are found, the phenology in these forests is still poorly understood. To characterize the phenological patterns and reveal the relationships between meteorological factors and phenology, we observed the leafing, flowering, and fruiting phenology in the tropical montane forests of Vietnam. Methods We observed the leafing, flowering, and fruiting phenology of 91 species every three months in five plots (elev. 1460–1920 m) in Bidoup-Nui Ba National Park, Vietnam, and analyzed how the number of species that were leafing, flowering, or fruiting varied in relation to precipitation, temperature, or daylength. Key results The leafing phenology showed a peak at the beginning of the wet season (April) and was significantly influenced by all of day length, precipitation, and temperature. The flowering phenology did not show any distinct peaks and was influenced by day length and precipitation. The 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 of the meteorological factors. Main conclusion The community-wide phenological patterns of leafing, flowering, and fruiting in the tropical montane forest of Bidoup-Nui Ba are unique among the tropical forests of East and Southeast Asia. In particular, our observation suggests that masting in tropical montane forests may be an ancestral state of both general flowering in tropical rainforests and masting found in temperate forests in East and Southeast Asia.

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The premise of the study

Though phenological studies in montane forests are important, particularly in tropical Asia where primitive angiosperms are found, the phenology in these forests is still poorly understood. To characterize the phenological patterns and reveal the relationships between meteorological factors and phenology, we observed the leafing, flowering, and fruiting phenology in the tropical lower montane forests of Vietnam.

Methods

We observed the leafing, flowering, and fruiting phenology of 91 species every three months in five plots (elev. 1460–1920 m) in Bidoup-Nui Ba National Park, Vietnam, and analyzed how the number of species that were leafing, flowering, or fruiting varied in relation to precipitation, temperature, or daylength.

Key results

The leafing phenology showed a peak at the beginning of the wet season (April) and was significantly influenced by all of day length, precipitation, and temperature. The flowering phenology did not show any distinct peaks and was influenced by day length and precipitation. The 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 of the meteorological factors.

Main conclusion

The community-wide phenological patterns of leafing, flowering, and fruiting in the tropical lower montane forest of Bidoup-Nui Ba are unique among the tropical forests of East and Southeast Asia. In particular, our observation suggests that masting in tropical lower montane forests may be an ancestral state of both general flowering in tropical rainforests and masting found in temperate forests in East and Southeast Asia.

Keywords (up to 5):

Introduction

In East and Southeast Asia, lowland and montane vegetation consist of various forest types. Lowland vegetation includes temperate forests, tropical seasonal forests, and tropical rain forests, among others. Montane vegetation, on the other hand, is comprised of tropical lower montane forests, higher montane forests, sub-alpine forests, and alpine forests (Corlett, 2007). Each of these forests displays specific phenological patterns (Kira, 1991). In 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). As a result, plants in temperate forests typically grow new leaves in spring, flower from spring to summer, and produce fruit mainly in autumn (Zhang et al., 2007; Edwards et al., 2017; Nagahama & Yahara, 2019). In a similar manner, tropical seasonal forests experience predictable changes in precipitation throughout the year, resulting in wet and dry seasons. Plants are able to monitor these changes in water availability to determine the progression of the seasons (Rathcke & Lacey, 1985). Consequently, in tropical seasonal forests, many 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 tropical rain forests, annual fluctuations in temperature and precipitation are much lower and more unpredictable than in temperate or tropical seasonal forests. Consequently, species in the tropical rainforests have low intensity blooms throughout the year or experience high intensity blooms only in years with exceptionally low rainfall and low temperatures (Sakai et al., 1999; Ichie et al., 2004; Nakagawa et al., 2019). This phenomenon is referred to as supra-annual flowering or general flowering (Sakai, 2002). Notably, species common to the tropical seasonal and rain forests usually bloom every year in the former but every few years in the latter (Kurten et al., 2018).

These generalizations about the phenology of tropical forests are based on observations made in lowland forests, which have been the focus of most previous studies. The phenology of tropical montane forests, found at elevations above 1000 m and having a different species composition from lowland forests (Kira, 1991), remains poorly understood in Asia. Although the transition from lowland to lower montane forest in Southeast Asia has a width of around 750–1200 m and altitude varies depending on the location (Ashton, 2014), phenological studies of tropical montane forests are of particular importance in Asia. Many primitive angiosperms can be found in these forests (Axelrod, 1966; Morley, 2001, 2018; Ohtani et al., 2021), and understanding their phenological patterns may provide insight into the ancestral phenological states of Asian forests.

