Oscillation, synchrony, and multi-factor patterns between cereal aphids and parasitoid populations in southern Brazil

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Abstract

In different parts of the world, aphid populations and their natural enemies are influenced by landscapes and climate. In the Neotropical region, few long-term studies have been conducted, maintaining a gap for comprehension of the effect of meteorological variables on aphid population patterns and their parasitoids in field conditions. This study describes the general patterns of oscillation in cereal winged aphids and their parasitoids, selecting meteorological variables and evaluating their effects on these insects. Aphids exhibit two annual peaks, one in summer–fall transition and the other in winter-spring transition. For parasitoids, the highest annual peak takes place during winter and a second peak occurs in winter–spring transition. Temperature was the principal meteorological regulator of population fluctuation in winged aphids and parasitoids during the year. The favorable temperature range is not the same for aphids and parasitoids. For aphids, temperature increase resulted in population growth, with maximum positive effect at 25°C. Temperature also positively influenced parasitoid populations, but the growth was asymptotic around 20°C. Although rainfall showed no regulatory function on aphid seasonality, it influenced the final number of insects over the year. The response of aphids and parasitoids to temperature has implications for trophic compatibility and regulation of their populations. Such functions should be taken into account in predictive models.

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Introduction

The ecological relations in agricultural environments are complex due to the interactivity of multiple factors. Therefore, the utilization of techniques and tools for the simultaneous analysis of the multifaceted influences of exogenous and endogenous factors is essential in the understanding and analysis of such bio systems, as well as in forecasting possibilities based on time series (Jonsson *et al.*, 2012; Malaquias *et al.*, 2017; Tougeron *et al.*, 2019).

Among the existing insect-pest species, aphids are among the most widespread worldwide, damaging wheat crops throughout their entire cycle (Dedryver *et al.*, 2010; Parizoto *et al.*, 2013; Rebonatto *et al.*, 2015; Brewer *et al.*, 2019). Biological control has been applied through parasitoids to reduce both direct and indirect damages caused by aphids in cereal crops (Andrade *et al.*, 2016; Yang *et al.*, 2017; Santos *et al.*, 2019). However, studies to detect the meteorological variables that influence population dynamics in aphid–parasitoid systems under field conditions are still scarce (Harrington *et al.*, 2007; Bell *et al.*, 2015; Honek *et al.*, 2018).

Climate changes significantly affect ecological variables in communities, such as abundance, seasonality, and co-occurrences (Furlong and Zalucki, 2017). These changes may trigger several consequences; for instance, alterations in phenology, richness, and abundance in the aphid–parasitoid systems in response to variables such as minimum temperature, and duration of frosts (Tougeron *et al.*, 2018). Therefore, understanding its impact is of utmost importance for agricultural and environmental management (Ovaskainen *et al.*, 2013).

Meteorological variables interfere in the bio-ecology of insects. The main meteorological variables studied in aphid–parasitoid systems are air temperature, rainfall, relative humidity of the air, photoperiod, speed, and wind direction (Meisner *et al.*, 2014; Bell *et al.*, 2015;
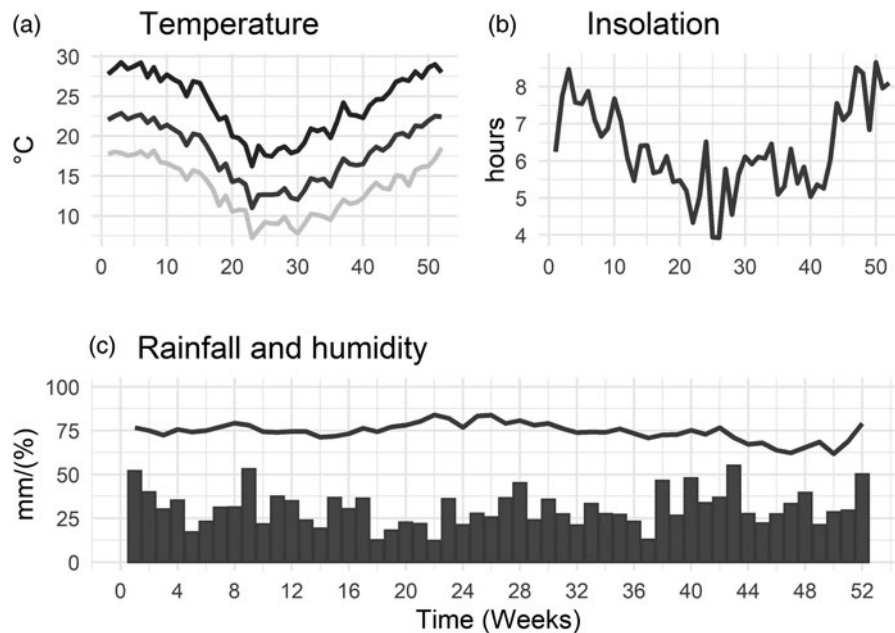
Figure 1. (a) Weekly mean for the air temperatures: maximum (dark gray), mean (gray), and minimum (light gray); (b) weekly mean for mean daily insolation; (c) weekly mean for relative humidity (%) (line) and rainfall (mm) (bars). Weather station of Passo Fundo, RS, Brazil, 2011–2018.

