


RESEARCH ARTICLE

Life tables for the diamondback moth (*Plutella xylostella*) in southeast Brazil indicate ants and spiders as leading mortality factors

Elizeu S. Farias  | Renata C. Santos | Daiane G. Carmo | João R. S. Soares |
Thiago L. Costa | Abraão A. Santos | Marcelo C. Picanço

Departamento de Entomologia, Universidade
Federal de Viçosa, Viçosa, Brazil

Correspondence

Elizeu S. Farias, Departamento de
Entomologia, Universidade Federal de Viçosa,
Viçosa, Minas Gerais 36570-900, Brazil.
Email: elizeu.farias@ufv.br, elizeusf21@
gmail.com

Funding information

Conselho Nacional de Desenvolvimento
Científico e Tecnológico, Grant/Award
Number: 140983/2017-1; Coordenação de
Aperfeiçoamento de Pessoal de Nível Superior,
Grant/Award Number: Finance code 001

Abstract

The diamondback moth (DBM), *Plutella xylostella* (Lep.: Plutellidae), causes significant losses in *Brassica* crops. Leaf consumption by the larvae reduces plant yield and causes the contamination of heading brassicas. Chemical control usually provides unsatisfactory results due to the quickly developed resistance of DBM populations to insecticides. Thus, natural control by biotic factors (predators, parasitoids, and entomopathogens) is crucial and should be managed upon knowledge of their role as DBM regulators. The leading mortality factors of DBM across the annual seasons in southeast Brazil were investigated by conducting 57 field life tables for 2 years. The highest and lowest total mortalities of DBM occurred in winter (99.7%) and autumn (94%). Predation was the main mortality factor in all seasons. Marginal parasitism rates were higher in spring and lower in autumn, and *Oomyzus sokolowskii* (Hym.: Eulophidae) accounted for almost 90% of total parasitism. The highest mortalities by rainfall were recorded in spring (44.5%), while physiological death and infection caused low mortalities ($\leq 6\%$) throughout the seasons. In addition, models were built to investigate the main predators acting on the DBM life stages; Araneae, *Brachymyrmex bruchi*, and *Tetramorium simillimum* (Hym.: Formicidae) were the predators associated with egg/L1 predation whereas *Solenopsis saevissima*, *T. simillimum* and *Camponotus* spp. (Hym.: Formicidae) were the ones responsible for L4/pupa predation. The L2/L3 stage was the least affected by predation, and the final model for this stage did not include any predator. In light of these findings, habitat manipulation and insecticide selectivity are discussed as measures to preserve the main predators and parasitoid.

KEYWORDS

apparent mortality, conservation biological control, Formicidae, k-values, marginal attack rate

1 | INTRODUCTION

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lep.: Plutellidae), is a destructive pest of *Brassica* crops (Furlong, Wright, & Dosdall, 2013; Philips, Fu, Kuhar, Shelton, & Cordero, 2014). *Plutella xylostella* larvae cause damage through defoliation, which reduces

plant yield (Philips et al., 2014). Besides, contamination of heading brassicas (e.g., cabbage, cauliflower and broccoli) with DBM larvae can render the product unmarketable (Vail, Kok, & Lentner, 1989). Insecticide-resistant DBM populations are reported throughout the world (Bacci et al., 2018; Steinbach, Moritz, & Nauen, 2017; Zago, Siqueira, Pereira, Picanço, & Barros, 2014). The often perceived

inefficacy of various insecticides in controlling the DBM has underlined the importance of naturally occurring mortality factors on this pest management.

Climate is one of the main factors regulating insect populations (Peacock, Worner, & Sedcole, 2006). The combined action of weather variables (e.g., temperature and rain) affects the pest both directly (e.g., causing mortality and physiological disorders, Pereira et al., 2007) and indirectly (e.g., affecting the duration of the pest life cycle and the foraging activity of natural enemies) (Fidelis et al., 2019). Also, predators, parasitoids and entomopathogens act on pests, reducing their populations. The importance of natural mortality factors varies considerably with the pest species. For instance, predators cause up to 77% and 26% mortality on *Planococcus citri* (Risso) (Hem.: Pseudococcidae) and *Neoleucinodes elegantalis* (Guenée) (Lep.: Crambidae), respectively (Rodrigues-Silva et al., 2017; Silva et al., 2017). Conversely, rainfall causes significant mortality (20%) on *Leucoptera coffeella* (Guérin-Méneville) (Lep.: Lyonetiidae) (Pereira et al., 2007), but not on *N. elegantalis* (Silva et al., 2017).

Ecological life tables are valuable tools for accessing the importance of the natural mortality factors of pests. By estimating the mortality by the acting factors throughout the pest life stages, one can determine the leading mortality causes (Morris & Miller, 1954; Southwood & Henderson, 2000). Based on this knowledge, measures can be undertaken to preserve/enhance the leading mortality factors (Naranjo, 2001; Rosado et al., 2013). Life tables for the DBM were generated in some countries viz. Canada, Australia and Japan (Dancau, Haye, Cappuccino, & Mason, 2020; Furlong, Shi, Liu, & Zalucki, 2004; Harcourt, 1963). However, to the best of our knowledge, none has been developed in Brazil.

We recently described how DBM populations fluctuate over the year in southeast Brazil due to the variation of weather variables (Farias et al., 2020). However, an understanding of the leading mortality factors of DBM is still lacking, especially regarding the forces regulating its population. Therefore, we developed life tables to determine the main natural enemies and their importance over the seasons in southeast Brazil. These findings could be used to implement conservation measures to preserve these natural enemies.

2 | MATERIAL AND METHODS

2.1 | Study site

This study was conducted from May 2017 to February 2019 in the experimental field (−20.767271, −42.868931) at the Universidade Federal de Viçosa, Viçosa, Minas Gerais state, Brazil. The region's climate is characterised as Cwb (dry winter and warm summer), according to the Köppen class (Peel, Finlayson, & McMahon, 2007). The area was surrounded by fragments of native vegetation (seasonal semi-deciduous forest) and small plots of corn, coffee, soybean and vegetables (tomato, brassicas, and cucurbits).

2.2 | Life tables

Horizontal life tables were carried out to assess the natural factors causing mortalities on DBM stages (egg/L1 [first instar larva], L2/L3 and L4/pupa) over the seasons. The dates of beginning and end of the life tables, and the temperature and rainfall data (recorded by an automated station located 200 m from the study site, INMET, 2019) are presented in Table 1. Eight replicates were held per season; however, some of them were defoliated by *Atta* sp. (Hym.: Formicidae) and the bird *Penelope jacquacu* (Spix's guan), resulting in a total of 57 replicates ($n = 14, 15, 13$ and 15 for winter, spring, summer and autumn, respectively).