According to Axelrod (1966), angiosperms evolved in tropical mountains during the Cretaceous period. As they expanded their distribution after the Cretaceous, deciduousness evolved as an adaptation to dry climates in the northern hemisphere, while evergreenness was maintained as an adaptation to climates without dry season in the southern hemisphere. Based on this hypothesis, the phenology of species growing in Southeast Asian tropical montane forests is considered ancestral in angiosperms. Thus, understanding the relationship between phenology and meteorological factors in these will help reconstruct the history of phenological divergence from tropical montane forests to tropical lowland and temperate forests.

The relationship between phenology and meteorological factors in the tropical montane forests of Southeast Asia has been well-studied in Mt. Kinabalu, Malaysia, with observations limited to eight species of *Medinilla* (Melastomataceae) by Nomura et al. (2003) for leafing and Kimura et al. (2009) for flowering and fruiting phenology. The average annual temperature at 1560 m in Mt. Kinabalu is 18.9 °C, and the average annual precipitation is 2714 mm. However, the precipitation decreases significantly during El Niño events. The average monthly temperature ranges from 16.5 °C (January) to 19.5 °C (September), and the average monthly precipitation changes from 100 mm (June) to 550 mm (November). Precipitation changes have a negative correlation with solar radiation.

The study of leafing phenology by Nomura et al. (2003) showed that tree species in lower mountain forests (elev. 1560 m) developed new leaves after the El Niño -caused dry period, while those in upper mountain forests (elev. 2590 m) developed new leaves during and after the dry period. However, tree species in the subalpine zone (elev. 3081 m) had continuous leaf development. This indicates that meteorological factors affecting leaf phenology varied with elevation. The other study of flowering and fruiting phenology by Kimura et al. (2009) at elevations 1600–1800 m showed that flowering occurred twice a year in June (when temperature rises) and January (when temperature fall) and was correlated only with temperature. Fruiting, however, occurred once a year for most species and was correlated with both temperature and solar radiation. It remains uncertain whether these patterns are prevalent among other native plant groups to Mt. Kinabalu.

Although Nomura et al. (2003) and Kimura et al. (2009) provide valuable data on the phenology of Asian tropical mountain forests, it is challenging to generalize their findings to all Southeast Asian montane forests. This is due to the varying climate conditions in Southeast Asia. For example, precipitation, which is often used as a cue for phenological changes, shows distinct annual changes in Mainland Southeast Asia, but indistinct changes in Mt. Kinabalu, resulting in different relationships between meteorological factors and phenology (Kumagai et al., 2005). Thus, the relationship between meteorological factors and phenology in Southeast Asian mainland lower montane forests may differ from that in Mt. Kinabalu.

In this study, we observed the phenology of leafing, flowering, and fruiting every three months in five plots located in the lower montane forests (1460–920 m) of Bidoup-Nui Ba National Park, Vietnam, in Mainland Southeast Asia. The monthly average temperature in Bidoup-Nui Ba National Park changes by only 3.6°C per year, with an average annual temperature of 18.7°C. However, 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). This results in a distinction between the dry season from December to March and the rainy season from April to November. The forest of Bidoup-Nui Ba National Park is primarily composed of broad-leaved evergreen trees from families such as Fagaceae and Lauraceae, with some deciduous tree species, such as *Acer* spp. (Sapindaceae), also commonly found (Nagahama et al., 2019).

Our study aimed to answer the following three questions:

- (1) What are the patterns of leafing, flowering, and fruiting in the lower montane forests of Bidoup-Nui Ba National Park, Vietnam?
- (2) Which meteorological factors are correlated with the patterns of leafing, flowering, and fruiting patterns in lower montane forests there?
- (3) What are the differences in the patterns of leafing, flowering, and fruiting between the lower mountain forests of Bidoup-Nui Ba National Park and other parts of the Southeast Asian tropics?

Methods

Study site

Leafing, flowering and fruiting phenology was observed in five plots located along an elevation gradient from 1460 m to 1920 m in Bidoup-Nui Ba National Park, located in Lam Dong Province, Central Highland of Vietnam (Table 1; Fig. 1a). The monthly average temperature in this area ranges from 16.7°C in January to 20.3°C in May (a difference of 3.6°C), and monthly precipitation varies from 10 mm in January to 281 mm in September (a difference of 271 mm; Fick & Hijmans, 2017; Fig. 1c–e). The wet season in this area occurs from April to November, and the dry season occurs from December to March.

Field 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 1; Fig. 1b). 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 elevations of five plots ranged from 1460 m (GL) to 1920 m (LB). In June 2018, we recorded girth and height for all trees and vine 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 morphology using taxonomic literature and type specimen images (Nagahama et al., 2019). For Fagaceae and Lauraceae, which have many similar species that are difficult to distinguish in the fields, we collected a specimen for each tree. Based on the number of individuals of each species, we selected around 20 dominant tree species in each plot, and for each of the selected dominant species, we selected five individuals with larger girth for phenological observations. Of the 100 species for which we recorded phenological states, some species had only one or two individuals due to misidentification in the first census in June 2018. We removed these seven species from the following analysis.

