



Temporal variation in abundance of mosquitoes (Diptera: Culicidae) in the subtropical Brazilian Atlantic forest

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ABSTRACT. Understanding the temporal variation in abundance patterns of vector or potential vector species, as well as the abiotic factors associated with these patterns, enables the creation of strategic measures aimed at preventing diseases spread by these organisms. Here, we evaluate through circular and linear analyses the temporal variation in abundance patterns of native mosquito species and verify how abiotic factors (temperature and rainfall) have influenced these patterns. For this purpose, fortnightly collections were carried out during one year in a remnant of the Atlantic Forest in Southern Brazil. We collected 1891 specimens belonging to 24 species. From those, 10 species were abundant enough to evaluate temporal variation in abundance patterns. We found different periods of occurrence for different species of mosquitoes and the distribution of abundances also differed throughout the year. Temperature was the main abiotic factor associated with temporal variation in abundance patterns presented by mosquito species. In this way, the application of these analyses is particularly interesting for the understanding of temporal variation in abundance patterns and subsequent adoption of preventive strategies for organisms of medical importance such as mosquitoes.

[Keywords: abiotic factors, circular analysis, climate change]

RESUMEN. Variación temporal de la abundancia de mosquitos (Diptera: Culicidae) en el Bosque Atlántico subtropical de Brasil. Comprender la variación temporal en los patrones de abundancia de vectores o de posibles especies de vectores, así como los factores abióticos asociados a estos patrones, permite crear medidas estratégicas dirigidas a prevenir las enfermedades que propagan estos organismos. En este trabajo evaluamos mediante análisis circulares y lineales la variación temporal en los patrones de abundancia de las especies nativas de mosquitos, y verificamos cómo los factores abióticos (temperatura y pluviosidad) influyen en estos patrones. Para ello se llevaron a cabo recolecciones quincenales durante un año en un remanente de la Mata Atlántica en el sur de Brasil. Recolectamos 1891 ejemplares pertenecientes a 24 especies. De esas, 10 especies fueron lo suficientemente abundantes para evaluar la variación temporal en los patrones de abundancia. Encontramos diferentes períodos de ocurrencia para diferentes especies de mosquitos, y la distribución de abundancias también difirió a lo largo del año. La temperatura fue el principal factor abiótico asociado con la variación temporal en los patrones de abundancia presentados por las especies de mosquitos. De esta manera, la aplicación de estos análisis es particularmente interesante para comprender la variación temporal en los patrones de abundancia y posteriormente adoptar estrategias preventivas para organismos de importancia médica como los mosquitos.

[Palabras clave: análisis circular, cambio climático, factores abióticos]

INTRODUCTION

A better understanding of the temporal variation in abundance patterns of vector or potential vector species, as well as the abiotic factors associated with these patterns, enables the creation of strategic measures aimed at preventing diseases spread by these organisms (Deichmeister and Telang 2011; Zittra et al. 2017). Although there are many studies that suggest the period of occurrence of mosquito species, most of them perform such inferences based only on the months of greater abundance (Silva and Lozovei 1998; Loetti et

al. 2007; Ferreira-de-Freitas et al. 2016; Santos et al. 2019, 2020), while others focus only on introduced species such as *Aedes aegypti* and *Aedes albopictus* (Reinhold et al. 2018).

For many species of mosquitoes, especially those already known for their vectorial capacity, the increase in abundance is mainly related to temperature (Reinhold et al. 2018; Franklins et al. 2019). This factor is preponderant, especially in temperate environments, where immatures go through a period of diapause during cold winters (Denlinger and Armbruster 2016). Considering that current

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climate changes predict an increase in the average temperature of the planet, the reduction of cold periods may lead to a high egg survival (e.g., Thomas et al. 2012), lower mortality of mosquito pupae and, consequently, cause greater abundance of adults during spring and summer (Ewing et al. 2016). Additionally, increasing season length also influences the number of successful generations per year (e.g., Buckley et al. 2017) and other life history traits can change under climate changes.

However, in tropical environments, which are generally much more diverse in species richness and ecological interactions than temperate environments, there are numerous factors that may interfere with the abundance of mosquito species, and they can still respond in different ways. It has been previously demonstrated that changes in the landscape can lead to an increase in some etiological agents which vector species may spread, such as those that cause malaria and yellow fever (Baeza et al. 2017; Wilk-da-Silva et al. 2020). Other studies point to the positive relationship between high temperatures and the abundance of some species of mosquitoes (Vieira et al. 2020). They also reveal that in tropical areas the seasonality of rainfall may be the main factor of variation in the composition and structure of mosquito communities (Julião et al. 2010).

Therefore, it is fundamental to determine whether and how the abundance of mosquito species varies through time and what ecological factors may be involved in these patterns. In this way, to access these kinds of information we can use circular and linear statistical analyses. These analyses have already been used, for example, to verify and compare seasonal patterns between different forest fragments (Morellato et al. 2000), to access the phenology of groups of specialist butterflies (Brito et al. 2014) and to evaluate phenological patterns and the biotic and abiotic factors related to them through space and time on moth pest species (Piovesan et al. 2018, 2019).

