ABRAÃO ALMEIDA SANTOS

THE ROLE OF CLIMATE ON THE MORTALITY, OCCURRENCE, AND POTENTIAL DISTRIBUTION OF *Ascia monuste orseis* (LEPIDOPTERA: PIERIDAE)

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Fitotecnia, para obtenção do título de *Doctor Scientiae*.

Orientador: Marcelo Coutinho Picanço

Coorientadores: Leandro Bacci
Rodrigo Soares Ramos

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“Quem aprende apanhando, pode ensinar sem bater.”

(Bráulio Bessa)

ABSTRACT

SANTOS, Abraão Almeida, D.Sc., Universidade Federal de Viçosa, October, 2020. **The role of climate on the mortality, occurrence, and potential distribution of *Ascia monuste orseis* (Lepidoptera: Pieridae)**. Adviser: Marcelo Coutinho Picanço. Co-advisers: Leandro Bacci and Rodrigo Soares Ramos.

In this thesis, we presented evidence on the role of climate in the natural history of the neotropical butterfly *Ascia monuste orseis* Godart (Lepidoptera: Pieridae). In the first chapter, we found that species occurrence increases during wet and warm conditions on agricultural crops since cold and dry conditions impair immature stages development (i.e., egg, larva, and pupa). In the second chapter, we investigated how variations on weather can affect the causes of natural mortality on immature stages. Our results indicated that variations on weather affect the mortality caused by failure, predations, and rainfall. Failure rates increased during cold and dry conditions, while under intense precipitation, rainfall caused mortality on eggs and larvae. Conversely, predation was higher during wet-warm seasons. However, we emphasized that these results were dependent on whether varied during immature development. Since *A. monuste orseis* is a pest of tropical brassica crops, in the last chapter, we investigated how the current climate and future scenarios can affect its potential distribution. Our models indicated that tropical areas seem to be suitable for species occurrence. However, under future scenarios, these areas tended to reduce, mostly to a host (cabbage) than the species. This thesis contributed to the knowledge about the natural history of *A. monuste orseis* and can be a guide to biosecurity protocols regarding the risk of pest introduction.

Keywords: Biosecurity. Tropical ecology. Neotropical entomology. Natural history. Ecological modelling.

RESUMO

SANTOS, Abraão Almeida, D.Sc., Universidade Federal de Viçosa, outubro de 2020. **O papel do clima sobre a mortalidade, ocorrência e distribuição potencial de *Ascia monuste orseis* (Lepidoptera: Pieridae)**. Orientador: Marcelo Coutinho Picanço. Coorientadores: Leandro Bacci e Rodrigo Soares Ramos.

Nesta tese nós apresentamos evidências sobre o papel do clima na história natural da borboleta neotropical *Ascia monuste orseis* Godart (Lepidoptera: Pieridae). No primeiro capítulo, nós mostramos que a ocorrência desta espécie em cultivos agrícolas é favorecida por condições quentes e úmidas, uma vez que a baixa temperatura e umidade foram prejudiciais para o desenvolvimento dos estágios imaturos da espécie (i.e., ovo, larva e pupa). Em seguida, nós investigamos como as variações climáticas podem afetar as causas naturais de mortalidade dos estágios imaturos. Assim, no segundo capítulo, nossos resultados indicaram que as variações de temperatura, umidade relativa e precipitação afetaram a mortalidade causada por chuva, falhas e predação. A mortalidade ocasionada pela chuva sobre ovos e larvas ocorreu em épocas de maior intensidade, enquanto que em estações de menor temperatura as falhas tenderam a aumentar. Por outro lado, a predação, em larvas e pupas, foi maior em épocas quentes. Contudo, ressaltamos que todos esses resultados foram dependentes do clima local e das variações observadas durante cada estágio de desenvolvimento do inseto. *Ascia monuste orseis* é uma praga em cultivos tropicais de brássicas, desse modo, no último capítulo, nós investigamos como o clima atual e futuros cenários podem afetar a distribuição potencial da espécie no mundo. Nossos modelos indicaram que áreas tropicais em outros continentes parecem ser adequadas para a ocorrência da espécie. No entanto, sob futuros cenários, essas áreas tenderam a diminuir, mas essa redução foi mais expressiva para um hospedeiro estudado (repolho) do que para o inseto. Desse modo, esta tese contribui para o conhecimento da história natural de *A. monuste orseis* e pode servir de guia para protocolos de biosegurança para o risco de introdução desta praga.

Palavras-chave: Biossegurança. Ecologia tropical. Entomologia neotropical. História natural. Modelagem Ecológica.

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1 GENERAL INTRODUCTION

Climate is the leading factor that determines species distribution, occurrence, development, survival, and reproduction (BROWN et al., 2004). Among the elements, the temperature affects individual metabolism, where, for instance, organisms development tended to increases, as temperature also increases (MARTINS et al., 2016). Thus, this factor is crucial for organisms biology and ecology. However, in areas where temperature does not change significantly across seasons, other factors, such as rainfall, also influence patterns of species natural history (POLLARD, 1988; BONEBRAKE et al., 2010).

Tropical climates are well defined by dry and wet seasons, which seem to determine species natural history from these regions. For instance, suitable areas for butterflies appear to be associated with wet and warm regions/seasons (DEVRIES, 1987; BONEBRAKE et al., 2010). While, the assemblages appear to reduce during dry conditions because it affects immature stages development and also hosts plants (BRABY, 1995; CHECA et al., 2014; POFFO et al., 2018). Thus, the natural history of butterflies from tropical regions may be determined by variations on dry and wet seasons.

Ascia monuste orseis Godart 1918 (Lepidoptera: Pieridae: Pierinae) is a neotropical butterfly distributed in South America (COURTNEY, 1986; DEVRIES, 1987). This species, during the larval stage, is a specialist pest of Brassicaceae family (Cruciferae) representing one of the major pests in these crops (SANTANA; ZUCOLOTO, 2011). Studies have shown the bioecology of *A. monuste orseis* in tropical areas and identified strategies for its maintenance.

Adults migrate to searching for the host during wet and warm seasons (SANTANA; RODRIGUES; ZUCOLOTO, 2017; POFFO et al., 2018) when flights are observed in a range from 19 °C to 39 °C (NIELSEN; NIELSEN, 1959). The oviposition is found mostly in the basal part of young leaves, which avoids predators action and improve immature development (CATTA-PRETA; ZUCOLOTO, 2003; BITTENCOURT-RODRIGUES; ZUCOLOTO, 2005). Eggs are oviposited in clusters, and it seems to increase larval hatching (SANTANA; ZUCOLOTO, 2016). However, cannibalism can occur by larvae that eat eggs. Nevertheless, this behavior depends on the interval time of hatching and food availability and seems to have a role in population control (BARROS-BELLANDA; ZUCOLOTO, 2001; ZAGO-BRAGA; ZUCOLOTO, 2004).

Ascia monuste orseis has five larval instars, and during that, caterpillars feed on leaves (SANTANA; RODRIGUES; ZUCOLOTO, 2017). However, this stage development depends on the age of leaf and its nitrogen content. For instance, when the caterpillars from the first instar feed on new leaves, they have a better development compared to those who feed on old (BITTENCOURT-RODRIGUES; ZUCOLOTO, 2009). Also, it was observed that *A. monuste orseis* has a better development in *Brassica oleracea* (kale) than *B. juncea* (mustard) due to its higher nitrogen content (BITTENCOURT-RODRIGUES; ZUCOLOTO, 2009).

Similar to eggs, caterpillars are also found in groups, and it seems to improve species defense against natural enemies (SANTANA; RODRIGUES; ZUCOLOTO, 2017). For instance, the per capitata risk of mortality in solitary larvae is higher compared to groups of 10 and 50 individuals (SANTANA; RODRIGUES; ZUCOLOTO, 2017). Although living in a group has a positive effect, in the last instars, larval dispersal increases to avoid the effects of food deprivation (BARROS-BELLANDA; ZUCOLOTO, 2002). However, it can be difficult, since larvae have low capacity to detect a host and can die due to predation and starving (BARROS-BELLANDA; ZUCOLOTO, 2003).

Regarding food deprivation, it was shown their negative effect during larval development and its impact on adults with relation to caterpillar instar. In the second instar, deprivation increases pupation time, while in the 4th reduces adult weight, and in both cases, a denial higher than 24 hours causes mortality (BARROS-BELLANDA; ZUCOLOTO, 2002). Also, when food is not available, larvae of fourth and fifth instars increases rates of cannibalism (SANTANA; ZUCOLOTO, 2011). However, caterpillars have a compensatory strategy to overcome it (high ingestion and biomass gain) if a new host is found, which does not impair species reproduction (BARROS-BELLANDA; ZUCOLOTO, 2002).

Overall, these studies have provided essential information regarding *A. monuste orseis* bioecology. However, there is a lack of knowledge about the role of climate on their occurrence, mortality, and potential distribution. Yet, some hypotheses to species occurrence were not proved, while information regarding the effects of local weather on natural enemies is available in short experiments.

The association between warm and wet conditions with *A. monuste orseis* occurrence is suggested since initial studies (e.g., LORDELLO; RODRIGUES, 1952). Because tropical climate has marked dry and wet seasons, it is understood the negative impact of drought periods on butterfly community (BONEBRAKE et al., 2010). These periods affect species reproduction, cause food deprivation to immature stages leading to high rates of mortality, and induce some reproductive strategies and migration (COURTNEY, 1986; BRABY, 1995; SHAHABUDDIN; TERBORGH, 1999; CHECA et al., 2014).

Oviposition of *A. monuste orseis* on *Brassica* crops appears to start in November, and it is observed until May - the wet and warm period in the tropical region (SANTANA; RODRIGUES; ZUCOLOTO, 2017). However, why are these conditions more suitable for *A. monuste orseis* occurrence? Field observations have suggested that adults are sensitive to variations in the temperature (NIELSEN; NIELSEN, 1959), and cold conditions may cause mortality in immature stages (SHIMA; GOBBI, 1981).

The causes of natural mortality of *A. monuste orseis*, in addition to climate, belong to host plant and natural enemies (predators, parasitoids, and pathogens). For instance, glucosinolates levels of *Brassica* species is a determinant factor for adults oviposition since those with high percentual are not suitable for immature development (COURTNEY, 1986; DEVRIES, 1987).

For eggs, the rates of mortality are low (DEVRIES, 1987) and one study observed predation by *Eriopis connexa* and *Coleomegilla maculate* (Coleoptera: Coccinellidae) but did not quantify it (LINK; COSTA, 1983). Also, parasitism is not related to *A. monuste orseis* during the egg stage (LORDELLO; RODRIGUES, 1952; LINK; COSTA, 1983).

Ants and wasps appear to be the leading natural factors in larval and pupal stage. In the first report about ants predation, RAMOS et al., (2012) identified this group as a predator only of pupae. However, SANTANA et al., (2017) suggest that ants can also predate larvae. Since this last one was conducted during the wet season, it may indicate a possible effect of weather on ants predation. Conversely, the role of wasps is well defined. They are voracious predators of the larvae, mostly during wet and warm seasons (PICANÇO et al., 2010; RAMOS et al., 2012). However, little is known about the rates of mortality caused by these factors and how variations on weather affect it.

Thus, in this thesis, we provided evidence for the knowledge gaps previously mentioned. We confirmed initial hypotheses regarding species occurrence on *Brassica* crops during wet and warm conditions (chapter 1) and shown that season and weather affect the mortality of immature stages caused by natural factors (chapter 2).

Finally, due to *A. monuste orseis* importance as a pest of *Brassica* crops and its sensibility to variations on weather, we also investigated their potential distribution under current and future climate scenarios (chapter 3). These scenarios suggest that the temperature will increase from 1.5 °C to 2.8 °C until 2050 (IPCC, 2014), and it can impact food security due to the risk associated with the introduction of pests and increases of suitable areas (RAMOS et al., 2019).

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2 CHAPTER 1

Wet and warm conditions contribute to the occurrence of the neotropical butterfly *Ascia monuste orseis* Godart (Lepidoptera: Pieridae) on *Brassica* crops

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ABSTRACT

Ascia monuste orseis Godart (Lepidoptera: Pieridae) is a neotropical butterfly distributed in South America. During the larval stage, this insect causes economic losses on *Brassica* crops. Wet and warm conditions are known to increase subspecies occurrence, but it remains unclear why these conditions are more suitable. In this study, we have shown that both conditions are highly favourable for *A. monuste orseis*. We determined the thermal requirements for immature development and then modelled *A. monuste orseis* occurrence using Climex algorithm. Two models were built: one for the year-round presence and other for seasonal suitability. We validated the models using subspecies occurrence records and monitoring in two Brazilian regions (Northeast and Southeast). The minimum, optimum and maximum temperature for immature development were estimated at 16.37, 29.16 and 34.95 °C, respectively. The model for year-round presence indicated tropical areas as highly suitable for *A. monuste orseis* occurrence (with 88% of accuracy) and the seasonal models showed unsuitable areas in some parts of South America during cold and dry periods. Such predictions were observed in the monitored areas where *A. monuste orseis* was not found. These results can be associated with the mortality caused by low temperature to immature stages, and drought conditions that may induce adults migration to moist habitats. Thus, we suggest that *A. monuste orseis* occurs mainly during wet and warm seasons on *Brassica* crops due to deleterious effects caused by cold and dry conditions. This information can be used to improve *A. monuste orseis* management in *Brassica* crops.

Keywords: Pierinae, modelling, climate, seasonal dynamic.

3 INTRODUCTION

Climate affects butterflies due to the direct impact on species biology, physiology, and distribution. Such implications are usually associated with fluctuations in the temperature, which affects survival, reproduction, foraging and migratory activities of species (Nielsen and Nielsen 1959; Braby 1995; Bonebrake et al. 2010; Poffo et al. 2018). For instance, the development of butterflies' immature stages varies according to temperature, and this effect can be estimated through laboratory experiments (e.g., Martins et al. 2016). During warm seasons, adults migrate to suitable areas (Checa et al. 2014; Poffo et al. 2018), and flight activity is higher at high temperatures (Nielsen and Nielsen 1959). Thus, the temperature has a direct impact on butterflies. However, in areas where oscillations are not drastic, other climate factors, such as rainfall, can also play a role in their occurrence (Jones and Rienks, 1987; Bonebrake et al. 2010; Checa et al. 2014).

Tropical climate shows a small variation in the temperature, but rainy periods are well defined (Peel et al. 2007). These variations can affect the butterflies' community negatively. For example, drought conditions decrease the abundance and richness of species due to a reduction in resource availability that impacts immature development (Shahabuddin and Terborgh 1999; Checa et al. 2014). Adults can be confined to moist refuges during dry periods, and diapause can be observed until the beginning of wet season (Braby 1995). Also, low humidity and drought conditions stimulate diapause initiation and maintenance (Jones and Rienks 1987) and cause mortality to immature stages (Da Silva et al. 2018). Thus, the patterns in tropical butterflies occurrence are likely to be associated with rainfall seasons.

Some methods can be applied to understand the patterns of species occurrence based on climate. Species distribution models, for instance, have been used to determine the probability of organisms presence based on biotic and abiotic factors and also to understand the effects of future climate scenarios (Franklin 2010). The modelling algorithm Climex is an useful tool to analyze butterflies distribution because, in addition to a model for their year-round presence, it also shows suitable areas according to seasons of the year (Kriticos et al. 2015; Ramos et al. 2019). Such models can indicate which seasons of the year offer suitable conditions for the butterflies and show the climate role on their seasonality.

Ascia monuste orseis Godart 1819 (Lepidoptera: Pieridae) is a neotropical butterfly distributed in South America. This subspecies is a pest of *Brassica* crops (e.g., cabbage and kale) and causes economic loss during immature stages (Liu 2005). Adults migrate to long distances to search for host, mates and suitable conditions for immature development (Poffo et al. 2018). Then, they oviposit in clusters (from five to 144 eggs) and larvae feed during this stage (~ 15 days) on leaves (Santana et al. 2017). Interestingly, this subspecies appears to occur mainly during warm and wet seasons on *Brassica* crops (Santana et al. 2017), and it is also found in moist areas throughout the year (Thiele et al. 2014; Melo et al. 2019). However, it remains unclear why these conditions are more suitable for *A. monuste orseis*.

In this study, we verified the underlying causes of higher *A. monuste orseis* occurrence in wet and warm conditions. For that, we initially determined the thermal requirements for the development of immature stages (i.e., eggs, larva, and pupa) and then used this information to create models using Climex algorithm. Two models were built: one for the potential distribution based on year-round suitability and other for the seasonal occurrence according to the month of the year (Kriticos et al. 2015). We validated these models using occurrence records of *A. monuste orseis* in South America and monitoring from areas in two Brazilian regions (Northeast and Southeast).

4 MATERIALS AND METHODS

4.1 THERMAL REQUIREMENTS

We performed the experiments using a population of *A. monuste orseis* established in 2016 from eggs collected in an organic brassica crop located in Coimbra (20° 50’ 27” S, 42°46’ 24” W), Minas Gerais, Brazil. We collected insects from this field again in 2017 and introduced them in the laboratory population to reduce the loss of genetic variability. The insects were reared under greenhouse conditions. Larvae were fed with leaves of kale (*Brassica oleracea* var. *acephala* L.) and adults with a mixture of honey and water (1:3). Plants of cabbage (*Brassica oleracea* var. *capitata* L.) were used for adult oviposition. We started the experiments in August 2017 and finished in December 2018.

The experiments were done at nine constant temperatures (15.0, 17.5, 20.0, 22.5, 25.0, 27.5, 30, 32.5, and 35 °C ± 1 °C), relative humidity 70 ± 5%, and 12 hours of photoperiod in incubators (Model EL202/3LED, EletroLab, São Paulo, Brazil). We selected this range of temperatures based on the related occurrence of *A. monuste orseis* on *Brassica* crops during seasons with high temperature (Santana et al. 2017), and because a small variation in temperature (~1 °C) can affect subspecies behaviour activity (Nielsen and Nielsen 1959).

For each temperature, 100 eggs were placed in the incubator. To do that, we previously left a cabbage plant in the greenhouse for adult oviposition for 30 minutes. Thus, we avoided possible damage to the eggs due to human mechanical removal from the plants since *A. monuste orseis* oviposit in clusters (Santana et al. 2017). After the eggs hatched, larvae were put in a plastic container (3000 mL) and fed kale leaves until the pupal stage. Assessments were performed every 24 hours, noting the number of living and dead insects. In each assessment, kale leaves (that served as substrate) were replaced.

The total number of days necessary for each stage to be completed (i.e., duration of eggs, larvae, and pupae in days) and its survival (%, y-axes) were regressed on temperature (x-axis) using Table Curve 2D software (Systat Software, San Jose, CA, USA) to obtain the initial parameters of the equations describing these relationships. The selected parameters were then adjusted using the package 'lme4' (Bates et al. 2015) in R software version 3.5.0 (R Core Team 2018) using generalized linear models (identity and binomial families, respectively, for development and survival) and confidence intervals (0.025 and 0.975 quantiles) were estimated by bootstrapping 1000 times. The overall significance of the models was obtained by comparing the fitted model to its respective null model (i.e., analysis of deviance) using the F and chi-squared tests (χ^2), respectively, for development and survival. We also estimated Nagelkerke pseudo R^2 as an additional goodness of fit measurement, in which values range from 0 to 1, with higher values indicating a better model fit (Nagelkerke 1991). The figure was plotted using SigmaPlot version 11.0 (Systat Software, Chicago, IL, USA).