We recorded phenological states as binary values: presence/absence of new leaves, flowers, and fruits, and used these values as species phenological states when at least one individual had them. 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 and often found only in very large trees. For those species, we also searched for flowering and fruiting trees around the plots and recorded any observed flowering and fruiting events, which were then included in our subsequent analyses.

Meteorological data collection

Data of precipitation and temperature were obtained from the weather database WorldClim (Fick & Hijmans, 2017). Data of day length was obtained the function 'daylength' from the R package 'geosphere' (Hijmans et al., 2017).

Categorizing phenological patterns

Considering sample size, data from five plots was pooled for the following analyses. The proportions of leafing, flowering, and fruiting species were calculated for 91 species observed in five plots using Excel for Mac (16.16.12). Phenological variation of 91 species was summarized by principal component analysis (PCA) and classified into by clustering analysis, with presence/absence data of new leaves, flowers, or fruits in seven observations. PCA was performed using the "prcomp" function in R (3.4.3; R core Team, 2017). Phenological similarity among species was calculated through squared Euclidean distance using the "dist" function in R (3.4.3) and dendrograms were constructed using the UPGMA method. Before performing PCA and clustering analysis, the presence of large multicollinearity between the explanatory variables was confirmed using the Variance Inflation Factor (VIF).

To verify the reliability of the UPGMA clustering results, non-hierarchical clustering was performed to the same data set using the Kmeans++ method. By comparing the results of UPGMA and Kmeans++, the number of clusters was determined for leafing, flowering, and fruiting phenology, respectively.

To assess whether the resulting clusters were unbiased towards any particular phylogenetic groups, we examined the distribution of top five families, Fagaceae (10 spp.), Symplocaceae (10 spp.), Lauraceae (9 spp.), Rosaceae (8 spp.), and Rubiaceae (8 spp.), on the dendrogram.

Relationship between phenology and meteorological factors

We used Generalized Linear Models (GLMs) with logit link function and binomial distribution of errors to investigate how the number of species that have leafing, flowering, or fruiting varied with precipitation, temperature, or daylength. The three meteorological factors were strongly correlated with each other (Appendix S1). Therefore, we used the following methods to summarize these correlated variations. First, we performed PCA for six variables, including temperatures, precipitations, and daylengths of current and previous months. We then 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 day length and precipitation, and another between day length and temperature. We calculated residuals for

each regression and tested the relationship using GLMs with day length, residual precipitation, and residual temperature as explanatory variables. All calculations were performed using R (3.4.3).

Comparison of phenological patterns among forests in East and Southeast Asia

Based on previous studies, we compared phenological patterns of leafing, flowering, and fruiting among nine well-studied locations of tropics, seasonal tropics, subtropics, and temperate (Table 2). We conducted a search for phenological studies in East and Southeast Asia using the keywords "leafing phenology", "flowering phenology", and "fruiting phenology". We selected areas where the visual observation of leafing, flowering, and fruiting phenology was conducted in the field for at least one year as well-studied areas for inclusion in our analysis. If the monthly phenological intensity, such as the number or proportion of flowering species, was not reported, the study was excluded from our analysis. We averaged each phenological record into a twelve-months record and calculated the proportions of leafing, flowering, and fruiting species for each month (Appendix S2). To determine phenological similarity between locations, we used the "dist" function in R (3.4.3) to calculate squared Euclidean distance and constructed dendrograms using the UPGMA method.

For the phenological data of Bidoup-Nui Ba, however, the observational records were only available for seven months (excluding February, March, May, August, and November). Thus, we constructed dendrograms: (1) using 21 proportion variables (3 phenological categories x 7 months) for nine areas including Bidoup-Nui Ba, and (2) using 36 proportion variables (3 categories x 12 months) for eight areas excluding Bidoup-Nui Ba. We then compared the topologies of those dendrograms. For the first data set, we performed PCA to summarize 21 variables into fewer principal components, and illustrated a biplot of PC1 and PC2 to interpret the result of the above clustering.

In addition, we calculated meteorological similarity between locations using monthly averages of day length (hours), temperature ($^{\circ}\text{C}$), and precipitation (mm) for nine locations, and constructed a dendrogram using the UPGMA method with squared Euclidean distance.

Results

Species composition

In five plots, we recorded a total of 3,965 tree individuals belonging to 60 families (Fig. 2). Fagaceae was the most abundant family (461 individuals; 11.6%) followed by Lauraceae with 422 individuals (10.6%), Rubiaceae with 368 individuals (9.3%), Symplocaceae with 325 individuals (8.2%), and Rosaceae with 197 individuals (5.0%). The remaining 2,193 individuals (55.3 %) belonged to the other 65 families or unknown families. Fifteen families were represented by only one individual.

