



# The impact of climate change on tritrophic interactions and crop production

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## SUMMARY

A major goal in agroecology is to sustainably maximize crop yield while minimizing pest damage. One way to accomplish this is utilizing the highly coevolved tritrophic interactions between crops, pests, and the natural enemies of those pests. With anthropogenic changes to global climate; however, there is an increased potential to alter these interactions. We investigated the effect of increasing carbon dioxide and temperature on crop yield of a common agricultural ecosystem: the cabbage species *Brassica oleracea*, specialized cabbage aphid *Brevicoryne brassicae*, and parasitic natural enemy *Diaeretiella rapae*. To evaluate crop yield under varying carbon dioxide and temperature conditions, an agent-based model was created using Netlogo. Percent crop loss, maximum pest population, and rate of parasitism were analyzed under three different temperature and carbon dioxide conditions: preindustrial, current, and 2050 projected. Crop loss was most significant at projected 2050 temperature and CO<sub>2</sub> conditions, with an  $18.71 \pm 6.86\%$  increase in crop loss compared to preindustrial times, and a  $10.63 \pm 7.73\%$  increase compared to current conditions. *Brevicoryne brassicae* population sizes steadily increased from preindustrial times, while the rate of parasitism (proportion of *Brevicoryne brassicae* parasitized per day) remained constant under all three climate conditions. Our model predicts anthropogenic climate change will exacerbate crop loss over time, likely due to projected pest population increases, unless mitigative measures are implemented.

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## INTRODUCTION

Anthropogenic climate change has become one of the greatest global concerns of the 21st century.

The current climate crisis began with the industrial revolution, which initially had positive health and economic impacts such as increased food production and more reliable access to water (Pingali, 2012). Today, the excessive use of fossil fuels paired with rapid deforestation has caused the concentration of atmospheric greenhouse gases, such as carbon dioxide (CO<sub>2</sub>) and methane, to reach the highest levels seen in human history (IPCC, 2018). This rise has disturbed key

environmental processes, accelerating species extinction, spread of disease, and destruction of communities (FAO, 2018).

One of the most notable effects of climate change is the exacerbation of food insecurity which can induce malnutrition and disease spread, chronic food deprivation, and income instability during periods of low crop output (FAO, 2018). Environmental changes such as an increased number of natural disasters, reduced ground and surface water availability, and the increase in Earth's average surface temperatures continue to impact the quality and quantity of crops (Wheeler

and von Braun, 2019). These changes disrupt entire agroecosystems through complex interactions between trophic levels, making it difficult to predict how individual crop species will be affected. Though substantial research has been conducted regarding how individual climate variables affect different species' distribution and behaviours, the interactive effects between the various factors in multi-trophic agricultural systems have not been thoroughly explored.

*Brassica oleracea*, more commonly known as the wild cabbage plant, is one of the most economically important crops in the world, with cultivars of the species including broccoli, cabbage, collard greens and cauliflower (Higdon et al., 2007). The high levels of essential nutrients make this species not only economically important, but nutritionally important as well (Higdon et al., 2007). One of the greatest threats to crop yields is the specialist cabbage aphid *Brevicoryne brassicae*. *B. brassicae* has been found to reduce crop yields of the wild cruciferous and cultivated *B. oleracea* species by up to 75% and can indirectly damage crops through the transmission of 30 known viruses (Gazmer et al., 2015; Capinera, 2001).

Though *B. oleracea* has various structural defenses, such as a waxy coating that resists aphid feeding, top-down regulation through predation and parasitism remains a primary method of population control. The generalist endoparasitic wasp *Diaeretiella rapae* is a highly evolved biological control. *B. brassicae* feeding has been found to induce a systemic wound response in *B. oleracea* plants, which attracts the *D. rapae* parasitoid through the release of 3-butenyl isothiocyanate emissions (Blande, 2017). The tritrophic interaction between *B. oleracea*, *B. brassicae*, and *D. rapae* can be found globally, with extensive research on the individual trophic levels, as well as the direct plant-herbivore and herbivore-parasitoid interactions. Several lab studies have demonstrated how changes in climate parameters, most notably elevated temperature and CO<sub>2</sub>, affect species development, behaviour, and interactions between the species. Understanding how changes affect a tritrophic system under the combined effects of temperature and CO<sub>2</sub> is complex, yet vital to understanding what changes in crop yields can be anticipated and prepared for in the coming years.