Potted cabbage plants (cv. Astro Plus) with eight leaves were kept in the lab ($25 \pm 5^\circ\text{C}$, RH $65 \pm 10\%$) for 12 h in wooden cages (two plants per cage) containing ~80 DBM adults from a laboratory-reared population. The plants were then carefully transported to the study site, sunken (protruding the plastic rim 2 cm below the soil) into the ground, and thoroughly inspected for DBM eggs. Two to four leaves (from different plant portions viz. upper, median and lower) were selected, and eggs from other leaves were removed using a fine brush (Size 4). Eggs from the selected leaves were counted, and this reading constituted the initial number of eggs (l_0). Subsequent assessments were performed twice daily (at 8 a.m. and 4 p.m.) by counting both the number of DBM (dead and alive) at each stage and predators on plants. Due to the small size of eggs and the leaf-mining habit of L1, plants were closely examined for egg/L1 mortality using illuminated hand-held magnifiers (30× magnification). The study plot contained 40 plants, including the infested ones, spaced 0.5×0.8 m apart. The plants were watered twice daily and did not receive any fertiliser or pesticide application.

Throughout the experiment, mortality was attributed to the acting factors (d_xFs) according to the following protocol: (a) individuals disappearing after rainfall events were considered dead by rain washing, (b) individuals dead by physiological disorders, infection (brownish coloured and soften larvae, and pupae covered by white spores), and parasitism were directly quantified in the assessments (Figure S1) and (c) predation by certain groups (such as Araneae, Figure S2) could be directly measured in the field, but for most cases (e.g., Formicidae, Figure S3), the predator did not leave any DBM body remnants. Therefore, individuals disappearing in the absence of rainfall were taken as dead by predation. The assessments ended when all pupae either died or emerged as adults, leaving an easily distinguishable empty cocoon (Figure S4).

Given the initial number of eggs (l_0), individuals entering each DBM stage (l_x), and dead individuals at each stage x (d_x), apparent and real mortalities (q_x and r_x , respectively) were calculated using Equations (1) and (2) (Southwood & Henderson, 2000):

$$q_x = d_x \div l_x \quad (1)$$

$$r_x = d_x \div l_0 \quad (2)$$

TABLE 1 Weather conditions and duration of the field experiments in Viçosa, MG, Brazil

| Year, season | Date | Temperature | | Rainfall | |
|-------------------|-------------------------------------|-------------|------------|---------------|-----------------|
| | | Mean (°C) | Range (°C) | Mean (mm/day) | Heavy rains (%) |
| 2017, autumn | May 25, 2017–June 21, 2017 | 17.6 | 7.3–28.9 | 0.51 | 0 |
| 2017, winter | 9/2/2017–September 21, 2017 | 18.7 | 7.5–30.2 | 0 | 0 |
| 2017, spring | November 30, 2017–December 19, 2017 | 22 | 16–31.3 | 13.73 | 12 |
| 2017/2018, summer | February 17, 2018–3/2/2018 | 22.7 | 17.4–31.4 | 3.5 | 0 |
| 2018, autumn | April 28, 2018–6/5/2018 | 18.0 | 5.5–29.1 | 0.33 | 0 |
| 2018, winter | August 14, 2018–September 21, 2018 | 18.3 | 8.7–30.6 | 1.33 | 0 |
| 2018, spring | November 13, 2018–November 26, 2018 | 21.4 | 15.8–29.8 | 10.71 | 14 |
| 2018/2019, summer | 2/8/2019–February 25, 2019 | 22.8 | 17.1–34.5 | 4.29 | 6 |

Note: The table is presented the dates of beginning and end of the assessments in each season, mean daily temperature (°C) and temperature range (minimum and maximum), and mean daily precipitation (mm/day) and percentage of days with heavy rains (precipitation >10 mm/hr).

Also, marginal mortality (*MM*) rates were estimated. The use of *MM* allowed us to attribute to each mortality cause (d_xF) its real importance, by estimating the mortality due to that factor in the absence of other synchronous d_xFs (Royama, 1981). For instance, measuring parasitism directly in the field can lead to an underestimation of this factor's role (Royama, 1981), because parasitised individuals can disappear by the action of other contemporaneous d_xFs . Hence, *MM* for parasitism was measured in the lab by collecting, at each season, five leaves (containing at least eight individuals) per life stage and rearing them ($25 \pm 5^\circ\text{C}$, $\text{RH } 65 \pm 10\%$, and 12 hr photoperiod) until adulthood (or parasitoid emergence). Also, *MM* for physiological death was measured separately (i.e., devoid of other d_xFs), by placing five plants (per season) individually into wooden cages (rain-protected by transparent plastic) and counting individuals dying at each stage. For rainfall, *MM* was taken as the apparent mortality (q_x) for this d_xF , because no other factor masks its action. Marginal mortality rates of predation and infection were derived from their own and relevant contemporaneous d_xFs apparent mortality (q_x) using Equation (3) (Elkinton, Buonaccorsi, Bellows, & Van Driesche, 1992; Naranjo & Ellsworth, 2005):

$$MM = qB \div (1 - qA) \quad (3)$$

where $qB = q_x$ of the factor (d_xF) of interest, and $qA = \text{sum of } q_x \text{ of contemporaneous } d_xFs \text{ potentially obscuring } qB$. For predation and infection, qA was attributed as being rainfall and rainfall + predation (i.e., only rainfall obscuring predation, and rainfall + predation obscuring infection), respectively.

From the *MM*, we calculated *k*-values (killing power) for each d_xF using the equation $k = -\log(1 - MM)$ (Royama, 1981). *k*-values are a practical presentation of *MM*, because they can (contrarily to *MM*) be added across pest stages and d_xFs , making them useful for further analyses or graphical representations. Also, provided the survival rates (emerging adults $\div I_0$), sex ratio ($SR = 0.5$; Harcourt, 1957) and fecundity (based on the mean temperatures recorded in each season, according to Ngowi et al., 2017), the net reproductive rate (R_0 , female offspring/female/generation) was calculated as:

$$R_0 = (\text{survival} \times SR \times \text{fecundity}) \div I_0 \quad (4)$$

2.3 | Natural enemies' identification

The relevant natural enemies (field-collected predators and parasitoids emerging in the lab) were kept in 90% ethanol. Parasitoids and Formicidae were identified by taxonomic experts. Other predators (Coleoptera, Hemiptera, Syrphidae, Neuroptera, and Vespidae) were identified by comparing the collected specimens with exemplars of the Regional Museum of Entomology at the UFV.

2.4 | Statistical analyses

All analyses were performed using R (R Core Team, 2019). Firstly, we analysed R_0 and *k*-values (pooled across all stages and d_xFs) as a function of season (Models 1 and 2) using generalised linear mixed models (GLMMs with gamma distribution and log-link; Bates, Mächler, Bolker, & Walker, 2015) which included year as random effect (1/year). Then, we checked for differences on *k*-values (pooled across all d_xFs) among DBM stages (egg/L1, L2/L3 and L4/pupa—Model 3) through GLMM with gamma distribution (log-link) including both year and season as crossed random effects (1/year + 1/season). Gamma distribution was adopted in both cases (models for R_0 and *k*-values) due to the right-skewed distribution of the response variables. Lastly, *MM* by predation (therein marginal predation rates), for each stage, was regressed against predator densities (Models 4 to 6) by linear mixed models (including year and season as crossed random effects), in order to identify the predators most accountable for that stage's predation. In this analysis, we only included predators whose frequency was >1% in the assessments. Inasmuch as the models had several predictors, they were simplified using a stepwise procedure (in both forward and backward directions) to identify the set of predictors yielding the lowest AIC value (i.e., the most parsimonious models).