Among the 19 dominant tree species in the LB plot (Appendix S3), *Claoxylon langbianense* A.Nagah. & Tagane (Euphorbiaceae; Nagahama et al., 2021) was the most common (45 individuals; 11.3%) almost twice as abundant as the second most common species, *Prunus wallichii* Steud. (Rosaceae; 36 individuals; 9.0%). In the CT plot, *Quercus bidoupensis* H.T.Binh & Ngoc (Binh et al., 2018) was the most common species (61 individuals; 10.4%) nearly three times as frequent as the second most common species, *Melicope pteleifolia* (Champ. ex Benth.) T. Hart. (Rutaceae; 22 individuals; 3.8%). In the HG plot, two species of Rubiaceae, *Diplospora* sp. (121 individuals; 7.8%) and *Urophyllum bidoupense* Yooprasert, Culham & Utteridge (Yooprasert et al., 2022; 109 individuals; 7.1%), had over 100 individuals within a plot. In the DIG plot, *Quercus* sp. (Fagaceae) was the most common species (63 individuals; 7.6%) followed by *Symplocos acuminata* (Blume) Miq. (Symplocaceae; 55 individuals; 6.6%) and *Litsea* sp. (Lauraceae; 41 individuals; 4.9%). In GL plot, *Adinandra donnaiensis* Gagnep. ex Kobuski (Pentaphylacaceae) was the most common species (48 individuals; 7.9%) followed by *Melicope pteleifolia* (Rutaceae; 46 individuals; 7.6%) and *Symplocos hayatae* K. Mori (Symplocaceae; 34 individuals; 5.6%). Among monitored tree species, only four species were deciduous species: *Meliosma pinnata* (Roxb.) Maxim. (Sabiaceae) in GL plot, and *Acer erythranthum* Gagnep., *A. campbellii* subsp. *flabellatum* (Rehder) A.E.Murray (Sapindaceae) and *Engelhardia serrata* Blume (Juglandaceae) in LB plot. The rest were evergreen species.

Phenological pattern

Among 91 monitored species, leafing, flowering, and fruiting events were recorded for 91 spp. (100.0 %), 65 spp. (71.4%), and 54 spp. (59.3 %), respectively. The number of leafing species varied seasonally by a factor of 4.6, ranging from 20 spp. (22.0%) in June to 91 spp. (100%) in April (Fig. 3a). The number of flowering species varied seasonally by a factor of 2.2, ranging from 15 spp. (16.5%) in September to 33 spp. (36.3%) in December (Fig. 3b). The number of fruiting species varied seasonally by a factor of 2.3, from 12 spp. (13.2%) in January to 27 spp. (29.7%) in July (Fig. 3c).

The phenological variations of leafing, flowering, and fruiting events were summarized into four principal components (Table 3; PC1 to PC4), which explained 77.6%, 77.8%, and 80.2% of the total variance of leafing, flowering, and fruiting events, respectively. In leafing, flowering, and fruiting data, all of the presence records in seven observation months positively impacted PC1. However, presence records had both positive and negative contributions to PC2, PC3, and PC4 (Table 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, respectively (Table 3). Eight species that had new leaves only in January and April had the highest PC1 scores (Appendix S4). Conversely, *Maesa perlaria* (Lour.) Merr., *Urophyllum bidoupense*, and *Saurauia napaulensis* DC. had new leaves in all seven times and had the lowest PC1 scores.

By a clustering analysis using the UPGMA method, 91 species can be classified into three groups, designated as Group 1–4 in Fig. 4. Species of Group 1 showed low frequency of new leaf growth and expanded new leaves in January and April but rarely in June, September, and October. This group included two deciduous species (*Acer erythranthum* and *Meliosma pinnata*) and 29 evergreen species. Species of Group 2 also showed low frequency of new leaf growth and expanded new leaves in January and April but not in December. This group included two deciduous species (*Acer flabellatum* and *Engelhardtia serrata*) and 18 evergreen species. Species of Group 3 showed high frequency of new leaf growth and expanded new leaves in most observed months. This group included 37 evergreen species. Species of Group 4 showed low frequency of new leaf growth, usually expanded new leaves usually in April and June, not in July, October, and September, and included only three evergreen species.

By conducting another clustering analysis using the Kmeans++ method, the clustering did not converge when K=4 (the number of clusters in UPGMA). When K=3, the result of clustering was agreed with the UPGMA clustering results for 83 species of the 91 total. However, Group 4 of the UPGMA clustering was not present.

Based on these two clustering results, the 91 species can be classified into three groups, designated as Group A–C (Fig. 4). Group A consisted of 31 species that showed new leaves at low frequency, and rarely expanded new leaves in September, October, and December. Group B consisted of 24 species that showed new leaves at high frequency and expanded new leaves in most observed months except October. Group C consisted of 37 species that showed new leaves at high frequency and expanded new leaves in October.