This study was conducted in a subtropical area, a transition between tropical and temperate climates. Specifically, the studied environment presents well-distributed rains throughout the year and temperature with four well-defined seasons, autumn and spring with mild temperatures, hot summer, and cold winter with frosts. Because in environments with marked seasonality of temperature insects generally show greater activity and

abundance in the hottest times of the year (Kishimoto-Yamada and Itioka 2015), here, we hypothesize that, since it is a subtropical environment, the different species of mosquitoes will present similar temporal variation in abundance patterns, and this pattern will be affected by the increase in temperature.

MATERIALS AND METHODS

Study area

This study was conducted in the Parque Natural Municipal Vale do Rio do Peixe, a forest fragment comprising approximately 300 ha, located in the municipality of Joaçaba, western Santa Catarina state, Southern Brazil (27°10'22" S - 51°30'23" W) (Figure 1). According to the Köppen climatic classification, the municipality climate is considered mesothermal humid with a cold winter (temperature range from -3 to 18 °C) and a hot summer (temperature above 22 °C) 'Cfa', annual precipitation of around 2000 mm and a relative annual humidity average of 76% (Alvares et al. 2013).

The region is part of the Atlantic rainforest biome, in the transition area (ecotone) between *Araucaria* and deciduous forests (Vibrans et al. 2012). The altitude range varies from 700 to 839 m a. s. l. A varied mosaic characterizes the local vegetation. The area is covered by primary forest in varying states of conservation, including preserved primary forest, primary forest amended by logging, forest fragment edges, glades, and ponds (Orlandin et al. 2017).

Sampling

Three sites were sampled in the forest fragment (c. 27°9'42.91" S - 51°35'15.55" W; c. 27°9'46.81" S - 51°35'1.47" W and c. 27°9'49.08" S - 51°34'50.67" W). Culicidae samplings were performed every 15 days, between October 2014 and October 2015 during the afternoon (Supplementary Material 1), by two people. Collections started at 1:00 p.m. and each site was sampled for 15 minutes, totaling 45 minutes. Blood-seeking mosquitoes were collected at the moment they landed on a collector, before the insect had the opportunity to bite (Reis et al. 2010). Mosquitoes were collected with a manual suction apparatus (Castro catcher) (Silver 2008) and transferred to killing jars. The identification to species level was performed using stereoscopic dissection microscopes, with the aid of

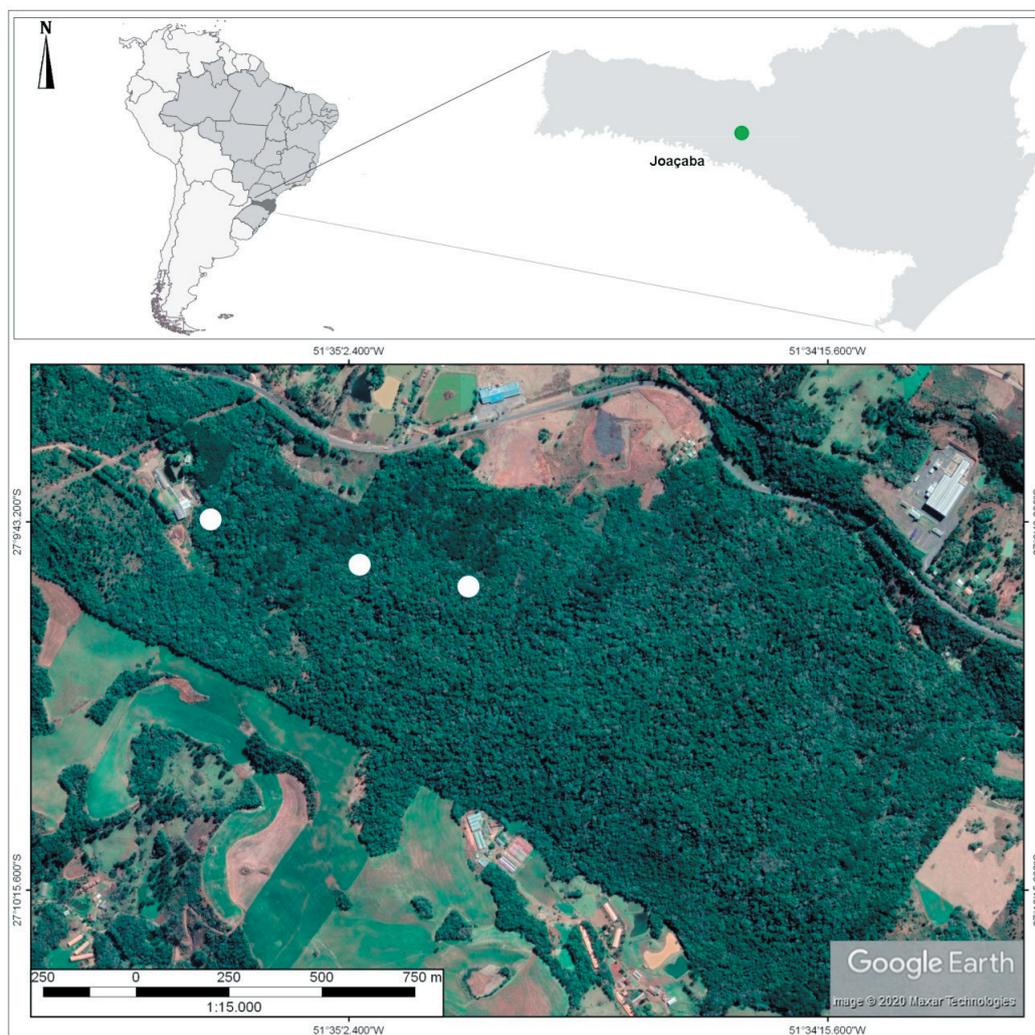


Figura 1. Ubicación del Parque Natural Municipal Vale do Rio do Peixe, en Joaçaba, Santa Catarina, sur de Brasil, donde se realizaron muestreos de Culicidae entre octubre de 2014 y octubre de 2015. Las tres áreas de muestreo están resaltadas en blanco. El mapa se construyó con el programa Quantum-GIS 2.18.12 (QGIS Development Team, 2017) a partir de imágenes de Google Earth (Google 2016).