All models were singular (i.e., with non-significant random effects), the reason why the random terms were dropped.

Significances (p -values) of the models were obtained by likelihood ratio tests (*lrtest* function, *lmtest* package; Zeileis & Hothorn, 2002) of the full models against null models (having only intercept). Significant differences among selected levels of nominal variables (DBM stage and season) were tested using pairwise differences of LS means (*lsmeans* package; Lenth, 2016). All models were checked for homoscedasticity and normality by checking residual plots. A detailed description of the models used in this manuscript is given in Table S1.

3 | RESULTS

3.1 | Natural enemies

Five hymenopteran species were found parasitizing DBM viz. *Cotesia* sp. Cameron (Braconidae), *Conura pseudofulvovariiegata* (Becker) (Chalcididae), *Aprostocetus* sp. Westwood and *Oomyzus sokolowskii* (Kurdjimov) (Eulophidae), and *Hyposoter* sp. Förster (Ichneumonidae) (Table 2). Thirty-six percent of all collected DBM were parasitised, and *O. sokolowskii* accounted for almost 90% of total parasitism.

Ants (Formicidae) and spiders (Araneae) were the most abundant predators, and appeared in 54.41 and 20% of the assessments, respectively (Table 3). Among the Formicidae, *Tetramorium simillimum* (Smith) was the most abundant, followed by *Brachymyrmex bruchi* Forel, *Pheidole* spp., *Camponotus* spp., *Solenopsis saevissima* (Smith), *Cardiocondyla emeryi* Forel and *Dorymyrmex brunneus* Forel. Syrphidae and Staphylinidae occurred in 4.73 and 1.51% of the readings, respectively, and the other predators were scarce (< 1% frequency).

3.2 | Life tables

The total mortality rates of DBM were not less than 94% over the entire study period, being slightly higher in winter (99.7%) and spring (99.6%) (Table 4). Based on the sum of real mortality (r_x) across the DBM stages, predation was the main mortality factor (d_xF) in all seasons. The highest mortalities by predation occurred in summer (96.1%) and winter (93.2%), followed by autumn (87.9%) and spring (54.9%). Mortality rates by parasitism were low (sum of $r_x \leq 2.2\%$),

irrespective of the season, because this factor was obscured by other contemporaneous d_xFs . Marginal rates (MM) of parasitism occurred in the L2/L3 and L4/pupa stages and were higher in spring and lower in autumn. The highest mortalities by rainfall were recorded in spring (44.5%). Physiological death appeared across all stages and seasons causing low mortality rates (sum of $r_x \leq 6\%$), whereas infection occurred low rates ($\leq 0.4\%$) only in autumn and winter (L4/pupa).

3.3 | Net reproductive rates and k -values

The net reproductive rate (R_0) and mean k -values (pooled across all d_xFs and pest stages) of DBM varied among seasons (R_0 : χ^2 (3) = 30.55, $p < 0.001$; k -values: χ^2 (3) = 43.64, $p < 0.001$). R_0 was significantly higher in autumn (7.630 female offspring/female/generation) compared to the other seasons (winter = 0.230, spring = 0.383 and summer = 0.718) (Figure 1). Conversely, k -values increased from winter to spring and then decreased towards autumn (Figure 2a). k -values also differed among the DBM stages (χ^2 (2) = 17.65, $p < 0.001$), being lower in L2/L3 compared to the other stages (Figure 2b). Predation was the prevailing d_xF in all stages. For egg/L1, rainfall was the second factor in importance, whereas parasitism was second to predation for the L2/L3 and L4/pupa stages.

3.4 | Marginal predation rates vs predator densities

The final model for marginal predation rates of egg/L1 included Araneae, *B. bruchi* and *T. simillimum* as predictors, all contributing positively to the dependent variable (Table 5). When *B. bruchi* densities increase from zero to two individuals per assessment, marginal predation rates increase from 72.3% to 95.5% (Figure 3b). The curves for Araneae and *T. simillimum* are slightly steeper, showing that when densities increase from zero to one individuals per assessment, predation rates are predicted to increase from 73.65% to 96.0% and 67.1% to 88.6%, respectively (Figure 3a and c). The model for L2/L3 only had Syrphidae, which was negatively related to marginal predation rates (Table 5). The model for L4/pupa had the ants *S. saevissima* and

| Parasitoid | Stage | Parasitism (%) |
|---------------|--|-----------------|
| Braconidae | <i>Cotesia</i> sp. Cameron | Larval |
| Chalcididae | <i>Conura pseudofulvovariiegata</i> (Becker) | Hyperparasitoid |
| Eulophidae | | 17.11 (90.14) |
| | <i>Aprostocetus</i> sp. Westwood | Hyperparasitoid |
| | <i>Oomyzus sokolowskii</i> (Kurdjimov) | Larval-pupal |
| Ichneumonidae | <i>Hyposoter</i> sp. Förster | Larval-pupal |
| Total | | 36.10 |

TABLE 2 Percentage parasitism of hymenopteran species associated with *Plutella xylostella* collected on cabbage

Note: Parasitism is expressed as the proportion of each species on total cases (parasitised and non-parasitised *P. xylostella*, $n = 576$) and on parasitised *P. xylostella* (within brackets, $n = 110$) in Viçosa, MG, Brazil (2017–2019).

TABLE 3 Percentage abundance and frequency of *Plutella xylostella* predators on cabbage ($n = 808$ individuals on 465 assessments)

| Predator | | Abundance (%) | Frequency (%) |
|---------------------------|---|---------------|---------------|
| Acari: Trombidiformes | | 0.50 | 0.86 |
| Araneae | | 13.37 | 20.00 |
| Coleoptera: Carabidae | <i>Elysus</i> sp. Walker | 0.25 | 0.43 |
| Coleoptera: Coccinellidae | <i>Harmonia axyridis</i> (Pallas) | 0.37 | 0.65 |
| Coleoptera: Staphylinidae | <i>Paederus</i> sp. | 0.87 | 1.51 |
| Diptera: Syrphidae | <i>Allograpta</i> spp. | 3.22 | 4.73 |
| Hemiptera: Miridae | <i>Tupiocoris</i> sp. China and Carvalho | 0.50 | 0.43 |
| Hymenoptera: Formicidae | | 80.07 | 54.41 |
| | <i>Camponotus</i> spp. | 7.55 | 12.04 |
| | <i>Solenopsis saevissima</i> (Smith) | 4.21 | 5.81 |
| | <i>Pheidole</i> spp. | 14.85 | 11.61 |
| | <i>Dorymyrmex brunneus</i> Forel | 1.11 | 0.86 |
| | <i>Brachymyrmex bruchi</i> Forel | 17.95 | 10.54 |
| | <i>Tetramorium simillimum</i> (Smith) | 32.43 | 25.16 |
| | <i>Cardiocondyla emeryi</i> Forel | 1.98 | 0.86 |
| Hymenoptera: Vespidae | | 0.37 | 0.65 |
| | <i>Polybia</i> sp. | 0.25 | 0.43 |
| | <i>Protonectarina sylveirae</i> (de Saussure) | 0.12 | 0.22 |
| Neuroptera: Hemerobiidae | | 0.50 | 0.86 |
| Total | | | 76.77 |

Note: The percentage values are the proportion of each species on the total number of predators (for abundance) and the number of predator appearances on the total number of assessments in Viçosa, MG, Brazil (2017–2019).