The top five families were scattered among Groups A, B and C, with the exception of Rubiaceae (2 spp. in Group B and 4 spp. in Group C; Table 4). For Fagaceae, 6 out of 10 spp. were included in Group A and the others were scattered in Group B and C. Similarly, for Lauraceae, 5 out of 9 spp. were included in Group A and the others were scattered in Group B and C.

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, respectively (Table 3). The 26 species had no flowering events and low PC1 scores, while three species (*Melicope pteleifolia*, *Diplospora* sp., and *Maesa* sp. in GL) flowered five or six times and had high PC1 scores (Appendix S4).

By a clustering analysis using the UPGMA method, 91 species can be classified into three groups designated

as Group 1–3 in Fig. 5. Species of Group 1 bloomed at the beginning of the wet season (April, June, and July), and rarely in October, and December. This group included 12 evergreen species. Species of Group 2 flowered at low frequency or did not bloom in our observation periods. This group included four deciduous species and 59 evergreen species. Species of Group 3 bloomed from the late wet season (October) to the dry season (December). This group included seven evergreen species.

By conducting another clustering analysis using the Kmeans++ method, the clustering did not converge when $K=3$. When $K=2$, Group A included 12 species of Group 1 and 17 species of Group 3 of the UPGMA clustering. All the rest 62 species of Group B were included in Group 2 species of the UPGMA clustering (Fig. 5).

Based on these two clustering results, 91 species can be classified into two groups, designated as Group A and B (Fig. 5). Twenty-eight species of Group A bloomed at high frequency and showed flowers at the beginning of the wet season (April, June, and July) and at the beginning of the dry season (November, and December). Sixty-three species of Group B bloomed at low frequency (31 spp.) or did not bloom (32 spp.). In this dendrogram, the top five families were scattered in Group A and B (Table 4). For Fagaceae and Symplocaceae, however, most species (9 out of 10 species in each) were included in Group B.

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, respectively (Table 3). The 37 species showed no fruiting events and 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 (Appendix S4).

By a clustering analysis using the UPGMA method, 91 species can be classified into two groups designated as Group 1 and 2 in Fig. 6. Species of Group 1 set fruits at high frequency, including 15 evergreen species. Species of Group 2 set fruits at low frequency or did not fruit, including four deciduous species.

By conducting another clustering analysis using the Kmeans++ method, the computation when $K = 2$ converged to the clustering of Group A and B: Group A included 15 species of UPGMA Group 1, and Group B included 9 and 67 species of UPGMA Group 1 and 2, respectively.

Based on these two clustering results, 91 species can be classified into two groups, designated as Group A and B (Fig. 6). Fifteen species of Group A set fruits at high frequency. On the other hand, 76 species of Group B set fruits at low frequency (39 spp.) or did not set (37 spp.). In this dendrogram, all species of Fagaceae and Rosaceae were included in Group B, 8 out of 9 spp. of Lauraceae were included in Group B, and species of Rubiaceae and Symplocaceae are more evenly distributed in Group A and Group B.

Relationship between phenology and meteorological factors

Both temperature and precipitation were highly correlated with day length (Appendix S5); correlation coefficients between temperature vs. daylength and precipitation vs. daylength were 0.89 and 0.83, respectively. Notably, the correlation between temperatures of current and previous months was weaker (0.78) and similarly, the correlation between the precipitations of current and previous months was 0.74. These values were lower than the correlation between the day lengths of current and previous months (0.87). Summary statistics of these six meteorological factors were obtained through a principal component analysis, and PC1 and PC2 accounted for 81.5% and 11.8% of the total variance, respectively. PC1 reflected whether six correlated variables showed higher or lower scores and was positive in the wet season and negative in the dry season (Fig. 7a). The high-PC1 season, from May to September, and the low-PC1 season, from December to March, corresponded to "summer" and "winter" in temperate forests of the northern hemisphere, respectively. PC2 reflected a ratio of current month's temperature and previous month's precipitation and was the lowest in April, a turning point from dry to the wet season, and the highest from October to November, a turning point from wet to dry season. All variables increased in the former turning point and decreased in the latter (Fig. 7b). The former turning-point season (April) and the latter turning-point season (October and November) corresponded to "spring" and "autumn" in temperate forests of the northern hemisphere,

respectively. The annual change in the residual precipitation of the previous month relative to the day length of that month was similar to the annual change in PC2 (Fig. 7c). Results of statistical tests using GLM with PC1 and PC2 as explanatory variables showed that the number of leafing species showed a 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 either PC1 ($p = 0.373$) or PC2 ($p = 0.097$).