Moiroux *et al.*, 2015). Temperature is one of the main factors that regulate the development of insects, since they possess limited thermoregulation (Alford *et al.*, 2014).

Systematic studies have been conducted on the flight phenology and seasonality of aphids and parasitoids, as well as their responses to meteorological variables have been conducted in Europe and Asia (Palearctic region) (Bell *et al.*, 2015; Holloway *et al.*, 2018). However, in the Neotropical region, this theme is still poorly known, thereby hindering the understanding of population oscillation patterns and its meteorological drivers, which are key factors for Integrated Pest Management. In the present study, multivariate statistical tools were employed to describe the population oscillation of aphids and parasitoids, the effect of meteorological variables on the ecological patterns observed and their implications for trophic compatibility.

Materials and methods

Study area

Samplings were conducted from the first week of January 2011 until the last week of December 2018 in a 5500 m^2 experimental area belonging to Embrapa Trigo, in the municipality of Coxilha, RS, Brazil (altitude of 710 m, lat of 28°11′42.8″S and long of 52° 19′30.6″W). According to Köppen and Geier, the climate in the region studied is of the Cfa type (Valério *et al.*, 2018).

Sampling

Populations of winged aphids associated with winter cereals and parasitoids were monitored with Moericke traps (yellow trays, 45 cm in length × 30 cm in width × 4.5 cm in height), filled with a water-based solution (2 liters), 40% formalin (0.3%), and detergent (0.2%). Each tray had two side orifices (5 mm of diameter), near the edge, protected with a thin net to prevent leaking and loss of solid content during the periods of precipitation. Four traps were placed around the edges of the experimental area. The traps were placed approximately 20 cm above ground, flush with bricks.

The use of Moericke traps favors the detection of aphids and parasitoids at the local level, allowing assumptions about the presence of primary hosts (crops) in the landscape, differing from suction traps that capture migrations from long distances (Pérez *et al.*, 2007; Bell *et al.*, 2015). The area was cultivated in a crop rotation system with black oats (*Avena strigosa* Schreb), white oats (*Avena sativa* L.), wheat (*Triticum aestivum* L.), triticale (*Tritico secale* Wittmack), and forage turnip (*Raphanus sativus* L.) in the fall–winter–spring transition. In the summer, soybeans (*Glycine max* L. Merrill), corn (*Zea mays* L.), and brachiaria grass (*Urochloa* sp.) were grown.

Every 7 days, the biological material of the trays was separated from the solution through a sieve, and maintained in glass flasks with 70% alcohol. Aphids and parasitoids were separated from other species of non-target insects that occurred, identified and quantified under a stereomicroscope. The aphid identification followed the dichotomous key by Pereira *et al.* (2009). The taxonomic systems based on Pennachio (1989), Tomanović *et al.* (2003), Starý and Lukáš (2009), Tomanovic *et al.* (2014), and Tomanović *et al.* (2018) were used to identify parasitoids. Data were stored on a TrapSystem platform (http://gpca.passofundo. ifsul.edu.br/traps/).

Meteorological data

Meteorological variables were obtained from the meteorological station of Passo Fundo (28°15′S, 52°24′W, 684 m), located 10 km from the study site, from which daily variables were obtained: minimum, maximum, and mean air temperature; accumulated rainfall (mm); relative humidity of the air (%); and mean daily insolation (hours) (fig. 1). The mean of the meteorological variables was calculated for the intervals between the collection of the traps (7 days).