TABLE 4 Life table parameters of *Plutella xylostella* on cabbage for the different seasons of the years 2017 and 2019 in Viçosa, MG, Brazil

| Season/x | Infection | | Parasitism | | Physiological death | | Predation | | Rainfall | | Σr_x |
|----------|---------------|-------|---------------|-------|---------------------|-------|---------------|-------|---------------|-------|--------------|
| | $q_x (r_x)$ | MM | $q_x (r_x)$ | MM | $q_x (r_x)$ | MM | $q_x (r_x)$ | MM | $q_x (r_x)$ | MM | |
| Winter | (0.001) | | (0.003) | | (0.06) | | (0.932) | | (0.002) | | 0.997 |
| Egg/L1 | | | | | 0.045 (0.045) | 0.001 | 0.810 (0.810) | 0.811 | 0.002 (0.002) | 0.002 | |
| L2/L3 | | | 0 (0) | 0.489 | 0.092 (0.013) | 0 | 0.699 (0.101) | 0.699 | 0 (0) | 0 | |
| L4/pupa | 0.015 (0.001) | 0.054 | 0.086 (0.003) | 0.320 | 0.088 (0.003) | 0.160 | 0.719 (0.022) | 0.719 | 0 (0) | 0. | |
| Spring | (0) | | (0) | | (0.001) | | (0.549) | | (0.445) | | 0.996 |
| Egg/L1 | | | | | 0 (0) | 0.057 | 0.305 (0.305) | 0.545 | 0.441 (0.441) | 0.441 | |
| L2/L3 | | | 0 (0) | 0.440 | 0 (0) | 0.072 | 0.717 (0.182) | 0.717 | 0 (0) | 0 | |
| L4/pupa | 0 (0) | 0 | 0 (0) | 0.929 | 0.02 (0.001) | 0.339 | 0.861 (0.062) | 0.921 | 0.065 (0.005) | 0.065 | |
| Summer | (0) | | (0.011) | | (0.003) | | (0.961) | | (0.016) | | 0.991 |
| Egg/L1 | | | | | 0 (0) | 0.060 | 0.843 (0.843) | 0.843 | 0 (0) | 0 | |
| L2/L3 | | | 0 (0) | 0.200 | 0.016 (0.002) | 0 | 0.554 (0.087) | 0.59 | 0.061 (0.01) | 0.061 | |
| L4/pupa | 0 (0) | 0 | 0.194 (0.011) | 0.697 | 0.007 (0) | 0.077 | 0.53 (0.031) | 0.6 | 0.116 (0.007) | 0.116 | |
| Autumn | (0.004) | | (0.022) | | (0.036) | | (0.879) | | (0) | | 0.940 |
| Egg/L1 | | | | | 0.011 (0.011) | 0 | 0.517 (0.517) | 0.517 | 0 (0) | 0 | |
| L2/L3 | | | 0 (0) | 0.020 | 0.03 (0.014) | 0.012 | 0.365 (0.172) | 0.365 | 0 (0) | 0 | |
| L4/pupa | 0.013 (0.004) | 0.037 | 0.076 (0.022) | 0.090 | 0.04 (0.011) | 0.190 | 0.663 (0.189) | 0.663 | 0 (0) | 0 | |

Note: $n = 14, 15, 13$ and 15 life tables for winter, spring, summer and autumn, respectively.

Abbreviations: x, *Plutella xylostella* stage; q_x , apparent mortality; r_x , real mortality; MM, marginal mortality, Σr_x , summation of r_x in the respective season, which corresponds to the total mortality.

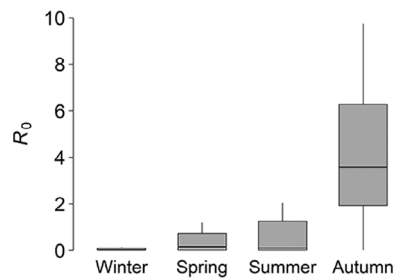


FIGURE 1 Box plots of R_0 (net reproductive rate of the population) for *Plutella xylostella* over the seasons (winter, spring, summer and autumn) in Viçosa, MG, Brazil. Box plots show median values (horizontal line), 25–75% interquartile range (box bounds), and 10th and 90th percentiles (whiskers)

Camponotus spp. (both marginally significant) and *T. simillimum* affecting the predation rates positively, while *B. bruchi* was negatively related to the dependent variable. An increment of 19.6%, 16.7% and 17.0% on L4/pupa marginal predation is expected when the densities

of *S. saevissima*, *T. simillimum* and *Camponotus* spp. increase from zero to one, zero to one and zero to 0.5 individuals per assessment, respectively (Figure 3d–f).

Overall, winter and summer had higher predator densities than spring and autumn (Figure 4). Spiders' densities varied little among the seasons. Conversely, ants' densities fluctuated considerably over the year, with *T. simillimum* and *B. bruchi* being more abundant in the summer, and winter having the highest densities of *S. saevissima* and *Camponotus* spp.

4 | DISCUSSION

Over the life tables, five hymenopteran species were found parasitizing DBM. Another study in Brazil reported a similar composition of DBM parasitoids in Central-West Brazil, with species from the genus *Apanteles*, *Cotesia*, and *Conura*, *Diadegma leontinae* Brèthes (an Ichneumonidae not found during our assessments) and *O. sokolowskii* (Guilloux, Monnerat, Castelo-Branco, Kirk, &

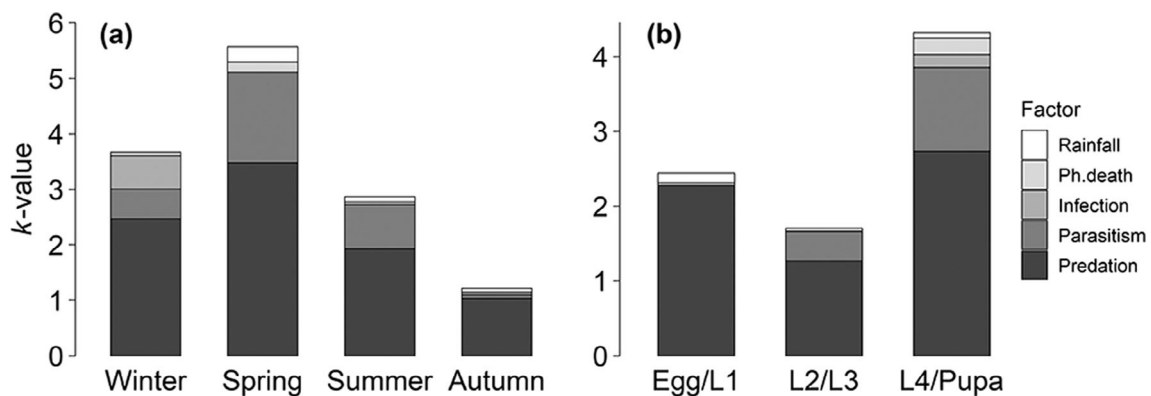


FIGURE 2 k -values (a) over the seasons (winter, spring, summer, and autumn) and (b) within each *Plutella xylostella* life stage (egg/L1, L2/L3 and L4/pupa) in Viçosa, MG, Brazil. Ph. death, physiological death; L1, first instar larva; L2, second instar larva; L3, third instar larva; L4, fourth instar larva