Figure 1. Location of the Parque Natural Municipal Vale do Rio do Peixe, in Joaçaba, Santa Catarina, Southern Brazil, where Culicidae samplings were carried out between October 2014 and October 2015. The three sampling areas are highlighted in white. Map constructed through the program Quantum-GIS 2.18.12 (QGIS Development Team, 2017) from Google Earth pictures (Google 2016).

literature and dichotomous keys from Lane (1953a,b), Consoli and Oliveira (1994) and Forattini (2002). Mosquitoes were deposited in the Zoology Laboratory of Universidade do Oeste de Santa Catarina (UNOESC), Joaçaba campus.

Predictor variables

To identify the predictive power of the factors responsible for the temporal variation in abundance patterns of the mosquitoes species, the following abiotic variables were considered: average temperature prior to

collection event at 60 days (T60), 30 days (T30) and 15 days (T15), and accumulated rainfall prior to collection event at 60 days (R60), 30 days (R30) and 15 days (R15) (Figure 2, Supplementary Material 2). These records were taken from the automatic station database query from the National Institute of Meteorology (INMET 2014) (Supplementary Material 3), which is located about five kilometers distant from the study site.

Additionally, we also recorded the local average temperature (LAT) and local average humidity (LAH) at each of the three

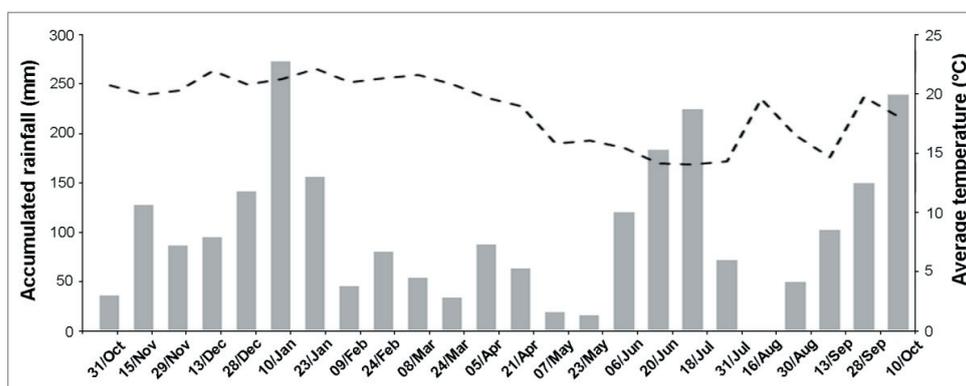


Figura 2. Variables meteorológicas registradas entre octubre de 2014 y octubre de 2015 en la consulta automática a la base de datos de la estación del Instituto Nacional de Meteorología (INMET). Barras: precipitación acumulada (mm) en los 15 días previos al muestreo de Culicidae; línea discontinua: temperatura promedio (°C) en los 15 días anteriores al muestreo de Culicidae.

Figure 2. Meteorological variables recorded between October 2014 and October 2015 at the automatic station database query from the National Institute of Meteorology (INMET). Bars: accumulated rainfall (mm) of 15 days prior to the collection event; dashed line: average temperature (°C) of 15 days prior to the collection event.

sampled sites, at the exact time of collection (Supplementary Material 4). For this procedure we used a Thermo Digital Hygrometer Digital Max./Min. 7429 Tfa Incoterm. Our average was based on the average of local temperature and the local humidity collected in the three sites because there was no statistical difference between them (Orlandin et al. 2020; Supplementary Material 4).

Circular statistical analyses

We used circular statistical analyses to assess the distribution of abundances of mosquito species over a 1-year period. These analyses transform value categories into angles ranging from 0° to 360° in a circle, where the 0 value is arbitrarily established (Zar 2010). In this case, for example, January or July may be attributed to the zero value without altering the logical processes of the tests. Thus, December and February are equally close to January, independently of the associated zero value. Therefore, the occurrence dates of a phenological observation are transformed to an angle proportional to the circularity of the 365 days in a year (e.g., $n^\circ \text{ days} \times 360/365$) (Supplementary Material 5).

We used Rao's spacing test to evaluate if the abundances of different mosquitoes species demonstrate uniform patterns across the year. Its application is recommended when the data do not present a unimodal distribution (Bergin 1991; Ribeiro et al. 2010). This test indicates the significance of the mean vector (μ), and the length of mean vector (r) determines

if the observations are concentrated (H1) or uniformly distributed (H0). When the mean angle is significant, we reject the null hypothesis (Morellato et al. 2000; Brito et al. 2014; Piovesan et al. 2018, 2019). After rejecting the hypothesis of uniform yearly abundances, the mean vector (μ) can be used to represent the concentration of abundances for a specified period of the year. This means that if higher species abundance is related to a specific part of the year, it can be understood to be the period of occurrence exhibited by a particular species (Piovesan et al. 2019). For this test, we used only the species that presented more than 10 specimens. All samples lacking significant values for the Rao's Spacing test were removed from further analyses. To perform circular statistical analyses, we used the Oriana 4.0 test version (Kovach 2011).