Data analysis

A non-parametric principal component analysis (PCA) (based on Spearman's correlation method) was conducted to identify an
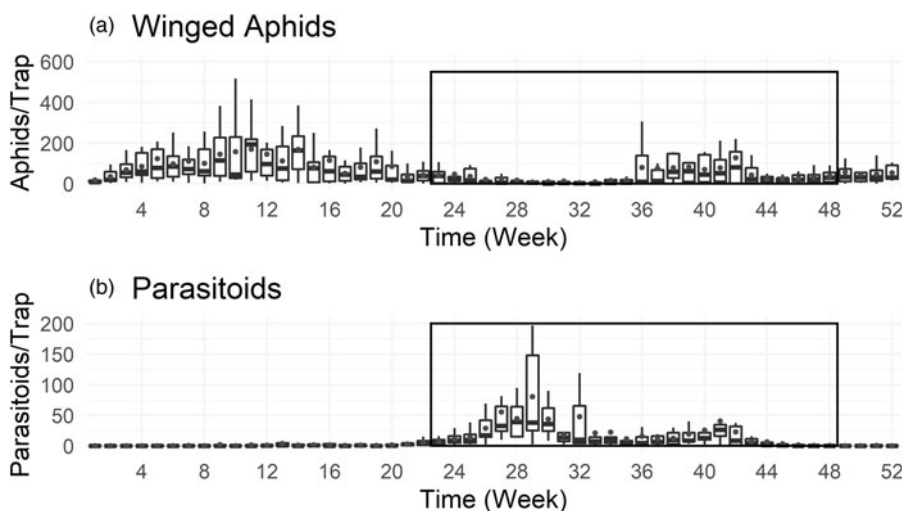
Figure 2. Boxplot of the population fluctuation of winged cereal aphids (a) and their parasitoids (b) over the weeks of the year during the period from January 2011 to December 2018. Red dots indicate the mean for each week. Area inside the rectangle indicates the period with the presence of the wheat crop. Coxilha, RS, Brazil.

existing correlation between variables using vector matrices and eigenvectors associated (v) regarding the meteorological data of the 8 years. For the PCA, the data were standardized by dividing the difference between each data point and the arithmetic mean of the variable of interest by its standard deviation. The components were selected according to the eigenvalues of the correlation matrix and based on the existence of eigenvalues >1 (Kaiser, 1974) and a minimum of 70% of explained variation. The selected PCA components were used as inputs in the subsequent statistical models, as they are orthogonal, and therefore not correlated.

The abundance of aphids and parasitoids per week was defined as the response variable (y) in two types of generalized additive mixed models (GAMM). The first one with errors fitted to the Negative binomial distribution and the second fitted to a Gaussian distribution. The models were parameterized according to the time component, expressed in weeks of the year (x_i); mean air temperature and mean daily insolation (x_j), expressed by the first main component of the PCA (PC1); the weekly rainfall accumulated and mean air humidity (x_k), expressed by the second main component of the PCA (PC2). In addition, two other variables, 'species (aphids and parasitoids)' and 'years' were added as random effects (b_l and b_m, respectively), according to equation 1. Also, a temporal autocorrelation function (weekly) was implemented using the autoregressive model (ARIMA) (ε_t) structure (Carvalho *et al.*, 2020). For the Gaussian model, the data were submitted to log transformation ($x + 0.5$). The Akaike information criterion (AIC) was used to select the best model (Akaike, 1973). The analysis was performed with the '*mgcv*' package (Wood, 2017) and the residual fit was assessed using the 'gam.check' function.

$$y_{ijkl} = \alpha + x_i + x_j + x_k + b_l + b_m + \varepsilon_{ijklm} + \varepsilon_t \qquad (1)$$

A second non-parametric PCA was performed, based on the Spearman correlation method to assess the relationship of annual aphid and parasitoid abundances and meteorological variables. For this analysis, a matrix was used containing the global abundance of each guild, as well as the variables mean air temperature and annual accumulated rainfall for each year of assessment. Both the first and the second PCA were performed using the 'prcomp' function, with biplots generated by the '*FactomineR*' package (Lê *et al.*, 2008).

We used the oscillation patterns of aphids and parasitoids obtained by the GAMM models to propose a risk zoning for sowing wheat crops in Southern Brazil based on the population fluctuation patterns obtained by the selected GAM models. The risk zone was carried out based on the aphid–parasitoid ratio, considering the response patterns of these communities to the mean air temperature, accumulated weekly rainfall, and recommended sowing date for the region (MAPA, 2008).

All analyses were performed using software R version 4.0.0 (https://www.r-project.org/).

Results

Winged aphids had greater abundance in the summer–fall transition (weeks 9–12) and the winter–spring transition (weeks 38–40) (fig. 2a). In the community of parasitoids, large populations were observed, especially during the winter (weeks 23–32), contrasting to the occurrence of winged aphids. The occurrence of parasitoids abundance also took place in another moment, the winter–spring transition. This period presented synchrony with the winged aphids' community (fig. 2b). In addition, taking into account both communities, the increase in population abundance was also related to a greater data variability, as shown in the boxplot interquartile range (fig. 2a, b).