The goal of our study is to assess how the aforementioned tritrophic interaction is affected under changing temperature and CO<sub>2</sub> conditions, and to determine how crop yield is affected in the system's native region of Western Europe. To achieve this goal, an agent-based model was developed simulating the tritrophic interaction under the climatic conditions of Western Europe. The following questions were investigated: (1) How do pre-industrial, current and projected temperature and CO<sub>2</sub> levels affect a crop yield within one growing season? (2) Do changing climatic conditions affect the population development of *B. brassicae*? (3) Do temperature and CO<sub>2</sub> conditions affect the efficacy of *D. rapae* as a biological control for *B. brassicae*?

## METHODS

### CLIMATE PARAMETERS

An agent-based model was created of the cabbage species *Brassica oleracea*, specialized cabbage aphid *Brevicoryne brassicae*, and generalist parasite *Diaeretiella rapae* using Netlogo (Wilensky, 1999). The model includes the climate parameters temperature (°C) and carbon dioxide (ppm) to investigate how anthropogenic climate change affects the tri-trophic system and crop yield. The model was run under preindustrial, current, and 2050 projected CO<sub>2</sub> and temperature conditions (Table 1). *B. oleracea* is native to Western Europe, so all temperature values are based on average European surface temperatures for the months of June to September, which reflects a typical crop season. There is some dispute as to what years fall under the pre-industrial era; however, we considered 1850 as pre-industrial in accordance with the National Oceanic and Atmospheric Administration.

### MODEL OVERVIEW

#### Herbivore and Parasitoid Development Time

In 2018, Soh et al. studied *B. brassicae* development time from nymph to adult at 5°C temperature increments, ranging from 10°C to 35°C. It was shown that development time decreases with increasing temperature (Soh et al., 2018). We used these measurements to obtain a polynomial regression for development time as a function of temperature (1). The following

regression determines the amount of time required for nymphs to reach adulthood and begin reproducing in the model where DT is development time (days) and T is temperature (°C) ( $R^2 = 0.99$ ):

$$(1) DT_{\text{herbivore}} = -0.0019T^3 + 0.1659T^2 - 4.8709T + 52.435$$

The development time of *D. rapae* has also been shown to decrease with increasing temperature. Saleh et al. 2014 recorded the total development time (in days) from egg to adult at 5°C temperature increments from 10°C to 30°C. This data was used to obtain a polynomial regression for development time as a function of temperature (2). The regression is used in the model to calculate the age at which parasitoid agents reach adulthood and can reproduce ( $R^2 = 0.99$ ):

$$(2) DT_{\text{parasitoid}} = -0.011T^3 + 0.759T^2 - 17.141T + 140.05$$

#### *Herbivore and Parasitoid Life Span*

The life span of *B. brassicae* is shown to decrease as temperature increases. Soh et al. 2018 recorded the life span of adult *B. brassicae* over the same 10°C to 35°C temperature range. To obtain the total lifespan from birth to death, the adult life span was added to the development time of *B. brassicae* and a polynomial regression was obtained with respect to temperature where TLS is total life span and T is temperature ( $R^2 = 0.91$ ). This function determines at what age herbivore agents die if they are not parasitized (3).

$$(3) TLS_{\text{herbivore}} = -0.0358T^2 + 0.209T + 34.87$$

An identical method was used to obtain the total lifespan function for *D. rapae* using data from Saleh et al. 2014 and linear regression ( $R^2 = 0.72$ ) (4).

$$(4) TLS_{\text{parasitoid}} = -0.8001T + 22.376$$

#### *Plant Dry Weight*

Researchers Stacey and Fellowes (2002) collected data on the dry weight of *B. oleracea* under ambient (350 ppm) and elevated (650 ppm) carbon dioxide. The average mass of *Brassica*

*oleracea* was found to increase when grown under elevated carbon dioxide conditions. To represent the increased average plant weight in the model, this data was used to obtain a linear regression for plant dry weight as a function of carbon dioxide (5).

$$(5) DW = 0.0036C + 1.236$$

where DW is dry weight (grams) and C is carbon dioxide (ppm) ( $R^2 = 1$ ) (5). The function was scaled to fit the energy parameters of the model, adjusted the maximum dry weight of a plant to the maximum energy level.