Based on the results of the statistical tests using GLM with daylength, residual precipitation, and residual temperature as explanatory variables, the number of leafing species showed a significant negative correlation with day length and residual precipitation and a 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 a significant negative correlation with daylength and residual precipitation, but did not show a 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 a significant correlation with any explanatory variables ($p = 0.918, 0.165, 0.504$ for day length, residual precipitation, and residual temperature, respectively).

Comparison of phenological patterns among forests in East and Southeast Asia

In the nine-location phenological similarity dendrogram, which was constructed using the proportions of leafing, flowering, and fruiting species in seven months (Fig. 8a, left side), Bidoup-Nui Ba was positioned at the outermost part, while Mt. Kinabalu was placed between Bidoup-Nui Ba and other seven areas. Among the seven areas, Fushan in Taiwan was positioned on the outermost part. In the inner part of Fushan, there were two clusters: a cluster consisting of two locations in Malaysia (Lambir and Pasoh) and two locations in Japan (Kanto and Kyushu), and another cluster consisting of Xishuangbanna in China and Khao Yai in Thailand. The eight-location phenological similarity dendrogram, which used data from twelve months (Fig. 8a, right side), showed a similar topology, with the exception that the two locations in Japan were now grouped together.

A principal component analysis was performed for the 21 variables (3 phenology categories x 7 months), resulting PC1 and PC2, which explained for 48.8% and 19.1% of the total variance, respectively. PC1 was primarily influenced by the proportions of leafing species in January, April, July, September, October, and December (Appendix S6). PC2 was primarily influenced by the proportion of leafing species in April, that of flowering species in September, October, and December, and the proportion of fruiting species in January, April, June, and December.

The meteorological similarity dendrogram of nine locations was constructed using monthly averages of day length, precipitation, and temperature. It was separated into two groups: Group 1 included six locations in China, Japan, Taiwan, Thailand, and Vietnam, and Group 2 included three locations in Malaysia and located at the base (Fig. 8b). Group 1 showed large, unimodal annual changes of day length, temperature, and precipitation, while Group 2 had high annual constancy of day length and temperature, and smaller, irregular annual change of precipitation.

Discussion

Key findings

In terms of species composition, the lower montane forest in Bidoup-Nui Ba National Park was similar to forests in Xishuangbanna, China, with Fagaceae being the most common family, followed by Lauraceae and Symplocaceae (Table 2). In terms of meteorological data, Bidoup-Nui Ba National Park was similar to Xishuangbanna, China and Khao Yai, Thailand (Fig. 8b). Seasons in Bidoup-Nui Ba were classified into the dry season, the wet season, and two transition stages including dry to wet transition around April and wet to dry transition around October. These two transition stages corresponded to “spring” and “autumn” in the temperate Northern Hemisphere climate. Under this pronounced seasonality, 91 monitored species showed high variabilities in leafing, flowering, and fruiting behaviors. They expanded new leaves at least once a

year, while leafing frequency largely varied between species. Twenty four of the 37 species with high new leaf development frequency expanded new leaves in all observed months except October, while the other species expanded new leaves in October, the transition stage from wet to dry season. Flowering frequency also varied among 91 species that were classified into the high frequency group (28 spp.) and the low frequency group (63 spp.). In the former, 12 species had flowers at the beginning of the wet season (April, June, and July) and other species had flowers at the beginning of the dry season (November, and December). Notably, 32 out of 91 species (35.2%) did not flower during the observation period. For fruiting phenology, 91 species were also classified into high frequency and low frequency groups, containing 15 spp. and 76 spp. (including non-fruiting 37 species), respectively.

In the following discussion, we will first characterize the phenological patterns in Bidoup-Nui Ba by comparing them with patterns in mainland SE Asia, China, Taiwan, and Japan. Second, we consider why the two clustering results based on the phenological patterns (Fig. 8a) and the meteorological data (Fig. 8b) were inconsistent. Finally, based on these considerations, we infer how different phenological patterns diverged in tropical montane forests, tropical lowland forests, and seasonal forests.