| <i>P. xylostella</i> stage | Term ^a | Slope \pm SE | <i>t</i> -value | <i>p</i> |
|----------------------------|-------------------------------|------------------|-----------------|----------|
| Egg/L1 | Intercept | 0.62 \pm 0.05 | 11.92 | <0.001 |
| | Araneae | 0.22 \pm 0.15 | 1.49 | 0.143 |
| | <i>Brachymyrmex bruchi</i> | 0.12 \pm 0.07 | 1.72 | 0.093 |
| | <i>Tetramorium simillimum</i> | 0.22 \pm 0.08 | 2.71 | 0.010 |
| L2/L3 | Intercept | 0.66 \pm 0.04 | 18.09 | <0.001 |
| | Syrphidae | −0.47 \pm 0.17 | −2.77 | 0.008 |
| L4/pupa | Intercept | 0.71 \pm 0.04 | 19.90 | <0.001 |
| | <i>Solenopsis saevissima</i> | 0.20 \pm 0.12 | 1.64 | 0.108 |
| | <i>Brachymyrmex bruchi</i> | −0.05 \pm 0.03 | −1.87 | 0.068 |
| | <i>Tetramorium simillimum</i> | 0.17 \pm 0.08 | 2.13 | 0.039 |
| | <i>Camponotus</i> spp. | 0.34 \pm 0.18 | 1.92 | 0.062 |

TABLE 5 Summary of linear models of marginal predation rates of *Plutella xylostella* life stages (egg/L1, L2/L3, and L4/pupa) against densities of predators (Araneae, Formicidae, Staphylinidae, and Syrphidae) in Viçosa, MG, Brazil (2017–2019)

^aFor all stages, full models included Araneae, *S. saevissima*, *Pheidole* spp., *B. bruchi*, *T. simillimum*, *Camponotus* spp., Staphylinidae and Syrphidae. A stepwise procedure combining both forward and backward selection was used to select the most parsimonious combination of predictors.

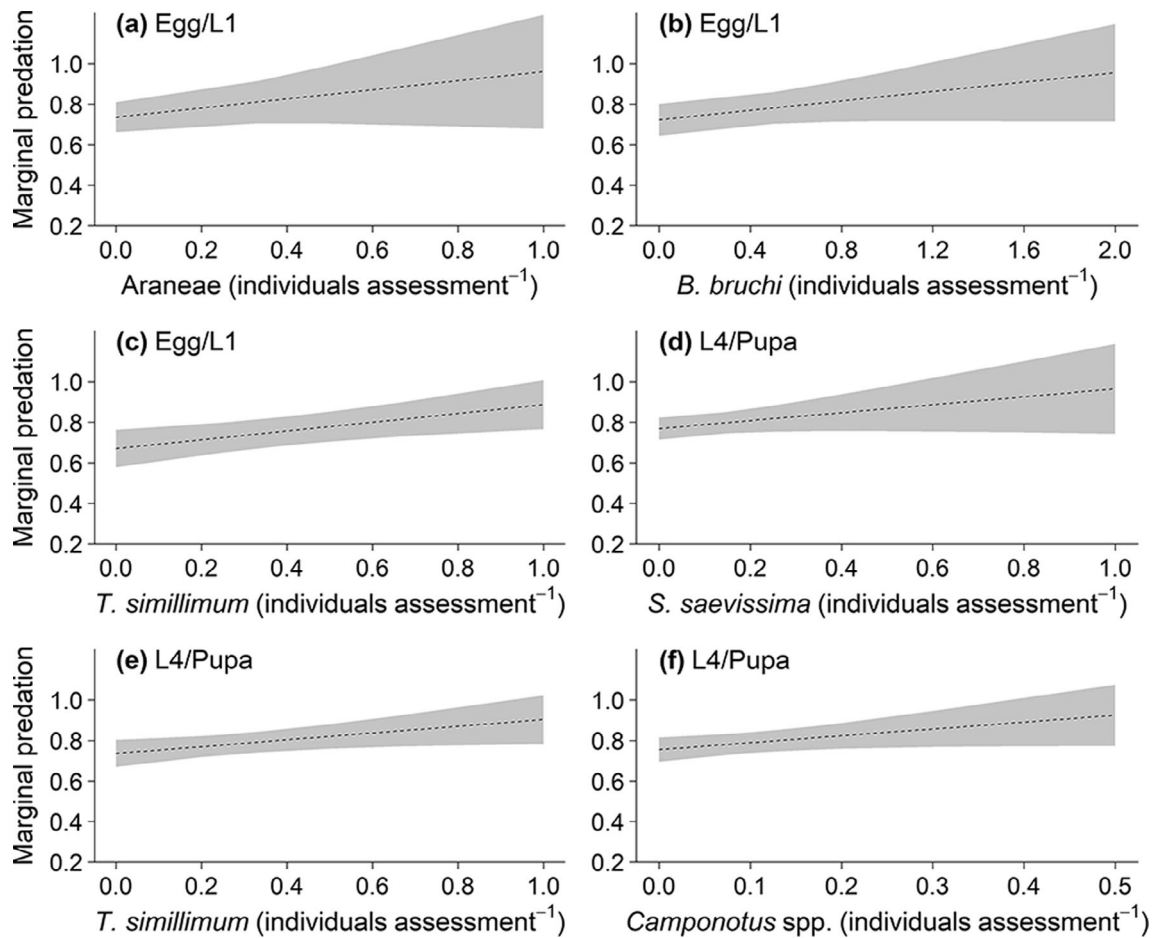


FIGURE 3 (a–f) Plots showing the effect of predator (*Araneae*, *Brachymyrmex bruchi*, *Tetramorium simillimum*, *Solenopsis saevissima* and *Camponotus* spp.) densities on marginal predation rates of *Plutella xylostella* life stages (egg/L1, L2/L3 and L4/pupa). Plots include model estimates (dashed black lines) and 95% confidence intervals (grey shadings). L1, first instar larva; L2, second instar larva; L3, third instar larva; L4, fourth instar larva

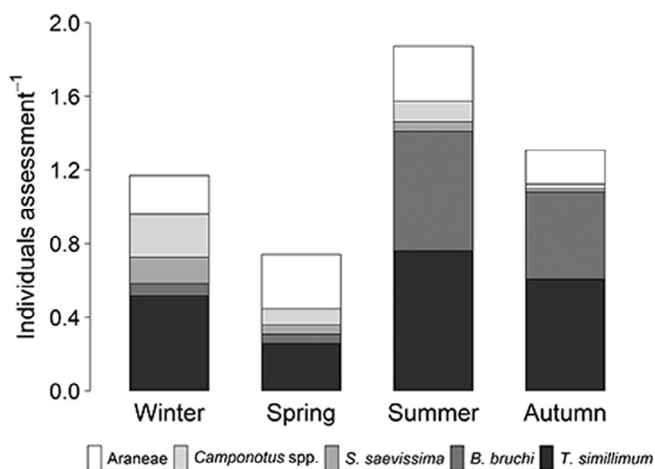


FIGURE 4 Densities of predators (*Araneae*, *Camponotus* spp., *Solenopsis saevissima*, *Brachymyrmex bruchi* and *Tetramorium simillimum*) on cabbage across seasons (winter, spring, summer and autumn) in Viçosa, MG, Brazil