Linear statistical analyses

First of all, to avoid autocorrelation for the average temperature (T) and for accumulated rainfall metrics (R), we generated models independently for each time scale (15, 30, and 60 days), using generalized linear models (GLM), based on non-normal distribution of residues (negative binomial). In order to determine the model with the greatest predictive power that is, the lowest corrected Akaike Information Criterion (AICc), models were selected, regardless of the time scale, for T and R abiotic factors. After selected the model with the greatest predictive power for T and R abiotic factors, we performed model building with multiple logistic regressions

(generalized linear model with binomial distribution). Through these models, the response variable, abundance of each mosquito species, was analyzed in relation to T, R, local average temperature (LAT), and local average humidity (LAH). These models produced were compared to null models, with no variables, and with only one constant parameter. For this test, the MASS package and the function glm.nb were used (Ripley et al. 2013). Subsequently, the generated models were ranked using the AICc and its weight (wAICc).

The weights drawn from the AICc varies from 0 to 1. Models with a wAICc closer to one yield the greater predictive power and are considered the most explanatory. The support provided by alternative models is determined by the differences in the AICc values and models with a $\Delta AICc < 2$ were considered equally plausible (Burnham and Anderson 2004; Burnham et al. 2011). As all the models are classified according to the $\Delta AICc$ value, the null model acts as a reference, enabling the identification and quantification of the variables having the best predictive power. These analyses were performed in the bbmle package, function AICctab (Bolker and Bolker 2013). Therefore, all linear statistical analyses were performed in an R environment (R Core Team 2015).

RESULTS

We collected a total of 1891 specimens belonging to 24 species of Culicidae (Table 1). Of this total, ten species were abundant enough to perform the phenological analysis. Of the ten species tested, nine showed abundances in non-uniform distributions through the year. Subsequently, we tested the prediction power of the abiotic factors measured on the temporal variation in abundance pattern of these species.

Circular statistical analyses

Phenological analyses showed that only *Mansonia titillans* did not present a statistically significant value, and this non-significant value may be related to the occasional low numbers of specimens sampled. However, circular analysis showed that phenological patterns were different between other species evaluated (Table 2, Figure 3).

Abundance of *Aedes crinifer* was concentrated with intensity in the month of August. *Aedes*

Table 1. Culicidae recolectados entre octubre de 2014 y octubre de 2015 en un fragmento de bosque ubicado en el municipio de Joaçaba, oeste de Santa Catarina, sur de Brasil (n=abundancia).

Table 1. Culicidae collected between October 2014 and October 2015 in a forest fragment located in the municipality of Joaçaba, western Santa Catarina, Southern Brazil (n=abundance).

Tribe	Species	n
Anophelini	<i>Anopheles lutzi</i> Cruz, 1901	2
Aedini	<i>Aedes crinifer</i> (Theobald, 1903)	63
	<i>Aedes scapularis</i> Rondani, 1848	63
	<i>Aedes serratus</i> Theobald, 1901	147
	<i>Aedes terrens</i> (Walker, 1856)	11
Mansoniini	<i>Psorophora ferox</i> (Van Humboldt, 1819)	387
	<i>Psorophora saeva</i> Dyar and Knab, 1906	1
	<i>Haemagogus leucocelaenus</i> (Dyar and Shannon, 1924)	1
	<i>Coquillettidia venezuelensis</i> (Theobald, 1912)	2
	<i>Mansonia titillans</i> (Walker, 1848)	12
Sabethini	<i>Runchomyia cerqueirai</i> (Stone, 1944)	5
	<i>Sabethes aurescens</i> (Lutz, 1905)	629
	<i>Sabethes chloropterus</i> (Humboldt, 1819)	1
	<i>Sabethes identicus</i> Dyar and Knab, 1907	38
	<i>Sabethes melanonymphe</i> Dyar, 1924	3
	<i>Sabethes purpureus</i> (Theobald, 1907)	1
	<i>Sabethes soperi</i> Lane and Cerqueira, 1942	1
	<i>Trichoprosopon compressum</i> Lutz, 1905	1
	<i>Trichoprosopon pallidiventer</i> (Lutz, 1905)	379
	<i>Wyeomyia fuscipes</i> Edwards, 1922	2
Wyeomyiini	<i>Wyeomyia leucostigma</i> Lutz, 1904	10
	<i>Wyeomyia limai</i> Lane and Cerqueira, 1942	126
	<i>Wyeomyia lutzi</i> (Lima, 1930)	2
	<i>Wyeomyia sabethea</i> Lane and Cerqueira, 1942	4

scapularis presented its period of occurrence between February and March, while *Aedes serratus* presented the mean vector in December, with two peaks of occurrence, one in November and another in January. Abundance of *Aedes terrens* was concentrated between January and February. However, this result needs to be interpreted with caution because this estimate is based on a low number of specimens.

