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Article

Fenología de las especies arbóreas de la Reserva Nacional Tambopata, Perú

Phenology of tree species of the *Tambopata* National Reserve, Peru

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Resumen

El ecosistema amazónico es uno de los más importantes del mundo y también uno de los menos estudiados, en especial su vegetación y sus fenofases. El objetivo del presente trabajo fue identificar y describir los patrones fenológicos de las especies arbóreas de gran porte más frecuentes de la Reserva Nacional Tambopata, Madre de Dios, Perú. El estudio se realizó entre los años de 2010 a 2017; mediante el establecimiento de cinco parcelas de 50 × 30 m por cada tipo de bosque: Bosque de Aguajal, Bosque de Bajío, Bosque Sucesional y Bosque de Tierra Firme. En cada parcela se marcaron e identificaron todos los individuos arbóreos con diámetro ≥ 10 cm, a 1.30 m por encima del suelo. Se hizo un análisis de especies indicadoras por hábitats y los taxones resultantes se observaron periódicamente, para evaluar las fenofases de botón floral, flor, fruto inmaduro y fruto maduro. Además, se evaluó la influencia de las variables precipitación y temperatura sobre sus respuestas fenológicas. Se registraron 1 958 individuos, pertenecientes a 57 familias, 173 géneros y 300 especies; destacan las familias Fabaceae, Moraceae y Annonaceae con el mayor número de taxa y Arecaceae con más individuos. Se analizaron ocho especies indicadoras, dos por cada tipo de bosque. Con excepción del Bosque de Aguajal, las fenofases botón floral y fruto maduro alcanzaron sus máximos valores en septiembre y diciembre-enero. Esta información contribuirá a un mejor entendimiento de la fenodinámica de cada uno de los tipos de bosques de la Reserva Nacional Tambopata.

Palabras clave: Análisis de fenofases, bosque amazónico, composición florística, especies indicadoras, fenodinámica, Madre de Dios

Abstract

The Amazonian ecosystem is one of the most important in the world and also one of the least studied, especially in regard to its vegetation and its phenophases. The objective of this study was to identify and describe the phenological patterns of the most frequent large tree species in the Tambopata National Reserve, Madre de Dios, Peru. The study was conducted between the years 2010 to 2017; by establishing five 50 × 30 m plots for each forest type: Aguajal Forest, Bajío Forest, Successional Forest and Tierra Firme Forest. In each plot, all tree individuals with a diameter ≥ 10 cm were marked and identified at 1.30 m above the ground. An analysis of indicator species by habitat was performed, and the resulting taxa were periodically observed to evaluate the flower bud, flower, immature fruit and mature fruit phenophases. In addition, the influence of precipitation and temperature variables on their phenological responses was evaluated. A total of 1 958 individuals were recorded, belonging to 57 families, 173 genera and 300 species; the Fabaceae, Moraceae and Annonaceae families stand out with the highest number of taxa and Arecaceae, with the highest number of individuals. Eight indicator species were analyzed, two for each forest type. Except in the Aguajal forest, the flower bud and mature fruit phenophases reached their maximum values in September and December-January. This information will contribute to a better understanding of the phenodynamics of each of the forest types in the Tambopata National Reserve.

Key words: Phenophase analysis, Amazon rainforest, floristic composition, indicator species, phenodynamics, Madre de Dios.

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Introduction

In recent decades, the effect of climate change, expressed in several types of environmental stress has received increasing attention, as evidenced in numerous recent studies (Häder and Barnes, 2019). The effects of climate change on plants are dramatic, because plants lack mobility. The abiotic factors that most affect plant phenology are: temperature (Körner and Basler, 2010), photoperiod and precipitation (Jackson, 2009); mainly in tropical and subtropical areas (Pires *et al*., 2018). Plant phenology is an integrative environmental indicator of climate change, expressed in the permanence, senescence or abscission of leaves, flowering and fruit ripening (Workie and Debella, 2018). In addition, phenology integrates other vital factors such as the duration, magnitude and timing of plant cycles (Pires *et al*., 2018).

In tropical regions, it is relatively easy to visualize blooms, especially in urban environments, hence their application in climate change impact assessments (Du *et al*., 2015). However, there is little research on tree communities that could explain the responses of plants to the effect of climate change (Davies *et al*., 2013). Phenological studies like the one conducted by Wolkovich *et al.* (2012) have been based on observations of a single species such as *Ginkgo biloba* L. (Matsumoto *et al*., 2003), or in taxa of a single genus such as *Protea* (Daru *et al*., 2019) and others with continental coverage.

In Amazonian forests, and specifically in Peru, phenological studies are scarce. Only the following have been conducted: seasonal phenological aspects in the *Tambopata* National Reserve (*Madre de Dios*, Peru) (Girardin *et al*., 2016), the climatic factors that determined the decline of vegetation in the 2005 and 2010 Amazonian droughts (Zhao *et al*., 2017) and of the relationships between insolation and precipitation on leaf production and leaf fall (Wagner *et al*., 2017).