Bordat, 2003). However, contrary to them, which reported *D. leontinae* and *Apanteles* sp. as the dominant parasitoids, *O. sokolowskii* was the prevailing species in our study, contributing almost 90% to DBM parasitism. As for the DBM predators, some of them (Acari, Araneae, Miridae, and Formicidae) were seen preying upon DBM during the assessments (Figures S2 and S3). Others (Carabidae, Coccinellidae, Neuroptera, Syrphidae, Staphylinidae and Vespidae) were reported as DBM predators in previous studies (Hosseini, Schmidt, & Keller, 2012; Miranda, Bylund, Grönberg, Larsson, & Björkman, 2011). Araneae and Formicidae were the most abundant predators. We could not sort by family all the collected Araneae, but three individuals found preying on DBM larvae were representatives of Linyphiidae (two individuals) and Dictynidae. Besides, *Cheiracanthium inclusum* (Hentz) (Eutichuridae), a reported DBM predator (Silva-Torres, Pontes, Torres, & Barros, 2010), appeared in our assessments.

The total DBM mortality (Σr_k) varied over the seasons, ranging from 94.0% to 99.7%. These values are comparable to those reported

in life tables conducted in Canada ($\geq 99.96\%$) (Dancau et al., 2020) and Japan ($\geq 94.21\%$) (Wakisaka, Tsukuda, & Nakasuji, 1991), and higher than those found in Australia (56% to 87% mortality) (Furlong et al., 2004). Irrespective of the season, predation was the prevailing d_xF in our study (especially in winter and summer). Among the DBM stages, L2/L3 was the one presenting the lowest MM rates. The k -value for the most important d_xF (predation) was lower for this stage. A reasonable explanation for this is the shorter duration of this stage compared to the others; L2/L3 comprises 21.11% of the total DBM developmental time, whereas egg/L1 and L4/pupa represent 32.74% and 46.15%, respectively (Steinbach et al., 2017). This indicates that artificial control measures (e.g., use of selective and bio-rational insecticides), when needed, should be focused on the L2/L3 stage, especially during autumn, to complement the action of naturally occurring mortality factors.

During spring, rainfall (44.5% mortality) was one of the leading mortality factors (together with predation), particularly in earlier stages (egg/L1). Wakisaka et al. (1991), investigating the effect of artificial precipitation (by means of water sprinkling) on DBM stages, reported up to 30% of eggs washed-off from the plants after water sprinkling; for eggs laid on the upper leaf side, this value was even higher (47%). Besides displacing eggs and larvae from the plant, rain droplets accumulate on the lipophilic surface of brassica leaves, forming larger drops that kill young larvae by drowning. Another indirect effect is the resulting preying of rain-dislodged larvae by soil-dwelling arthropods (Dancau et al., 2020). We also observed substantial pupa mortalities ($q_x = 11.6\%$) following heavy rains during summer. The higher importance of rain mortality in spring compared to summer (both comprising the rainy season for the study region), is due to the higher frequency of heavy rains (precipitation >10 mm/hr, Jarraud, 2008) on the former.

Based on its low r_x rates, parasitism was strongly obscured by the other d_xFs . Overall, the highest and lowest k -values for parasitism occurred in spring and autumn, respectively. Also, k -values of parasitism (mainly represented by *O. sokolowskii*) were higher for L4/pupa than for L2/L3. Studies accessing the *O. sokolowskii* preference for different DBM stages report higher parasitism in L4 compared to L2 and L3 (Sow, Arvanitakis, Niassy, Diarra, & Bordat, 2013; Talekar & Hu, 1996), which support our findings.

When regressing marginal predation rates against densities of the most frequent predators, no predator was positively related to L2/L3 predation. For the other stages, spiders and *T. simillimum* were the predators associated with egg/L1 predation, and *S. saevissima*, *T. simillimum* and *Camponotus* spp. were the ones responsible for L4/pupa predation. The importance of ants to DBM control has been shown by a comprehensive study by Agarwal, Rastogi, and Raju (2007). Using sentinel larvae and exclusion experiments, they found six species (including two species of *Camponotus*) foraging on DBM larvae, with *Pheidole* sp. and *Tetramorium* sp. being the primary species involved. Also, previous studies have found *T. simillimum* to predate on larvae of the curculionids *Hypothenemus hampei* (Ferrari) and *Diaprepes abbreviatus* (L.) (Armbrecht & Gallego, 2007; Whitcomb, Gowan, & Buren, 1982). As for the spiders, their role in the biological

control of pests, including DBM, has been extensively acknowledged (Ma, Li, Keller, Schmidt, & Feng, 2005; Quan et al., 2011; Suenaga & Hamamura, 2015).

In light of these findings, conservation measures are important for maintaining natural enemies' populations in brassica crops. Crop cultivation (e.g., ploughing and grass-cutting) contributes to reducing spider densities in agroecosystems, both by causing direct mortality and leading spiders to move out of the area (Bogya & Markó, 1999; Thorbek & Bilde, 2004). Therefore, in brassica crops from the study region, tilling should be avoided and ground cover (e.g., grassy or non-brassica weeds on the inter-rows) be maintained to preserve spider populations. Besides, the use of selective insecticides (IGRs, diamides, spinosyns, and Bt-based products) is a measure that could be deployed to preserve both predatory ants (Araújo et al., 2017; Barros, Silva-Torres, Torres, & Rolim, 2018) and spiders (Markó, Keresztes, Fountain, & Cross, 2009; Pekar, 2002). During spring (season with higher parasitism rates), chemical control should be avoided to the maximum extent, because *O. sokolowskii* is reportedly sensitive to several insecticides (Bacci et al., 2018; Cordero, Bloomquist, & Kuhar, 2007; Haseeb, Amano, & Liu, 2005), including IPM-compatible ones (e.g., spinosyns and IGRs). Habitat diversification is another means of enhancing pest biological control (Wilkinson & Landis, 2005). By increasing habitat complexity (through intercropping and polyculture, among other practices), alternative resources such as pollen, nectar and shelter are provided, which increase the abundance and diversity of natural enemies (Rezende, Venzon, Perez, Cardoso, & Janssen, 2014; Togani, Venzon, Souza, Santos, & Sujii, 2019).

Estimates of net reproductive rates (R_0) were low from winter to summer (exhibiting an increasing pattern) and plainly higher in autumn. Contrariwise, the mean k -values (pooled across all d_xFs and pest stages) follow a reverse direction, decreasing towards autumn. R_0 is a parameter that measures the tendency of the population to either increase in size ($R_0 > 1$), decrease ($R_0 < 1$) or remain stable ($R_0 = 1$) (Southwood & Henderson, 2000). Based on the values found in our study, DBM populations would exhibit higher growth during autumn, decrease drastically in winter, and grow steadily in the spring and summer towards autumn. However, the climate plays a major role in regulating DBM dynamics. Lower values of temperature and relative humidity favour this pest, which results in higher DBM densities in winter, decreasing towards autumn (Farias et al., 2020). Our study shows how the natural mortality factors of DBM would act if this pest was equally abundant in all seasons. By artificially infesting plants with DBM in periods in which the pest densities were supposed to be low (summer and autumn), a temporal asynchrony of DBM with their main natural enemies (i.e., high DBM densities and low predator densities) might have occurred (Roy, Brodeur, & Cloutier, 2005; Van Nouhuys & Lei, 2004). This is evidenced by the lowest predator densities in spring and autumn, the seasons with lowest mortalities by predation.