Psorophora ferox showed abundance concentrated mainly in late January. Similarly,

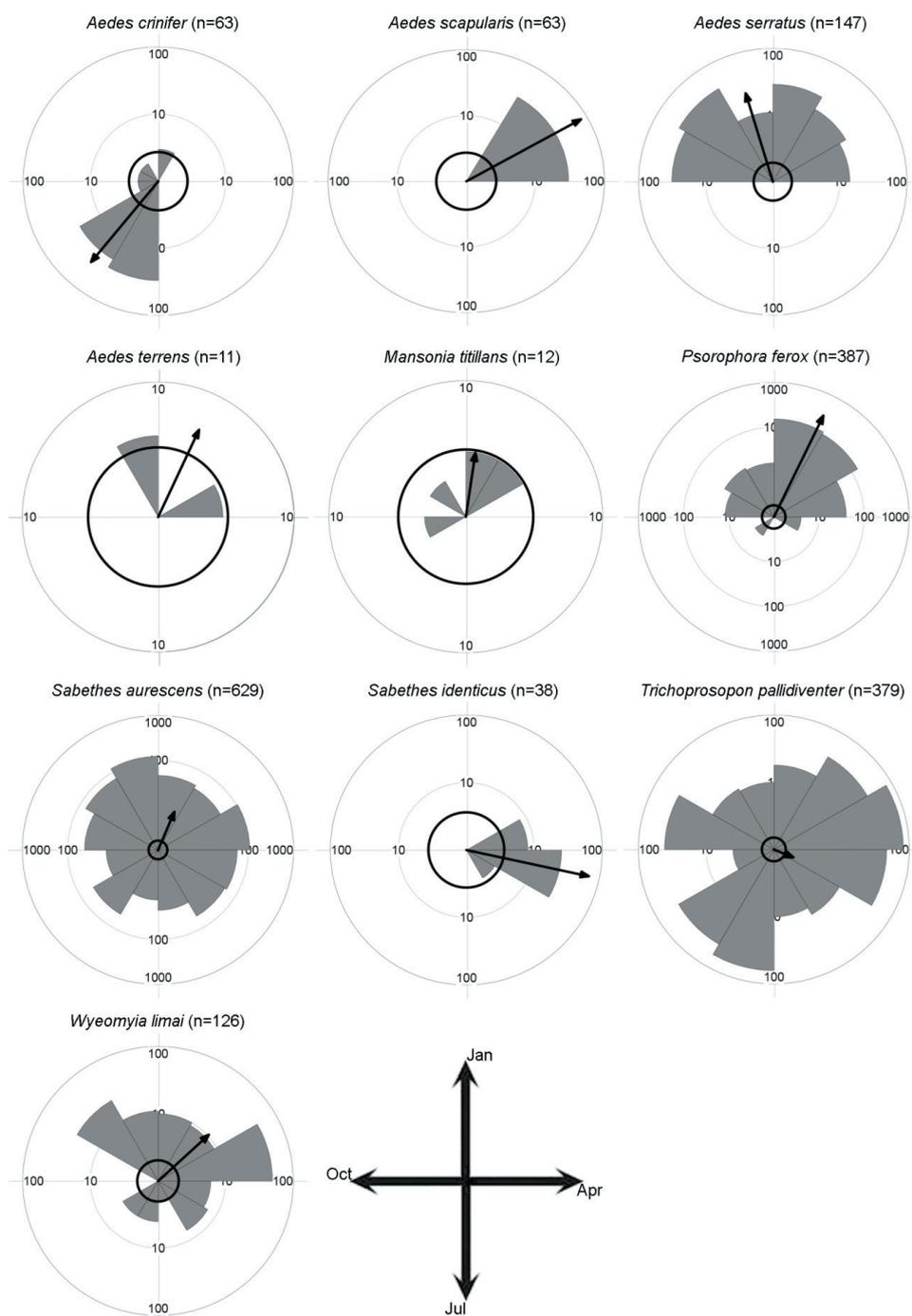


Figura 3. Parcela circular de la abundancia de especies de mosquitos recolectadas entre octubre de 2014 y octubre de 2015, durante la tarde, en un fragmento de bosque en el municipio de Joaçaba, oeste de Santa Catarina, sur de Brasil. Los vectores (flechas) indican el período de ocurrencia medio (vector medio: μ), mientras que su longitud representa la concentración de abundancia de mosquitos a lo largo del tiempo (longitud del vector medio: r). El círculo en negrita representa la relación entre abundancia (N) y concentración (r), e indica la significancia (e.g., un círculo en negrita mayor que las flechas indica una falta de significación estadística).

Figure 3. Circular plot of the abundance of mosquitoes species collected between October 2014 and October 2015, during the afternoon, in a forest fragment located in the municipality of Joaçaba, western Santa Catarina, Southern Brazil. Vectors (arrows) indicates the mean occurrence period (mean vector: μ), while its length represents the concentration of mosquito abundance throughout time (length of mean vector: r). Bold circle represents the relationship between abundance (N) and concentration (r) indicating significance (e.g., bold circle greater than arrows indicates a lack of statistical significance).