Eight species of winged cereal aphids and seven species of parasitoids were observed in the current study (table 1). Among the aphid species, greater abundance of *R. padi* was found. This species corresponded to 90% of the total abundance of winged aphids captured. In addition to *R. padi*, species such as *S. avenae*, *S. graminum*, *R. maidis*, *R. rufiabdominalis*, and *M. dirhodum* showed relative abundances above 1%. The aphids *S. maydis* and *S. flava* exhibited abundances below 1%.

In the parasitoid communities, the species found with greater abundance were as follows: *A. platensis*, followed by *D. rapae*, *A. uzbekistanicus*, and *A. rhopalosiphi*. The species *E. plagiator*, *A. ervi*, and *L. testaceipes* showed the lowest relative abundances (<5%) (table 1). Taking into account the total population of aphids and parasitoids (table 1), the proportion found during the study period was 5.72 winged aphids/parasitoid. This proportion varied throughout the year, according to the population oscillation of the communities (fig. 2).

In the PCA (fig. 3a), it was found that the variables: minimum [$v = 0.55$], mean [$v = 0.57$], and maximum air temperatures

Table 1. Species, number of individuals (*N*) and relative abundance (A) of winged aphids and parasitoids associated with cereal crops

Aphid species	*N*	A (%)
Rhopalosiphum maidis (Fitch, 1856)	477	1.50
Rhopalosiphum padi (Linnaeus, 1758)	28,824	90.00
Rhopalosiphum rufiabdominalis (Sasaki, 1899)	420	1.31
Schizaphis graminum (Rondani, 1852)	722	2.25
Sipha flava (Forbes, 1884)	56	0.17
Sipha maydis (Passerini, 1860)	38	0.12
Sitobion avenae (Fabricius, 1775)	1122	3.50
Metopolophium dirhodum (Walker, 1849)	373	1.16
Total	32,038	100
Parasitoid species		
Aphidius ervi (Haliday, 1834)	87	1.55
Aphidius platensis (Bréthes, 1913)	3439	61.39
Aphidius rhopalosiphi (DeStefani, 1902)	381	6.80
Aphidius uzbekistanicus (Luzhetzki, 1960)	408	7.28
Diaeretiella rapae (Mc'Intosh, 1855)	1043	18.62
Ephedrus plagiator (Nees, 1811)	174	3.11
Lysiphlebus testaceipes (Cresson, 1880)	70	1.25
Total	5602	100

Coxilha, RS, Brazil, 2011–2018.

[$v = 0.56$], as well as the mean daily insolation [$v = 0.21$] had a greater contribution in PC1 (49.70% of the explained variance). The variables accumulated weekly rainfall and relative humidity of the air had a greater contribution in PC2 (30.03% of explained variance), with *eigenvectors* $v = -0.67$ and -0.66, respectively. Moreover, Spearman's rank correlation indicated significant correlation between the air temperatures and the daily mean insolation ($r > 0.5$; *P* value <0.05), and between the mean relative humidity of the air and accumulated rainfall ($r > 0.5$; *P* value <0.05). Thus, only the variables mean air temperature and accumulated weekly rainfall were maintained for the interpretations of PCs on subsequent statistical models (fig. 3b, c).

The Gaussian model (AIC = 7539) performed better than the Negative binomial model (AIC = 15,141) for the populations of winged aphids of cereals. The increase in PC1 scores (temperature) resulted in a higher abundance (in log) of winged aphid (edf = 1.86; *F* = 1.99; *P* < 0.001) with a linear relationship (fig. 4a). The maximum positive effect was observed around 25°C (figs 3b and 4a). The PC2 (rainfall) negatively influenced the abundance of winged aphids with a slightly nonlinear trend (edf = 2.14; *F* = 7.22; *P* < 0.001). The cumulative weekly rainfall was mostly lower than 100 mm, thereby influencing the confidence interval tail to the right (figs 3c and 4b).

For parasitoids, the Gaussian model (AIC = 5328) also performed better than the Negative binomial model (AIC = 16,525). The smoothed effects of PC1 were significant (edf = 2.36; *F* = 1.48; *P* < 0.001) with the maximum positive effect being around 20°C (figs 3b and 4c). The effect of temperature on parasitoids showed a nonlinear trend, indicating different patterns of response to temperature than aphids (fig. 4c). The accumulated weekly rainfall also exhibited negative effect on the abundance of parasitoids

(edf = 2.48; *F* = 5.99; *P* < 0.001). This relationship was also slightly nonlinear and influenced by low frequency of rainy weeks above 100 mm (figs 3c and 4d).