4.2 CLIMEX MODELS

The algorithm Climex (version 4.0) is an approach for species distribution models that predicts suitable areas where the species can tolerate the climatic conditions based on previous information of current occurrence (Kriticos et al. 2015). Also, it is possible to understand how the species respond to climatic variables at different temporal scales (e.g., weekly growth index - GIw). Thus, we can estimate the potential geographical distribution and the seasonal suitability of a species concerning the climate.

Information regarding the known geographical distribution of the species and laboratory data (e.g., thermal requirements) are required to fit a model in Climex (Kriticos et al. 2015). After obtained the estimated parameters, they are validated using independent data (e.g., locations where species is found) to obtain the accuracy of the model. Thus, we created a model for the potential distribution of *A. monuste orseis* using information from areas where it occurs, and the thermal requirements found in this study. Based on this model, we generated the seasonal models and created maps for the years evaluated in the fields (2008 and 2011).

For the potential distribution, Climex generates the Ecoclimatic Index (EI) using ‘Compare locations’ function. This index is a result of growth (e.g., temperature and moisture indexes) and stress indexes (e.g., cold, hot, dry, and wet) which gives an overall measure of the suitability of the location for yearly by a species. EI ranges from 0 to 100, where 0: the area is inadequate for species establishment; 0 – 30: less favourable climate conditions for species growth and development; > 30 highly favourable climate conditions. For the seasonal suitability, the software informs the GIw that describes favourable conditions for population growth in a scale from 0 to 1 using ‘Compare locations/years’ function. Values close to 0 indicate inappropriate periods for species growth. The closer this value is to 1, the more the conditions of the period are favorable. For both models, Climex generates maps and, in the case of GIw, sequences by month/year (Kriticos et al. 2015).

4.3 MODEL CALIBRATION

We fitted the model based on biological data of *A. monuste orseis* (see indexes description below). We found 98 occurrence records of the species in the literature that were used to validate our potential distribution model. These data are available in a supplementary file in the online version of the article.

For the potential distribution, we used CliMond 10´-gridded data (available on https://www.climond.org/). This data represents a historical climate for over 30 years (1961-1990) centered in 1975. We used the average of monthly temperature (minimum and maximum), precipitation, and relative humidity at 09:00 and 15:00 hours. The model was validated based on the match between EI suitable categories (i.e., > 0) and the occurrence records.

Temperature index

Based on the thermal requirements' experiment, eggs did not hatch at 15 °C and all larvae died above 35 °C. We estimated the temperature of 16.37 °C as the minimum and 29.13 °C as the optimum for the development of *A. monuste orseis* (Fig. 1). Thus, we used the values of 15 (DV0), 16.37 (DV1), 29.13 (DV2), and 35 °C (DV3) as temperature indexes (Table 1).

Moisture index

Ascia monuste orseis occurrence is associated with wet areas and seasons. For instance, its presence on *Brassica* crops is related to seasons with high precipitation patterns (Thiele et al. 2014; Melo et al. 2019). Thus, values of moisture were set up to 0.10 (lower soil moisture threshold), 0.40 (lower optimum soil moisture), 1.60 (upper optimum soil moisture), and 2.0 (upper soil moisture threshold) (Table 1). These values provided better results for our model and matched the occurrence records.

Stress indices

Cold

We set the temperature threshold for cold stress at 15 °C, as eggs did not hatch, and the cold stress accumulation in -0.0005 per week to match with areas of *A. monuste orseis* occurrence (Table 1).

Heat

At 35 °C, we noted that larvae of *A. monuste orseis* died four days after eggs hatched, so we used this temperature as the threshold for heat stress. For heat stress accumulation rate, we adopted 0.0001 week^{-1} (Table 1).

Dry

Ascia monuste orseis mostly occurs in areas with high relative humidity and it is sensitive to changes in this variable (Thiele et al. 2014; Santana et al. 2017; Melo et al. 2019). Thus, the dry stress threshold moisture level and dry stress accumulation rate were set at 0.20 and -0.01 week^{-1}, respectively (Table 1).

Wet

Although *A. monuste orseis* occurs in rainy areas (Thiele et al. 2014; Melo et al. 2019), rainfall may cause adult mortality during migratory flights (Poffo et al. 2018) and to larvae in early instars through drowning (Picanço et al. 2010). Thus, wet stress parameter and wet stress accumulation rate (both dimensionless) were set at 2.5 and 0.015 (Table 1).

Monthly climate data

To build the seasonal models, we used a monthly time series (1901-2017) from the Climatic Research Unit (CRU) version 3.26 (https://crudata.uea.ac.uk/cru/data/hrg/). We chose monthly average minimum and maximum temperatures, and precipitation in the years of 2008 and 2011, when field data was collected (see below).

4.4 MONITORING THE OCCURRENCE OF *A. MONUSTE ORSEIS*

Two brassica areas, one in the Northeast and other in the Southeast Brazilian region (1569 km apart), were monitored for one year (January to December). We performed fortnightly evaluations by counting the number of eggs and larvae of *A. monuste orseis*. Climate data (rainfall, mean temperature, and relative humidity) were obtained from the Brazilian National Institute of Meteorology automatic stations (http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep).

Area 1 (~ 0.5 ha) was located in Viçosa, Minas Gerais state, Southeast region (20° 46’ 12” S, 42° 52’ 07” W; altitude 750 m) and consisted of cabbage plants grown without pesticide application. This area was evaluated in 2008 and 20 plants randomly selected were assessed in each sampling date.

Area 2 (~ 0.6 ha) was located in Areia Branca, Sergipe state, Northeast region (10° 46’ 23” S, 37° 22’ 41” W; altitude 178 m), consisting of kale plants also grown without pesticide applications. This field was monitored in 2011. At each assessment, 30 kale plants were randomly selected and surveyed in this field.

We plotted the climate data, the weekly growth index from seasonal models, and the observed number of *A. monuste orseis* per plant in the sampled fields (y-axis) against months (x-axis) for both fields. These graphs were designed using ‘ggplot2’ (Wickham 2016) package in R (R Core Team 2018).

5 RESULTS

5.1 THERMAL REQUIREMENTS

The developmental time and survival of immature stages of *A. monuste orseis* varied according to the temperature (Fig. 1). Eggs did not hatch at 15 °C after 80 days, and the developmental time reduced as temperature increased (pseudo R^2= 0.85; F= 349.2; P<0.001; Fig. 1A). For instance, at 17.5 °C egg development was completed in 14 days, while above 30 °C, it was less than 4 days. Conversely, its survival increased as a response to increases in the temperature with values close to 100% (pseudo R^2=0.48; χ2=378.52; P<0.001).

A similar response was observed during larvae's developmental time (pseudo R^2 = 0.89; F = 834.69; P < 0.001), but we noticed a different response for survival (pseudo R^2=0.40; χ2= 283.80; P < 0.001; Fig. 1B). Initially, larvae survival tended to increase in response to temperature with values up to 75% between 25-30 °C. However, it decreased markedly at temperatures above 30 °C and the larvae did not survive at 35 °C during the experiment. This effect was confirmed using 20 larvae at this temperature and, again, we did not observe their development.

For pupae, we checked if they develop at 35 °C before carrying out the analysis. Then, we also rechecked this effect with 20 pupae and we did not observe any development. Overall, the developmental time of pupae had the same tendency as the other immature stages (pseudo R^2 =0.75; F=268.21; P<0.001; Fig. 1C). Still, we were not able to determine its survival curve because a survivorship similar to or higher than 80% was observed in all evaluated temperatures.

5.2 POTENTIAL DISTRIBUTION

Based on the parameters fitted, our model had 88.77% of accuracy, i.e., 87 out of 98 occurrence records were matched suitable categories (blue and orange colours, Fig. 2). The potential distribution model indicated that areas in the tropical zone were highly favourable for the occurrence of *A. monuste orseis* and few areas in the subtropical zone, such as Argentina, the South Brazilian region, and Paraguay were less favourable.

5.3 SEASONAL MODELS AND FIELD VALIDATION

The seasonal models showed that GIw varies among months [2008 (Fig. 3) and 2011 (Fig. 4)]. Large unsuitable areas (i.e., GIw equal to zero) were observed mostly from June to September, comprising the driest periods in South America (Alvares et al. 2013).

In area 1, the temperature ranged from 15 °C (winter) to 23 °C (summer), with rainfall occurring mostly from January to April, September, and December. Also, the lowest relative humidity was registered in September (Area 1, Fig. 5).The GIw for this area had values close to 1 from January to April, with a steep decline from May to June (Area 1, Fig. 6). Then, GIw increased from August to December. The highest density of *A. monuste orseis* was recorded in January, with peaks in August and November. From February to July, and also September-October, the subspecies did not occur (Area 1, Fig. 6).

In area 2, the temperature varied from 25 °C (winter) to 29 °C (summer), rainfall was concentrated in March-April, and relative humidity ranged from 72 to 78% (Area 2, Fig. 5). The GIw values were close to zero only in November and December (Field 2, Fig. 6). Fitted values were moderate (~ 0.25) from January through March, then increased until May, with a plateau until September, and progressively declined until December. The pest was generally well distributed year-round in area 2, with peaks in February, June, and September. In December, the pest was not detected (mean density = 0) (Area 2, Fig. 6).

6 DISCUSSION

We found that the immature development of *A. monuste orseis* occurs from 16.37 to 34.95 °C (Fig. 1), indicating that the species is limited to warm areas. Our model for the year-round suitability permanent occupancy indicates that tropical regions are highly suitable for *A. monuste orseis* (Fig. 2). However, the seasonal model indicated large unsuitability in regions with cold and dry periods (Fig. 3 and 4), which was supported by our findings in the two monitored areas (Fig. 6). Thus, we confirmed that the occurrence of *A. monuste orseis* on *Brassica* crops is favoured by wet and warm conditions.

Tropical species usually have narrow thermal ranges since temperature fluctuation is low over the year in the tropical zone (Bonebrake et al. 2010). Although mild compared to temperate species, thermal variations have an impact in the biology of tropical lepidopterans. For instance, low temperatures increase developmental time of *Byciclus anynana* Butler (Fischer et al. 2010), trigger species migration (Bonebrake et al. 2010), and reduce Pieridae species occurrence (Pollard 1988). Additionally, high temperatures (> 30 °C) reduce flight activity of *Ascia monuste* L. (Nielsen and Nielsen 1959) and cause larva and pupa desiccation in *Neoleucinodes elegantalis* Guenée (Da Silva et al. 2018). Hence, the thermal requirements for the development of immature *A. monuste orseis* support the permanent model that suggests tropical areas as highly favourable for its presence. However, because this region has dry and wet seasons, such change can also play a role in species occurrence.

The seasonal models indicated reductions in the number of suitable areas for *A. monuste orseis* during the dry season (June-September). Previous studies support this finding, as dry conditions have been reported to cause habitat contraction of other tropical species (Braby 1995; Checa et al. 2014). For example, dry stress reduces suitable areas for *N. elegantalis* in South America (Da Silva et al. 2018). Dry seasons decrease species richness and abundance of tropical butterflies, mainly due to the reduction of food supply (and nutritional quality of host plants) for adults and immatures (Shahabuddin and Terborgh 1999; Checa et al. 2014). Hence, dry conditions reduce suitable areas for *A. monuste orseis* due to adverse effects on subspecies survival and host plants availability.

Conversely, butterflies have some strategies to survive during adverse conditions (Bonebrake et al. 2010). Species from the genus *Eurema* (Pieridae) shows three different adaptive strategies during dry seasons in Australia: continuous breeding and opportunistic migration, opportunistic breeding when conditions are favourable, and strictly seasonal breeding (Jones and Rienks 1987). For *A. monuste*, the first strategy seems to be adopted. This species was reported in Cordoba (Argentina) flying towards wet areas with higher food supply (Poffo et al. 2018). Another strategy is the retreat to moist refugia (Bonebrake et al. 2010) because microclimate has a decisive role in structuring the community of butterflies (Checa et al. 2014). Thereby, we hypothesise that during dry periods *A. monuste orseis* move into moist habitats (e.g., fragments of native vegetation), and when conditions become favourable, they return to *Brassica* crops (continuous breeding and opportunistic migrations strategy). To support our hypothesis, the species can be found in wet habitats (forests and conservation parks in urban areas) (Thiele et al. 2014; Melo et al. 2019) during dry seasons, while its occurrence on *Brassica* crops appears to be restricted to wet and warm seasons (Santana et al. 2017).

Our field data and the fitted GIw provided evidence for this hypothesis. In area 1 (Southeast), the subspecies did not occur during the coldest and driest months (i.e., June and July), as predicted by the seasonal model. In area 2 (Northeast), GIw indicated November and December as less favourable for species presence. For both fields, the fitted GIw were supported by field data. These results indicate that dry and cold conditions are limiting for *A. monuste orseis* occurrence on *Brassica* crops. Differences on the pest seasonality among fields might be related to climate of the regions and indicate that, within tropical areas, temporal dynamics of species differ for populations spaced apart geographically (Sutcliffe et al. 1996). However, caution is needed when interpreting these results since our evaluations were not performed in the same year for the different areas and a long time series data is necessary to confirm it (e.g., 30 years, Walter et al. 2019).

Nonetheless, climate conditions are not the only factor determining the subspecies occurrence, since the GIw indicated suitable conditions in some months, but *A. monuste orseis* was not found. A further explanation is the role of natural enemies on species populations. Ants and wasps cause high immature mortality rates in a short period of time, especially when pest density is high (Santana et al. 2017). Thus, it is possible that these natural enemies suppressed *A. monuste orseis* populations during the sampling intervals, and we were not able to observe the subspecies occurrence. In addition, we noted the presence of other *Brassica* fields in the study region, which could also be a resource to *A. monuste orseis* (Ramos et al. 2019).

We have provided information of *A. monuste orseis* occurrence on *Brassica* crops based on laboratory experiment and climate models validated by field-collected data, for year-round presence and seasonal suitability. Thus, we confirmed that this species could occur during wet and warm seasons because cold and dry conditions compromise the insect performance. Based on that, we have some recommendations to improve *A. monuste orseis* control. As *Brassica* crops are usually cultivated year-round in South America (Santos et al. 2019; Farias et al. 2020), we suggest that scouting measures should be enforced during wet and warm conditions. When possible, we recommend planting during dry and cold conditions since these conditions are adverse for *A. monuste orseis* occurrence on *Brassica* crops.

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Author’s contribution

AAS and MCP conceived the research. AAS, DGC, and RCS conducted the thermal requirements experiments. EGF performed field evaluation in 2008 (Southeast), while AAS and LB performed in 2011 (Northeast). MCP analyzed thermal requirements data and AAS created Climex models. AAS wrote the first manuscript version. AVR and ESF edited and made critical reviews. All authors read and approved the final version of the manuscript.

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Table 1

Parameters fitted in the model of *Ascia monuste orseis* using Climex algorithm (version 4.0).

Index	Parameter	Values	Unit
Temperature	DV0 = lower threshold	15.00	°C
	DV1 = lower optimum threshold	16.37	°C
	DV2 = upper optimum threshold	29.13	°C
	DV3 = upper threshold	34.95	°C
Moisture	SM0 = lower soil moisture threshold	0.10	a
	SM1 = lower optimum soil moisture	0.40	a
	SM2 = upper optimum soil moisture	1.60	a
	SM3 = upper soil moisture threshold	2.00	a
Cold stress	TTCS = temperature threshold	15.00	°C
	THCS = stress accumulation rate	-0.0005	$week^{-1}$
Heat stress	TTHS = temperature threshold	35.00	°C
	THHS = stress accumulation rate	0.0001	$week^{-1}$
Dry stress	SMDS = soil moisture threshold	0.20	a
	HDS = stress accumulation rate	-0.01	$week^{-1}$
Wet stress	SMWS = soil moisture threshold	2.50	a
	HWS = stress accumulation rate	0.015	$week^{-1}$

a: dimensionless indices of soil moisture (0 = over dry; 1 = field capacity).

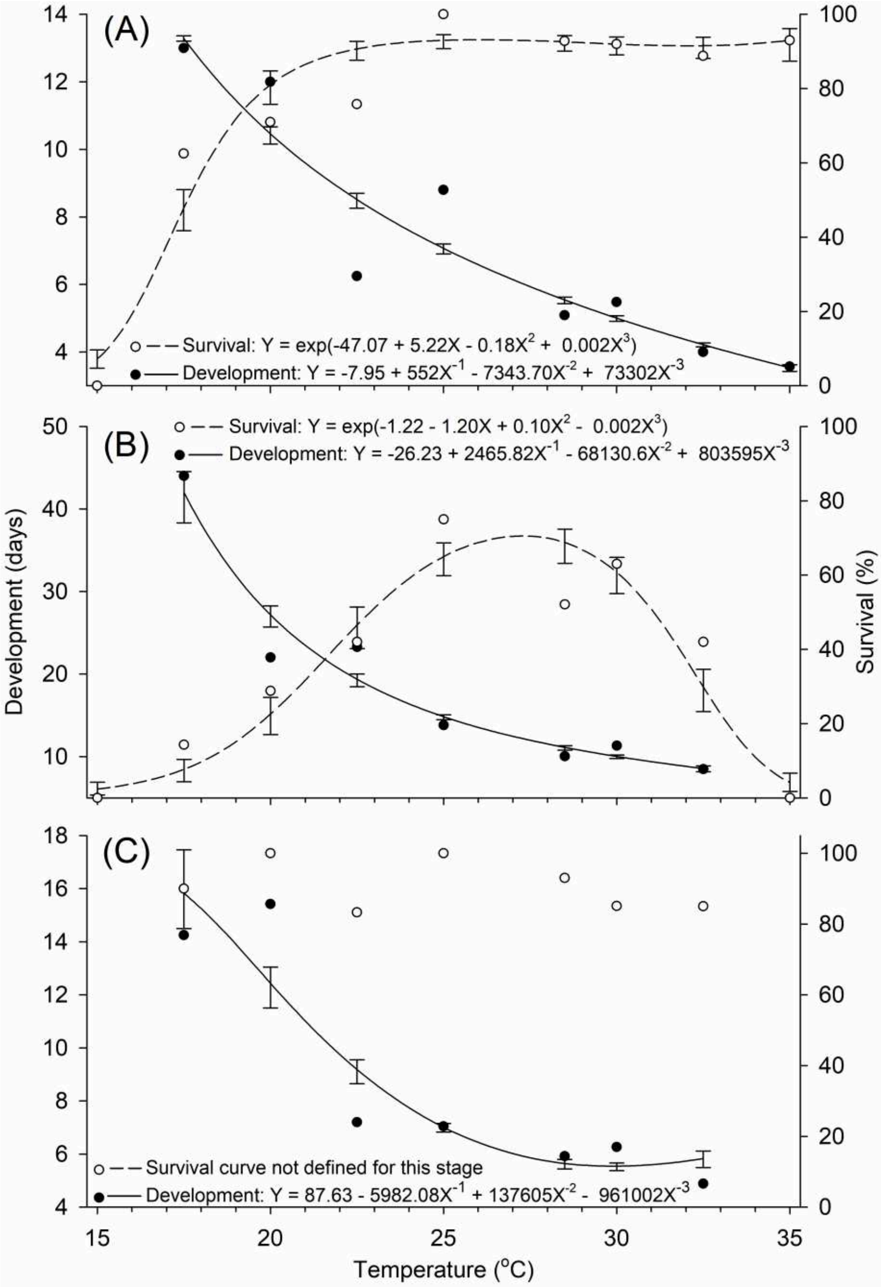

Fig. 1

Duration (in days - A) of the development of egg, larval, and pupal stages of *Ascia monuste orseis* and its survival (B) as a function of temperature (°C). Estimated confidence intervals at 95% of probability are shown for evaluated temperatures. We did not include biological data for 15 °C because egg hatching did not occur at this temperature. Also, at 35 °C, egg hatching was observed but larvae and pupae did not survive. Thus, we only included 35 °C in egg analysis. Pupae survival was higher than 80% for all temperatures.