Therefore, the objectives of this study were to identify and describe the phenological patterns of the most frequent tree species in the Amazonian Forest of the *Tambopata* National Reserve.

Materials and Methods
Study area

The research was conducted between January 2010 and December 2017, in the *Tambopata* National Reserve (TNR) of the *Tambopata* Research Center (*Tambopata* Research Center/*TRC*), located at 250 masl, at coordinates 433162 E - 8548037 N, near the border of the *Bahuaja Sonene* National Park, *Madre de Dios* region, Peru (Figure 1). The study area covers an area of 1 613 ha, with an average annual precipitation of 2 925 mm and an average annual temperature of 25 °C.

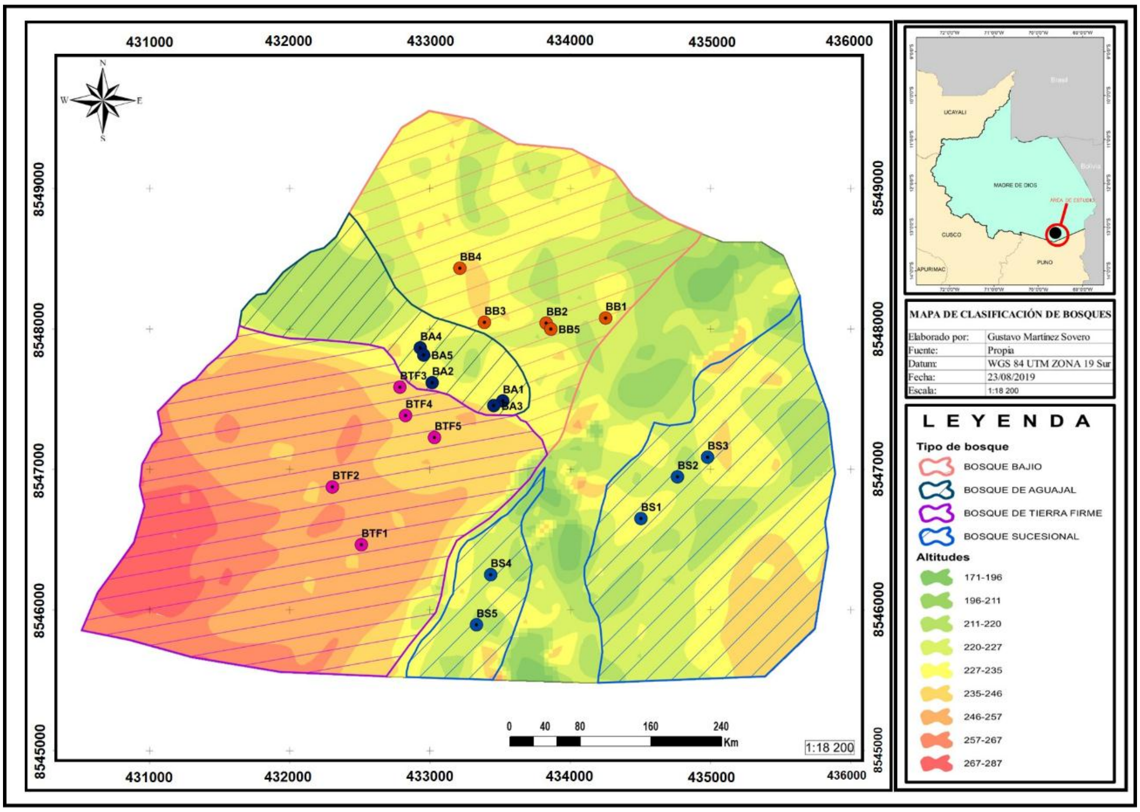


Figure 1. Location of the study area and distribution of plots in the TNR, *Madre de Dios*, Peru.

Ribeiro *et al*. (1999) classified the area into four forest types: *Aguajal* Forest (AF), with flooded soils almost all year round and predominantly *Mauritia* *flexuosa* L.f. (*aguaje*); *Bajío* Forest (BF), with occasionally flooded soils and with few emerging species such as *Dipteryx micrantha* Harms (*shihuahuaco* or *cumaru*) and *Ceiba pentandra* (L.) Gaertn. (*ceiba* or *kapok* tree); Successional Forest (SF), located in the river plain and dominated by fast-growing taxa like *Erythrina poeppigiana* (Walp.) O.F. Cook and *E. ulei* Harms, *Triplaris americana* L. (*tangarana*) and patches of *Guadua* sp. (bamboo); and *Tierra Firme* Forest (TFF), with clayey soils with emerging species such as *Hymenaea courbaril* L. (West Indian locust) and *Eschweilera coriacea* (DC.) S.A. Mori.

