# ISSUES: FIGURE SET An inquiry-based approach for teaching Type III functional responses in ecology

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A bee on a yellow flower

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A male hoverfly (Photo by Alvesgaspar, CC BY-SA 3.0, via Wikimedia Commons)

**THE ISSUE:**

Maize (also known as corn) has played an important role in human agriculture ever since its domestication by indigenous peoples of Mexico some 10,000 years ago. The crop is now planted across the world, including in China. However, several invasive pests, including the fall armyworm *Spodoptera frugiperda*, have threatened this crop and lowered yield. *Eupeodes corollae*, an endemic syrphid hoverfly, has been proposed as a biological control agent. Here, students will explore the antagonistic relationship between *S. frugiperda* and *E. corollae*, with both species feeding on larvae of the other species and learn about type III functional responses. This Figure Set teaches about a reciprocally antagonistic ecological system, with systems and evolution being cross-cutting themes of the 4-Dimensional Ecology Education (4DEE) framework. In addition, this Figure Set also facilitates students’ examination of environmental ethics (as pertaining to biological control agents) and agricultural ecosystems, allowing for students to learn about human-environment interactions.

**FOUR DIMENSIONAL ECOLOGY EDUCATION (4DEE) FRAMEWORK**

* **Core Ecological Concepts:**
  + Ecosystems
    - Trophic levels
    - Predation
    - Networks
    - Regulators
* **Ecology Practices:**
  + Quantitative reasoning and computational thinking
    - Data analysis and interpretation
  + Designing and critiquing investigations
    - Evaluating claims
  + Working collaboratively
* **Human-Environment Interactions:**
  + Ethics
    - Environmental ethics
  + How humans shape and manage resources/ecosystems/the environment
    - Agricultural ecosystems
* **Cross-cutting Themes:**
  + Systems
  + Spatial and temporal
    - Evolution

**STUDENT-ACTIVE APPROACHES:**

Think/pair/share, jigsaw

**STUDENT ASSESSMENTS:**

Instructors can collect responses to the questions in this Figure Set as a formative assessment or may alternatively wish to transform some of these questions into multiple-choice clicker questions as students are working on the Figure Set.

**CLASS TIME:**

One 75-minute class period

**COURSE CONTEXT:**

Mid- to upper-level ecology class for biology majors; requires students to be familiar with predator-prey interactions, trophic levels, interspecific competition, evolutionary mechanisms, and type I and II functional responses. This Figure Set could be used in conjunction with Jean et al. (2023), which introduces Type I and Type II functional responses (https://tiee.esa.org/vol/v19/issues/figure\_sets/jean/abstract.html).

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**OVERVIEW**

**WHAT IS THE ECOLOGICAL ISSUE?**

Maize (*Zea mays*), typically known as corn to consumers, is a major agricultural crop that is used extensively for food, industrial processes, and fuel (Erenstein, Jaleta, Sonder, Mottaleb, & Prasanna, 2022). Demand for maize is expected to increase steadily in the coming decades, driven by increases in human population and the corresponding increase for maize as animal feed (Hubert, Rosegrant, van Boekel, & Ortiz, 2010). Thus, given this importance of maize, it is critical for ecologists to better understand the potential threats to maize production in order to mitigate such threats.

This Figure Set examines efforts to protect maize production in China, which is one of the world’s leading producers of maize. The country ranks second (behind the United States) in total maize production and produces over a fifth of the world’s maize each year, highlighting the importance of investigating ecological interactions that may impact maize production (Hou et al., 2020; Ranum, Peña-Rosas, & Garcia-Casal, 2014). One of these threats is the fall armyworm (*Spodoptera frugiperda*), an agricultural pest that is native to North and South America. This armyworm is migratory and has been rapidly expanding its range to other locations, reaching China in December 2018 and causing damage to over one million hectares of maize and other crops in each of the following years (Tay, Meagher, Czepak, & Groot, 2023; Zhou, Wu, Zhang, & Wu, 2021). The emergence of this invasive species, and the subsequent ecological and agricultural consequences of this introduction, have necessitated a search for strategies to combat the pest.

One strategy that has been proposed is the use of biological control agents, i.e., the release of other organisms to limit a pest population’s growth. One possible biocontrol agent is the hoverfly *Eupeodes corollae*, which is known to eat *S. frugiperda* larvae. Interestingly, adult *S. frugiperda* are also known to prey on *E. corollae* larvae, leading to bidirectional predation from both species (Li & Wu, 2022). This Figure Set guides students through critically thinking about a series of experiments that investigates this system and interactions between the two species, allowing students to evaluate the potential of *S. frugiperda* as a biological control agent for maize (Li et al., 2021). In addition to guiding students to think about experimental design, environmental ethics, and human-environment interactions, the Figure Set will introduce the concept of Type III functional responses.