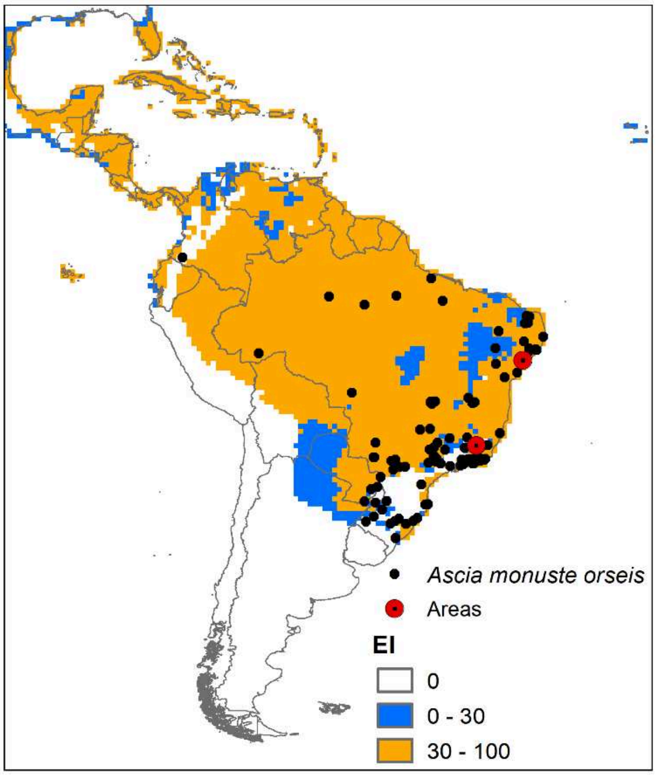

Fig. 2

Occurrence records of *Ascia monuste orseis* (black circles) and the year-round presence model for its current distribution in South America based on Ecoclimatic Index (EI, from 0 to 100). The areas in white are unfavourable for subspecies occurrence (0), while blue and orange colours are less (0-30) and highly favourable (30-100), respectively. Red circles indicate the location of two areas evaluated to validate the seasonal models.

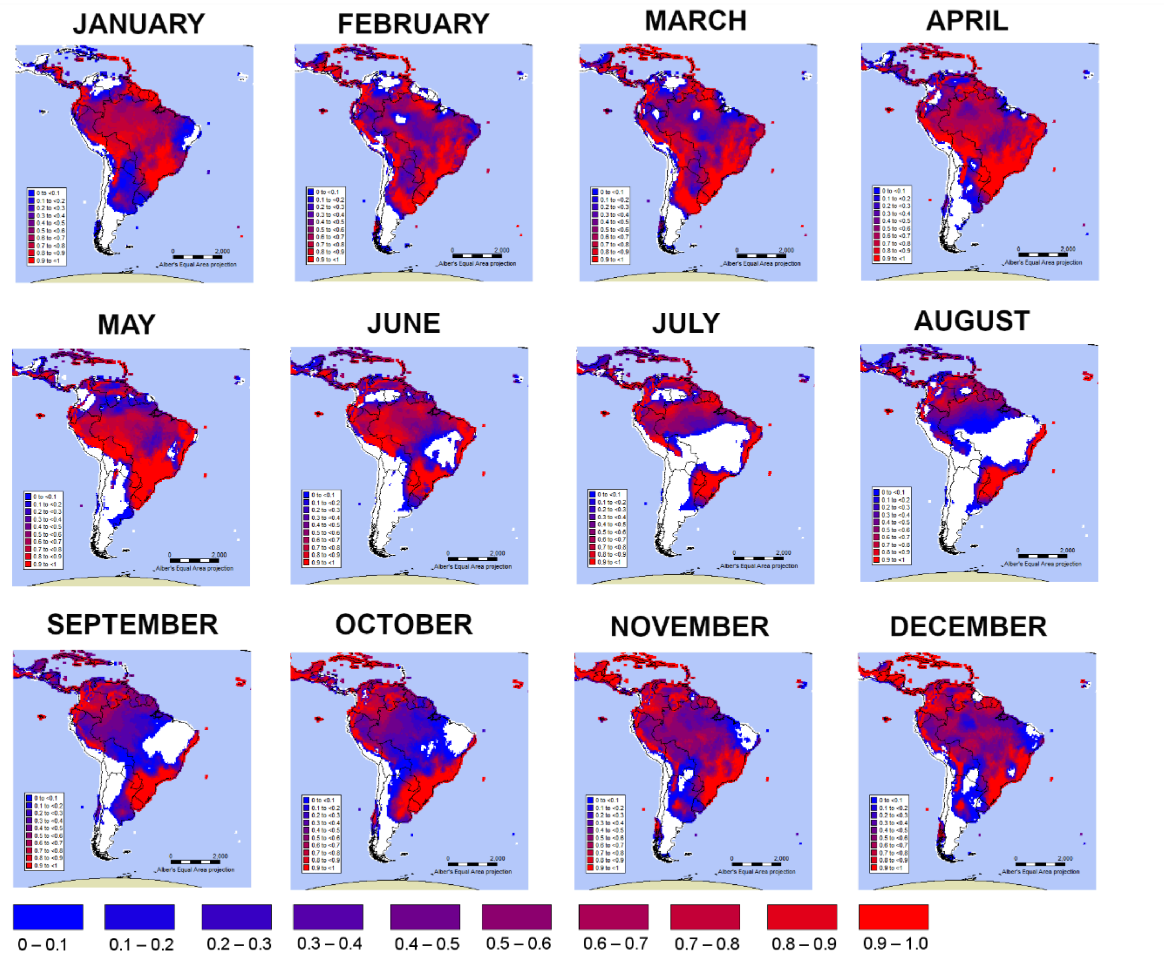

Fig. 3

Weekly Growth Index (GIw; from 0 to 1) by month for *Ascia monuste orseis* in South America for the year 2008. White colour indicates that the GIw equals zero.

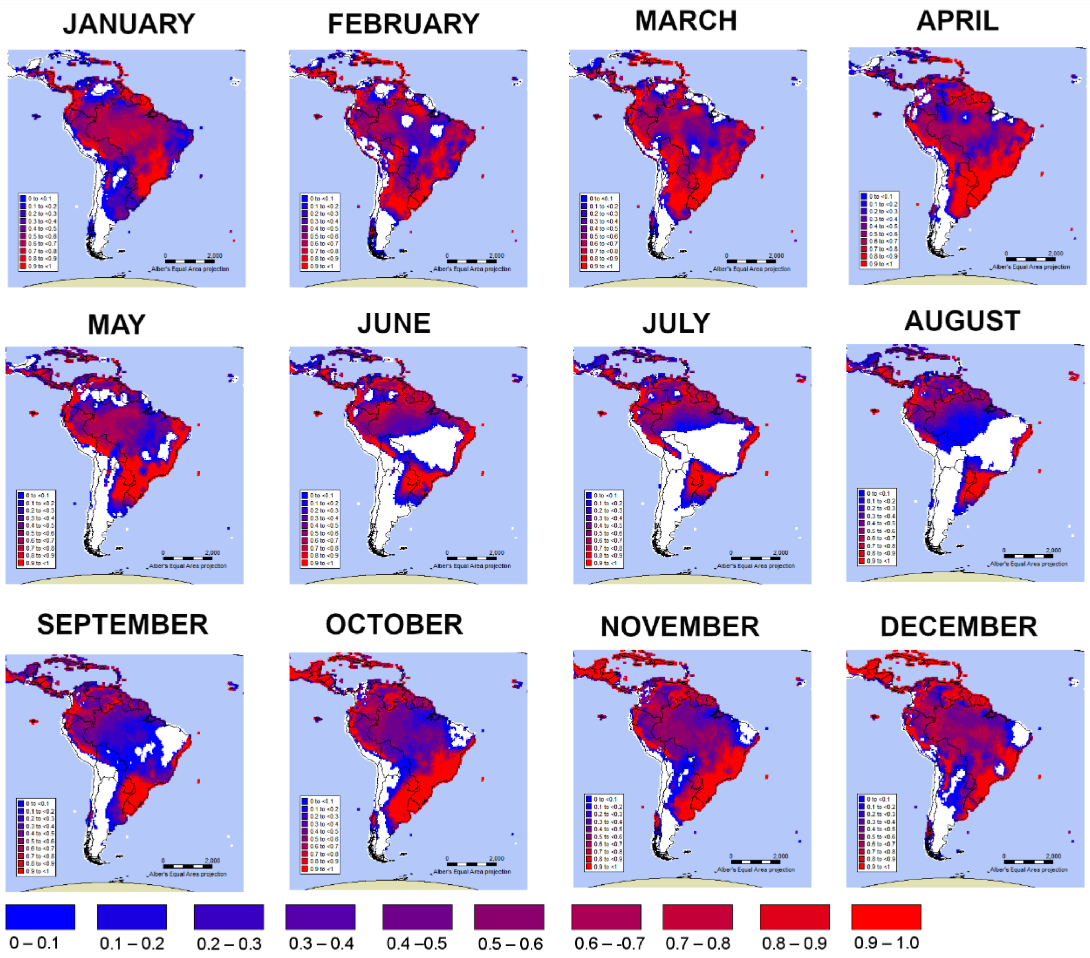

Fig. 4

Weekly Growth Index (GIw; from 0 to 1) by month for *Ascia monuste orseis* in South America for the year 2011. White colour indicates that the GIw equals zero.

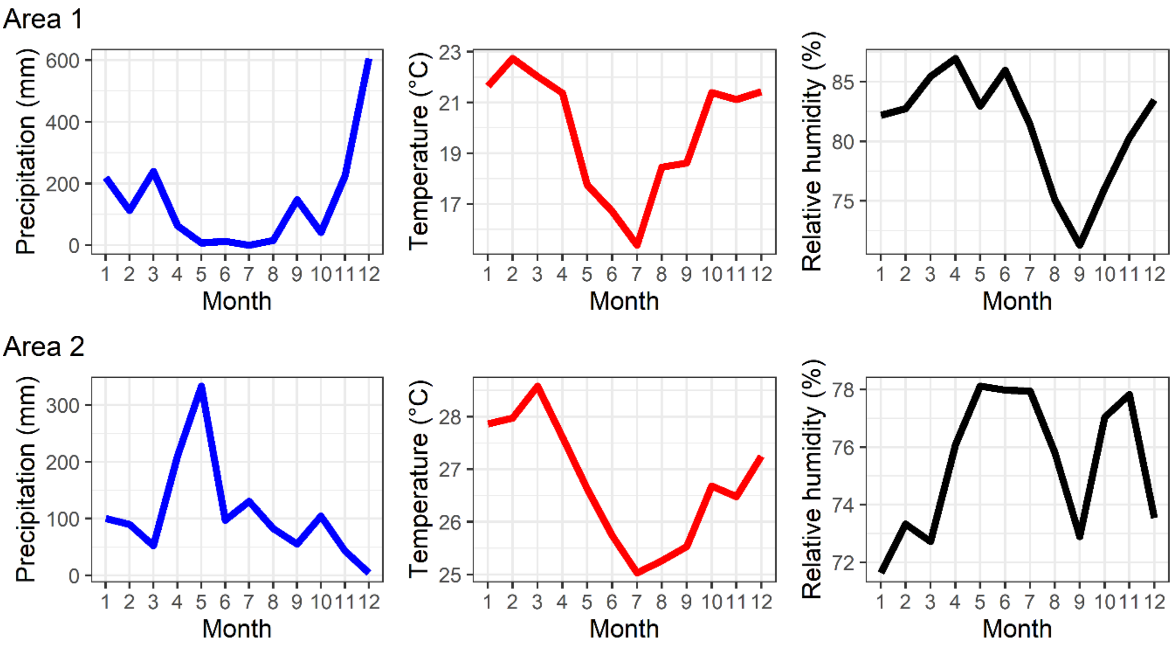

Fig. 5

Monthly cumulative rainfall and average temperature and relative humidity from areas 1 (Viçosa, Minas Gerais State, Southeast region, Brazil, 2008) and 2 (Areia Branca, Sergipe State, Northeast region, Brazil, 2011).

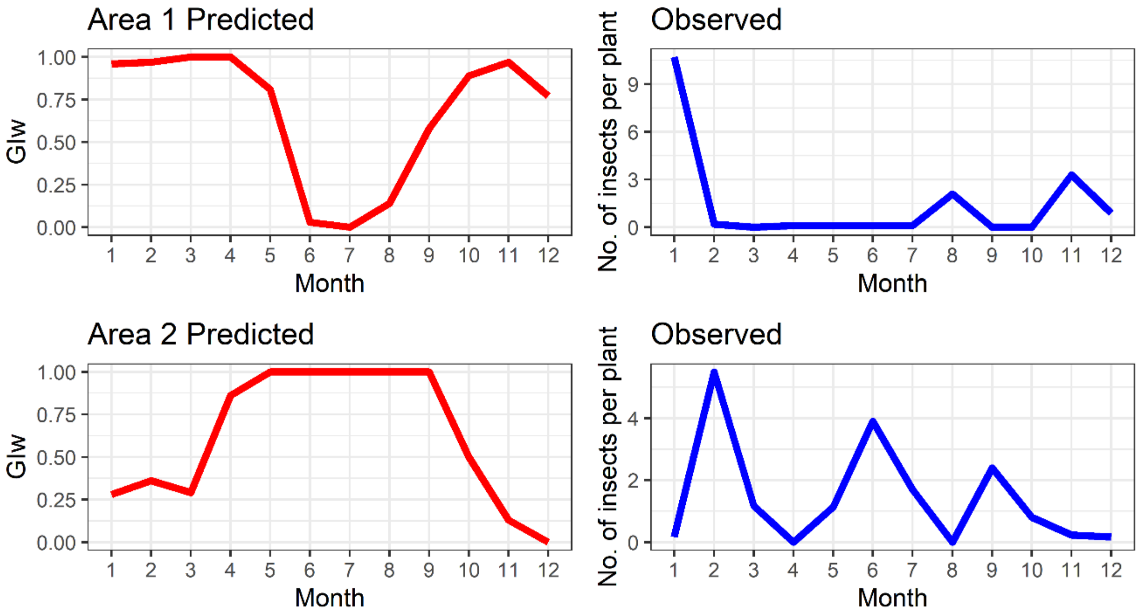

Fig. 6

Predicted Weekly Growth Index (GIw) and observed densities of *Ascia monuste orseis* (eggs and larvae per plant) in areas 1 (Viçosa, Minas Gerais State, Southeast region, Brazil, 2008) and 2 (Areia Branca, Sergipe State, Northeast region, Brazil, 2011). GIw ranges from 0 (no growth) to 1 (high growth).

APPENDIX – CHAPTER 1 SUPPLEMENTARY MATERIAL

Location (State, Country)	Reference
Acre, Brazil	(Paiva and Fazolin 2005)
Alagoas, Brazil	(Broglio-Micheletti et al. 2008; Da Silva et al. 2013)
Amazonas, Brazil	(Cardoso 1999)
Bahia, Brazil	(Zacca et al. 2011; Lima and Zacca 2014; Paluch et al. 2016)
Ceará, Brazil	(Costa et al. 2013)
Distrito Federal, Brazil	(de Castro and Montalvão 2019)
Espírito Santo, Brazil	(Pratissoli et al. 2007; Freitas et al. 2016)
Maranhão, Brazil	(Pereira et al. 2018)
Mato Grosso, Brazil	(Bogiani et al. 2012; Vargas et al. 2018)
Mato Grosso do Sul, Brazil	(Herzog et al. 2005)
Minas Gerais, Brazil	(Picanço et al. 1997; Mata and Lomonaco 2013; Dias et al. 2016; Vicente et al. 2016; Souza et al. 2016; Andrade and Teixeira 2017; Pereira and Cruz 2018; Henriques et al. 2019)
Pará, Brazil	(Costa et al. 1982; Kato and Poltronieri 1984; Monteiro et al. 2016)
Paraná, Brazil	(Pereira et al. 2003; Brandão Filho et al. 2011, 2014; Garcia-Salik et al. 2014; Pizzatto et al. 2016; Pérez et al. 2017)
Pernambuco, Brazil	(Nobre et al. 2008; Carvalho Neto et al. 2017; Melo et al. 2019)
Rio de Janeiro, Brazil	(Monteiro et al. 2009; Soares et al. 2011; Passos et al. 2018)
Rio Grande do Norte, Brazil	(Lima and Haji 1993)
Rio Grande do Sul, Brazil	(Iserhard 2003; Camargo 2006; Giovenardi et al. 2008; Biermann 2009; Molina and Di Mare 2010; Gerhardt et al. 2012; Bellaver et al. 2012; Kogler et al. 2014; Thiele et al. 2014; Hauschild 2016; Signorini et al. 2016; Dorneles et al. 2019)
São Paulo, Brazil	(Lordello and Rodrigues 1952; Mielke and Casagrande 1997; Barros-Bellanda and Zucoloto 2002; Scaglia et al. 2003; Medeiros and Júnior 2005; Bolfarini et al. 2006; Costa et al. 2009; Santana and Zucoloto 2011; Schlick-Souza et al. 2011; Mariscal 2013; Damato et al. 2018)
Santa Catarina, Brazil	(Carneiro et al. 2008)
Missiones, Argentina	(Bustos 2008, 2009)
Nariño, Colombia	(Zethelius 2003)
Naranjal, Paraguai	(Groth et al. 2018)

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7 CHAPTER 2

Season and weather affect the mortality of immature stages of *Ascia monuste orseis* (Lepidoptera: Pieridae) caused by natural factors

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ABSTRACT

In this study, we evaluated the causes of mortality in immature stages of *Ascia monuste orseis* Godart (Lepidoptera: Pieridae) over each of four seasons, for two years, on an experimental cabbage plot using life tables. We addressed two key questions: i) Do the mortality rates caused by a factor vary by season? ii) How does the local weather contribute to such variation? We identified five causes of mortality (failure, pathogens, parasitism, predation, and rainfall) that together tended to be higher during wet-warm conditions with values up to 94%. However, each cause and its mortality rate varied among seasons. Failure was observed in all stages and tended to increase during cold conditions with a negative relationship with air temperature and relative humidity, and positive for precipitation. Larva and pupa predation increased during warm conditions and was positively associated with both air temperature and relative humidity. Conversely, in seasons with intense precipitation, pupa predation was reduced and had a negative relationship. Rainfall caused mortality of eggs and larvae, mostly during intense events, and egg mortality also showed a positive and significant association with precipitation. Larval parasitism was low, and pathogens were noted in larvae and pupae, but we did not find variation by season for these factors. Our results indicate that mortality caused by failure, predation, and rainfall on immature stages of *A. monuste orseis* can vary among seasons and appear to be related to local weather. These findings improve our comprehension of how local weather affects the immature stages of a neotropical pest and the mortality factors associated therein.