The temporal component of the GAMM model, expressed as weeks of year, indicated a significant effect on the abundance (log) of winged aphids (edf = 8.40; *F* = 40.13; *P* < 0.001). Aphids presented higher populations during summer, autumn, and spring. The reduction in aphid population during winter is due to thermal influence. During this season, there is a prevalence of temperature below 20°C. Although spring shows higher temperatures than winter, providing a higher number of insects, the populations face the effects of maturation and wheat harvest (fig. 5a). The time component showed that time has a significant effect on the abundance (log) of parasitoids (edf = 8.75; *F* = 83.81; *P* < 0.001). There was a higher number of insects during winter and the beginning of spring, coinciding with the vegetative and reproductive period of wheat (fig. 5c).

The second PCA showed variation in the annual abundances of aphids and parasitoids, as well as its relation with the variables of mean air temperature and precipitation. The explained variance for PC1 and PC2 was 88.78%, with 52.02 and 36.76 for PC1 and PC2, respectively. A positive correlation was observed between the annual abundance of aphids and parasitoids whereas annual rainfall showed a negative correlation with PC1. In PC2, a positive correlation of total abundance of aphids and mean air temperature was observed with this component, whereas the abundance of parasitoids was negatively correlated. These relations can be observed in the vector arrangement of Biplot (fig. 6).

The oscillation pattern observed in the insects may have implications for the risk of barley yellow dwarf virus (BYDV) transmission by aphids in response to the wheat sowing date (fig. 7a). The sowing window takes place within 22nd to 29th weeks of the year (1 June to 20 July) (MAPA, 2008) in the studied area. A risk gradient based on the aphid–parasitoid ratio can be determined within this period. Sowing at the beginning of the recommended season also occurs at a time when there is a high proportion of aphids in relation to the parasitoids, which is the period most likely to transmit the virus. The later the sowing takes place, the lower the aphids/parasitoids proportion will be, thereby lowering the virus transmission risks (fig. 7b).

Discussion

This study described the occurring species and population oscillation of cereal winged aphids and their parasitoids in southern Brazil, based on a historical series. It is possible that these species have been introduced from other regions of the planet along with the primary producers of these trophic networks: cultivated grasses such as wheat, barley, and oat. With the increase of wheat in the area cultivated, initially without effective natural enemies, aphids became important pests (Rebonatto *et al.*, 2015). Winged aphid oscillation patterns are well described in temperate regions, predominantly in the northern hemisphere (Van den Eynde *et al.*, 2020). This study was carried out in the south of Brazil, below the Tropic of Capricorn, where the climate is considered subtropical of the Cfa type (Valério *et al.*, 2018).