Data collection and sample processing

The plots were installed according to the guidance of the Research Center's trail system. Twenty 50 × 30 m plots were evaluated —five for each forest type—, representing 3.5 times the 20 × 20 m area recommended for a subplot (Phillips *et al.*, 2016). In each plot, all tree individuals with a *DBH* (diameter at 1.30 m above the ground) ≥ 10 cm were registered. The registered individuals (n= 1 958) were collected, herborized and identified through virtual visits to botanical collections: Tropicos (https://www.tropicos.org/), *The Plant List* (http://www.theplantlist.org/), and GBIF (https://www.gbif.org/), as well as consultations with specialists and visits to physical herbaria close to the study area: the Alwyn Gentry Herbarium (AGH), the Vargas herbarium (CUZ), and the *Oxapampa* Herbarium of the Central Forest (HOXA).

Subsequently, they were ordered by families according to the system proposed by the Group for the Phylogeny of Angiosperms (APG IV, 2016); the specimens were deposited in the TNR Herbarium. Next, it was proceeded to identify indicator taxa by forest type, based on the fidelity and affinity of the species by type of habitat (Dufrêne and Legendre, 1997), whose individuals were monitored monthly with binoculars in order to evaluate the following phenophases: flower bud, flower, unripe fruit, and ripe fruit. A modification of the Fournier scale was used for phenological data collection (1974) on the absence/presence of phenophases, where 0 indicates absence, and 1, presence. Precipitation and temperature data for the study period were obtained from the TNR Meteorological Station and the *Puerto Maldonado* Meteorological Station. (*Madre de Dios*).

Data analysis

Three matrixes —floristic, phenological, and environmental— were constructed. Based on the floristic matrix, an *NMDS* (*Non-metric Multidimensional Distance Scaling*) ordination analysis was carried out (Kruskal, 1964) which uses the dissimilarity matrix between plots, applying Bray-Curtis distance. In addition, a PERMANOVA analysis (Permutational Multivariate Analysis of Variance) was performed to verify significant differences between the groups formed, and the rarefaction method was used to compare species richness between forest types (habitats); the maximum number of species was estimated based on the Chao2 index as a measure of sampling efficiency (Colwell, 2013). An *ISA* analysis (Indicator Species Analysis), which determines the significance of the species under analysis based on a *Monte Carlo* test, was carried out to verify the indicator species by habitat types (Dufrêne and Legendre, 1997) in order to test the null hypothesis that the species under study had no indicator value (*IndVal*).

Subsequently, the influence of environmental variables on phenological variables was verified by means of a *CCA* analysis (Canonical Correlation Analysis) (McCune and Grace, 2002). The ratio between the precipitation and temperature averages and the averages of the phenophases of the indicator species was estimated by forest type for each monthly average during the years 2010 to 2017. Finally, the correlation of these months with the phenophases under study for the indicator species was verified. A *Monte Carlo* test with 1 000 permutations was utilized to determine the significance of the ordination. All analyses were performed with the R 3.6.3 statistical environment (R Core Team, 2021) and the Fitopac 2.1 software (Shepherd, 2010).

Results

Floristic composition

In the four forest types, 1 958 individuals were recorded, grouped into 57 families, 173 genera, and 300 species. The families with the highest number of genera were Fabaceae (19), Euphorbiaceae (12), Malvaceae (12), Moraceae (12), and Annonaceae (11). The families with the greatest number of species were Fabaceae (36), Moraceae (27), and Annonaceae (18), and the ones that grouped most individuals were Arecaceae (607), Euphorbiaceae (144), Fabaceae (142), and Myristicaceae (122) (Table 1). In addition, 68 species were registered for the *Aguajal* Forest, 142 for the *Bajío* Forest, 82 for the Successional Forest and 158 for the *Tierra Firme* Forest; it should be noted that one species was observed in more than one forest type.

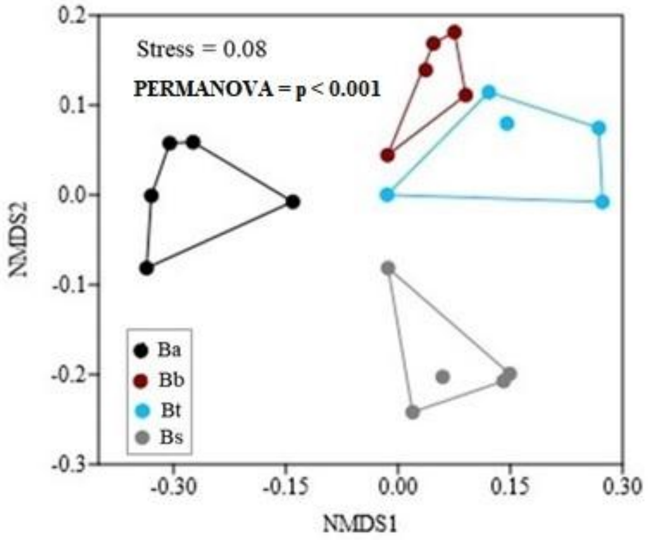
Table 1. Relationship of families and number of genera, species and individuals, evaluated in the *Aguajal* forest (AF), *Bajío* forest (BF), Successional Forest (SF), and *Tierra Firme* Forest (TFF) in the TNR, *Madre de Dios*, between 2010-2017.