Keywords: Pierinae; Tropical ecology; Life table; Population ecology; *Brassica*.

8 INTRODUCTION

Environmental factors affect many aspects of insect development and ecology including generation time, migration, or mortality (Brown et al., 2004; Peterson et al., 2009). Understanding how species respond to such stimuli is important for appropriate management strategies, whether for conservation or pest management (Farias et al., 2020; Peterson et al., 2009). Yet despite the vast majority of the 250 000 extant Lepidopteran species occurring within tropical latitudes, most of our understanding of their ecology comes from temperate systems, especially agricultural pests from the Pieridae family (e.g., *Pieris* spp.) (Bonebrake et al., 2010; Courtney, 1986). As both pollinators and pests, this dearth of knowledge leaves the role of tropical populations in ecosystem services or disservices particularly vulnerable to change.

Tropical climates are well recognized by variation in precipitation that determines two seasons across the year – dry (autumn and winter) and wet (spring and summer) (Peel et al., 2007). These conditions seem to determine tropical butterfly abundance, distribution, and life cycle (Bonebrake et al., 2010). For instance, in Australian tropical savanna, dry seasons reduce species abundance through adverse effects on immature stages and their host plants (Jones and Rienks 1987; Braby 1995). Migration to moist refugia can be observed during these conditions to overcome negative effects on larvae such as desiccation and failure (Jones and Rienks, 1987; Poffo et al., 2018). But these effects can also extend to the factors that influence population size in the field (Sutcliffe et al., 1996).

Predators are one of the main natural enemies of lepidopteran larvae in neotropical areas and they can be affected by dry-wet seasons (Santana et al., 2017; Santos et al., 2018). Wasps reduce foraging activity under decreased temperatures and also intense precipitation (Kasper et al., 2008). During dry-warm conditions, ant species occurrence increases (Ennis and Philpott 2019) but seems to reduce in cold conditions (Rosado et al., 2013). Thus, there is a dynamic process in the neotropical climate where alterations on dry-wet conditions affect not only butterfly ecology, but also natural factors of mortality.

Ascia monuste orseis Godart (Lepidoptera: Pieridae) is a neotropical butterfly from South America where variation in temperature is a deterministic factor for its distribution and occurrence (Santana et al., 2017; Santos et al., 2019). The species is considered an important pest of *Brassica* crops in the neotropics, responsible for losses up to 100% (Alam, 1992). This species responds positively to wet-warm seasons and in dry-cold conditions it seems to contract to moist refugia (Santos et al., 2020, unpublished data). Females lay eggs in clusters (from 5 to 144 eggs) on the abaxial surface of leaves, and when they hatch, the larvae feed on plants during this entire stage (Santana et al., 2017; Santana and Zucoloto, 2016). Pupae can be found on soil and also on branches and the abaxial surface of leaves (AAS, personal observation). Predators, particularly ants and wasps, seem to influence immature populations of *A. monuste orseis* in the field during warm conditions (Picanço et al., 2010; Santana et al., 2017). However, it is unclear how variations on climate conditions can affect immature stages and their mortality since previous studies only measured changes over a single season.

Ecological life tables gather information about the natural history of a species, such as mortality factors according to life stage (Bellows et al., 1992). While such information is mostly used to determine key mortality factors, it can also provide insight into the causes of mortality and weather variables (Bellows et al., 1992; Peterson et al., 2009). To gain this insight, we constructed 70 life tables under field conditions over two years to evaluate the natural mortality factors of immature stages of *A. monuste orseis*. We addressed two key questions: i) Do the mortality rates caused by a factor vary by season? ii) How does the local climate contribute to such variation?

9 MATERIALS AND METHODS

9.1. STUDY AREA

The study was conducted in an experimental area within ~100 m of native vegetation fragments comprising seasonal semi-deciduous forest at the Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais state, Brazil (20°46'12.6"S, 42°52'07.4"W). The climate corresponds to the Cwb Köppen-Geiger class (dry autumn/winter and wet summer/spring) (Peel et al., 2007). We obtained hourly data on air temperature, precipitation, and relative humidity from an automated weather station located 400 m from the experimental area.

9.2. COHORT ESTABLISHMENT

Initially, we established a rearing of *A. monuste orseis* in a greenhouse (March 2016). Eggs and larva were collected in organic *Brassica* crops (cabbage, cauliflower, broccoli, and kale) located in Coimbra, Minas Gerais state, Brazil. We reared larvae with kale leaves and adults received a mixture of honey and water (1:3). Cabbage plants were used for adult oviposition. We restocked the colony twice per year with immature stages of *A. monuste orseis* from organic *Brassica* crops to preserve genetic diversity.

9.3. LIFE TABLES

We constructed life tables in each of the four seasons over two years (n = 8 seasons): autumn (April-May 2017/2018), spring (October-November 2016/2017), summer (January 2017/February 2018), and winter (June-July 2017/ July-August 2018). Autumn and winter corresponded to the dry seasons, while spring and summer the wet ones. In each season, we established a cabbage plot (cv. Astro Plus) containing four rows of 10 plants each, spaced 1 x 0.5 m (n = 40 plants/plot). Seeds were sown to seedling starter trays in a greenhouse and seedlings were transplanted to the field 30 days after sowing. We grew the plants following the general recommendations for cabbage cultivation (Filgueira, 2008), without the use of pesticides and watering the plants twice a day.

In each season, the experiment was carried out in 10 plants of cabbage randomly distributed among the rows in the plot. We cultivated plants of cabbage (cv. Astro Plus) in 5-liter plastic pots, in a greenhouse, following the same procedures described above (Filgueira, 2008). Seedlings were transferred to the pots at the same time the plot was established. When the potted plants had 7-10 leaves, we left them in the colony greenhouse for two hours for adult oviposition. Then, we transferred the potted cabbage plants containing the eggs to the field (i.e., plot) and started the evaluations. We buried the pots in the ground, so all the plants were in the same soil level to allow the access of crawling insects. One leaf per plant containing an egg cluster (see average and standard deviation values in table 1 – lx) was used to evaluate the cohort mortality.

A total of 10 life tables (i.e., 10 plants) were conducted per plot (i.e., season). However, due to difficulties in the rearing, we had only five life tables in spring and winter of 2018. Therefore, 70 life tables were conducted in total (autumn = 20, spring = 15, summer = 20, and winter = 15).

9.4. DETERMINATION OF MORTALITY FACTORS

The causes of mortality were monitored during the development of the immature stages up to adult emergence. The continuous observation was made twice a day (08:00 – 10:00 am and 03:00 – 05:00 pm) based on natural enemy activity (Santana et al., 2017). Two observers made continuous observations, and the number of insects was recorded before and after observations. We categorized the mortality factors as failure, parasitism, predation, pathogens, and rainfall. However, when we were not able to detect a cause of mortality, it was noted as "unknown".

Failure was defined for each development stage according to the following criteria. Egg and pupa failure were noted when eggs did not hatch and adults did not emerge, respectively. For the larvae, the incomplete molting was used as a cue of failure. Finally, we also included adults with abnormal development (e.g., deformed wings) in this category.

Parasitoids adults attack initial instars (1st to 3rd). However, mortality caused by parasitism can be observed in the 5th instar, when the pupa of the parasitoid is external to the larva’s body (Santana et al., 2017). Thus, although we found parasitoids attacking initial instars of *A. monuste orseis*, we only considered it as a factor of mortality when the larva of *A. monuste orseis* presented the pupa of these organisms.

Predation was noted directly by continuous observations. For instance, the main species of predatory ants attacking *A. monuste orseis* in our study showed a group-predation behavior, removing individual larva and pupa from the plant and taking them to their nest (Santana et al., 2017). However, wasps, another major group of predatory insects, did not attack as a group. Instead, individual wasps attacked and cut larva and pupa into small pieces before carrying them to their nest, with recurrent flights from the plant to the nest (Santana et al., 2017). Predation of *A. monuste orseis* eggs rarely occurs (Catta-Preta and Zucoloto, 2003) and, in our study, it happened once during autumn 2018. Ants, parasitoids, and wasps were collected, assembled, and identified at the UFV Integrated Pest Management Laboratory. Ants were identified by Professor Jacques Hubert Charles Delabie (Universidade Estadual de Santa Cruz, Ilhéus, Bahia state, Brazil) and Júlio Cézar Mário Chaul (Departamento de Entomologia, UFV). Wasps were identified based on Jacques et al., (2012).

Mortality due to pathogens was evaluated by counting larvae and pupae with red/black color as a cue of bacteria and viruses infection. Mortality caused by rainfall was determined by performing evaluations immediately after the occurrence of precipitation. We noted that rain knocked eggs from the plants and impaired the clusters. An indirect effect was also detected following intense precipitation, where eggs on the abaxial surface of the leaves get covered in mud and desiccate as the mud dries. For larvae, an indirect effect also occurred but, in this case, the larvae did not feed on leaves covered with mud. In these cases, we considered rainfall as the cause of mortality.

9.5 LIFE TABLE ANALYSIS

We constructed multiple decrement life tables for the immature stages of A. monuste orseis using the techniques of Carey (1993) and Peterson et al., (2009) incorporated into the M-DEC spreadsheet program (Davis et al., 2011). In M-DEC, the variables are defined as: x-the life stage index, lx-the number of individuals entering the stage, dx-the number of individuals dying in a stage, alx-the fraction of the cohort living at the beginning of the stage, adix-fraction of the original cohort dying in stage x due to cause i, adx-fractions of deaths in stage x from all causes, and aqx-the probability of dying in stage x in the presence of all causes (Davis et al., 2011).

9.6. STATISTICAL ANALYSIS

All analyses were performed in R version 3.5.1 (R Core Team, 2018). First, we tested the effect of seasons (explanatory variable, x-axis) on: (i) the duration of the life tables, (ii) total mortality, and (iii) mortality of the immature stages of *A. monuste orseis* caused by natural factors (dependent variables, y-axes). Model (i) (count data that are not proportions) was analyzed under poisson error distribution (link function = log). Models (ii) and (iii) (count data expressed as proportions) were analyzed under binomial error distribution (link function = logit) (Crawley, 2013).

We ran these models using generalized linear mixed models (GLMM) (function 'glmer', package lme4, Bates et al., 2015) to account for the random variation of plots and autocorrelation of plants (Bolker et al., 2009). Thus, we included plant nested within plots as a random effect (1|plot/plant). We also added the number of individuals (lx in table 1) as weights in models (ii) and (iii) because we used proportions as dependent variables. We checked all models with diagnostic plots of scaled residuals plotted against fitted values, as well as goodness-of-fit tests on the scaled residuals to check uniformity, overdispersion, and zero-inflation using the package DHARMa (Hartig, 2018). When seasons had a significant effect, means were compared by multiple pairwise comparisons using least-square means at $\alpha = 0.05$ (function 'emmeans', package emmeans, Lenth, 2020).

Finally, when we found a significant effect of seasons on the mortality caused by a factor within a stage (models iii), we also investigated how this mortality (y-axis) was affected by air temperature, precipitation, and relative humidity (x-axes). In this case, we used the average values of each weather variable during the developmental stage of *A. monuste orseis* in the models. We also ran these models using generalized linear mixed models (GLMM) (function 'glmer', package lme4, Bates et al. 2015) including plant nested within plot as a random effect (1|plot/plant) and added the number of individuals as weights for the reasons previously mentioned (Bolker et al. 2009). All models were checked as described above using the package DHARMa (Hartig 2018). We designed graphics for significant effects using the package ggplot2 (Wickham 2016) and climate variables were plotted using Sigma Plot software version 11.

10 RESULTS

10.1. IMMATURE DEVELOPMENT

The number of days necessary for immature development (from egg to adult emergence) varied among seasons ($\chi2 = 88.64$; df = 3; $P < 0.0001$), with a faster development in summer (average ± SD, 23.85 ± 3.91 days) compared to autumn

(38.65 ± 4.70 days), spring (37.40 ± 5.26 days), and winter (42.37 ± 2.19 days) (Fig. 1).

10.2. NATURAL MORTALITY FACTORS OF *A. MONUSTE ORSEIS*

The total mortality caused by natural factors varied among seasons ($\chi2$ = 24.29; df = 3; $P < 0.001$) with higher values during summer (average ± SD, 94.18 ± 3.15%) and lowest in winter (89.22 ± 9.45%) (Fig. 2).

During egg development, we identified failure and rainfall as the main causes of mortality (Table 1, Fig. S1 supplementary material). Predation by *Geocoris* sp. only occurred in one life table during autumn 2018. In addition to failure and rainfall, parasitism (*Cotesia* sp.), pathogens, and predation (ants and wasps) were observed during larva development (Table 1, Fig. S2 supplementary material). Also, this stage had the highest probability of death in all seasons. For pupa, we observed failure, pathogens, and predation (ants and wasps) (Table 1, Fig. S3 supplementary material).

The ant species predating *A. monuste orseis* were *Ectatomma edentatum* Roger, *Camponotus* sp., *Pheidole* sp., *Pseudomyrmex termitarius* Smith, *Solenopsis saevissima* Smith, and *Tetramorium simillimum* Smith. Wasps were identified as *Mischocyttarus* sp., *Polistes* sp., *Polybia bifasciata* Saussure, *Polybia ignobilis* Haliday, *Polybia paulista* Ihering, and *Polybia* sp.

10.3. MORTALITY, STAGES, AND SEASONS

The mortality of immature stages of *A. monuste orseis* caused by failure, pathogens and predation varied along seasons (Table 1). Death by rainfall appears to be associated with spring and summer. For parasitism, no tendency was observed as it only happened during autumn and summer 2018 in two and one life tables, respectively (Table 1). Therefore, models for this factor were not possible to perform. Our analysis indicated that the mortality of *A. monuste orseis* was related to the seasons and developmental stage of this insect.

Eggs failure was lower during summer and higher in winter ($\chi2$ = 232.81, df = 3, $P < 0.0001$; Fig. 3), while the rates of mortality by rainfall was higher only in spring ($\chi2$ = 592.67, df = 3, $P < 0.0001$; Fig. 3).

Larvae failure had higher values during winter and lowest in summer ($\chi2$ = 157.66, df = 3, P < 0.0001; Fig. 4). Conversely, an inverse relationship was found for predation, increasing during summer, and reducing in winter ($\chi2$ = 253.06, df = 3, P < 0.001; Fig. 4). We did not find a relationship between the mortality caused by pathogens ($\chi2$ = 2.55, df = 3, P = 0.46) and rainfall ($\chi2$ = 1.10, df = 3, P = 0.32) with seasons.

For pupae, failure increased during winter ($\chi2$ = 10.58, df = 3, P = 0.01; Fig. 5) and there was no effect due to pathogens ($\chi2$ = 1.07, df= 3, P = 0.78). However, predation rates increased during summer ($\chi2$ = 24.80, df = 3, P < 0.0001; Fig. 5).

10.4. CONTRIBUTION OF CLIMATE

In the previous section, we found that season affected the rates of mortality caused by failure, predation, and rainfall on immature stages of *A. monuste orseis*. Thus, we further investigated how these variations were associated with weather variables.

We verified that weather conditions varied during the development of the immature stages of *A. monuste orseis* (Fig. 6). For instance, the air temperature ranged from 15 to 25 °C during egg and pupal stages, and from 11 to 26 °C for larvae (Fig. 6). Precipitation was higher during the pupal stage with values up to 40 mm, while a precipitation less than 25 mm was registered for eggs and larvae (Fig. 6). Finally, relative humidity varied more during pupa development (40-90 %) than egg (60-90 %) and larva (55-95 %; Fig. 6). Our models indicated that these variations contributed to the mortality rates observed (Table 2).

The mortality caused by egg failure was negatively associated by air temperature and relative humidity, and positively by precipitation. For rainfall, in this stage, precipitation was positively related, but relative humidity had a negative effect (Table 2).

For larva mortality factors, failure rates were negatively associated with both air temperature and relative humidity, and positively with precipitation. All weather variables had a significant and positive association with predation (Table 2).

For pupa mortality, all weather variables showed significant associations with the observed rates (Table 2). Air temperature and relative humidity were negatively correlated with failure, but the opposite effect was detected for precipitation.

Conversely, precipitation had a negative relation on predation, while temperature and relative humidity corroborated that.

11 DISCUSSION

The results of our study suggest that the duration of *A. monuste orseis* life cycle and the total mortality caused by natural factors vary among seasons. The mortality caused by failure, predation, and rainfall varied by season and was related with air temperature, precipitation, and relative humidity in a weather-stage dependent relationship. These findings improve our comprehension of how local weather affects the immature stages of a neotropical pest and the mortality factors associated therein.

Tropical climates are known by small variations around temperature but defined by rainy seasons. The dynamic of populations could then be expected to respond to changes in precipitation rather than the temperature. However, in our study, variations on immature development may be more associated with the latter. For instance, immature development took 42 days in winter, while in summer it was only 25 days. The minimum temperature required for *A. monuste orseis* is estimated to be 16.35 °C, and below 15 °C eggs do not hatch (Santos et al., 2020, unpublished data). We noted during our experiments that the temperature tended to vary below 15 °C in autumn, spring, and most of winter. These cold conditions would have caused stress on *A. monuste orseis*, reducing their rate of metabolism and leading a longer time to development or, in some cases, its mortality (Brown et al., 2004).

The probability of death was consistently higher during *A. monuste orseis* larval development. In part this could be explained by the time required to complete development and how this increases the probability of mortality (Bellows et al., 1992). However, other traits also play a role in that aspect. Female adults of *A. monuste orseis* appear to use the abaxial leaf surface as an oviposition site to avoid predators (Catta-Preta and Zucoloto, 2003) and they oviposit eggs in clusters as a strategy to improve hatch rates (Santana and Zucoloto, 2016). It results in a group of larvae feeding on leaves, which increases the mortality risk for the group as a whole, especially by natural enemies as plant volatiles can be a cue for predators and parasitoids, although the per capita risk is lower (Santana et al., 2017). Pupae also seem susceptible to the effects of natural factors (e.g., predation) as they are only resting until the adult stage, but their thick cuticle may reduce mortality caused by abiotic factors (DeVries, 1987; Lindstedt et al., 2019). Thus, these aspects help explain our results regarding the causes of mortality observed and their relationship with climate factors.

Failure occurs in all stages and appears negatively associated with temperature and relative humidity. As stated previously, eggs of *A. monuste orseis* do not hatch under a continuous temperature of 15 °C, and dry conditions reduce suitable areas for species occurrence (Santos et al., 2020, unpublished data). Variation in temperature, mostly below this threshold, coupled with low relative humidity, may have affected species contributing to failure rates in all stages (Jones and Rienks, 1987). We must also mention the effect of allelochemicals from host plant on larva failure, as glucosinolates presented on *Brassica* plants reduces their survival (Schlick-Souza et al., 2011). However, it is difficult to detect such an effect in the field. For pupa and larva failure, we found an exception to precipitation that appeared positively associated with the mortality rates, which indicates that precipitation may cause mechanical damage to these stages. This is intriguing especially for the pupal stage because of the extra physical protection conferred by its exoskeleton (Lindstedt et al. 2019). Therefore, further investigation on the mechanical impacts of rainfall on pupae is required.