In summary, this study describes how natural mortality of DBM fluctuates due to the acting factors whose intensities vary across seasons. Predation, the leading mortality factor throughout the year, is exerted mainly by ants and spiders. Parasitism, in turn, is particularly important in regulating DBM during spring. Conservation measures

should be undertaken to preserve predators (especially spiders and ants) and parasitoids (mostly represented by *O. sokolowskii*).

ACKNOWLEDGEMENTS

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001, and Fundação de Amparo à Pesquisa do Estado de Minas Gerais—FAPEMIG. E.S.F. gratefully acknowledges the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship grant (process number: 140983/2017-1). Special thanks to the taxonomic experts Angélica Pentead-Dias (UFSCAR, Brazil) and Marcelo Tavares (UFES, Brazil) for parasitoid identification; and Jacques Delabie (CEPEC/CEPLAC, Brazil) and Julio Chaul (UFV, Brazil) for Formicidae identification.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ORCID

Elizeu S. Farias  <https://orcid.org/0000-0001-8167-6974>

REFERENCES

- Agarwal, V. M., Rastogi, N., & Raju, S. V. S. (2007). Impact of predatory ants on two lepidopteran insect pests in Indian cauliflower agroecosystems. *Journal of Applied Entomology*, 131, 493–500.
- Araújo, T. A., Picanço, M. C., Ferreira, D. O., Campos, J. N., Arcanjo, L. P., & Silva, G. A. (2017). Toxicity and residual effects of insecticides on *Ascia monuste* and predator *Solenopsis saevissima*. *Pest Management Science*, 73, 2259–2266.
- Armbricht, I., & Gallego, M. C. (2007). Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata*, 124, 261–267.
- Bacci, L., Rosado, J. F., Picanço, M. C., Gönring, A. H. R., Galdino, T. V. S., & Martins, J. C. (2018). Failure control of *Plutella xylostella* (Lepidoptera: Plutellidae) and selectivity of their natural enemies to different insecticides. *Journal of Plant Protection Research*, 58, 161–167.
- Barros, E. M., Silva-Torres, C. S. A., Torres, J. B., & Rolim, G. G. (2018). Short-term toxicity of insecticides residues to key predators and parasitoids for pest management in cotton. *Phytoparasitica*, 46, 391–404.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bogya, S., & Markó, V. (1999). Effect of pest management systems on ground-dwelling spider assemblages in an apple orchard in Hungary. *Agriculture, Ecosystems and Environment*, 73, 7–18.
- Cordero, R. J., Bloomquist, J. R., & Kuhar, T. P. (2007). Susceptibility of two diamondback moth parasitoids, *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) and *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae), to selected commercial insecticides. *Biological Control*, 42, 48–54.
- Core Team, R. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Danau, T., Haye, T., Cappuccino, N., & Mason, P. G. (2020). Something old, something new: Revisiting the diamondback moth (Lepidoptera: Plutellidae) life table after 65 years. *Canadian Entomologist*, 152, 70–88.
- Elkinton, J. S., Buonaccorsi, J. P., Bellows, T. S. Jr, & Van Driesche, R. G. (1992). Marginal attack rate, *k*-values and density dependence in the analysis of contemporaneous mortality factors. *Researches on Population Ecology*, 34, 29.
- Farias, E. S., Santos, A. A., Ribeiro, A. V., Carmo, D. G., Paes, J. S., & Picanço, M. C. (2020). Climate and host plants mediating seasonal dynamics and within-plant distribution of the diamondback moth (*Plutella xylostella*). *Crop Protection*, 134, 105172.
- Fidelis, E. G., Farias, E. S., Lopes, M. C., Sousa, F. F., Zanoncio, J. C., & Picanço, M. C. (2019). Contributions of climate, plant phenology and natural enemies to the seasonal variation of aphids on cabbage. *Journal of Applied Entomology*, 143, 365–370.
- Furlong, M. J., Shi, Z., Liu, S.-S., & Zalucki, M. P. (2004). Evaluation of the impact of natural enemies on *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) populations on commercial *Brassica* farms. *Agricultural and Forest Entomology*, 6, 311–322.
- Furlong, M. J., Wright, D. J., & Dosdall, L. M. (2013). Diamondback moth ecology and management: Problems, progress, and prospects. *Annual Review of Entomology*, 58, 517–541.
- Guilloux, T., Monnerat, R., Castelo-Branco, M., Kirk, A., & Bordat, D. (2003). Population dynamics of *Plutella xylostella* (Lep., Yponomeutidae) and its parasitoids in the region of Brasília. *Journal of Applied Entomology*, 127, 288–292.
- Harcourt, D. G. (1957). Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. II. Life-history, behaviour, and host relationships. *The Canadian Entomologist*, 89, 554–564.
- Harcourt, D. G. (1963). Major mortality factors in the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). *The Memoirs of the Entomological Society of Canada*, 95, 55–66.
- Haseeb, M., Amano, H., & Liu, T. X. (2005). Effects of selected insecticides on *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) and *Oomyzus sokolowskii* (Hymenoptera: Eulophidae), parasitoids of *Plutella xylostella* (Lepidoptera: Plutellidae). *Insect Science*, 12, 163–170.
- Hosseini, R., Schmidt, O., & Keller, M. A. (2012). Detection of predators within *Brassica* crops: A search for predators of diamondback moth (*Plutella xylostella*) and other important pests. *African Journal of Agricultural Research*, 7, 3473–3484.
- INMET (2019). *BDMEP – Banco de Dados Meteorológicos para Ensino e Pesquisa*. Retrieved from <http://www.inmet.gov.br/projetos/rede/pesquisa/>
- Jarraud, M. (2008). *Guide to meteorological instruments and methods of observation* (WMO-no. 8). Geneva, Switzerland: World Meteorological Organisation.
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69, 1–33.
- Ma, J., Li, D., Keller, M., Schmidt, O., & Feng, X. (2005). A DNA marker to identify predation of *Plutella xylostella* (Lep., Plutellidae) by *Nabis kinbergii* (Hem., Nabidae) and *Lycosa* sp. (Aranea, Lycosidae). *Journal of Applied Entomology*, 129, 330–335.
- Markó, V., Keresztes, B., Fountain, M. T., & Cross, J. V. (2009). Prey availability, pesticides and the abundance of orchard spider communities. *Biological Control*, 48, 115–124.
- Miranda, F., Bylund, H., Grönberg, L., Larsson, L., & Björkman, C. (2011). Population density and killing capacity by predators of eggs and larvae of the diamondback moth in Nicaragua. *Environmental Entomology*, 40, 333–341.
- Morris, R. F., & Miller, C. A. (1954). The development of life tables for the spruce budworm. *Canadian Journal of Zoology*, 32, 283–301.
- Naranjo, S. E. (2001). Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*. *Crop Protection*, 20, 835–852.
- Naranjo, S. E., & Ellsworth, P. C. (2005). Mortality dynamics and population regulation in *Bemisia tabaci*. *Entomologia Experimentalis et Applicata*, 116, 93–108.
- Ngowi, B. V., Tonnang, H. E. Z., Mwangi, E. M., Johansson, T., Ambale, J., Ndegwa, P. N., & Subramanian, S. (2017). Temperature-dependent phenology of *Plutella xylostella* (Lepidoptera: Plutellidae): Simulation