Families	No. of Genera	No. of Species	Forests/No. of individuals				Total No. of (indiv.)
			AF	BF	SF	TFF	
Anacardiaceae	3	4	0	4	8	1	13
Annonaceae	11	18	20	17	33	14	84
Apocynaceae	3	7	1	4	7	25	37
Araliaceae	2	2	0	2	2	7	11
Arecaceae	9	10	308	126	124	49	607
Bignoniaceae	3	4	1	0	3	6	10
Boraginaceae	1	2	0	1	1	4	6
Burseraceae	3	6	5	5	2	9	21
Calophyllaceae	1	1	6	0	0	0	6
Cannabaceae	2	2	0	7	0	0	7
Capparaceae	1	1	3	0	3	0	6
Caricaceae	1	1	0	4	0	0	4
Celastraceae	2	3	0	1	0	0	1
Chrysobalanaceae	2	6	6	3	0	5	14
Clusiaceae	2	2	2	0	0	1	3

Combretaceae	2	2	0	4	9	1	14
Ebenaceae	1	1	0	0	0	1	1
Elaeocarpaceae	1	4	2	4	2	5	13
Euphorbiaceae	12	16	27	8	37	72	144
Fabaceae	19	36	14	26	54	48	142
Icacinaceae	1	1	0	1	0	0	1
Lacistemataceae	1	1	0	1	0	0	1
Lamiaceae	1	2	0	0	0	2	2
Lauraceae	6	14	2	10	15	16	43
Lecythidaceae	4	5	10	6	0	16	32
Linaceae	1	1	2	0	0	1	3
Macgraviaceae	1	1	0	0	0	1	1
Malpighiaceae	1	1	1	0	0	0	1
Malvaceae	12	14	40	27	11	34	112
Melastomataceae	1	4	1	1	1	3	6
Meliaceae	0	13	1	62	16	16	95
Moraceae	12	27	7	41	31	27	106
Myristicaceae	4	8	7	57	35	23	122
Myrtaceae	3	5	0	1	0	7	8
Nyctaginaceae	2	5	1	7	1	14	23
Ochnaceae	1	1	0	2	0	0	2
Olacaceae	3	3	0	1	0	6	7
Opiliaceae	1	1	0	1	0	2	3
Phyllanthaceae	2	2	2	1	0	0	3
Phytolacaceae	1	1	0	2	0	0	2
Picramniaceae	1	1	0	1	0	0	1
Piperaceae	1	2	0	0	2	0	2
Polygonaceae	2	2	0	2	34	2	38
Putranjivaraceae	1	1	0	0	0	1	1
Rubiaceae	7	7	0	2	11	3	16
Rutaceae	2	2	0	1	0	7	8
Sabiaceae	1	2	0	0	0	2	2
Salicaceae	2	6	0	8	8	5	21
Sapindaceae	2	4	0	5	5	0	10
Sapotaceae	4	14	4	13	1	23	41
Simarubaceae	1	1	1	0	0	2	3
Siparunaceae	1	2	0	1	0	4	5

Staphylaceae	1	1	0	1	0	0	1
Trigonaceae	1	1	0	1	0	0	1
Urticaceae	3	12	4	16	39	20	79
Violaceae	3	3	0	4	0	7	11
Vochysiaceae	1	1	0	0	0	1	1
Total	173	300	478	492	495	493	1 958

The TNR forests with the greatest similarity were the *Tierra Firme* Forest and the Successional Forest. On the other hand, the most dissimilar were the *Aguajal* Forest and the Successional Forest. Such differences are reflected in the graph in Figure 2 of the *NMDS* with Bray-Curtis stress = 0.08 and significant variance ($p<0.001$).



AF = *Aguajal* Forest; BF= *Bajío* Forest; TFF = *Tierra Firme* Forest; SF = Successional Forest. Each point represents a 50 × 30 m plot in the TNR, *Madre de Dios.*

Figure 2. *NMDS* of species in the four study forests.

Likewise, the rarefaction and extrapolation methods, based on the samples, showed a difference between the specific richness and the environmental heterogeneity of the communities, allowing us to find greater richness in the *Tierra Firma* and *Bajío* forests (Figure 3).