Larva predation appears to be positively affected by all-weather factors. It indicates that predation tended to be higher during wet-warm conditions. High predation levels by ants are observed during warm weather (Ennis & Philpott 2019; Weseloh 1988), as cold conditions reduce foraging (Rosado et al., 2013). Also, wasps generally increase foraging activity during these seasons (Kasper et al. 2008; Santana et al. 2017). Similar to larva, pupa predation also had a positive effect from air temperature and relative humidity, but we noted a negative effect from precipitation. It is important to note that precipitation levels were higher during pupal development compared to the larval phase. Thus, we suggest that the intensity of precipitation might have determined predators activity in our study. This effect on ant and wasp activity is noted in other systems and in both cases, it reduces or stops their foraging (Wirth & Leal 2001; Kasper et al., 2008).

Rainfall seems to cause significant mortality on eggs only during intense precipitation. Though female choice seems to be useful to avoid predation, it may expose eggs to rainfall effects. Such an effect was already indicated under controlled conditions (Rahman et al., 2019), and we confirmed it in the field. In addition, the larva was indirectly affected by rainfall, since sand covers basal leaves after intense rain and may cause wear on larva mandibles (Lopresti et al., 2018). Conversely, since the larva is a mobile stage, they probably moved to clean leaves to overcome it.

Pathogens and parasitoids were not found to be related to climate and presented low rates of mortality. Two possible reasons could explain this. First, in natural environments, the rates of infection and parasitism are higher compared to agricultural areas which are mostly in simplified landscapes (Bianchi et al., 2006). Although our experimental area was close to forest vegetation, it only had cabbage as host, and this may not have been enough to maintain these organisms. Second, both processes require time to occur, with mortality observed afterward. For instance, parasitoids seek initial instars to oviposit (1st-3rd) (Santana et al. 2017), while pathogens (among other factors) depend on the amount of food intake by the larva to result in an infection, which mostly occurs on 4-5th instar (Barros-Bellanda & Zucoloto 2002). In that time lag, predators likely catch a prey already ‘killed’ (i.e., in the process of death) by these factors, as ants and wasps tended to attack later instars of *A. monuste orseis* larva (Santana et al. 2017).

Our findings show that the mortality caused by failure, predation, and rainfall on immature stages of *A. monuste orseis* varied by season. Air temperature, precipitation, and relative humidity seem to be related to this variation; however, it depends on how these weather variables change during each immature stage development. Our results highlight the importance of local weather studies to understand the natural history of neotropical species.

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Table 1 Multiple decrement life tables (probability of dying from a factor in the presence of other causes) for immature stages of *Ascia monuste orseis* (Lepidoptera: Pieridae). Values represent the average (standard deviation) from 20 (autumn and summer) and 15 (spring and winter) ecological life tables conducted in Viçosa, Minas Gerais state, Brazil (n = 70).

Season/Stage	lx	aqx	alx	adx	Failure	Pathogens	Parasitism	Predation	Rainfall	Unknown
autumn										
Egg	54.45 (17.28)	0.21 (0.15)	1.00 (0.00)	0.21 (0.15)	0.21 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.01)
Larva	42.35 (14.73)	0.74 (0.16)	0.79 (0.15)	0.58 (0.15)	0.20 (0.16)	0.02 (0.04)	0.03 (0.03)	0.29 (0.16)	0.00 (0.02)	0.07 (0.11)
Pupa	9.60 (5.88)	0.27 (0.31)	0.21 (0.14)	0.21 (0.14)	0.02 (0.03)	0.03 (0.05)	0.00 (0.00)	0.02 (0.03)	0.00 (0.00)	0.01 (0.02)
Total				1.00 (0.00)	0.43 (0.19)	0.05 (0.06)	0.03 (0.03)	0.31 (0.17)	0.00 (0.02)	0.08 (0.11)
spring										
Egg	84.73 (13.73)	0.45 (0.16)	1.00 (0.00)	0.45 (0.16)	0.17 (0.12)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.22 (0.14)	0.07 (0.08)
Larva	45.67 (14.59)	0.79 (0.07)	0.55 (0.16)	0.44 (0.14)	0.13 (0.12)	0.02 (0.04)	0.00 (0.00)	0.20 (0.15)	0.01 (0.03)	0.08 (0.10)
Pupa	9.27 (4.38)	0.30 (0.24)	0.11 (0.05)	0.11 (0.05)	0.01 (0.01)	0.02 (0.03)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)
Total				1.00 (0.00)	0.30 (0.17)	0.05 (0.06)	0.00 (0.00)	0.21 (0.15)	0.23 (0.15)	0.14 (0.13)
summer										
Egg	59.95 (15.94)	0.17 (0.13)	1.00 (0.00)	0.17 (0.13)	0.09 (0.12)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06 (0.08)	0.03 (0.07)
Larva	49.30 (10.29)	0.75 (0.15)	0.83 (0.13)	0.62 (0.16)	0.11 (0.10)	0.00 (0.00)	0.00 (0.01)	0.42 (0.20)	0.01 (0.04)	0.07 (0.12)
Pupa	11.85 (6.38)	0.62 (0.23)	0.21 (0.14)	0.21 (0.14)	0.03 (0.07)	0.03 (0.04)	0.00 (0.00)	0.07 (0.08)	0.00 (0.00)	0.01 (0.05)
Total				1.00 (0.00)	0.24 (0.18)	0.03 (0.04)	0.00 (0.01)	0.49 (0.23)	0.07 (0.11)	0.11 (0.14)
winter										
Egg	66.13 (18.92)	0.34 (0.15)	1.00 (0.00)	0.34 (0.15)	0.34 (0.15)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Larva	44.50 (13.18)	0.69 (0.19)	0.66 (0.15)	0.46 (0.18)	0.32 (0.15)	0.01 (0.02)	0.00 (0.00)	0.13 (0.12)	0.00 (0.00)	0.01 (0.02)
Pupa	13.93 (7.75)	0.52 (0.23)	0.21 (0.14)	0.21 (0.14)	0.06 (0.06)	0.01 (0.02)	0.00 (0.00)	0.03 (0.04)	0.00 (0.00)	0.00 (0.00)
Total				1.00 (0.00)	0.71 (0.14)	0.02 (0.03)	0.00 (0.00)	0.16 (0.12)	0.00 (0.00)	0.01 (0.02)

Note: lx – number of individuals alive at the beginning of stage x; aqx—the probability of dying in stage x in the presence of all causes; alx—the fraction of the cohort living at the beginning of the stage; adx—fractions of deaths in stage x from all causes (1: failure, 2: parasitism, 3: pathogens, 4: predators, 5: rainfall, and 6: unknown)

Table 2 Summary of the generalized linear mixed models with binomial distribution (logit link) with the effects of air temperature, precipitation, and relative humidity on the mortality of eggs, larvae, and pupae of *Ascia monuste orseis* caused by natural factors (failure, rainfall and predation).

Stage/Factor	Term	Estimate	SE	z value	*P*
Eggs					
Failure	Intercept	6.03	1.23	4.90	**<0.001**
	Air temperature	-0.22	0.02	-9.23	**<0.001**
	Precipitation	0.004	0.001	2.51	**0.01**
	Relative humidity	-0.03	0.01	-3.44	**<0.001**
Rainfall	Intercept	9.63	1.74	5.53	**<0.001**
	Air temperature	-0.04	0.18	-0.23	0.81
	Precipitation	0.04	0.02	1.99	**0.04**
	Relative humidity	-0.22	0.05	-3.72	**<0.001**
Larvae					
Failure	Intercept	12.61	0.93	13.44	**<0.001**
	Air temperature	-0.27	0.01	-13.77	**<0.001**
	Precipitation	0.01	0.004	3.27	**0.001**
	Relative humidity	-0.10	0.009	-11.08	**<0.001**
Predation	Intercept	-9.26	0.89	-10.3	**<0.001**
	Air temperature	0.17	0.01	8.8	**<0.001**
	Precipitation	0.01	0.003	4.89	**<0.001**
	Relative humidity	0.06	0.009	7.32	**<0.001**
Pupae					
Failure	Intercept	73.70	16.20	4.55	**<0.001**
	Air temperature	-2.37	0.55	-4.31	**<0.001**
	Precipitation	0.17	0.04	4.40	**<0.001**
	Relative humidity	-0.46	0.09	-5.00	**<0.001**
Predation	Intercept	-18.27	2.03	-9.07	**<0.001**
	Air temperature	0.47	0.05	8.86	**<0.001**
	Precipitation	-0.02	0.004	-7.27	**<0.001**
	Relative humidity	0.10	0.01	5.62	**<0.001**

Note significant *P* values are boldfaced.

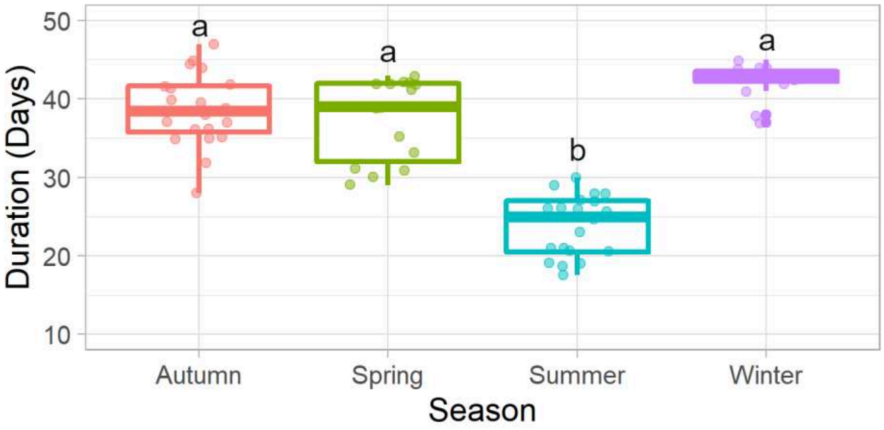

Fig. 1. Duration (in days) of ecological life tables of *Ascia monuste orseis* (Lepidoptera: Pieridae) along the four seasons over two years in Viçosa, Minas Gerais state, Brazil. Similar letters indicate no difference among seasons (*P* < 0.05). Boxplots show median values and interquartile range.

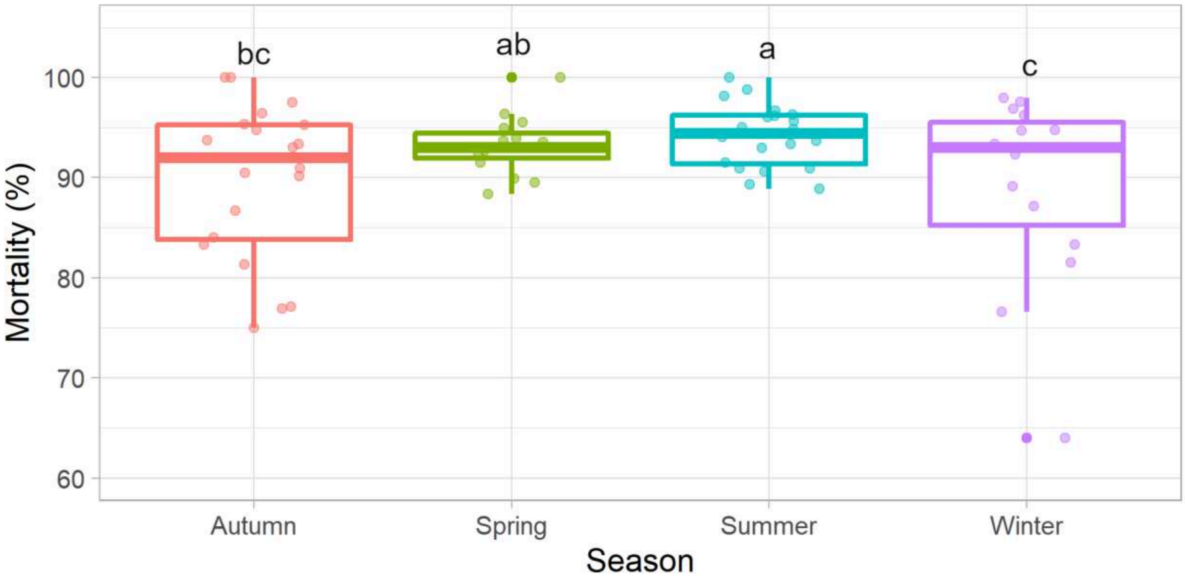

Fig. 2. Total mortality (%) caused by natural factors on immature stages of *Ascia monuste orseis* (Lepidoptera: Pieridae) at different seasons of the year in Viçosa, Minas Gerais state, Brazil. Similar letters indicate no difference among seasons ($P < 0.05$). Boxplots show median values and interquartile range.

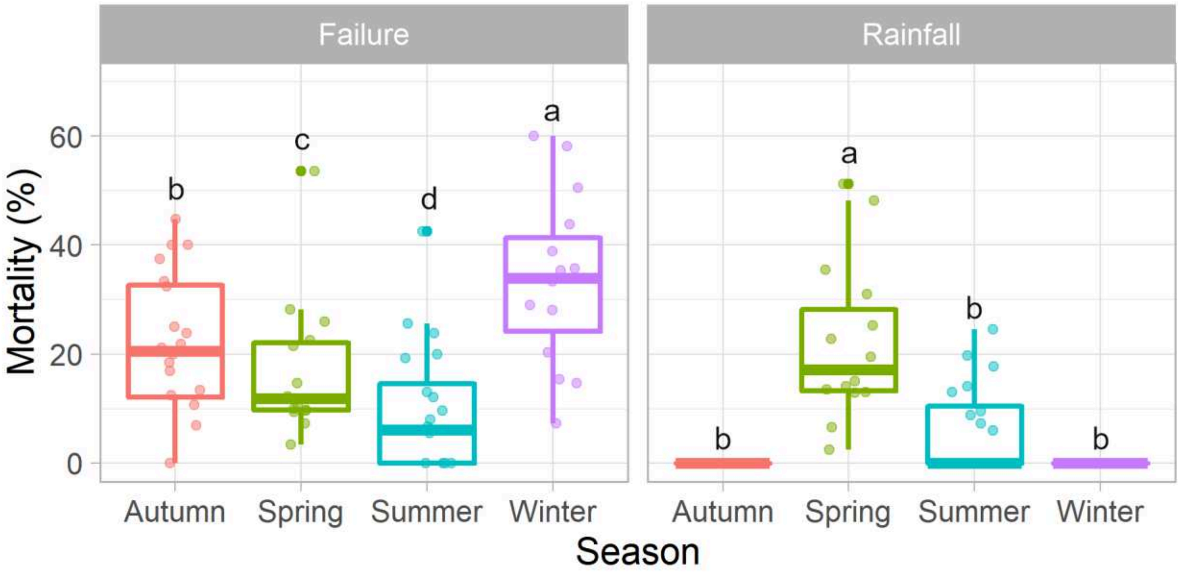

Fig. 3. Mortality (%) caused by failure and rainfall on eggs of *Ascia monuste orseis* (Lepidoptera: Pieridae) at different seasons of the year in Viçosa, Minas Gerais state, Brazil. Similar letters indicate no difference among seasons (*P* < 0.05). Boxplots show median values and interquartile range.

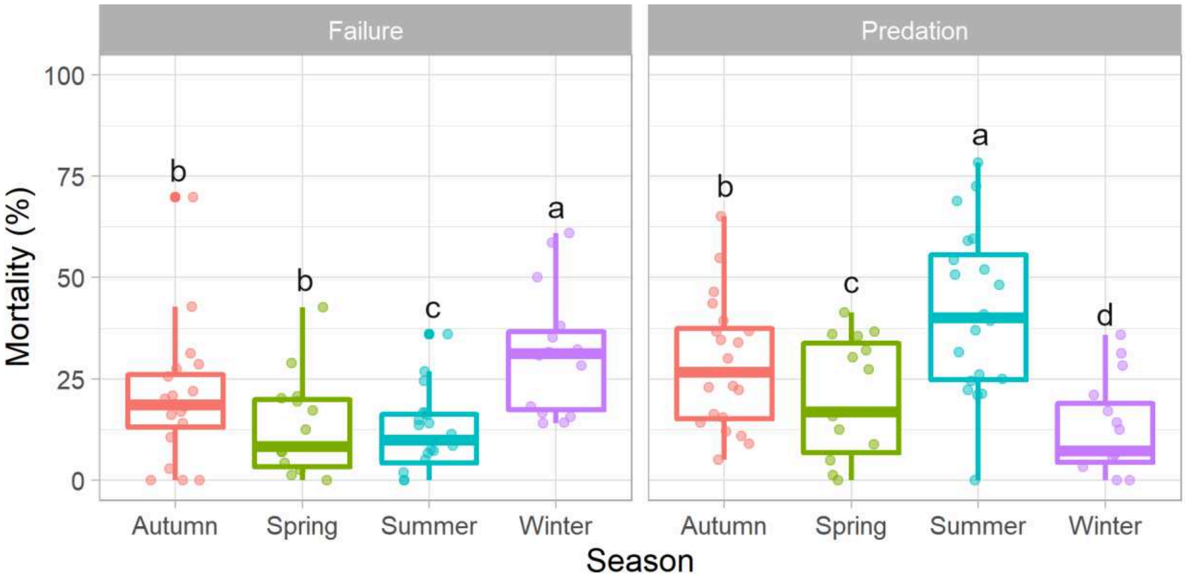

Fig. 4. Mortality (%) caused by failure and predation on larvae of *Ascia monuste orseis* (Lepidoptera: Pieridae) at different seasons of the year in Viçosa, Minas Gerais state, Brazil. Similar letters indicate no difference among seasons ($P < 0.05$). Boxplots show median values and interquartile range.