Our results indicate aphids exhibiting two annual peaks, one in the summer–fall transition, and the other, in the winter–spring transition. The parasitoid populations also presented a bimodal pattern, with the first peak in full winter, and the second, in the winter–spring transition. Therefore, there was great asynchronicity between the first peak of aphids and parasitoids. On the
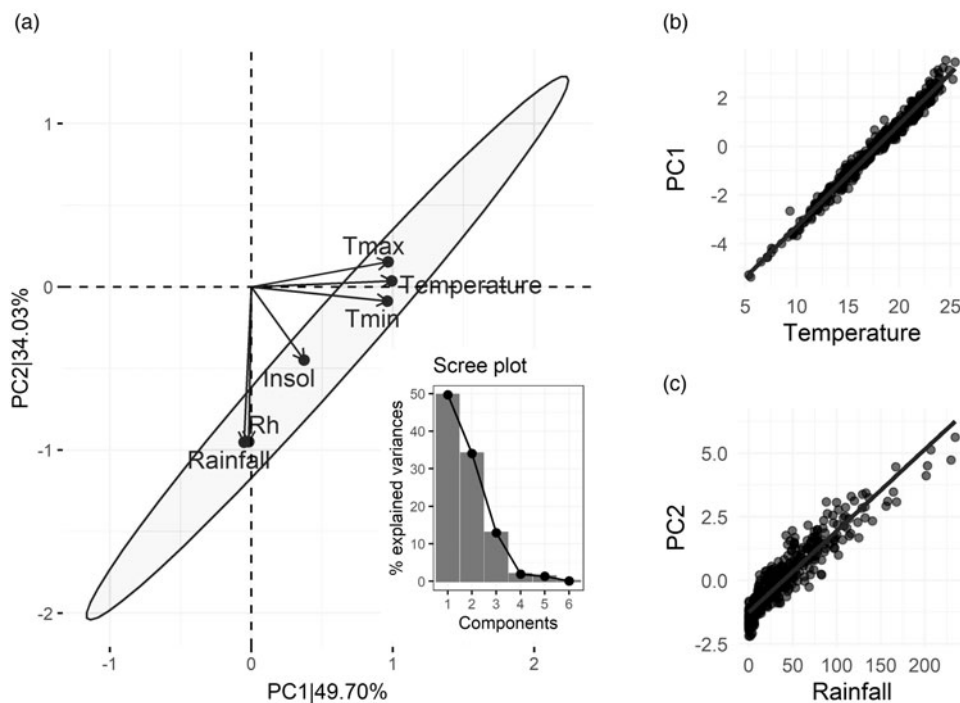
Figure 3. (a) Principal component analysis (PCA) partitioning the variance of meteorological variables: accumulated weekly rainfall (Rainfall); mean relative humidity (Rh); mean daily insolation (Insol); and air temperatures: minimum (Tmin), mean (Temperature), and maximum (Tmax). Weather station of Passo Fundo, RS, Brazil, 2011–2018. (b) Relationship between the first main component of the PCA and the mean air temperature. (c) Relationship between the second main component of the PCA and the accumulated weekly rainfall.
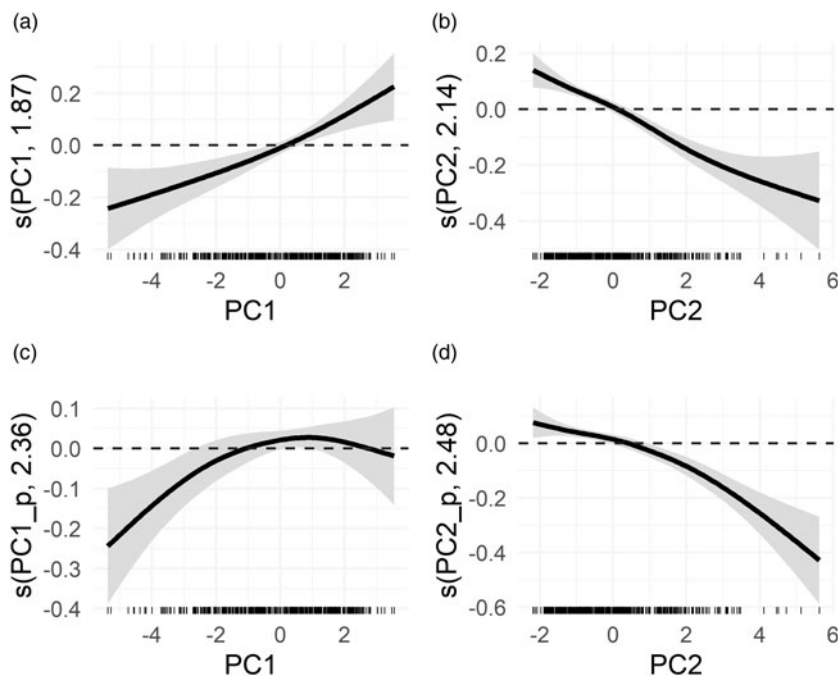
Figure 4. Smoothed splines of the linear components mean air temperature and accumulated weekly rainfall for winged cereal aphids (a and b) and their parasitoids (c and d). Shaded areas indicate the 95% confidence interval. Dashed red line indicates marginal zone between positive and negative effects of independent variables on populations.

other hand, there was a lower delay between aphids and parasitoids for the second peaks. Thus, it is necessary to understand which factors cause the population oscillation pattern observed.