#### *Plant Nutritional Quality*

Stacey and Fellowes (2002) showed that under ambient CO<sub>2</sub>, the proportion of nitrogen present in plant tissues decreases. Nitrogen is a primary metabolite vital to *B. brassicae* growth; its decrease leads to a phenomenon known as compensatory feeding, where herbivory increases to compensate for decreased acquisition of nutrients (DeLucia et al., 2012). Stacey and Fellowes observed this phenomenon by recording an increase in *Brevicoryne brassicae* percent fat by weight with increasing CO<sub>2</sub>. To quantify increased herbivory as a function of CO<sub>2</sub>, a linear regression was obtained for aphid percent fat by weight as a function of CO<sub>2</sub> and used to determine biomass loss due to herbivory in the model (6).

$$(6) DW = 0.0036C + 1.236$$

where PF is percent fat by weight and C is carbon dioxide (ppm) ( $R^2 = 1$ ). The function was scaled to fit the energy parameters of the model.

#### *Output parameters and statistical analysis*

Each trial of the model was run for 100 ticks (representing days) to reflect the typical duration of a crop season (Brouwer and Heibloem, 1986). Percent crop loss, parasitism rate, and maximum herbivore population were analyzed under preindustrial, current, and 2050 projected temperature and CO<sub>2</sub> conditions (Table 1). Percent crop loss is the percentage of crops lost over one growing season. Parasitism rate is the average number of herbivores parasitized per day over one growing season. Maximum herbivore population is the largest population achieved over

one growing season. The model was run 25 times under each set of climate conditions. Starting populations for *D. rapae*, *B. brassicae*, and *B. oleracea* were held constant at 50, 50, and 700 respectively.

The effect of each climate condition on percent crop loss, maximum herbivore population, and rate of parasitism were analyzed with an ANOVA test followed by a post-hoc Tukey's test. Temperature and CO<sub>2</sub> were treated as one combined categorical variable titled 'Climate Condition', based on the year being modelled. Percent crop loss, maximum herbivore population, and rate of parasitism were all treated as numerical dependent variables. Rate of parasitism was arcsine square root transformed to meet the equal variance assumption for ANOVA. All statistical analyses were performed using R v3.5.2 (R Development Core Team, 2019).

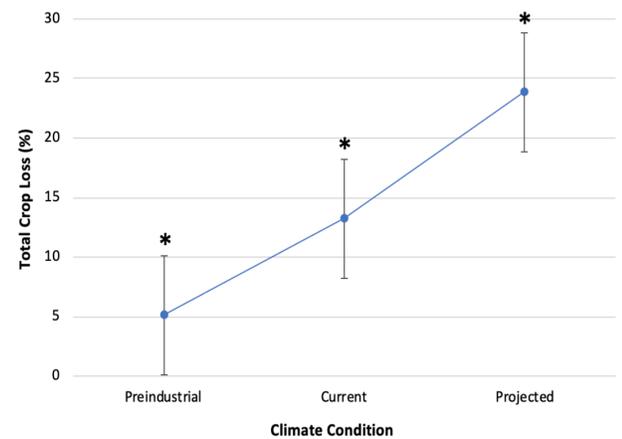
**Table 1.** Temperature data (°C) based on average European surface temperatures from June to September for the years 1850, 2018, and a projected value for 2050 (European Environment Agency, 2018). Global concentration of atmospheric carbon dioxide data (ppm) for the years 1850, 2019, and a projected value for 2050. 1850 and 2018 data are from the National Oceanic and Atmospheric Administration (2019). 2050 projection is from the Organisation for Economic Co-operation and Development (Marchal et al., 2011).

Climate Condition	Year	Temperature (°C)	CO <sub>2</sub> (ppm)
Preindustrial	1850	15.2	280
Current	2018	17	410
Projected	2050	18.2	500

## RESULTS

### PERCENT CROP LOSS

The percent crop loss is the proportion of crop yield lost at the end of the growing season. This proportion consistently increased as carbon dioxide and temperature increased, indicating a positive linear relationship as observed in Figure 1. Climate condition was found to have a significant effect on average percent crop loss ( $F_{2,57} = 70.717$ ,  $P = 3.634e-16$ ). A significant difference between average total crop loss was observed under all three climate conditions (Figure 1). The most severe crop loss was observed under 2050 projected conditions, while significantly milder crop loss was observed under 1850 preindustrial conditions. The model predicts an  $18.71 \pm 6.86\%$  increase in crop loss in the year 2050 compared to preindustrial times, and a  $10.63 \pm 7.73\%$  crop loss increase in 2050 compared to 2018.