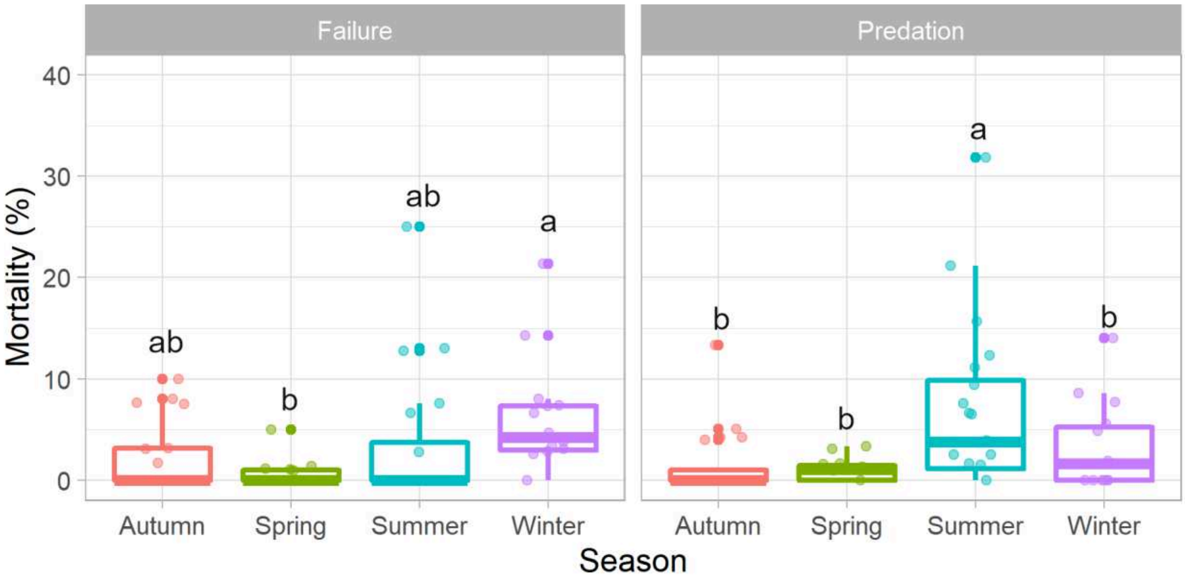

Fig. 5. Mortality (%) caused by failure and predation on pupae of *Ascia monuste orseis* (Lepidoptera: Pieridae) at different seasons of the year in Viçosa, Minas Gerais state, Brazil. Similar letters indicate no difference among seasons ($P < 0.05$). Boxplots show median values and interquartile range.

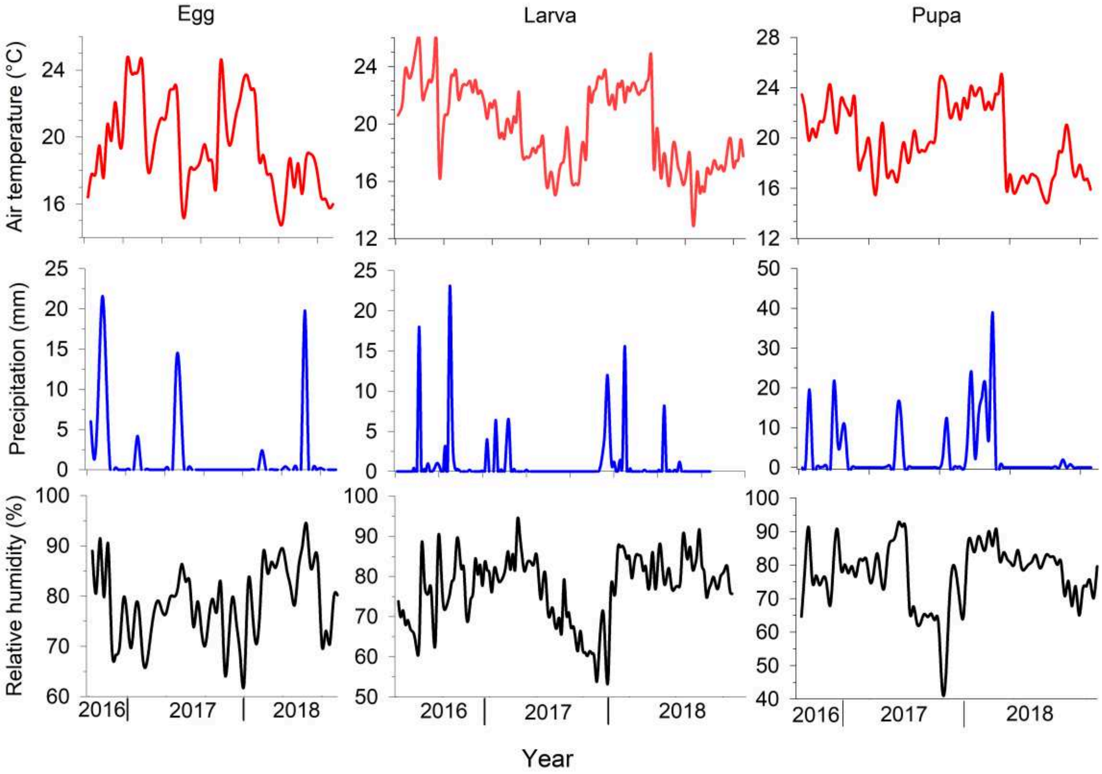

Fig. 5. Average daily air temperature and relative humidity, and daily accumulated precipitation recorded during the ecological life table experiments of *Ascia monuste orseis* in Viçosa, Minas Gerais state, Brazil. Climate variables were obtained from a weather station located 400 m from the experimental area.

APPENDIX – CHAPTER 2 SUPPLEMENTARY MATERIAL

Fig. S1. Natural mortality factors on eggs of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Failure

Rainfall

Fig. S2. Natural mortality factors on larva of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Failure

Fig. S2 (cont.). Natural mortality factors on larva of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Pathogens

Parasitism

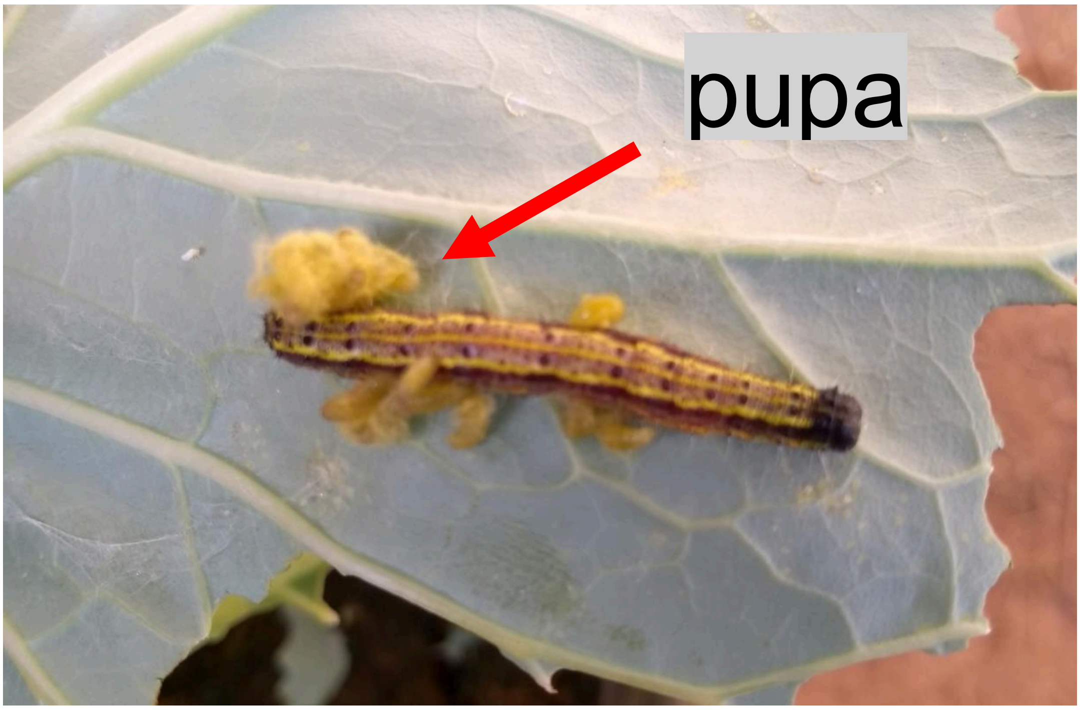

Fig. S2 (cont.). Natural mortality factors on larva of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Predation - Ants

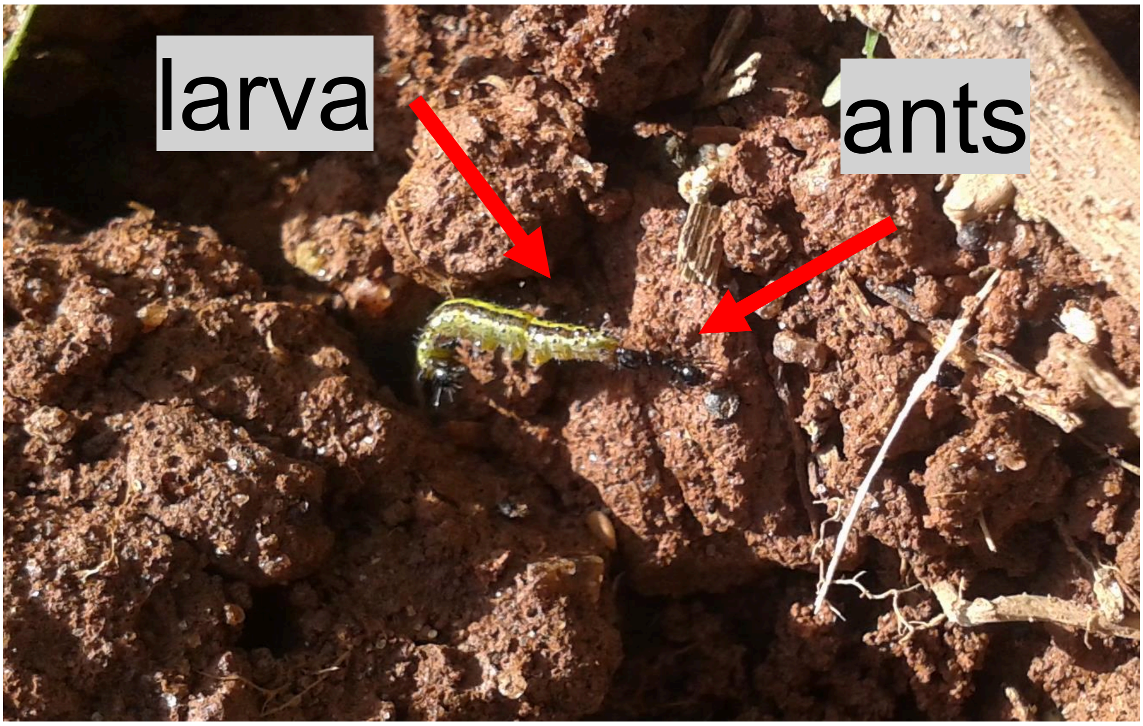

Fig. S2 (cont.). Natural mortality factors on larva of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Predation - Wasps

Fig. S2 (cont.). Natural mortality factors on larva of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Rainfall

Fig. S3. Natural mortality factors on pupa of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Failure

Pathogens

Fig. S3. Natural mortality factors on pupa of *Ascia monuste orseis* (Lepidoptera: Pieridae). Viçosa, Minas Gerais, Brazil.

Predation – Ants

Predation - Wasps

12 CHAPTER 3

Distribution models for *Ascia monuste* and the host *Brassica oleracea* var. *capitata*

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ABSTRACT

The butterfly *Ascia monuste* L. (Lepidoptera: Pieridae) is a specialist pest of brassica crops in neotropical regions where it significantly impacts crop production. Understanding the actual and potential distribution of the pest and its hosts in current and future climates may help government agencies to mitigate and manage potential incursions. Here, we use MaxEnt algorithm to model the current distribution of both *A. monuste* and its host, *Brassica oleracea* var. *capitata* L. (cabbage) and then model the likely impact of projected climate change (RCP 4.5 and 8.5 scenarios) on their potential future distributions. While *A. monuste* is currently restricted to the American continent, we show that under current conditions the potential distribution of both the butterfly and cabbage includes areas of Africa, Asia, Oceania and Europe to some extent. The annual temperature range and mean annual temperature were found to be the strongest predictors associated with the distribution of both species. Under a projected climate change scenario, suitable areas in the tropical climate zone are expected to decrease for both species. However, in temperate regions, the suitable area for cabbage is expected to increase but will remain unsuitable for the pest. Our results highlight the need for strategies to prevent the introduction of *A. monuste* to other areas of the tropical climate zone and for the development of management practices in the neotropical region.

Keywords: biosecurity, climate change, neotropical pest.

13 INTRODUCTION

Ascia monuste L. (Lepidoptera: Pieridae) is an important pest of brassica crops produced in the neotropical region (Barros-Bellanda & Zucoloto, 2005; Liu, 2005). The butterfly is currently distributed across large areas of Central and South America, and a small part of North America (Southern Florida and East coast; Alam, 1992; Barros-Bellanda & Zucoloto, 2005; Liu, 2005; Poffo et al., 2018). This species comprises seven subspecies and several forms share the same hosts, i.e., *Brassica* species (Pease, 1962; Liu, 2005). The larvae of *A. monuste* feed on leaves throughout their entire development phase, causing substantial damage to crops (Liu, 2005; Santana, Zago, & Zucoloto, 2011). The adults can then migrate over long distances in search of oviposition sites (Hayward, 1953; Barros-Bellanda & Zucoloto, 2002; Poffo et al., 2018), and oviposit on leaves in clusters of varying sizes from 5 to 144 eggs (Santana, Rodrigues, & Zucoloto, 2017).

Temperature appears to regulate the distribution of *A. monuste* in the neotropical region where this species can be found on brassica crops during the warm seasons, from November to May (Santana et al., 2017). The adults' daily activity is positively correlated with temperature, up to about 19 °C (Nielsen & Nielsen, 1959). The seasonal flights are observed in both spring and summer from morning till late afternoon (Hayward, 1953; Poffo et al., 2018). Rainfall also appears to regulate its occurrence, as adults cease migration during rain (Poffo et al., 2018) and larvae, especially early instars, can be killed by storms (Picanço et al., 2010). The large-scale migration and broad diet of this species suggests a broad climate tolerance and therefore high potential for invading tropical regions worldwide.

Among varieties of *Brassica oleracea*, cabbage (*B. oleracea* var. *capitata* L.) is one of the most commonly cultivated species (Šamec, Pavlović, & Salopek-Sondi, 2017). The annual yield is estimated at 55 million tons of fresh heads produced on 2.6 million hectares with China, India, Russian Federation, Republic of Korea and Ukraine representing the largest producers (FAO, 2019). Cabbage is an important export product for several countries including China, the United States of America, Netherlands, and Mexico (FAO, 2019). This crop is of particular importance from a nutritional perspective as its contains glucosinolates and other bioactive products that can have positive effects on disease treatments (Cartea & Velasco, 2008).

Climate modelling can be used to understand the potential distribution of a pest, and alert agricultural agencies in geographical regions that are suitable for pest, enabling targeted strategies for early detection and eradication (Waage & Mumford, 2008). The establishment of a pest in any new area relies on the presence of a host (Kumar, Neven, & Lisa, 2014). Following arrival in Spain from South America, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) became established and subsequently spread into European countries that grow tomato (Desneux et al., 2010). Thus, mapping both the potential distribution of both a pest and its hosts can inform areas of potential occupancy to implant biosecurity actions (Waage & Mumford, 2008; Kumar et al., 2014).

In this study, we model the current distribution and the potential effect of climate change on both the distribution of *A. monuste*, and its host, cabbage (*B. oleracea* var. *capitata*). We aim to, first, determine the regions in the world that are currently suitable for both species and should, therefore, develop crop biosecurity strategies. Second, we aim to elucidate how climate change (IPCC, 2014) may cause changes in the distribution of *A. monuste* and cabbage.

14 METHODS

Species distribution modeling is a tool for identifying suitable areas for species based on the environmental variables of known occurrence sites (Phillips & Elith, 2010). We used MaxEnt algorithm to predict the current and future potential distributions of *A. monuste* and cabbage. As the basis of our model, we used climate variables from the current distribution area of the two species and then investigated shifts in the distribution of host and pest under different climate scenarios.

14.1 CURRENT DISTRIBUTION

We collected information on the distribution of both species (latitude and longitude) from published articles, reports, and online databases (GBIF, 2018a; 2018b). For *A. monuste*, the information regarding subspecies was not included. We obtained 46 and 715 records for *A. monuste* and cabbage, respectively. However, to minimize spatial autocorrelation among data points (Boria, Olson, Goodman, & Anderson, 2014), we applied spatial filtering using the spThin package (Aiello-lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015) in R version 3.5.0 (R Core Team, 2018). Filtered occurrence points were > 10 km apart (Boria et al., 2014), ensuring that each cell could have only one occurrence point due to the spatial resolution of 5 km used for the environmental data in the models. This filter resulted in 44 data points for *A. monuste* and 357 for cabbage (Figure 1A and C, respectively).

14.2 ENVIRONMENTAL DATA AND CLIMATE CHANGE SCENARIO

Initially, we obtained 19 environmental variables for each data point from WordClim version 1.4 dataset at ~ 5 km spatial resolution (http://www.worldclim.org/bioclim), sufficient to support climatic variables on a global scale (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These environmental variables include monthly precipitation and mean, minimum, and maximum temperature recorded between 1960 and 1990 (Hijmans et al., 2005). The variables included in our models were selected by Pearson correlation via SDMtools in ArcGIS (Brown, 2014), and by applying biological criteria, since temperature and precipitation are the most important factors that influence the growth and development of *A. monuste* and *B. oleracea* var. *capitata* (Nielsen & Nielsen, 1959; Liu, 2005; FAO, 2019). To avoid multicollinearity, i.e., when a correlated variable is already in the model (Franklin, 2009), we included only one variable from a group of highly correlated variables ($r \geq |0.75|$; Supporting Information 1). Six environmental variables in total were inserted: annual mean temperature (bio 1), mean diurnal temperature range (bio 2), annual temperature range (bio 7), mean annual precipitation (bio 12), precipitation of driest month (bio 14) and precipitation seasonality (bio 15).

The climate change scenarios used were RCP 4.5, and 8.5 (Representative Concentration Pathways) developed by Hadley Center Global Environmental Model (HadGEM2-ES) for the years 2050 and 2070. These scenarios predict the temperature change from 1.1 to 2.6 °C to RCP 4.5, and 2.6 to 4.8 °C in the RCP 8.5 by the end of the 21st century. The first scenario is a moderate scenario and likely to occur (Tollefson, 2018), whereas the second is an extreme climate change scenario (IPCC, 2014).

14.3 MODEL DEVELOPMENT, SELECTION, AND EVALUATION

Models were developed in MaxEnt (version 3.3.3k), also known as a correlative maximum entropy-based model, which is a presence-only data method for predicting the potential distribution of species (Phillips, Anderson, & Schapire, 2006). The probability distribution is generated using species presence data and background information from environmental variables (Phillips et al., 2006). We chose MaxEnt because it is relatively robust to small sample sizes (in this study for *A. monuste*) and no absence data are required (Pearson, Raxworthy, Nakamura, & Townsend-Peterson, 2007; Phillips et al., 2006).

A total of 50,000 background points were randomly selected for each species representing areas of current occurrence. This number was chosen because it is an appropriate background number to work on a global scale (Jarnevich, Stohlgren, Kumar, Morisette, & Holcombre, 2015). A bias surface was generated for each species using a kernel density estimate in SDMtools (Brown, 2014), offsetting the effect of sampling intensity and potential sampling bias (Jarnevich et al., 2015). We combined the models resulting from five different transformations of environmental variables [feature classes: (L) linear, (Q) quadratic, (P) product, (T) threshold, and (H) hinge] and also applied a range of regularization multipliers (RMs). These RMs reduce the number of parameters and control the model complexity as follows: values > 1 result in simpler models with less discriminating power and broader species potential distribution; values < 1 are inappropriate for global prediction (Jarnevich et al., 2015; Elith et al., 2011). The values of RM used were 1, 1.5 and 2.0 and were used with different feature classes combinations (i.e., L, Q, P, T, and H) in each modeling run (see Table 1). For all models performed in MaxEnt, we selected a logistic output.