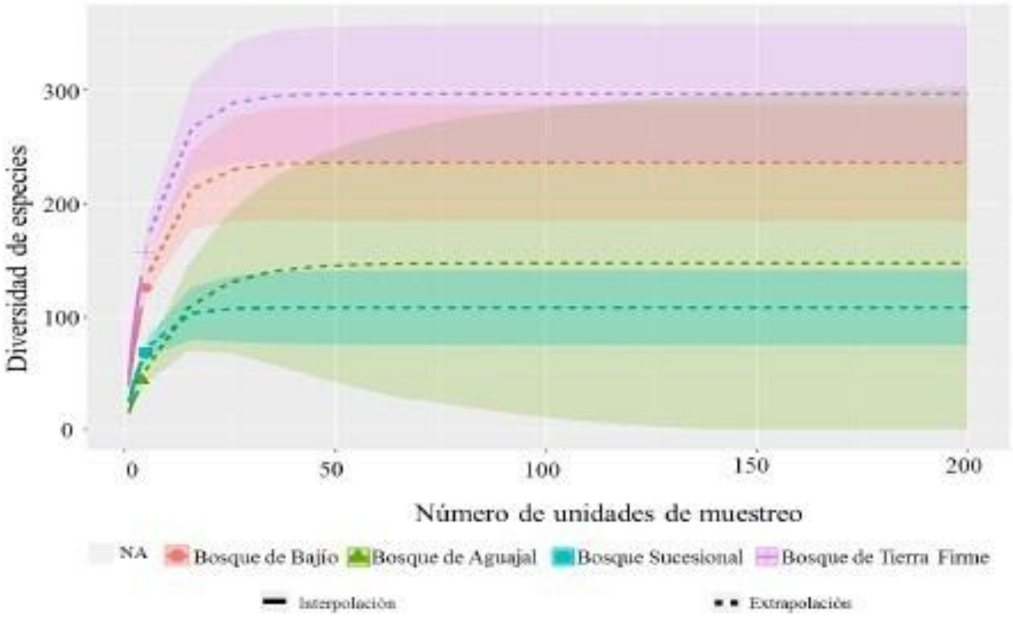


Figure 3. Richness rarefaction curve estimated using the Chao2 index for the TNR forests, *Madre de Dios.*

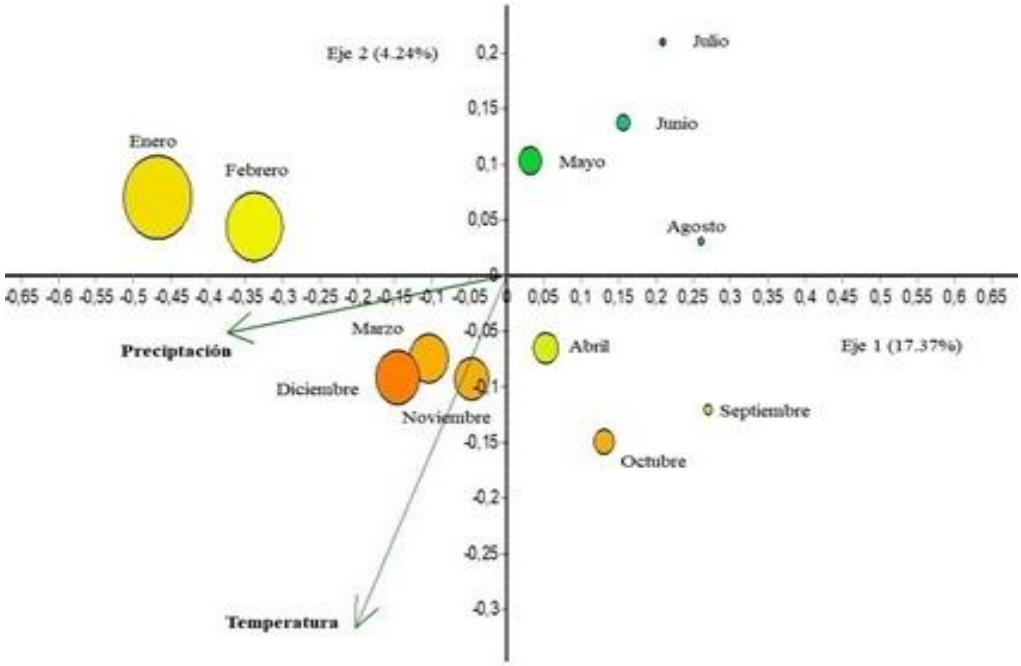
Analysis of indicator species

ISA identified eight species as indicator species for the respective forests, the most prominent being: *Mauritia flexuosa* and *Euterpe precatoria* Mart., for the *Aguajal* Forest; *Iriartea deltoidea* Ruiz & Pav., for the *Bajío* Forest; *Erytrhina ulei*, for the Successional Forest and *Quararibea malacocalyx* A. Robyns & S. Nilsson, for the *Tierra Firme* Forest (Table 3).

Table 3. Indicator species selected by *ISA* and used for the *CCA* analysis of the forests evaluated in the TNR.