**Figure 1:** The average percentages of crop loss (% ± SE) under preindustrial (1850), current (2018), and future (2050) climate conditions are  $5.16 \pm 3.87$ ,  $13.24 \pm 5.25$ , and  $23.87 \pm 5.67$  respectively. Climate condition includes temperature (°C) and carbon dioxide (ppm) (refer to Table 1). Climate condition had a significant effect on percent crop loss ( $F_{2,57} = 70.717$ ,  $P = 3.634e-16$ ). Significant differences between climate conditions and total crop loss are denoted with an asterisk (\*). Sample size is 20 for all groups.

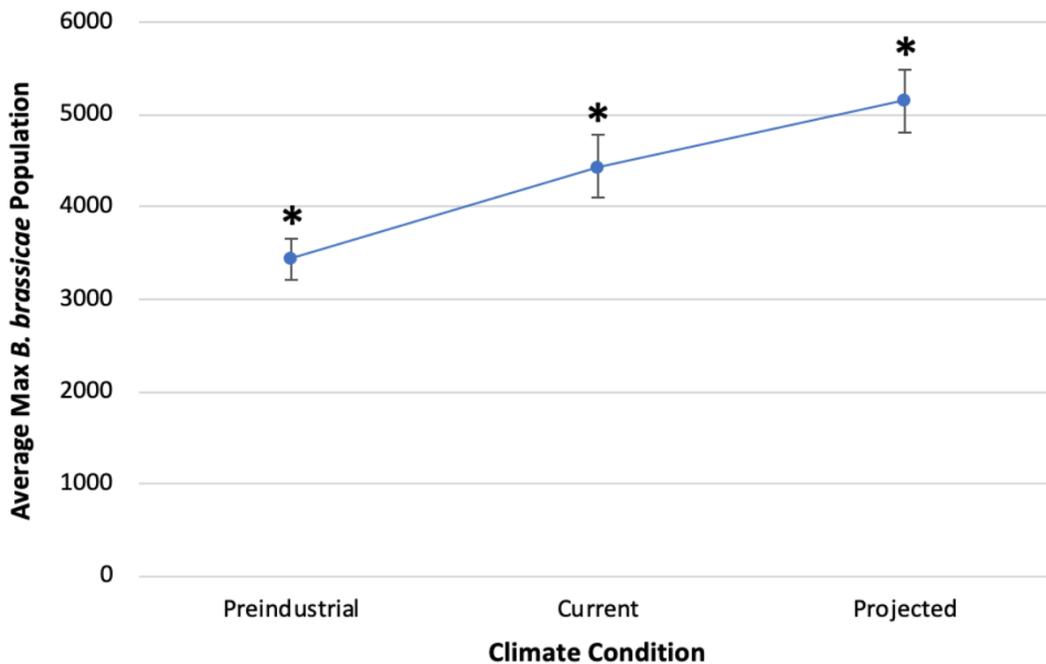
## MAXIMUM HERBIVORE POPULATION

The maximum herbivore population is the peak number of *B. brassicae* aphids during the growing season. As temperature and carbon dioxide increased, the population of *B. brassicae* was observed to increase. Figure 2 indicates that the effect of climate condition on maximum herbivore population is positive and approximately linear. Climate conditions were found to have a significant effect on the maximum herbivore population achieved ( $F_{2,57} = 116.85$ ,  $P = 2.2e-16$ ). A significant difference between average