We eliminated extrapolations outside the environmental range using the MaxEnt option ‘fade-by-clamping’. The contribution and permutation importance of each environmental variable in the model were estimated using the ‘jackknife’ test. Also, we checked whether the models generated were congruent with biological logic. To do this, we analyzed whether the predictors created based on the response curves to environmental variables were sound in terms of biological logic (Kumar et al. 2014). Models that were incongruent with this logic were eliminated from further evaluations.

To select the best model, we calculated the Bayesian Information Criterion (BIC) using ENMTools (Warren, Glor, & Turelli, 2010). We chose this criterion because, when relatively few data points are used, BIC estimates the true model complexity better than tests that involve quantifying the area under the receiver operating characteristic curve (AUC; Warren & Seifert, 2011), and it has a higher penalty for the model complexity than the Akaike Information Criterion (AIC) (Kumar, Neven, Zhu, & Zhang, 2015). Similar to AIC, a smaller BIC value (ΔBIC < 2) means a ‘better’ model (Franklin, 2009).

We evaluated the selected models using AUC values and true skill statistic (TSS; Allouche et al. 2006; Franklin 2009). The AUC values were obtained by training the models by cross-validation using ten replicates. These AUC values vary between 0 and 1, where values of > 0.5, 0.5 - 0.7, 0.7 - 0.9 and > 0.9, indicate, respectively, random, poor, satisfactory and good model performance (Manel, Williams, & Omerod, 2001). We also computed TSS values in R version 3.5.0 (R Core Team, 2018). The TSS is a threshold dependent metric, ranging from -1 to +1, that indicates the proportion of real presences that are accurately predicted. TSS values of > 0.5, > 0.7 and > 0.9 indicate respectively acceptable, good and excellent projection. Values of zero or less indicate a high frequency of erroneous predictions of presence and absence, and hence, a random projection (Jiménez-Valverde, 2014).

14.4 DISTRIBUTION OF *A. MONUSTE* AND *B. OLERACEA* VAR. C*APITATA*

The distribution of *A. monuste* and cabbage was extracted from MaxEnt logistic outputs using ArcGIS 10.5.2. The areas were classified as unsuitable and suitable for both species based on maximum test sensitivity plus specificity (TSH values in Table 1), a method for threshold selection when only presence data are available (Liu, White, & Newell, 2013). We created an overlap map for each project using the suitable classes for both species. These maps identify the areas that are suitable for *A. monuste* and cabbage in the same projection. We also computed the number of pixels related to suitable areas to determine the percentage reduction of suitable areas under each climate change scenario. Both analyses were performed using the spatial analyst tool in ArcGIS.

15 RESULTS

15.1 MODEL PERFORMANCE

Based on the AUC evaluation, the best model for *A. monuste* had a high performance, while cabbage had a satisfactory performance (Table 1). For both species, the TSS values indicated reasonable projections (Table 1).

Temperature variables had a significant contribution and permutation importance in the distribution models for both species (Table 2), as demonstrated by the outcome of the Jackknife test (Figure S1). Among the temperature variables, annual temperature range was the best predictor for the distribution of both *A. monuste* and cabbage, followed by the annual mean temperature (Table 2). For both species, the probability curves for presence based on each of these variables showed biological logic (Figure S2 for *A. monuste* and S3 for cabbage).

15.2 SPECIES DISTRIBUTIONS

While *A. monuste* is currently restricted to the American continent (Figure 1A), our modelling indicates that the tropical climate zones of Africa, Asia, and Oceania, as well as a small part of Europe, are currently suitable for *A. monuste* (Figure 1B). For cabbage we find both tropical and temperate regions are currently suitable (Figure 1C and D), including the five major producers of China, India, Russian Federation, Republic of Korea, and Ukraine (Figure 1D).

Under both climate change scenarios, the suitable areas will reduce for both species, particularly for cabbage in the tropical zone, and more so under the more extreme RCP 8.5 climate change scenario than under the RCP 4.5 scenario (Figure 2). For *A. monuste*, a reduction of 13 and 15% in suitable areas can be expected by the 2050 year under the RCP 4.5 (Figure 2A) and 8.5 (Figure 2B) scenarios, respectively, while for cabbage these values were 43% (Figure 2C) and 54% (Figure 2D). However, for the crop, the suitable areas increased in the temperate zone (e.g., Europe and Russian Federation), in both scenarios. We found that suitable areas for cabbage were also suitable for *A. monuste* in the tropical climate zone and a few temperate regions, as indicated by the overlapping projections (Figure 3). However, overall, with climate change, there was a very substantial decrease (69% for RCP 4.5

and 74% for RCP 8.5) in the overlapping areas for *A. monuste* and cabbage (Figure 3).

Projecting to 2070, we found a similar pattern of change. Suitable areas for both species continued to decrease in tropical climate zone, while for cabbage the suitable area increased in the temperate zone, particularly in Europe, where only a small area becomes suitable for *A. monuste* (Figure S4).

16 DISCUSSION

Under current climate conditions, several areas in tropical regions and a small part of the temperate zone are found to be suitable for the neotropical pest *A. monuste*, with these areas all suitable for cabbage. We find that while suitable areas in the tropical zone will be smaller for the host in future climates, the remaining areas will be suitable for the pest.

The model for the current distribution of *A. monuste* showed that, in addition to its presence in the Americas, several regions in the tropical climate zone and a small part of Europe are likely suitable for this pest. The finding that the annual temperature range and the mean annual temperature are the best predictors for the distribution of *A. monuste* is not surprising. Tropical climates are warm and, compared to temperate climates, both seasonal and day-to-day variation in temperature are small (Seidel, Fu, Randel, & Reicher, 2008). Therefore, compared to temperate organisms, tropical organisms exhibit low thermal ranges (Bonebrake, Ponisio, Boggs, & Ehrlich, 2010). Both the migratory and egglaying activity of *A. monuste* occurs in spring and summer where the highest temperature is observed in the neotropical region (Hayward, 1953; Nielsen & Nielsen, 1959; Poffo et al., 2018), and small temperature variations can affect this activity (Nielsen & Nielsen, 1959). As a result, the model for the current distribution of *A. monuste* predicts that areas with lower variation in temperature throughout the year, such as tropical regions, are suitable for this pest.

The general decrease in the distribution of *A. monuste* under the climate change scenarios can be understood in the context of the direct negative effect of increased temperature on insect physiology, leading to rapid development but reduced survival and fecundity (Martins et al., 2016). Moreover, high temperatures can also reduce flight activity (Nielsen & Nielsen, 1959; Bonebrake et al., 2010). The subspecies *A. monuste monuste* has optimal survival and fecundity at 25 °C (Liu, 2005), while flight frequency is reduced at a temperature above 30 °C and ceases entirely above 40 °C (Nielsen & Nielsen, 1959). In tropical regions, shifts in precipitation patterns and longer dry spells are likely to occur (Seidel et al., 2008). Coupled with increased temperature, which we found to be the best environmental predictor, this will likely decrease the suitable areas as more extended periods of high temperatures (likely above 30 ºC) will negatively impact the physiology and behavior of *A. monuste*.

Varieties of *B. oleracea* are cultivated worldwide as a result of domestication and breeding (Rodríguez, Soengas, Cartea, Sotelo, & Velasco, 2014). Our model showed that both temperate and tropical regions are suitable for cabbage production. It makes sense that the annual mean temperature was the best predictor for the distribution, as high temperatures reduce crop establishment, yield, and quality through inhibition of the photosystem II followed by decreases on the capacity of photosynthetic electron transportation (Díaz, De Haro, Muñoz, & Quiles, 2007; Rodríguez et al., 2014). However, the selection of cabbage populations with heat tolerance has already permitted their establishment in tropical areas (Rodríguez et al., 2014). Therefore, in addition to temperate areas, tropical regions are also suitable for cabbage production, as shown by the current distribution model.

Drier conditions will become more frequent in future climates and will reduce the total area suitable for cabbage production. Our model confirms this for cabbage distribution in the years 2050 and 2070, notably in tropical regions and in North America, probably as a result of the heat stress associated with the long dry spells (Seidel et al., 2008). By contrast, suitable areas for cabbage will increase in Europe and Russia, and this may be associated to positive effects of climate change in northern areas resulting in suitable temperatures for the crop (Olesen & Bindi, 2002).

We showed that the potential areas suitable for both *A. monuste* and cabbage include countries where both species are currently present as well as countries in Asia and Africa where only the host is currently present. The latter countries that are growing this crop may potentially see incursions and establishment of *A. monuste*, as has been reported in areas in Brazil (Picanço et al., 2010), Mexico (Liu, 2005) and the West Indian Islands (Alam, 1992). However, the overlap projection does not necessarily cover the whole potential area of *A. monuste*, as other *Brassica* hosts, such as kale (*B. oleracea* var. *acephala* L.) and mustard (*B. juncea* L.; Barros & Zucoloto, 1999), were not included in our model.

The climate change models used to assess the distribution of *A. monuste* and cabbage represent intermediate (RCP 4.5) and very high greenhouse gas emissions (RCP 8.5) scenarios (IPCC, 2014). While there was a decrease in suitable areas for both species, this decrease was higher under the more extreme scenario, and the impact was larger on cabbage than on *A. monuste*. This makes biological sense as the occurrence of *A. monuste* under field conditions coincides with warm seasons (Santana et al., 2017). Although higher temperature affects the flight *A. monuste* (> 30 °C), flight only ceases entirely above 40 °C (Nielsen & Nielsen, 1959). For cabbage, temperatures above 30 °C cause a reduction in the rate of photosynthesis which also leads a decrease in growth (Díaz et al., 2007; Rodríguez et al., 2014). Furthermore, in the genus *Brassica,* wild species (e.g., *B. fruticulosa*) can be much more tolerant to heat stress than agricultural species (Díaz et al., 2007). Thus, it is expected that climate change will affect cabbage more than it will affect *A. monuste*.

Apart from limitations due to modeling criteria, the lack of inclusion of biotic factors can limit the predictive value of species distribution models. The populations of *A. monuste* are regulated by natural enemies such as birds, entomopathogens, parasitoids, spiders, and wasps (Picanço et al., 2010; Santana et al., 2017). Cabbage crops are exposed to weed, diseases, and other pests that can lead to losses (Dillard, Bellinder, & Shah, 2004; Fidelis et al., 2019). These biotic interactions can impact species distribution and were not included in our models. Also, our models do not display the suitable areas for species in each season (or month) of the year, and some of the areas may be unsuitable for *A. monuste* and cabbage during parts of the year. Given these limitations, the results of this study should be interpreted with some caution.

While the models showed that the tropical climate zone is suitable for *A. monuste* and cabbage, this pest is currently found only in America (Pease, 1962; Alam, 1992; Liu, 2005; Poffo et al., 2018). The absence from other continents is likely due to the lack of migration (Franklin, 2009), e.g., through physiological difficulties posed by natural barriers such as deserts and sea (Johnson, 1960; Poffo et al., 2018). This emphasizes the role of humans in pest invasion, introducing it in other countries intentionally or unintentionally (Waage & Mumford, 2008). While natural barriers limit the migration of *A. monuste* to tropical climate zones, human transport can be a mode of invasion. The transportation of eggs due to their relatively small size, compared to larvae and pupa, and presence on leaves (Liu, 2005; Santana et al., 2017) are particularly prone to human-aided dispersal. The recent introduction of *T. absoluta* in Europe reflects this, where until 2006, this pest only occurred in South America. Its introduction into Europe has affected the tomato crops leading to losses of up to 100% (Desneux et al., 2010). This example, combined with our results, underscores the need for agricultural biosecurity about the accidental introduction of *A. monuste*, as prevention is the most crucial aspect to avoid pest introduction (Waage & Mumford, 2008).

In this sense, several actions could be undertaken to increase biosecurity. Affected areas that export substantial fresh head cabbage, such as Mexico (FAO, 2019; Liu, 2005), should execute local control and pest eradication, to minimize the risk of introduction of *A. monuste* to other areas. In addition, for countries that import cabbage, surveillance, and quarantine are needed to prevent the risk of introduction from existing sources (Waage & Mumford, 2008). Our study can serve as a guideline to identify current and future areas that are at risk of an incursion of *A. monuste*.

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Table1. Summary of MaxEnt model performance statistics for *Ascia monuste* and *Brassica oleracea* var. *capitata*. The best model, highlighted in bold, was selected using a Bayesian Information Criterion (ΔBIC < 2).

Description		Selection	Evaluation		TSH
Features	RM	BIC (ΔBIC)	AUC (±SD)	TSS (±SD)	
A. monuste					
LQ	**2**	**1313.3 (0.7)**	**0.902 ± 0.022**	**0.814 ± 0.156**	**0.314**
LQP	2	1313.8 (2.5)	0.901 ± 0.019	0.737 ± 0.103	0.365
LQP	1.5	1316.0 (2.6)	0.912 ± 0.017	0.762 ± 0.108	0.356
LQPT	1	1316.1 (5.1)	0.947 ± 0.035	0.688 ± 0.133	0.387
LQP	1	1317.5 (3.6)	0.911 ± 0.041	0.754 ± 0.111	0.350
B. oleracea var. *capitata*					
LQ	**1.5**	**10916.8 (0.9)**	**0.841 ± 0.014**	**0.615 ± 0.069**	**0.403**
LQP	1	10924.4 (2.3)	0.847 ± 0.025	0.625 ± 0.055	0.431
LQ	2	10931.2 (2.9)	0.846 ± 0.021	0.613 ± 0.042	0.429
LQP	1.5	10931.3 (7.0)	0.846 ± 0.018	0.624 ± 0.049	0.443
LQ	1	10934.2 (5.8)	0.846 ± 0.035	0.627 ± 0.038	0.448

Abbreviations: L, Q, P, T, and H: linear, quadratic, product, threshold, and hinge features, respectively; RM: Regularization Multiplier; AUC: Area Under the ROC curve; TSS: true skill statistic; TSH: threshold suitable habitat; SD is standard deviation, derived from ten cross-validation replicates.

Table 2. Contribution (C) and permutation importance (PI, %) of each environmental variable in the distribution models for *Ascia monuste* and *Brassica oleracea* var. *capitata.*

Variables	C (%)	PI (%)
Ascia monuste		
Annual mean temperature (bio 1, °C)	2.28	12.19
Mean diurnal temperature (bio 2, °C)	0.84	2.87
Temperature annual range (bio 7, °C)	94.45	82.44
Mean annual precipitation (bio 12, mm)	0.31	1.07
Precipitation of driest month (bio 14, mm)	1.76	1.27
Precipitation seasonality (bio 15, CV)	0.36	0.16
Brassica oleracea var. *capitata*		
Annual mean temperature (bio 1, °C)	38.48	69.64
Mean diurnal temperature (bio 2, °C)	1.99	10.00
Temperature annual range (bio 7, °C)	53.06	12.01
Mean annual precipitation (bio 12, mm)	4.56	6.08
Precipitation of driest month (bio 14, mm)	0.30	2.23
Precipitation seasonality (bio 15, CV)	1.61	0.04

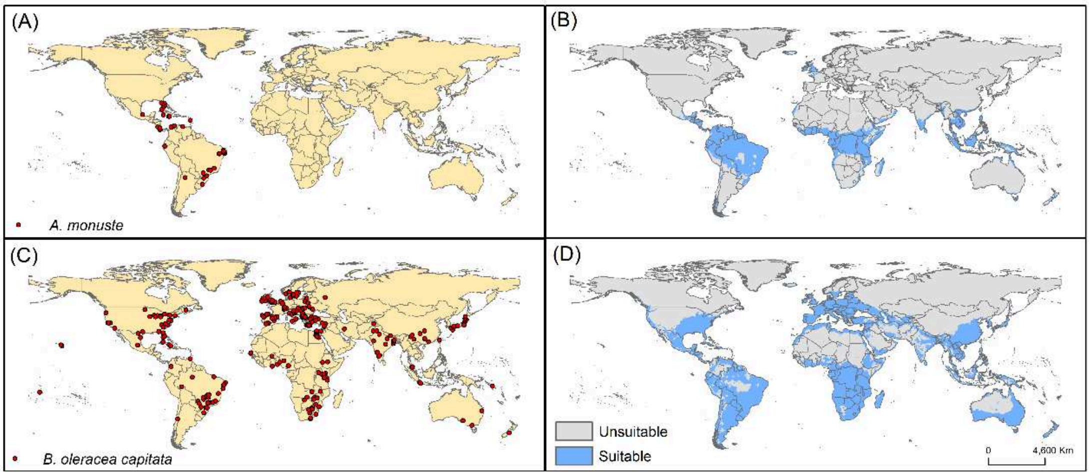

Figure 1**.** Occurrence and current potential distribution for *Ascia monuste* (1A-B) and *Brassica oleracea* var. *capitata* (1C-D).

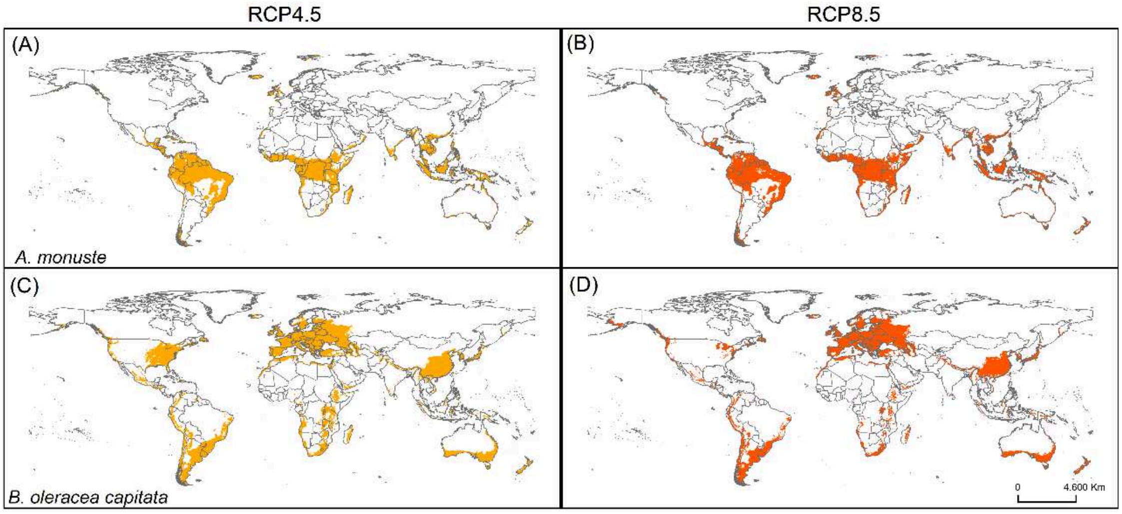

Figure 2. Distribution models under climate change scenarios RCP 4.5 and 8.5 for *Ascia monuste* (1A-B) and *Brassica oleracea* var. *capitata* (1C-D) for the year 2050. Colours represent suitable areas for the species.