As for winged aphids, the parameters mean air temperature (°C) and accumulated weekly rainfall (mm) affected the populations in short-time. These parameters are related to the development rate, reproduction, and mortality of aphids, directly influencing the development of winged insects (Leslie *et al.*, 2009; Wang *et al.*, 2015; Honek *et al.*, 2018; Wiest *et al.*, 2020). The increase in air temperature caused an increase in the development rate, resulting in massive growth and greater development of winged morphotypes (Auad *et al.*, 2009). The negative effect of accumulated precipitation on the population abundance of winged aphids corroborates the results obtained previously (Rebonatto *et al.*, 2015; Chamuene *et al.*, 2018; Soares *et al.*, 2020). Precipitation affects the population of aphids, increasing mortality, both by drowning and by the increase in air relative humidity, providing favorable environment for entomopathogenic fungi (Soares *et al.*, 2020).
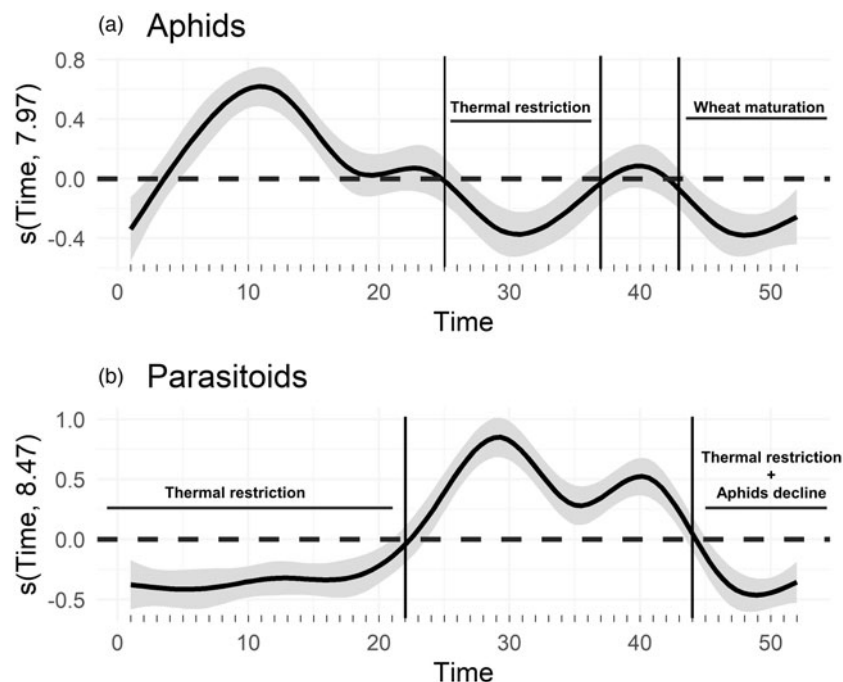
Figure 5. Smoothed splines of the linear time component, expressed in weeks of the year, for winged cereal aphids (a) and their parasitoids (b). Shaded areas indicate the 95% confidence interval. Dashed line indicates marginal zones between positive and negative effects of independent variables on populations.
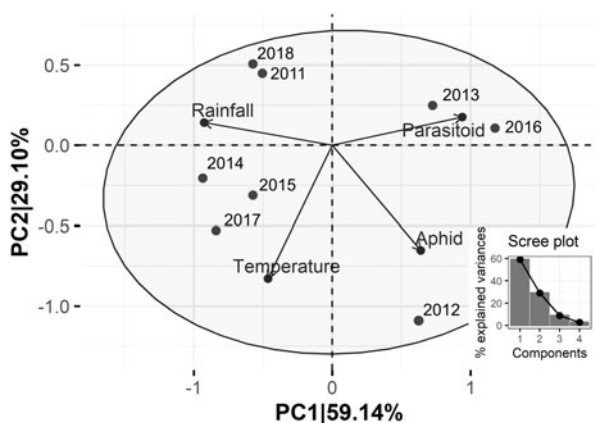

Figure 6. Principal component analysis (PCA) partitioning the variance of meteorological variables: annual rainfall accumulated (Rainfall), mean annual air temperature (Temperature), and the abundance of winged aphids (Aphid) and their parasitoids (Parasitoids) between the years of evaluation. Coxilha, RS, Brazil, 2011–2018.

Although the current study investigated the population dynamics of aphids and related parasitoids, the availability and quality of host plants are yet to be studied. This is an important issue because these factors may influence aphids directly and parasitoids indirectly (Honek *et al.*, 2018). Future studies considering the transition of the host in agricultural landscapes may complement the current results, addicting factors are capable of helping the interpretation of oscillation patterns (Finlay and Luck, 2011).

The absence of synchrony between aphids and parasitoids during the first peak can be due to the effect of temperature. The response of parasitoids to air temperature was first observed by Santos *et al.* (2019). Parasitoids of the *Aphidius* genus (the dominant genus in this study) have faster development in temperatures between 15 and 25°C, and temperatures closer to 20°C are

optimum for population growth. At temperatures above 25°C, both the reproduction rate and parasitism tend to decrease (Jerbi-Elayed *et al.*, 2015). The parasitoid *D. rapae* (the second most abundant species) presents a temperature range similar to the *Aphidius* genus (Basheer *et al.*, 2014).