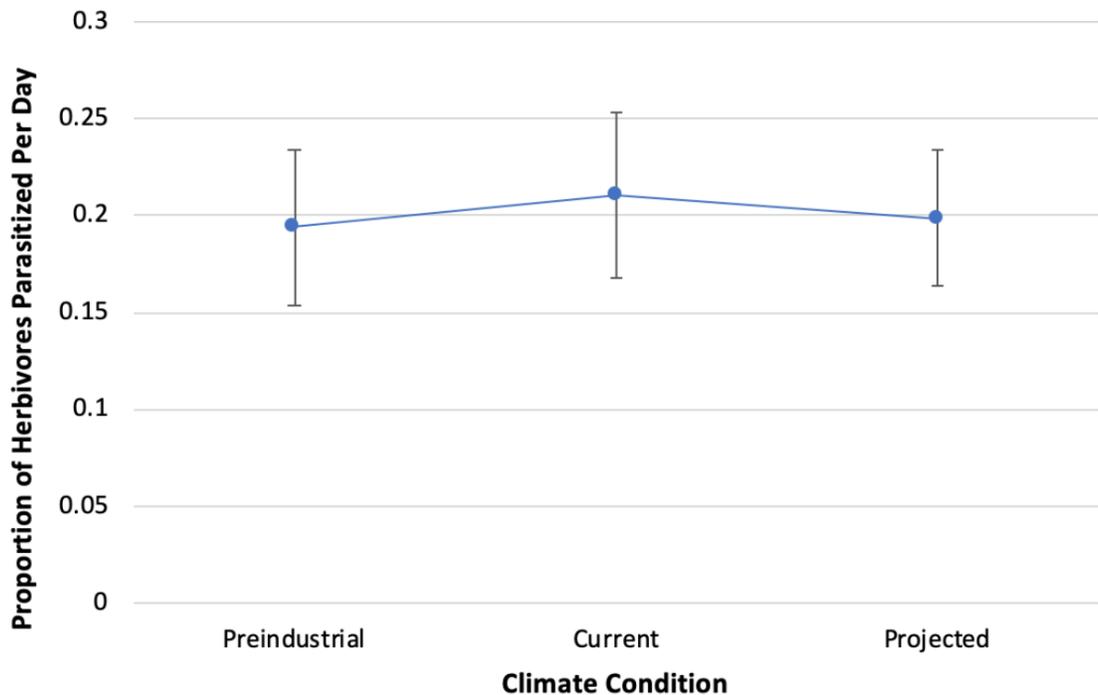
maximum herbivore population was observed under all three climate conditions (Figure 2). The model suggests herbivore populations will increase in 2050 by  $49.65 \pm 13.98\%$  from 1850 and a  $16.08 \pm 11.70\%$  from 2018.

## RATE OF PARASITISM

The rate of parasitism is a measure of the proportion of aphids parasitized per day. Climate condition was not found to have a significant effect on average rate of parasitism ( $F_{2,57} = 0.9859$ ,  $P = 0.3794$ ), which remained notably consistent within the range of 0.15 to 0.26 as illustrated in Figure 3.



**Figure 2:** Average max *B. brassicae* populations ( $\pm$  SE) achieved under preindustrial (1850), current (2018), and future (2050) climatic conditions are  $3443.0 \pm 225.8$ ,  $4438.8 \pm 336.3$ , and  $5152.4 \pm 342.7$  respectively. Climate condition includes temperature ( $^{\circ}\text{C}$ ) and carbon dioxide (ppm) (refer to Table 1). Climate condition had a significant effect on max *B. brassicae* population ( $F_{2,57} = 116.85$ ,  $P = 2.2e-16$ ). Significant differences between climate conditions and total crop loss are denoted with an asterisk (\*). Sample size is 20 for all groups.



**Figure 3:** Average max *B. brassicae* populations ( $\pm$  SE) achieved under preindustrial (1850), current (2018), and future (2050) climatic conditions are  $3443.0 \pm 225.8$ ,  $4438.8 \pm 336.3$ , and  $5152.4 \pm 342.7$  respectively. Climate condition includes temperature ( $^{\circ}\text{C}$ ) and carbon dioxide (ppm) (refer to Table 1). Climate condition had a significant effect on max *B. brassicae* population ( $F_{2,57} = 116.85$ ,  $P = 2.2e-16$ ). Significant differences between climate conditions and total crop loss are denoted with an asterisk (\*). Sample size is 20 for all groups.