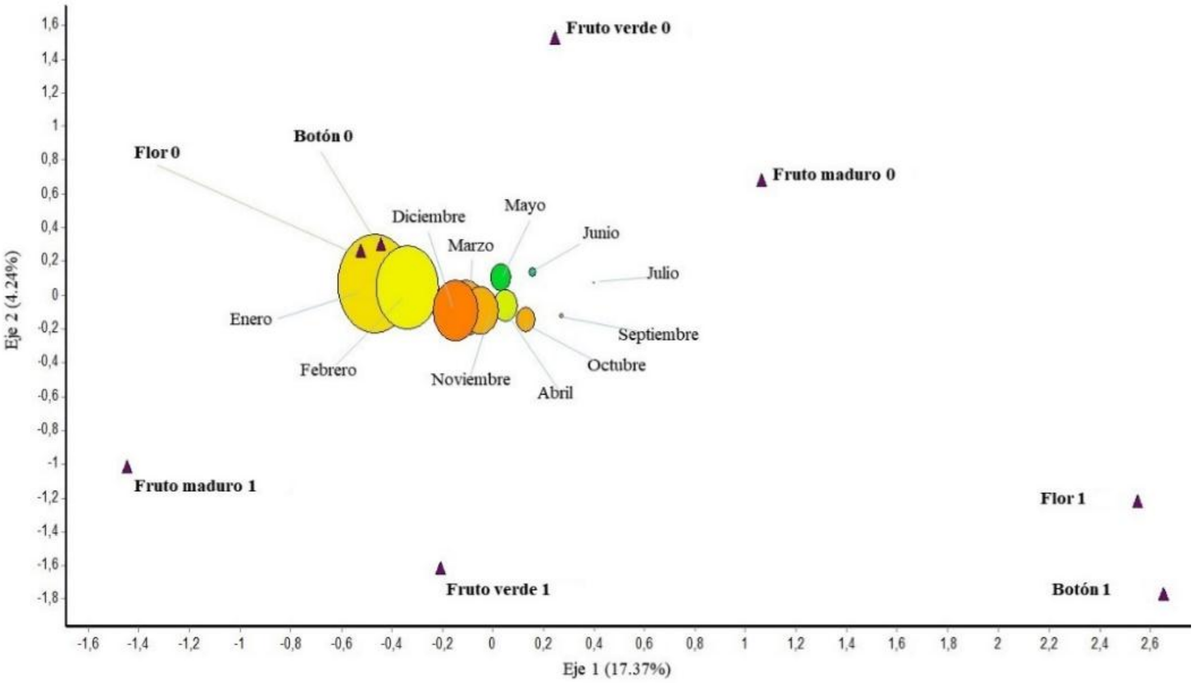
Type of Forest	Species	IndVal	*p* -value
Aguajal Forest	*Mauritia flexuosa* L.f.	1	0.005
	Euterpe precatoria Mart.	0.973	0.005
Bajío Forest	*Iriartea deltoidea* Ruiz & Pav.	0.959	0.005
	Otoba parvifolia (Markgr.) A.H. Gentry	0.722	0.030
Successional Forest	*Erythrina ulei* Harms.	0.946	0.005
	Spondias mobin L.	0.843	0.005
Tierra Firme Forest	*Quararibea malacocalyx* A. Robyns & S. Nilsson	0.849	0.005
	Tetragastis panamensis (Engl.) Kuntze	0.775	0.030

The *CCA* analysis, based on the phenophase records of the indicator species and the environmental variables of temperature and precipitation proved to be significant (MS = 0.001); with the precipitation variable strongly correlated to axis 1 (-0.99), and the temperature variable, to axis 2 (-0.84). In the graph with 22 % cumulative variation (Figure 4), it is observed that both environmental variables were highly correlated with the November to March period, precisely the months with the highest temperatures and precipitation, which correspond to the neotropical summer. Likewise, the button (2.65) and flower (2.55) phenophases presented the highest canonical values for axis 1; ripe fruit (-1.61) and unripe fruit (1.52) registered the highest values for axis 2 (1.52). (Figure 5).



Larger circles = Months with greater influence of precipitation; Color scale = Influence of the temperature variable, where variations of blue and green depict the months with the lowest temperatures, and yellow and orange, the months with the highest temperatures.

Figure 4. *CCA* of environmental variables in the forests evaluated in the TNR, *Madre de Dios*.



Larger circles = Months with greater influence of precipitation; Color scale = Influence of the temperature variable, where variations of blue and green depict the months with the lowest temperatures, and yellow and orange, the months with the highest temperatures.

Figure 5. *CCA* of phenophases in the TNR, *Madre de Dios*. Larger circles: months with greater influence of precipitation.

The analysis of the phenophases of the indicator species (Table 4) showed that, in the *Aguajal* Forest, the flower bud phenophase began in October and reached its maximum value in November (21 %), and the highest values for ripe fruit were reached in December (16 %) and January (15 %). In the *Bajío* Forest the highest value for the flower bud phenophase (17 %) was obtained in September, and for ripe fruit, in December (29 %). In the Successional Forest the maximum value for the flower bud phenophase (14 %) was recorded in September, and for ripe fruit (23%), in December; in the *Tierra Firme* Forest, the highest value for the flower bud phenophase was observed in September (35 %), and in January (24 %) for ripe fruit.

Table 4. Register of the phenophases of indicator species and mean of environmental variables in the TNR, *Madre de Dios* (2010-2017).