Tabla 2. Estadísticas descriptivas derivadas del análisis circular de la abundancia de especies de mosquitos recolectadas entre octubre de 2014 y octubre de 2015 durante la tarde, en un fragmento de bosque ubicado en el municipio de Joaçaba, oeste de Santa Catarina, sur de Brasil. μ : vector medio; d/m: día y mes correspondientes a μ ; r: longitud del vector medio (es una medida de concentración y puede variar entre 0 [cuando hay tanta dispersión que no se puede describir un ángulo medio] y 1 [cuando todos los datos se concentran en la misma dirección]); CSD: desviación estándar circular (la raíz cuadrada de menos 2 veces el logaritmo de la longitud media resultante dividida por el número de observaciones); CSDd: días relacionados con CSD; U: prueba de espaciado de Rao (el estadístico de prueba agrega las desviaciones entre puntos consecutivos, cada uno ponderado por el número total de observaciones en el conjunto de datos); P: valores P.

Table 2. Descriptive statistics derived from circular analysis of the abundance mosquitoes species collected between October 2014 and October 2015 during the afternoon, in a forest fragment located in the municipality of Joaçaba, western Santa Catarina, Southern Brazil. μ : mean vector; d/m: day and month corresponding to μ ; r: length of mean vector (it is a measure of concentration and may vary from 0 [when there is so much dispersion that a mean angle cannot be described] and 1 [when all the data are concentrated at the same direction]); CSD: circular standard deviation (the square root of minus 2 times the log of the mean resultant length divided by the number of observations); CSDd: days related to CSD; U: Rao's spacing test (the test statistic aggregates the deviations between consecutive points, each one weighted by the total number of observations in the dataset); P: P-values.

Species	μ	d/m	r	CSD	CSDd	U	P
<i>Aedes crinifer</i>	219.62°	4/aug	0.78	40.29°	±39	297.14	<0.01
<i>Aedes scapularis</i>	60.39°	28/feb	0.95	17.76°	±17	320	<0.01
<i>Aedes serratus</i>	342.92°	4/dec	0.69	48.99°	±48	332.88	<0.01
<i>Aedes terreus</i>	25.05°	24/jan	0.71	47.18°	±46	198.51	<0.01
<i>Mansonia titillans</i>	8.42°	08/jan	0.47	69.93°	±68	168.98	>0.05
<i>Psorophora ferox</i>	25.88°	25/jan	0.83	34.16°	±33	344.18	<0.01
<i>Sabethes aurescens</i>	22.90°	22/jan	0.31	87.91°	±86	346.19	<0.01
<i>Sabethes identicus</i>	102.15°	10/apr	0.92	23.25°	±22	303.16	<0.01
<i>Trichoprosopon pallidiventer</i>	112.05°	20/apr	0.15	110.61°	±109	338.09	<0.01
<i>Wyeomyia limai</i>	47.44°	15/feb	0.51	66.63°	±65	311.43	<0.01

Sabethes aurescens showed concentrated abundance at the end of January, but with three peaks throughout the year, in March, August, and December. On the other hand, abundance of *Sabethes identicus* was concentrated in April. *Trichoprosopon pallidiventer* also showed a period of occurrence in April, but we exercise caution with this observation because although the mean vector is significant, the size of this vector indicates that the significance is low. Finally, *Wyeomyia limai* concentrated its abundance in February, presenting two peaks of occurrence, in November and March.

Linear statistical analysis

Among the nine species tested, the abundance of two (*Sa. identicus* and *Tr. pallidiventer*) was not related to the abiotic factors we assessed. On the other hand, the other species showed to be affected mainly by temperature (Table 3).

The best model that explained the abundance of *Ae. crinifer* was the association between the lowest average temperatures of 30 days before the collections and accumulated rainfall of 60 days before the collections (T30+R60). For *Ae. scapularis*, the highest average temperatures of

60 days before the collections associated with a lower accumulated rainfall of 30 days before the collections (T60+R30), was the best model that explained its abundance. The abundance of *Ae. serratus* was positively affected by the highest average temperatures of 30 days before collection (T30) and to a lesser extent by its association with local average humidity rates at the time of collection (T30+LAH). While for *Ae. terreus*, the highest average temperatures of 30 days before the collection (T30) was the best model that explained its abundance. The abundance of *Ps. ferox* was better explained by the association between the highest average temperatures of 30 days before the collections and the accumulated rainfall of 60 days before the collections (T30+R60). Among the sabethines, local average temperature (LAT) and, to a lesser extent, the association between this and local average humidity (LAT+LAH) explained the abundance of *Sa. aurescens*. While for *Wy. limai* highest average temperatures of 60 days before the collections associated with lower local humidity (T60+LAH) and, to a lesser extent, the lower accumulated rainfall of 15 days that preceded the collections (T60+R15) were the models that best explained its abundance.

Table 3. GLM mejor clasificados para la variación temporal de la abundancia de mosquitos, relacionados con las siguientes variables climáticas: temperatura promedio antes del evento de recolección a los 60 días (T60), 30 días (T30) y 15 días (T15); precipitación acumulada antes del evento de recolección a los 60 días (R60), 30 días (R30) y 15 días (R15), y temperatura media local (LAT) y humedad media local (LAH).

Table 3. Best-ranked GLMs for temporal variation of mosquito abundance, related to the following climatic variables: average temperature prior to collection event at 60 days (T60), 30 days (T30) and 15 days (T15); accumulated rainfall prior to collection event at 60 days (R60), 30 days (R30) and 15 days (R15), and local average temperature (LAT) and local average humidity (LAH).