Phenological characteristic in Bidoup-Nui Ba

By summarizing the above-mentioned variability, the overall phenological patterns in the tropical lower montane forest of Bidoup-Nui Ba, Vietnam were characterized as follows. First, leafing phenology had a low peak at the beginning of the wet season (April), and was significantly associated with day length, precipitation, and temperature. This observation is consistent with previous observations in tropical seasonal forests where many plants have a peak of leafing in either wet or dry season (Wright & van Schaik, 1994). Second, flowering phenology did not show any distinct peak, although it was associated with day length and precipitation. This phenological pattern was different from a previous observation study in the tropical lowland forest showing a peak of flowering at the end of the dry season (Kitamura *et al.*, unpublished). Third, 32 out of 91 species (35.2%) did not flower during the observation period, suggesting that those species have masting habit. Among these non-flowering species, *Lithocarpus* and *Quercus* (Fagaceae) are of the same genera as species known to exhibit masting in temperate forests (Shibata *et al.*, 2019; Wang *et al.*, 2022). This is the first report suggesting the occurrence of masting species in tropical montane forests of Southeast Asia, although masting species have been observed in montane forests of South India (Mohandass *et al.*, 2016) and tropical seasonal lowland forest in Thailand (Kurten *et al.*, 2018). However, there is a possibility that some species did not flower due to their immaturity, as we observed that some species such as *Calophyllum rugosum* P.F.Stevens (Calophyllaceae), *Platsea latifolia* Blume (Metteniusaceae), *Beilschmiedia bidoupensis* Komada, Tagane & Yahara (Komada *et al.*, 2022), and *Acer campbellii* subsp. *flabellatum* in the plots did not flower even though the taller trees outside of the plots were in flowering or fruiting. Further studies, including tree size and maturity data for each species, are needed to conclude that some tree species of lower montane forest in Bidoup-Nui Ba show masting habits. Fourth, fruiting phenology showed a low peak from the mid-wet season (July) to the early dry season (December) and was not significantly associated with any meteorological factor. Again, this observation was different from a previous study in the tropical lowland forest showing a peak of fruiting early in the wet season (Kurten *et al.*, 2018). In summary, tree species in the lower montane forests of Bidoup-Nui Ba are highly variable in leafing, flowering, and fruiting behaviors, and the phenological patterns observed there were different from previous observations in tropical lowland forests with dry season in spite that the climate in Bidoup-Nui Ba shows a pronounced seasonality in precipitation.

These phenological patterns in the lower montane forests of Bidoup-Nui Ba were similar to those of Mt. Kinabalu with high intensities of flowering and fruiting events throughout the year (Fig. 8a). Here, we define the term “intensity” to describe the proportion of species active in leafing, flowering, or fruiting in a particular observation month. Unlike Bidoup-Nui Ba and Mt. Kinabalu, the phenological patterns in the other areas showed more pronounced seasonality in the intensities of flowering and fruiting events, with some low-intensity months. These differences in phenological intensity may be the one of the key factors characterizing forest phenology and are not necessarily consistent with the meteorological differences among

forests (Fig. 8).

Comparison between the phenological similarities and the meteorological similarities

The discrepancies between the clustering results based on the phenological patterns (Fig. 8a) and the meteorological data (Fig. 8b) suggested that not only day length, temperature, and precipitation included in this study's analyses, but also some other meteorological factors affected forest phenology. If the three meteorological factors are sufficient to explain forest phenology, the phenological patterns in Bidoup-Nui Ba are expected to be similar to those in Xishuangbanna, where three meteorological factors show similar seasonal patterns. In reality, however, the phenological patterns differed between Bidoup-Nui Ba, with a high intensity of leafing and flowering throughout the year, and Xishuangbanna, with distinct peaks of leafing and flowering within the year. Moreover, if the three meteorological factors are sufficient to explain forest phenology, its patterns are expected to differ between Bidoup-Nui Ba and Mt. Kinabalu, due to meteorological differences between them, especially in precipitation (Kumagai et al., 2005). In reality, however, the phenological patterns of two montane forests were similar in high intensities of flowering and fruiting events throughout the year.

Compared to lowlands, there are more days when clouds cover tropical mountains (Karger et al., 2021). Though the number of cloudy days was not monitored in our observations in Bidoup-Nui Ba National Park, tree trunks in the HG plot were covered by mosses, suggesting that the forest was often covered with clouds. Previous study (Sklénar et al., 2008) summarized the effects from the occurrence of clouds to the ecology of mountain ecosystems as follows: (i) considerable quantities of water can be provided indirectly through cloud or fog water deposition, (ii) reduced evapotranspiration during the day prevents development of water stress in the plants, (iii) reduced temperature oscillations minimize the risk of night frosts, and (iv) low temperatures affect metabolic rates of plants (Hedberg, 1964; Sarmiento, 1986; Breckle, 2002; Sklénar et al., 2008). Due to those effects, many plants in tropical mountains may grow or reproduce without the resting season and show high-intensity phenology in leafing, flowering, and fruiting throughout the year, as in the lower montane forests of Bidoup-Nui Ba and Mt. Kinabalu.

Diversification of phenological patterns among forests in East and Southeast Asia

Given the above similarities and differences of phenological patterns 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 the adaptive evolution of angiosperms in East and Southeast Asia.

According to the paleobotanical (Axelrod, 1966; Morley, 2001, 2018) and molecular-ecological studies (Ohtani et al., 2021), 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. It is also suggested that, before the entry of angiosperms into the lowland Cretaceous record, they evolved chiefly in moist tropical to warm temperate upland regions (Axelrod, 1966). Therefore, when inferring how phenological patterns diverged between various forest types, we can assume that tropical lower montane forests have ancestral states of leafing, flowering, and fruiting phenology (Fig. 9). This assumption does not preclude reverse changes, but rather helps in considering reverse changes.