The effect of the year, generally grouped as a random variable in mixed models, is a key factor to be considered in studies that aim to explain abundances and community structures (Werner *et al.*, 2020). In the region under study, rainfall was well distributed throughout the year, with little influence on seasonality. However, its negative effect on aphid populations is evident in the high abundance of aphids in dry years. Warmer years were positively associated with the abundance of winged aphids, whereas colder years were more beneficial for parasitoids. Therefore, for hot dry years, a greater abundance of aphids is expected, whereas in cold dry years, a greater number of parasitoids is expected, resulting in a greater reduction in aphids population. Studies in wider time scales, for instance, variations between years in the final abundance, propitiate detection of the ways that aphids and parasitoids populations respond to variations in climatic or agricultural landscapes (Harrington *et al.*, 2007; Tougeron *et al.*, 2019; Zhao and Reddy, 2019). Interannual variations may affect the changes of strategies in parasitoids hibernation, anticipation of migration, and alteration of aphids population size (Bell *et al.*, 2015; Andrade *et al.*, 2016; Tougeron *et al.*, 2018). The effects of the year may have consequences in the trophic compatibility of the organisms and should be taken into account in the studies of species interactions at different trophic levels.

The delay in the occurrence of parasitoids in relation to the first aphid outbreak is related to the effects of temperature on both guilds, as explained previously. This delay is particularly relevant for wheat grown in southern Brazil. Considering the observed oscillation patterns, a risk gradient for wheat was generated based on the aphid–parasitoid ratio. In this scenario, wheat sowing carried out later (even within the recommended time –
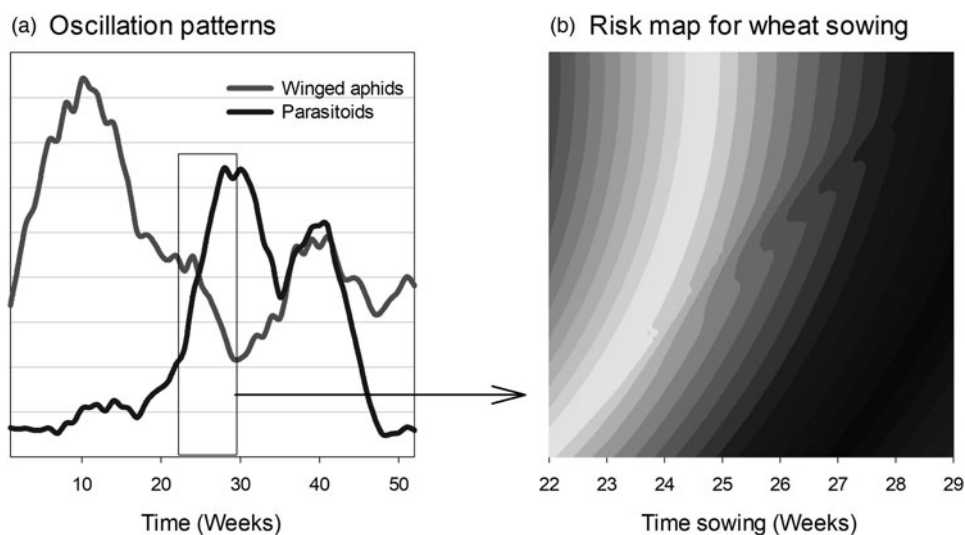
Figure 7. (a) Smoothed splines estimated by the GAMM models indicating the population oscillation patterns of winged cereal aphids (light gray line) and their parasitoids (dark gray line) throughout the year. Rectangle indicates time zone indicated for sowing wheat in the study region according to the Ministry of Agriculture, Livestock and Supply (MAPA, 2008); (b) risk map for wheat sowing based on the proportion of winged aphids and parasitoids caught in traps. Colors indicate levels of risk, from white (highest risk) to black (lowest risk).

22nd to 29th weeks of the year) tends to be climatically more favorable for parasitoids, expanding the potential biological control and reducing the risks of BYDV transmission by aphids. Despite this, quantification of the direct effect of parasitoids on aphids is an essential step for understanding the population dynamics and aphid's management (Fidelis *et al.*, 2019). Therefore, forecasting models that aid in decision making on the management of aphids and virus transmission must be taken into account in the aphids–parasitoids relation. These assumptions, based on the data of winged populations, need to be corroborated with parasitism data measured in field conditions.

Finally, our results show the population oscillation dynamics in cereal winged aphids and their parasitoids in the South of Brazil. The different results shown by aphids and parasitoids in response to temperature have important implications for trophic compatibility and should be taken into account in predictive models analyzing the impact of parasitoids on wheat aphids. In addition, we observed that rainfall is related to the intensity of occurrence of populations, with no implication for seasonality.

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