Variables	ΔAICc	df	w	AICc	Variables	ΔAICc	df	w	AICc	Variables	ΔAICc	df	w	AICc
<i>Ae. crinifer</i>				<i>Ae. scapularis</i>				<i>Ae. serratus</i>						
T30 + R60	0	4	0.8251	75.51	T60 + R30	0	4	0.7113	59.06	T30	0	3	0.5861	112.1
T30	5.2	3	0.062	81.6	T60	2.6	3	0.1971	62.53	T30 + LAH	1.7	4	0.2473	113
R60	5.4	3	0.0551	81.83	T60 + LAH	5	4	0.0573	64.1	T30 + R15	2.9	4	0.1371	114.1
T30 + LAH	6	4	0.0421	81.47	R30	7.1	3	0.0206	67.05	LAT	7.3	3	0.0149	119.5
LAT + R60	8.3	4	0.0132	83.79	LAT + R30	9.8	4	0.0052	68.91	Null model	9.8	2	0.0044	122.5
Null model	12.8	2	0.0014	89.87	Null model	9.9	2	0.005	70.52	LAT + R15	9.9	4	0.0042	121.1
LAT	14.6	3	<0.001	90.97	LAT	12.1	3	0.0017	72.03	LAT + LAH	10.2	4	0.0035	121.5
LAH	14.6	3	<0.001	91.03	LAH	12.5	3	0.0014	72.48	R15	12.3	3	0.0012	124.5
LAT + LAH	17.3	4	<0.001	92.84	LAT + LAH	14.7	4	<0.001	73.77	LAH	12.4	3	0.0012	124.5
<i>Ae. terrens</i>				<i>Ps. ferox</i>				<i>Sa. aurescens</i>						
T30	0	3	0.6416	36.7	T30 + R60	0	4	0.761	134.8	LAT	0	3	0.4434	199.2
T30 + R15	2.6	4	0.1717	38.43	T30	3.4	3	0.141	139.1	LAT + LAH	1.5	4	0.2059	199.9
T30 + LAH	2.9	4	0.1527	38.66	T30 + LAH	4.1	4	0.098	138.9	T60	2.6	3	0.1208	201.8
LAT	8	3	0.0119	44.68	LAH	23.1	3	<0.001	158.8	LAT + R15	2.8	4	0.1099	201.1
Null model	8.7	2	0.0082	46.04	R60	24.1	3	<0.001	159.9	T60 + LAH	4.1	4	0.0567	202.4
LAT + LAH	9.6	4	0.0053	45.37	LAT + LAH	24.6	4	<0.001	159.4	T60 + R15	4.2	4	0.0546	202.5
LAT + R15	10.7	4	0.0031	46.46	Null model	25.6	2	<0.001	162	Null model	9	2	0.005	208.8
LAH	10.8	3	0.0029	47.48	LAT + R60	25.8	4	<0.001	160.6	R15	10.5	3	0.0023	209.8
R15	11.1	3	0.0025	47.78	LAT	26.4	3	<0.001	162.1	LAH	11.3	3	0.0015	210.6
<i>Sa. identicus</i>				<i>Tr. pallidiventer</i>				<i>Wy. limai</i>						
R60	0	3	0.342	62.66	Null model	0	2	0.392	184.7	T60 + LAH	0	4	0.4078	121
Null model	1	2	0.206	64.3	LAH	2.1	3	0.137	186.2	T60 + R15	0.6	4	0.2966	121.6
LAT + R60	2.5	4	0.1	64.22	R15	2.3	3	0.126	186.4	LAT + R15	3	4	0.093	124
LAH	2.7	3	0.09	65.33	T15	2.5	3	0.113	186.6	LAT	3.2	3	0.0809	125.1
T30 + R60	2.8	4	0.084	64.57	LAT	2.6	3	0.105	186.7	T60	3.3	3	0.0773	125.2
T30	3.2	3	0.068	65.88	LAT + LAH	4.9	4	0.033	188.1	LAT + LAH	5.6	4	0.0249	126.6
LAT	3.5	3	0.059	66.16	T15 + LAH	5	4	0.033	188.1	R15	7.7	3	0.0088	129.6
LAT + LAH	5.2	4	0.026	66.93	T15 + R15	5.1	4	0.031	188.3	Null model	8.5	2	0.0057	131.1
T30 + LAH	5.3	4	0.024	67.03	LAT + R15	5.1	4	0.03	188.3	LAH	8.8	3	0.0049	130.8

DISCUSSION

Among the 24 species sampled here, eight (*Ae. scapularis*, *Ae. serratus*, *Cq. venezuelensis*, *Hg. leucocelaenus*, *Ma. titillans*, *Ps. ferox*, *Sa. chloropterus* and *Sa. soperi*) are known to be vectors of some etiological agent that cause diseases such as yellow fever, other encephalitises and filariasis (Guedes 2012; Hanley et al. 2013; Abreu et al. 2019). Of these, three (*Ae. scapularis*, *Ae. serratus* and *Ps. ferox*) were among the most abundant mosquito species (Table 1).