- and visualization of current and future distributions along the eastern Afromontane. *PLoS One*, 12, e0173590.
- Peacock, L., Worner, S., & Sedcole, R. (2006). Climate variables and their role in site discrimination of invasive insect species distributions. *Environmental Entomology*, 35, 958–963.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644.
- Pekar, S. (2002). Susceptibility of the spider *Theridion impressum* to 17 pesticides. *Journal of Pest Science*, 75, 51–55.
- Pereira, E. J. G., Picanço, M. C., Bacci, L., Della Lucia, T. M. C., Silva, E. M., & Fernandes, F. L. (2007). Natural mortality factors of *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) on *Coffea arabica*. *Biocontrol Science and Technology*, 17, 441–455.
- Philips, C. R., Fu, Z., Kuhar, T. P., Shelton, A. M., & Cordero, R. J. (2014). Natural history, ecology, and management of diamondback moth (Lepidoptera: Plutellidae), with emphasis on the United States. *Journal of Integrated Pest Management*, 5, D1–D11.
- Quan, X., Wu, L., Zhou, Q., Yun, Y., Peng, Y., & Chen, J. (2011). Identification of predation by spiders on the diamondback moth *Plutella xylostella*. *Bulletin of Insectology*, 64, 223–227.
- Rezende, M. Q., Venzon, M., Perez, A. L., Cardoso, I. M., & Janssen, A. (2014). Extrafloral nectaries of associated trees can enhance natural pest control. *Agriculture, Ecosystems and Environment*, 188, 198–203.
- Rodrigues-Silva, N., Campos, S. O., Farias, E. S., Souza, T. C., Martins, J. C., & Picanço, M. C. (2017). Relative importance of natural enemies and abiotic factors as sources of regulation of mealybugs (Hemiptera: Pseudococcidae) in Brazilian coffee plantations. *Annals of Applied Biology*, 171, 303–315.
- Rosado, J. F., Bacci, L., Martins, J. C., Silva, G. A., Gontijo, L. M., & Picanço, M. C. (2013). Natural biological control of green scale (Hemiptera: Coccidae): A field life-table study. *Biocontrol Science and Technology*, 24, 190–202.
- Roy, M., Brodeur, J., & Cloutier, C. (2005). Seasonal activity of the spider mite predators *Stethorus punctillum* (Coleoptera: Coccinellidae) and *Neoseiulus fallacis* (Acarina: Phytoseiidae) in raspberry, two predators of *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Biological Control*, 34, 47–57.
- Royama, T. (1981). Evaluation of mortality factors in insect life table analysis. *Ecological Monographs*, 51, 495–505.
- Silva, E. M., Silva, R. S., Silva, N. R., Milagres, C. C., Bacci, L., & Picanço, M. C. (2017). Assessment of the natural control of *Neoleucinodes elegantalis* in tomato cultivation using ecological life tables. *Biocontrol Science and Technology*, 27, 525–538.
- Silva-Torres, C. S. A., Pontes, I. V. A. F., Torres, J. B., & Barros, R. (2010). New records of natural enemies of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) in Pernambuco, Brazil. *Neotropical Entomology*, 39, 835–838.
- Southwood, T. R. E., & Henderson, P. A. (2000). The construction, description, and analysis of age-specific life-tables. In T. R. E. Southwood & P. A. Henderson (Eds.), *Ecological methods* (pp. 404–436). Oxford, UK: Blackwell Science.
- Sow, G., Arvanitakis, L., Niassy, S., Diarra, K., & Bordat, D. (2013). Life history traits of *Oomyzus sokolowskii* Kurdjumov (Hymenoptera: Eulophidae), a parasitoid of the diamondback moth. *African Entomology*, 21, 231–238.
- Steinbach, D., Moritz, G., & Nauen, R. (2017). Fitness costs and life table parameters of highly insecticide-resistant strains of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) at different temperatures. *Pest Management Science*, 73, 1789–1797.
- Suenaga, H., & Hamamura, T. (2015). Effects of manipulated density of the wolf spider, *Pardosa astrigera* (Araneae: Lycosidae), on pest populations and cabbage yield: A field enclosure experiment. *Applied Entomology and Zoology*, 50, 89–97.
- Talekar, N. S., & Hu, W. J. (1996). Characteristics of parasitism of *Plutella xylostella* (Lep., Plutellidae) by *Oomyzus sokolowskii* (Hym., Eulophidae). *Entomophaga*, 41, 45–52.
- Thorbeck, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, 41, 526–538.
- Togni, P. H. B., Venzon, M., Souza, L. M., Santos, J. P. C. R., & Sujii, E. R. (2019). Biodiversity provides whitefly biological control based on farm management. *Journal of Pest Science*, 92, 393–403.
- Vail, K. M., Kok, L. T., & Lentner, M. (1989). Broccoli yield response to selected levels of cabbage looper (Lepidoptera: Noctuidae) larvae in southwestern Virginia. *Journal of Economic Entomology*, 82, 1437–1443.
- Van Nouhuys, S., & Lei, G. (2004). Parasitoid-host metapopulation dynamics: The causes and consequences of phenological asynchrony. *Journal of Animal Ecology*, 73, 526–535.
- Wakisaka, S., Tsukuda, R., & Nakasuji, F. (1991). Life tables of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) and effects of rainfall, temperature and host plants on survival and reproduction. *Japanese Journal of Applied Entomology and Zoology*, 35, 115–122.
- Whitcomb, W. H., Gowan, T. D., & Buren, W. F. (1982). Predators of *Diaprepes abbreviatus* (Coleoptera: Curculionidae) larvae. *The Florida Entomologist*, 65, 150–158.
- Wilkinson, T. K., & Landis, D. A. (2005). Habitat diversification in biological control: The role of plant resources. In F. L. Wackers, P. C. J. van Rijn, & J. Bruin (Eds.), *Plant-provided food for carnivorous insects: A protective mutualism and its applications* (pp. 305–325). Cambridge, UK: Cambridge University Press.
- Zago, H. B., Siqueira, H. A. A., Pereira, E. J., Picanço, M. C., & Barros, R. (2014). Resistance and behavioural response of *Plutella xylostella* (Lepidoptera: Plutellidae) populations to *Bacillus thuringiensis* formulations. *Pest Management Science*, 70, 488–495.
- Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News*, 2, 7–10.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Farias ES, Santos RC, Carmo DG, et al.

Life tables for the diamondback moth (*Plutella xylostella*) in southeast Brazil indicate ants and spiders as leading mortality factors. *Ann Appl Biol*. 2020;1–10. <https://doi.org/10.1111/aab.12656>