## DISCUSSION

### EFFECTS OF CLIMATIC CONDITIONS ON CROP YIELDS

In this study, increased temperature and  $\text{CO}_2$  levels significantly increased percent crop loss. This can be explained by numerous factors, including the significant increase in maximum *B. brassicae* population under elevated climate conditions as well as compensatory feeding (Stacey and Fellowes, 2002). Elevated temperatures have consistently elicited a negative response among *Brassicae* crops, with effects ranging from a mild decrease in quality and output to catastrophic yield decrease at extremely high temperatures (Schaubberger et.al, 2017; Zhao et al., 2017; Kaur et al., 2017). Thermal stress has been shown to impair plant photosynthetic activity, reduce the dry weight of seedlings, and reduce leaf water content of *B. oleracea* which directly affects crop survival (Rodríguez et al., 2015).

In contrast to the effects of temperature, elevated carbon dioxide has been shown to increase *B. oleracea* dry mass, leaf area, and number of leaves as represented in our model (Stacey and Fellowes, 2002). This phenomenon occurs because stomatal conductance is regulated by atmospheric  $\text{CO}_2$  concentration, which ensures crops are able to intake  $\text{CO}_2$  while regulating the diffusion of water out of the stomata (Taub, 2010). In elevated conditions, plants are able to intake greater amounts of  $\text{CO}_2$  while maintaining a low stomatal conductance, resulting in significant increases in monocrop yields, noting 12-14% in wheat, rice and soybean crops (Taub, 2010). The elevated  $\text{CO}_2$  changes the composition of the plant as well, resulting in decreased nitrogen concentrations due to increased non-structural carbohydrate concentrations.

## EFFECTS OF CLIMATIC CONDITIONS ON APHID POPULATIONS

In this model, we found maximum *B. brassicae* populations increased with increasing temperature and CO<sub>2</sub>. This can be attributed to decreased *B. brassicae* development time under elevated temperature conditions (Soh et al., 2018). Faster development allows nymphs to reach reproduction age within a shorter period, in turn shortening the generation time. This has been seen in other aphids, such as corn aphids as well (Asin and Pons, 2001). Though the exact mechanism by which temperature influences development rate is unclear, studies have attributed it to feeding behaviour changes, nutritional quality of the plants, and physiological sensitivity to temperature which all have strong influences on *B. brassicae* development (Özder and Sağlam, 2013).

A meta-analysis of 80 field and lab studies investigating the effects of elevated temperature and CO<sub>2</sub> confirmed the trend of increasing aphid populations found in our model, noting that decreased development time, increased fecundity, and increased herbivory caused high proliferation rates (Srinivasa Rao et al. 2016). These increases were most notably observed among phloem feeders such as *B. brassicae* and species with high nitrogen requirements. In addition to herbivory induced crop damage (Xie et al., 2014), the increased number of adult aphids may potentially increase migration and virus transmission, further compounding the damages induced by aphid populations.

## RATE OF PARASITISM AND BIOLOGICAL CONTROL

To combat the extensive damage induced by *B. brassicae*, *D. rapae* is often cited as a primary method of biological control through parasitism (Moayeri et al., 2013). In our model, the rate of parasitism indicates the efficacy of *D. rapae* as a biological control against *B. brassicae* under various climatic conditions. The average proportion of aphids parasitized was approximately 0.2, with no significant difference between the three climate conditions (Figure 3). The parasitism rate is effective in pre-industrial conditions; however, it loses efficacy in current and future conditions, noted by the increase in

maximum herbivore populations and increased crop loss (Figures 1 & 2).

Based on equations (3) and (4), elevated temperature affects the lifespan of *D. rapae* to a greater extent than the *B. brassicae* lifespan, which likely played a key factor in the inability to increase parasitism at higher temperatures (Soh et al., 2018; Saleh et al., 2014). *D. rapae* only parasitizes *B. brassicae* individuals in the nymphal stage; suggesting the decrease in herbivore development time decreased the timespan to parasitize the aphid, reducing the potential for population regulation. Population regulation of *B. brassicae* by *D. rapae* at elevated temperatures has been studied by researchers Moayeri et al. (2013), who found that within the temperature range of 17-30°C, *D. rapae* exhibited a type II functional response. This indicates that the initial rate of parasitism will increase as *B. brassicae* density increases, however it will eventually plateau and be limited by the time required to parasitize a herbivore (Moayeri et al., 2013). These findings coincide with the findings of our model, as the average rate of parasitism remained consistent with increasing densities of *B. brassicae*.