As expected, we found a large number of species presenting their periods of occurrence

in the hottest periods of the year; in particular, most species of Aedini presented this pattern. However, the peaks occurred at different times, and even the distribution of abundance during the year was different for each species. The temporal variation in abundance patterns found here also differed from those found for most of these species in other studies (Forattini et al. 1995; Maciá 1997; Loetti et al. 2007; Ferreira-de-Freitas et al. 2016; Orlandin et al. 2017; Santos et al. 2019, 2020). However, when we look at some such species, their associations with higher-temperature periods of the year become evident. *Aedes scapularis*, *Ae. serratus* and *Ps. ferox* were species that presented

peaks of abundance at different times during the hottest period of the year (Forattini et al. 1995; Ferreira-de-Freitas et al. 2016; Santos et al. 2019). Additionally, the abundance of these species was positively affected by temperature and generally associated with precipitation. In environments with higher average temperatures, the abundance of these species is apparently broadened throughout the year, while in environments with lower average temperatures abundance seems to be more concentrated into a shorter period of the year (Maciá 1997; Loetti et al. 2007). Moreover, *Ae. scapularis*, *Ae. serratus* and *Ps. ferox* are flood water mosquitoes, therefore, their abundance is also dependent of water dynamics of temporary pools.

The opposite seems to happen in *Ae. crinifer*. Several studies point to an affinity of this species with milder periods of the year, but at different times (Maciá 1997; Loetti et al. 2007; Ferreira-de-Freitas et al. 2016; Orlandin et al. 2017). This species may actually be characteristic of environments with milder climate, since it was collected abundantly in several studies conducted in Southern Brazil and Argentina (Maciá 1997; Loetti et al. 2007; Ferreira-de-Freitas et al. 2016; Santos et al. 2020). On the other hand, the abundance of this species decreases in environments with higher annual average temperatures (Medeiros-Sousa et al. 2013; Carvalho et al. 2014). However, the abundance of *Ae. crinifer* was not affected only by milder temperatures, but rather, by its association with accumulated rainfall. The immature *Ae. crinifer* develops in temporary puddles created by rain (Urcola and Fischer 2019). Thus, the relationship with rainfall could explain the occurrence of this species in greater abundance at different times of the year found in different studies.

On the other hand, the sabethines, except *Sa. identicus*, presented abundances distributed in practically all the months of the year. *Sabethes aurescens*, *Tr. pallidiventer* and *Wy. limai* are species whose immature development occurs in internodes of bamboos and taquaras, and are generally sampled abundantly throughout the year in environments with high concentrations of this vegetation (Lozovei 1998, 2001; Zequi and Lopes 2001), as in the present study. Furthermore, there are indications that these species, in general, are less affected by variation in abiotic conditions, such as temperature and rainfall (Guimarães et al. 2000). However, in our study, *Wy. limai* and *Sa. aurescens* were affected by abiotic

factors, but in different ways. The sabethines are usually acrodendrophiles and diurnal, performing their blood repast in the canopy of trees (Silva et al. 2020), and may descend to ground level during periods of the day when the heat is more intense (Guimarães and Victório 1986). This behavior could explain why temperature influenced the abundance of these species. It is likely that the time of collection events, during the hottest period of the day, coincided with the moment that these species descended from the treetops, becoming more active at ground level.

The abundance of *Tr. pallidiventer* remained constant throughout the study and was not influenced by any of the abiotic factors measured here. This result contradicts that found in another study conducted at the same site (Orlandin et al. 2017), in which the authors found a relationship between the average and minimum temperature at the time of collection and the abundance of *Tr. pallidiventer*. However, the study performed by Orlandin et al. (2017) was conducted during the evening twilight, a day period that shows marked differences in temperature, especially when compared between winter and summer. Thus, it is likely that the abundance and occurrence of this species, throughout the year, are basically controlled by the availability of sites for oviposition.

Our results suggest that the modifications predicted in the current climate change context mainly related to temperature may affect species in different ways. In the case of Aedini, due to the concentration of abundance occurring in warmer times of the year, it is expected that with an increase in average temperature the abundance of these species will be more evenly spread across more months of the year. In contrast, in *Ae. crinifer*, this temporal window may decrease, restricting haematophagic activities only to the nocturnal period, since it can be found at different times of day and night (Ferreira-de-Freitas et al. 2016; Orlandin et al. 2017; Santos et al. 2020), or even concentrate its abundance only in the winter season. On the other hand, since the abundance of *Sa. aurescens*, *Wy. limai* and *Tr. pallidiventer* was distributed throughout the year, it is likely that the variation in annual temperature and precipitation is not so important for the occurrence of these species and their presence is much more impacted by availability of oviposition substrates.

In conclusion, we observed that different species presented different temporal variation in abundance patterns throughout the year. Although the abundance of some species was indeed observed to have been by temperature, as we hypothesized, precipitation and other factors intrinsic to each species may affect their seasonality and the distribution of abundances throughout the year. Although circular analysis tools are still little used, they have proved to be useful to evaluate the phenological patterns of several organisms (Morellato et al. 2000; Ribeiro et al. 2010; Forrest 2016; Piovesan et al. 2018). The application of such analyses is particularly interesting for a species' seasonal occurrence and/or how the abundances of species are distributed throughout the year. Having this information, it is possible to adopt preventive strategies for organisms of medical importance

such as mosquitoes (Deichmeister and Telang 2011; Zittra et al. 2017). Although we have identified different patterns for different species, it is important to note that monitoring occurred only for one year and in only one period of the day. For a better understanding of the phenological patterns of these species it is necessary that the samples are performed over a longer period of time and in different environments (e.g., monitoring different types of breeding sites). Having achieved this, it will be possible to assess the impact of abiotic factors thresholds, and evaluate what role annual or supra-annual phenomena (e.g., El Niño) (Forrest 2016; Piovesan et al. 2018) and the landscape play on phenological patterns of mosquito species.

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