Types of forests	**Monthly average (2010-2017)**			**Phenophases**							
				Bud		**Flower**		**Unripe fruit**		**Ripe fruit**	
	M	**T (°C)**	**Pp (mm)**	**0 (%)**	**1 (%)**	**0 (%)**	**1 (%)**	**0 (%)**	**1 (%)**	**0 (%)**	**1 (%)**
***Aguajal* Forest**	J	25.5	505.3	100	0.0	99.7	0.3	79.7	**20.3**	84.7	**15.3**
	F	25.4	434.0	99.8	0.2	99.9	0.1	83.3	16.7	87.1	12.9
	M	25.7	316.9	99.8	0.2	99.0	1.0	83.7	16.3	88.7	11.3
	A	25.3	224.3	98.8	1.2	96.4	3.6	81.5	18.5	96.1	3.9
	M	24.2	208.9	96.7	3.3	91.8	8.2	83.3	16.7	93.9	6.1
	J	23.7	130.8	97.0	3.0	93.6	6.4	79.3	20.7	92.7	7.3
	J	23.1	88.4	98.9	1.1	93.1	6.9	78.7	21.3	91.8	8.2
	A	24.2	87.3	99.1	0.9	91.8	8.2	76.9	23.1	88.9	11.1
	S	25.2	105.8	99.8	0.2	98.7	1.3	76.4	23.6	88.2	11.8
	O	25.7	192.5	87.0	13.0	99.6	0.4	81.4	18.6	87.9	12.1
	N	25.7	286.4	78.9	**21.1**	87.2	**12.8**	80.5	19.5	85.8	14.2
	D	25.9	344.3	99.4	0.6	95.1	4.9	76.0	**24.0**	84.3	**15.7**
***Bajío* Forest**	J	25.5	505.3	98.3	1.7	98.4	1.6	66.8	**33.2**	71.1	**28.9**
	F	25.4	434.0	99.6	1.4	99.5	0.5	73.2	26.8	74.0	**26.0**
	M	25.7	316.9	99.4	1.6	99.6	0.4	72.0	28.0	75.4	24.6
	A	25.3	224.3	100	0.0	99.8	0.2	74.7	25.3	82.2	17.8
	M	24.2	208.9	96.9	3.1	99.0	1.0	76.7	23.3	84.3	15.7
	J	23.7	130.8	96.1	3.9	95.7	4.3	78.8	21.2	79.8	20.2
	J	23.1	88.4	90.9	9.1	92.4	7.6	85.7	14.3	80.5	18.5
	A	24.2	87.3	90.4	9.6	86.5	3.5	85.4	14.6	78.0	22.0
	S	25.2	105.8	83.4	**16.6**	81.2	**8.8**	81.0	19.0	77.5	22.5
	O	25.7	192.5	96.5	3.5	92.3	**7.7**	70.5	29.5	81.3	18.7
	N	25.7	286.4	95.8	4.2	94.2	5.8	64.3	**35.7**	77.9	22.1
	D	25.9	344.3	99.0	1.0	97.6	2.4	62.8	**37.2**	70.8	**29.2**
Successional Forest	J	25.5	505.3	99.5	0.5	100	0.0	83.4	16.6	79.6	20.4
	F	25.4	434.0	99.4	0.6	99.2	0.8	87.9	12.1	83.2	16.8
	M	25.7	316.9	99.0	1.0	99.6	0.4	89.3	10.7	90.7	9.3
	A	25.3	224.3	97.1	2.9	99.3	0.7	87.9	12.1	96.7	3.3
	M	24.2	208.9	91.0	9.0	99.3	0.7	84.0	16.0	98.4	1.6
	J	23.7	130.8	92.0	8.0	99.0	0.1	79.9	20.1	99.0	1.0
	J	23.1	88.4	90.8	9.2	98.0	2.0	83.0	17.0	95.4	4.6
	A	24.2	87.3	90.5	9.5	92.8	7.2	81.3	18.7	96.0	4.0
	S	25.2	105.8	86.0	**14.0**	96.1	3.9	78.2	21.8	93.1	6.9
	O	25.7	192.5	95.8	4.2	90.0	**10.0**	67.2	**32.8**	91.7	8.3
	N	25.7	286.4	99.0	1.0	98.6	1.4	67.0	**33.0**	83.0	17.0
	D	25.9	344.3	99.4	0.6	100	0.0	76.0	24.0	77.2	**22.8**

Tierra Firme Forest	J	25.5	505.3	99.7	0.3	100	0.0	81.9	18.1	76.0	**24.0**
	F	25.4	434.0	99.0	1.0	100	0.0	99.3	0.7	92.0	8.0
	M	25.7	316.9	92.2	7.8	96.8	3.2	100	0.0	98.2	1.8
	A	25.3	224.3	90.1	9.9	96.5	3.5	98.8	1.2	98.3	1.7
	M	24.2	208.9	87.8	12.2	93.0	7.0	96.5	3.5	100	0.0
	J	23.7	130.8	95.8	4.2	91.0	9.0	95.2	4.8	100	0.0
	J	23.1	88.4	99.1	0.9	99.0	1.0	93.6	6.4	98.6	1.4
	A	24.2	87.3	90.5	9.5	97.7	2.3	93.6	6.4	99.1	0.9
	S	25.2	105.8	65.5	**34.5**	74.1	**25.9**	95.0	5.0	96.8	3.2
	O	25.7	192.5	94.5	5.5	95.6	4.4	60.1	**39.9**	96.3	3.7
	N	25.7	286.4	99.7	0.3	99.7	0.3	62.0	**38.0**	92.0	8.0
	D	25.9	344.3	99.0	1.0	99.5	0.5	70.9	29.1	83.9	**16.1**

Discussion

Floristic composition

It is important to know the dimensions of floristic heterogeneity in order to describe and understand the dynamic patterns of species and their interaction with the environment. The present study shows that the indicator species analyzed herein are frequently cited in local floristic studies (Baez and Garate, 2017; Dueñas and Garate, 2018; Alvarez-Montalván *et al.,* 2021). Families such as Fabaceae, Moraceae and Arecaceae are listed as representative of the Peruvian Amazonian forests (Vásquez *et al*., 2010; Ureta, 2015, Alvarez-Montalván *et al.,* 2021).