*D. rapae* parasitism was not sufficient in preventing increased crop loss, thus the rapid population growth of *B. brassicae* suggests the need for additional population control. Other predators such as syrphid fly maggots, lady beetle adults and larvae, and lacewing larvae and plant extracts are biologic controls that can be used in conjunction with *D. rapae* (Gill et al., 2013). In addition to this, agricultural methods can be employed such as plowing the field following each harvest to reduce the spread of aphids and survival of eggs (Gill et al., 2013). With predictions of increased crop damage under the changing climate, finding suitable and effective methods for controlling *B. brassicae* and other economically detrimental aphids is crucial to improving global food security.

## LIMITATIONS

Tritrophic interactions and the factors which affect them are highly complex, resulting in numerous limitations to this model. Increased plant dry weight and compensatory feeding as a result of decreased nutrient quality were two vital

factors to include in the model. However, due to limited field data, the linear regression for plant dry weight (5) was based on only two means at 350 and 650 ppm CO<sub>2</sub> with a sample size of 24 (Stacey and Fellowes, 2002). The linear regression for *B. brassicae* percent fat by weight (6) was also obtained using two means at 350 and 650 ppm with sample size 10 (Stacey and Fellowes, 2002). Thus, the regressions have low statistical power and are only approximations of how plant dry mass and herbivory changes with CO<sub>2</sub>. In the future, regressions involving data points at more CO<sub>2</sub> concentrations with a greater sample size would be needed to improve the approximation. Equations (1) through (4) had greater statistical power, however all functions used in the model would be more accurate with a greater sample size and more temperature and CO<sub>2</sub> data points.

There are numerous environmental and biological factors which could be added to increase the accuracy of the model. For example, *B. oleracea* has been shown to release herbivore-induced plant volatiles (HIPVs) as a defense response to herbivory, which attracts various parasitoid species including *D. rapae* (Bruinsma et al., 2009). When grown under elevated CO<sub>2</sub> conditions (650 ppm), Klaiber et al. (2012) found a significant change in the chemical composition of *B. oleracea* HIPVs. In particular, terpene emissions after 10 weeks of elevated CO<sub>2</sub> exposure were significantly reduced, however the resulting effect on *D. rapae* attraction is still unknown (Klaiber et al., 2013). In addition to this, including water cycle disturbances such as droughts and floods would increase the model's ability to predict future crop yield (IPCC, 2018).

Future research could investigate beyond the proposed tritrophic interaction by introducing additional species. This could include adding another biological control, such as the ladybird beetle *Hippodamia convergens*, and comparing its efficacy to *D. rapae*. The model could also be improved by accounting for *B. oleracea* interactions with temperature and CO<sub>2</sub> sensitive soil microbes, a complex interaction which provides *B. oleracea* with nutrients and could affect crop quality and yield (Classen et al., 2015).

## CONCLUSION

The present study aimed to investigate the effect of increasing carbon dioxide and temperature on crop yield by modeling the tritrophic interaction between the cabbage plant *B. oleracea*, specialist aphid *B. brassicae*, and natural parasitic enemy *D. rapae*. Crop loss was found to increase significantly as anthropogenic climate change progressed, with an expected  $10.63 \pm 7.73\%$  increase in crop loss under 2050 climate conditions compared to 2018. Additionally, herbivore populations were found to increase significantly between preindustrial, current, and projected climate conditions while rate of parasitism remained constant. This model can be further developed with additional parameters such as herbivore-induced plant volatiles and changes in *B. oleracea*-soil microbe interactions. Furthermore, this model can be applied to the study of climate change mitigation strategies such as the use of parasitoids as a biological control. This allows us to predict the magnitude of interference needed to protect crop yields while ensuring the balance of the agroecosystem is maintained.

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## AUTHORSHIP AND CONTRIBUTIONS

Geetha Jeyapragasan found the appropriate tritrophic interaction collected seed data for the model, while Frances Lorenz derived the framework of the model. Both members created the Netlogo Model, and the results were statistically analyzed by Frances Lorenz. Geetha Jeyapragasan wrote the introduction, discussion, and conclusion while Frances Lorenz wrote the methods, results and limitations.

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