**FIGURE SETS TABLE**

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| --- | --- | --- |
| **Figure Set** | **Student-active Approach** | **Cognitive Skill** |
| Investigating effects of reciprocal predation: Exploring biological control and type III functional responses | Small group work; think/pair/share; jigsaw | Interpretation, analysis, application |

**Learning Objectives:**

Students will be able to

* + Identify and explain the significance of Type III functional responses
  + Compare and contrast Type III functional responses to Type I and Type II functional responses
  + Critically interpret graphs showing functional responses
  + Explain the significance of biological control agents and the potential impact on agriculture
  + Discuss the ethical implications of biological control agents
  + Design experiments to test functional responses
  + Describe potential impacts of human agriculture on ecosystems
  + Predict the impact of various ecological changes, including how they may impact various evolutionary mechanisms (e.g., random genetic drift)

**Student Assessment:**

There are several possible modes of assessment. For instance, this Figure Set can be collected and used as a formative assessment, or instructors can transform some of the questions into poll questions. Instructors can also develop questions relating to functional responses for additional homework or quiz questions.

**FIGURE SET BACKGROUND**

This Figure Set introduces a case study examining efforts to protect the growth of maize (corn), a major agricultural crop, in China, from the fall armyworm (*Spodoptera frugiperda*). The fall armyworm is an invasive species that migrated to China in December 2018, devastating maize fields and leading to severe declines in maize production. Several options have been considered to control and limit the impact of *S. frugiperda*, including both the use of pesticides as well as biological control agents. One such potential biological control agent is the hoverfly *Eupeodes corollae*, which preys on *S. frugiperda* larvae.

This Figure Set uses this case study and a series of associated experiments that test predation of *E. corollae* on *S. frugiperda* (and vice versa) to introduce students to type III functional responses and guide students to think critically about the different types of functional responses. Questions are also designed to elicit critical thinking about predator-prey interactions, evolutionary consequences, and the bioethics of utilizing biological control agents. The Figure Set requires students to have prior knowledge about type I and type II functional responses. Instructors may wish to consult another Figure Set published in *Teaching Issues and Experiments in Ecology* that guides students to think about biological control agents and type I and type II functional responses (Hsu, 2018) and deploy this Figure Set as a follow up to the original Figure Set.‬‬‬‬‬‬‬‬‬‬‬‬‬‬‬‬

**STUDENT INSTRUCTIONS**

B

**Part 1: Review of functional responses**

We have previously learned how prey consumption rates by predators can be characterized by functional responses.

1. What are functional responses?
2. How are Type I and Type II functional responses different? Provide a biological explanation for the differences.
3. How might scientists use functional response information about a set (or sets) of species?

**Part 2: Introduction to study system and evolutionary connections**

We will be exploring functional responses using a case study of maize grown in China. Maize (*Zea mays*), often sold as corn in grocery stores, is a major agricultural crop and is used for food, industry, and fuel. Demand for maize is expected to increase over the next few decades, largely driven by maize being used for animal feed. China is one of the world’s leading producers of maize.

1. Think about humans planting agricultural crops like maize. How do you think such human activities may impact local ecosystems as well as biodiversity in the area?
2. What could potentially threaten the yield of agricultural crops? Brainstorm and list two to three possible factors that could lead to lower agricultural productivity.
3. One major threat to maize production in China is the agricultural pest *Spodoptera frugiperda*, also known as the fall armyworm. This armyworm is native to North and South America but spread suddenly to Africa in 2016 and to China by 2019. What ecological factors do you think could contribute to the rapid spread of *S. frugiperda*? Explain your reasoning.
4. *Spodoptera frugiperda* has spread from its native range, with several populations of this pest increasing in size. Which evolutionary force is expected to decrease in influence as a population increases in size? What is the impact of increased population size on genetic variation, and why is this important? Explain.
5. Other research has identified that there are high levels of gene flow between populations of *S. frugiperda*. Predict the impact of this gene flow on genetic variation in *S. frugiperda* populations and justify your response.