Also, the specific grouping of individuals by forest type allows to establish close similarities between habitats. Thus, the *NMDS* clustering analysis showed that habitats with higher numbers of tree individuals, such as the *Bajío* Forest and the *Tierra Firme* Forest, were more similar than forests with lower numbers of individuals. On the other hand, it has been pointed out that the analysis has the disadvantage of generating more than one response; therefore, it is necessary to carry out procedures to determine the lowest stress value (Rocha-Loredo *et al*., 2010). In this sense, the reliability of the analysis performed is valid, since the stress value was below 0.1.

In addition, the direct comparison of the observed richness by habitat type showed how habitats not correlated by cluster analysis exhibited more species, as in the *Bajío* Forest and the Successional Forest. However, none of the forest types reached the stability in the number of taxa indicated by the indicator coefficient Chao2. Moreover, with the same rarefaction analysis, Samaniego *et al*. (2015) did not obtain differences in richness. In contrast, Silva *et al*. (2016) indicated that the stability of the rarefaction curve in the *Tapajós* National Forest was observed, especially for secondary forests.

Analysis of the phenological responses of the indicator species

The relationships between the different habitat types and meteorological parameters exhibited greater variations in phenological responses in the *Tierra Firme* Forest, which may indicate greater sensitivity to changes in temperature and precipitation. On the other hand, when correlating the environmental parameters under study for the *Aguajal, Bajío* and Successional Forests, these appear to be more influenced by temperature than by precipitation. Lack of precipitation or extreme drought and temperature —depending on the duration periods (Siegmund *et al*., 2016) — affect the arboreal individuals of the *Tierra Firme* Forest found in the Amazonian region (Zhao *et al*., 2017). One of the immediate indicators is the loss of forest greenness and leaf senescence, which leads to the accumulation of organic material, decay, and an increase of CO_2. In this regard, the study by Pires *et al*. (2018), carried out in an Atlantic Forest reserve in *Rio de Janeiro*, determined a weak relationship between the climate conditions and the dynamics of fruit formation and maturation, which was related to the phenodynamics of flowering. Contrarily, the present study showed that the presence of immature and ripe fruits decreased ostensibly with the approach of the months of June to September, when rainfall reached its lowest values.

The phenological behavior of plants, as an indicator of climate change, is being researched and monitored in various parts of the world (Workie and Debella, 2018). In these studies, phenological behavior will play a decisive role in the analysis and interpretation of climatic components in time and space (Pires *et al*., 2018), as may be observed in the study documented herein. For this reason, apart from other environmental factors not considered, the effect of temperature and precipitation on the establishment of the phenophases of the evaluated species was significant.

On the other hand, tropical forests are characterized by a highly diverse phenology due to the lack of a well-defined cold season that affects and restricts their growth. For this reason, it is possible to observe species with flowers and fruits all year round, others that flower and bear fruit only once a year, or only once in several years (Pires *et al*., 2018). Similarly, most tropical woody plants produce new leaves and flowers suddenly rather than continuously; thus, their phenological changes represent adaptations to biotic and abiotic factors (Van Schaik *et al*., 2003).

It is important to highlight that, although the contribution of the results of the present study is limited, it constitutes a support base for local scientific knowledge and reflects the need to integrate greater numbers of species in order not to discriminate possible taxa that may be fundamental for the understanding of the phenodynamics of the study area. Therefore, the conservation of the reserve and its habitats is imperative.

Conclusions

The results show that the indicator species found in this study, in addition to representing the most abundant families in the Peruvian Amazonia, proved that their phenophases are correlated with temperature and precipitation. However, they merely provide an initial pattern of the phenology of the species, so that further research in this line is recommended in order to fill scientific gaps and contribute to the conservation of the area.

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Conflict of interest

The authors declare no conflict of interest.

Contributions by author

Gustavo A. Martínez-Sovero: project planning, field data collection and review of the manuscript; Consuelo Rojas-Idrogo: project planning and supervision and review of the manuscript; Guillermo E. Delgado-Paredes: drafting and review of the manuscript; Felipe Zuñe-Da Silva: data analysis; Alexander Huamán-Mera: drafting and review of the manuscript; Yuriko Murillo-Domen: drafting and review of the manuscript; Donald J. Brightsmith: drafting and review of the manuscript. All team members approved the final manuscript.

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