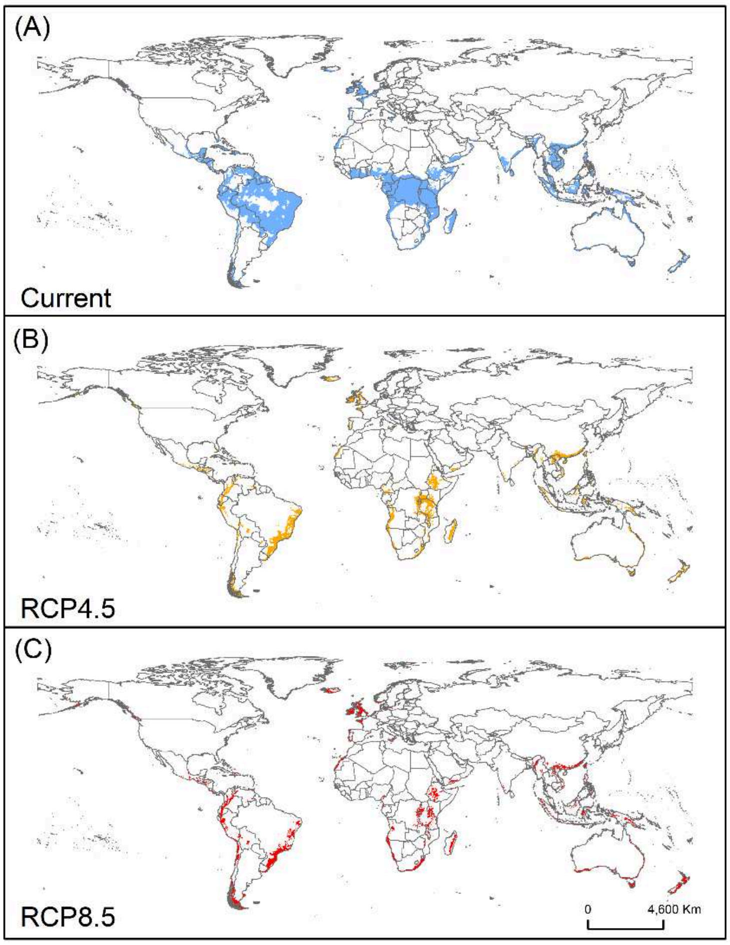

Figure 3. Suitable areas for *Ascia monuste* and *Brassica oleracea* var. *capitata* under current (3A) and climate change scenarios RCP 4.5 (3B) and 8.5 (3C). Colours represent suitable areas for both species under the same projection

APPENDIX – CHAPTER 3 SUPPLEMENTARY MATERIAL

Table S1. Pearson's correlation coefficients between all environmental variables. Only one variable from a group of variables that presented high correlation (r ≥ |0.75|) was included. Bold font indicates variables in the final model.

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio2	0.521																		
bio3	0.839	0.387																	
bio4	-0.833	-0.210	-0.891																
bio5	0.896	0.707	0.613	-0.513															
bio6	0.968	0.355	0.888	-0.936	0.764														
bio7	-0.730	0.015	-0.826	0.971	-0.358	-0.876													
bio8	0.812	0.533	0.638	-0.501	0.845	0.704	-0.387												
bio9	0.938	0.439	0.808	-0.861	0.792	0.949	-0.781	0.609											
bio10	0.935	0.621	0.660	-0.585	0.988	0.825	-0.455	0.865	0.831										
bio11	0.980	0.425	0.891	-0.926	0.795	0.996	-0.847	0.731	0.950	0.848									
bio12	0.378	-0.245	0.565	-0.554	0.119	0.486	-0.615	0.252	0.375	0.200	0.454								
bio13	0.455	-0.104	0.581	-0.567	0.233	0.527	-0.589	0.370	0.413	0.303	0.511	0.896							
bio14	0.055	-0.375	0.221	-0.245	-0.139	0.167	-0.346	-0.066	0.107	-0.075	0.123	0.709	0.392						
bio15	0.367	0.514	0.282	-0.190	0.429	0.269	-0.069	0.449	0.260	0.412	0.317	-0.173	0.138	-0.517					
bio16	0.445	-0.124	0.581	-0.569	0.215	0.522	-0.595	0.352	0.408	0.286	0.504	0.922	0.993	0.429	0.094				
bio17	0.083	-0.372	0.255	-0.275	-0.121	0.197	-0.375	-0.044	0.135	-0.054	0.153	0.744	0.429	0.994	-0.515	0.466			
bio18	0.224	-0.202	0.353	-0.337	0.026	0.282	-0.389	0.254	0.153	0.100	0.265	0.797	0.743	0.558	-0.104	0.761	0.581		
bio19	0.249	-0.242	0.431	-0.405	0.055	0.357	-0.475	0.074	0.307	0.112	0.316	0.754	0.584	0.671	-0.273	0.610	0.698	0.374	

Note: bio1 = annual mean temperature; **bio2 = mean diurnal temperature**; bio3= isothermality; bio4= temperature seasonality; bio5 = maximum temperature of warmest month; bio6 = maximum temperature of coldest month; **bio7 = temperature annual range**; bio8 = mean temperature of wettest quarter; bio9 = mean temperature of driest quarter; bio10 = mean temperature of warmest quarter; bio11 = mean temperature of coldest quarter; **bio12 = mean annual precipitation**; bio13 = precipitation of wettest month; **bio14 = precipitation of driest month**; **bio15 = precipitation seasonality**; bio16 = precipitation of wettest quarter; bio17 = precipitation of driest quarter; bio18 = precipitation of warmest quarter; bio19 = precipitation of coldest quarter.

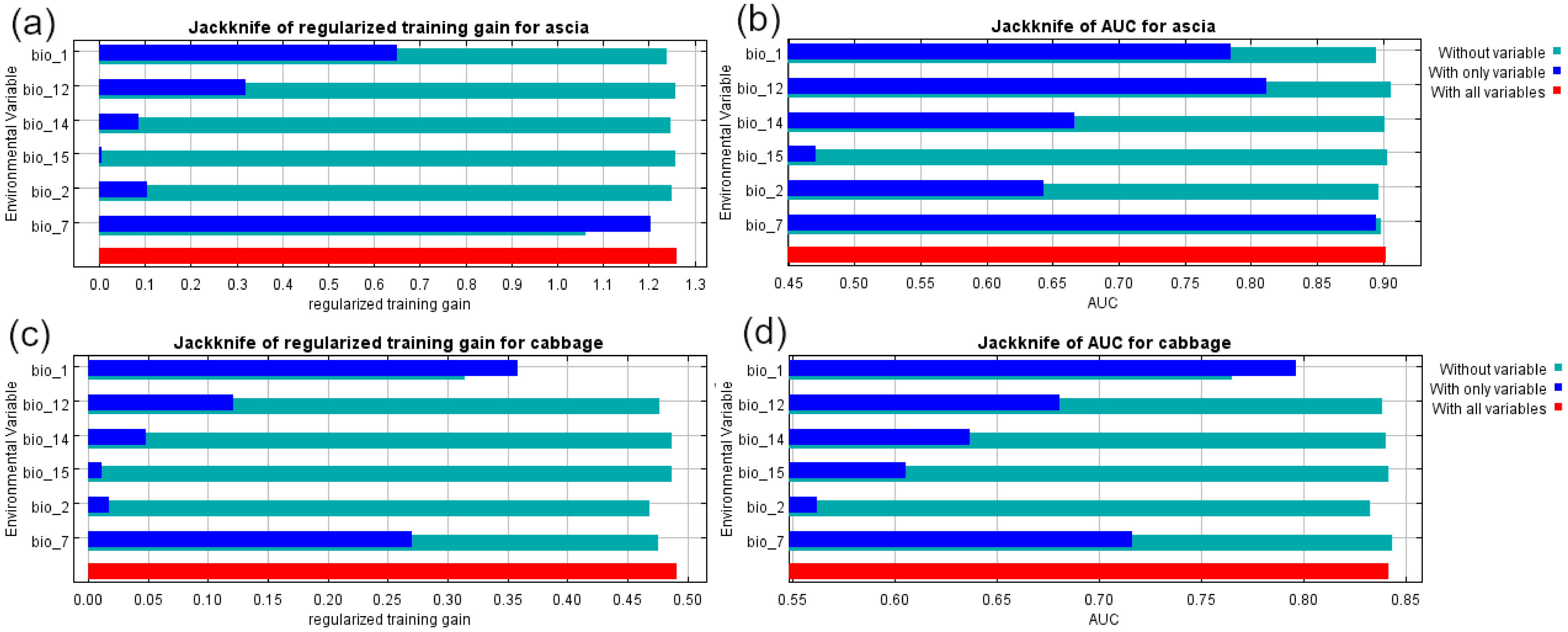

Figure S1

The relative importance of the environmental variables for *Ascia monuste* (A-B) and *Brassica oleracea* var. *capitata* (C-D) based on a Jackknife test of (A-C) regularized training gain and (B-D) Area under the ROC Curve (AUC).

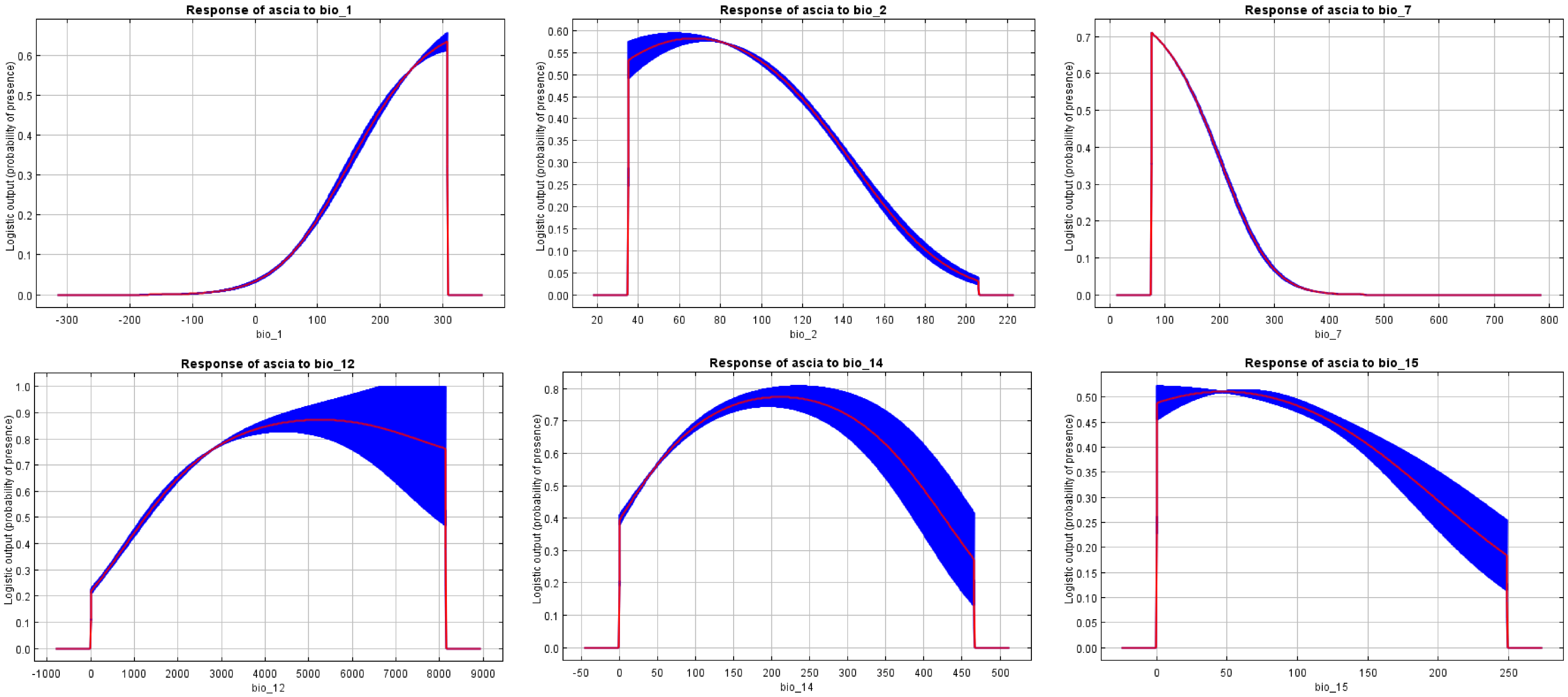

FIGURE S2

The probability of presence (y-*axis*) curves based only on bio 1, 2, 7, 12, 14 and 15 (x-*axis*), respectively, for *A. monuste*. Blue region represents a standard deviation based on ten cross-validation replicates.

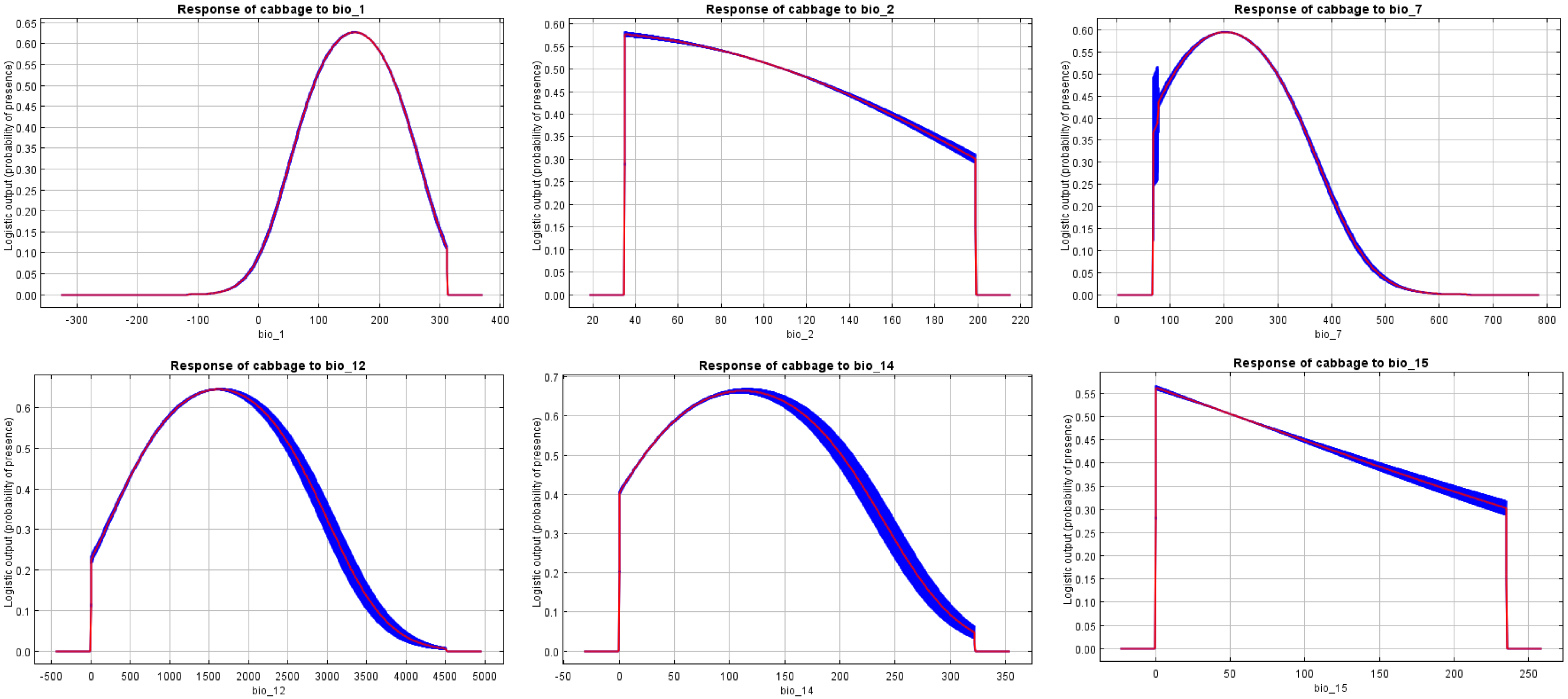

Figure S3

The probability of presence (y-*axis*) curves based only on bio 1, 2, 7, 12, 14 and 15 (x-*axis*), respectively, for *Brassica oleracea* var. *capitata*. Blue region represents a standard deviation based on ten cross-validation replicates.

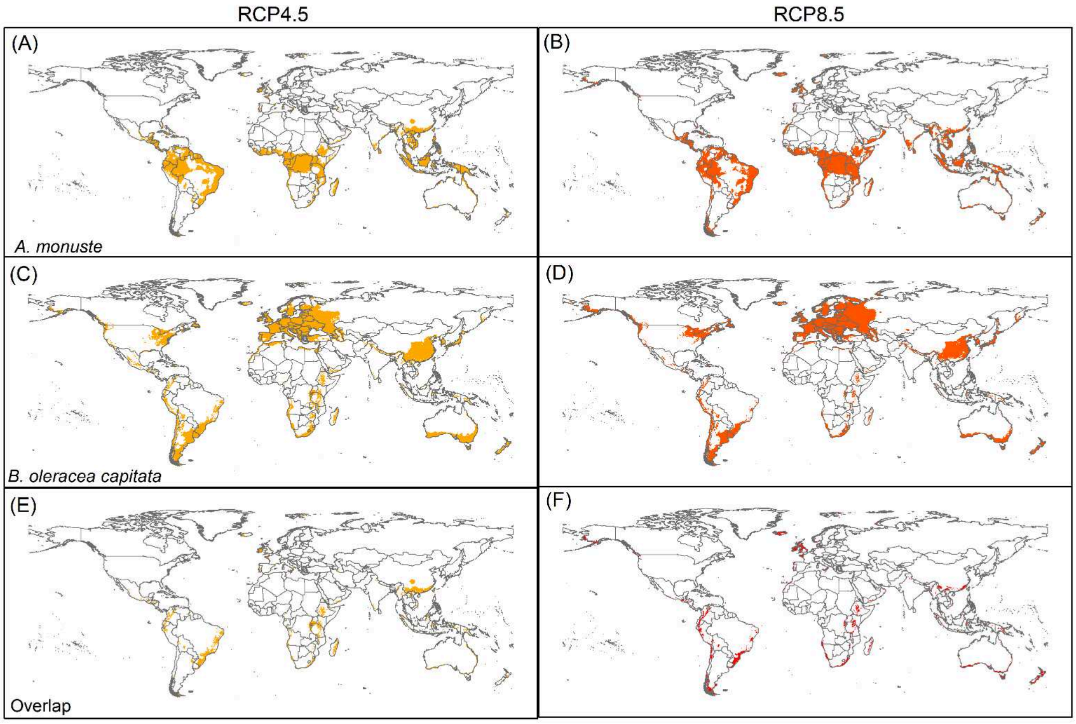

Figure S4

Models of global climate suitability for *Ascia monuste* (A-B) and *Brassica oleraceae* var. *capitata* (C-D) under RCP4.5 and 8.5 climate change scenario for the 2070 year. E and F an overlap maps with suitable conditions for both species.

17 GENERAL CONCLUSIONS

We provided evidence that *A. monuste orseis* can occur on *Brassica* crops during wet and warm seasons because cold and dry conditions compromise the insect performance. We also shown that variations on local weather can affect the causes of natural mortality in a local dependent relation. In addition, projecting the potential distribution of *A. monuste orseis* and the host cabbage, we show that under current climate conditions, suitable areas includes tropical regions in other continents. However, under a projected climate change scenario, these suitable regions are expected to decrease for both species. Thus, this thesis contributed to the knowledge about the natural history of *A. monuste orseis* and can be a guide to biosecurity protocols regarding the risk of pest invasion.