First, during the process of distribution expansion from tropical lower montane forest to tropical lowland forest (process 1 of Fig. 9), some plants weakened their seasonal patterns as a result of adaptation to lowland climates, resulting in reduced intensities of leafing, flowering, and fruiting through a year. In contrast, other plants, including masting species in tropical lower montane forests, retained their abilities to respond to changes in temperature and precipitation, resulting in supra-annual flowering events occurring after irregular drought and low temperature, known as general flowering.

Second, during the process of distribution expansion from tropical lower montane forests to tropical seasonal forests (process 2 of Fig. 9), plants reduced phenological intensities as a result of adaptation to severe drought in lowland climates, resulting in annual patterns of leafing and flowering in the dry season, and fruiting in the

wet season. In this process, some plants evolved deciduousness for adaptation to severe drought (Axelrod, 1966).

Third, phenological changes similar to the process 2 are considered to have occurred during the processes of geographical migration from tropical rain forest areas to tropical seasonal forest areas (process 3 of Fig. 9), resulting in annual patterns of leafing and flowering in the dry season, and fruiting in the wet season. In this process, some plants evolved deciduousness for adaptation to severe drought (Axelrod, 1966).

Fourth, during the processes of geographical migration from the tropical seasonal forest areas to subtropical seasonal forest areas (process 4 of Fig. 9), plants adapted to the lower temperature, where annual patterns of leafing and flowering in spring, and fruiting in autumn emerged.

Fifth, during the processes of geographical migration from the subtropical forest areas to warm-temperate forest areas (process 5 of Fig. 9), plants adapted to the cooler temperature in winter, resulting in high-peaked annual patterns of leafing and flowering in spring, and fruiting in autumn. In this process, only some groups, including Fagaceae, are considered to retain masting habits.

This hypothetical framework explains that high-intensity patterns of leafing and flowering phenology are found in montane forests, longer and scattered patterns of leafing and flowering phenology are found in low-latitude areas, and shorter and concentrated patterns of leafing and flowering phenology are found in high-latitude areas (Fig. 8a). Based on this framework, we suggest that phenological traits may change in future by sensitively responding to climate changes. However, it should be noted that the framework of Figure 9 is a simplification of the complicated changes in tree phenology observed in various forest types. To develop a more realistic framework, we need to describe and compare community-wide phenological patterns in various forests in more locations in East and Southeast Asia.

Conclusion

In conclusion, the community-wide phenological patterns of leafing, flowering, and fruiting in the tropical lower montane forest of Bidoup-Nui Ba are unique among tropical forests of East and Southeast Asia. Particularly, our observation suggests that masting of tropical lower montane forest can be an ancestral trait to both general flowering in tropical rain forests and masting found in temperate forests in East and Southeast Asia. These considerations are derived from the first quantitative observations of the leafing, flowering, and fruiting phenology in the tropical lower montane forest of continental Asia, and comparisons of community-wide phenological patterns among various forest types observed in East and Southeast Asia.

This study also suggested that not only day length, temperature, and precipitation, but also some other meteorological factors, such as cloud cover days may have affected forest phenology. Cloud forests in the tropics are known as terrestrial ecosystems that are rich in species and endemics (Karger et al., 2021). Further studies on the influence of cloud cover days on phenology are needed using meteorological data including the data of near-global, fine-grain monthly cloud frequencies from 15 year of Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images (Wilson & Jetz, 2016).

Further quantitative studies describing community-wide phenological patterns are also needed to determine whether similar patterns are observed in plant communities under similar climatic conditions or not. Also, we need to consider the phylogenetic constraint among species for more precise comparison. In recent years, community-level phenological shifts have been reported in several areas (e.g. CaraDonna et al., 2014; Chen et al., 2017), suggesting that significant change will occur in synchronized ecosystems in response to future climate change. To deepen our understanding of phenological responses to climate change, we need additional detailed studies of phenology throughout Asia.

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Contributions:

AN (Nagahama) and TY lead the study and significantly contributed to data analysis and interpretation. AN (Nagahama), ST, NVN, HTB, TQC, NTN, KT, MZ, HT, HN, AN (Naiki), and TY contributed to field surveys in Vietnam and collecting phenological data. AN (Nagahama), ST, NVN, HTB, TQC, EM, HT, HN, AN (Naiki), and TY contributed to species identifications. SK contributed to field surveys in Thailand and collecting phenological data. All authors reviewed the manuscript draft and revised it critically on intellectual content. All authors approved the final version of the manuscript to be published.

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