**Part 3: Impacts of fall armyworm and potential solutions**

1. The fall armyworm has caused significant damage to maize in China, decimating over one million hectares of this crop. Predict the consequence of the fall armyworm’s invasion on the common cutworm (*S. litura*), which is a native predator of maize in China. Then draw a graph to illustrate your prediction, labelling all axes.
2. *Spodoptera litura* has a number of predators, including wasps and other insects. Predict the impact of the *S. frugiperda* invasion on 1) wasps and other insects that feed on *S. litura* and 2) on the natural predators of wasps and other insects. Justify your response. Then draw a graph to illustrate your prediction, labelling all axes.
3. The application of pesticides that kill *S. frugiperda* has been proposed as one potential solution to reduce its damage to maize crops in China. Brainstorm one argument in favor of using pesticides and one argument against using pesticides. Be sure to brainstorm and think about the potential ecological impacts of the use of pesticides. Are there any ethical concerns with using pesticides?
4. Another approach that has been suggested to limit the impacts of *S. frugiperda* is the use of biological control agents, i.e., the release of natural predators. For instance, the hoverfly *Eupeodes corollae is known to eat S. frugiperda* larvae. Brainstorm one argument in favor of using biological control agents and one argument against using biological control agents. Be sure to think about the potential ecological impacts of the use of biological control agents. Are there any ethical concerns with using biological control agents?
5. Adult *S. frugiperda* also prey on *E. corollae* larvae, leading to bidirectional predation from both species. Predict how such an ecological relationship between these two species may influence population dynamics of both species. What information would be helpful to determine the impacts of this relationship? How could this complicate the use of *E. corollae* as a biological control agent?

**Part 4: Exploring functional responses**

1. To investigate the potential effectiveness and impact of *E. corollae* as a biological control agent, scientists from the China Agricultural University and Chinese Academy of Agricultural Sciences conducted a series of experiments to test the functional response of 1) *E. corollae* predation on *S. frugiperda* larvae and 2) *S. frugiperda* predation on *E. corollae* larvae. Outline below how you would design an experiment to test such functional responses.
2. Results from one of the experiments are shown below. The different shapes and lines on the graph represent experiments done with different ages (i.e., developmental stages) of predator and prey – these details are not important; instead, focus on the relationship between prey density and the number of prey consumed that is depicted in each of these graphs. How would you describe this relationship? Do these data support 1) a type 1; 2) a type 2; or 3) another type of functional response? Explain and justify your response.

A graph of a number of insects

Description automatically generated with medium confidence

**Figure 1. A.** Functional response curves of different hoverfly (*Eupeodes corollae*)development stages (represented by the different symbols) feeding on fall armyworm (*Spodoptera frugiperda)*. **B.** Functional response of fall armyworm (*S. frugiperda)* feeding on hoverflies (*E. corollae)* Different developmental stages of the prey are shown with different symbols. Note the different scales between graphs A and B. Figures and captions modified from Li et al. (2021). Reprinted under Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International license (CC BY-NC-ND 4.0).

1. Based on these data, which species likely has a higher rate of absolute predation on the other? I.e., which species will likely be able to eat more than the other species, everything else being equal? Remember to examine the axes values carefully in each of the above graphs. Explain your reasoning.
2. After examining both functional responses, do you think *E. corollae* wouldbe an effective biological control agent of *S. frugiperda* in China? Explain your reasoning.

**Part 5: Drawing conclusions**

1. This type of functional response seen in both graphs is known as a Type III functional response**.** (Though both graphs show the same type of functional response, you may wish to focus on the lines on the second graph, where it is likely a little easier to visualize the relationship.) Draw a graph that shows type I, type II, and type III responses and label your axes. After drawing this graph, in what ways is Type III a) similar and b) different from type I and type II functional responses? Explain.
2. Functional responses are often modeled by assuming that predators need time to first locate, handle, and then consume prey. For example, some predators may forage for prey, which may be unevenly distributed in the environment. Predators may search for a while before finding a cluster of prey and recognizing that location as an abundant area for prey. Using this framework, explain the trends seen in the type III functional response.

**NOTES TO FACULTY**

*Overview*

This Figure Set is designed for an upper-division ecology class and requires students to be familiar with experimental design, including knowing about controls and independent versus dependent variables. In addition, the Figure Set requires students to have prior knowledge of type I and type II functional responses. The instructor may wish to deploy another Figure Set published by the author in *Teaching Issues and Experiments in Ecology* that introduces the concept of functional responses and biological control agents (Hsu, 2018). The current Figure Set is designed to augment the original Figure Set published in 2018 (available at https://tiee.esa.org/vol/v13/issues/figure\_sets/hsu/abstract.html), which does not include any coverage of Type III functional responses outside of a potential out-of-class extension that asks students to research Type III functional responses. Here, this Figure Set builds upon students’ knowledge of type I and type II functional responses to challenge students to think critically about type III functional responses in the context of authentic experiments involving the fall armyworm *Spodoptera frugiperda* and the hoverfly *Eupeodes corollae*. ‬‬‬‬‬‬‬‬‬‬‬‬‬‬‬

These experiments were conducted recently (with the corresponding paper published in 2021) given the spread of the fall armyworm, which is an invasive agricultural pest that has devastated maize and other agricultural crops worldwide (Barros, Torres, Ruberson, & Oliveira, 2010; De Groote et al., 2020; Feldmann, Rieckmann, & Winter, 2019; Goergen, Kumar, Sankung, Togola, & Tamò, 2016; Li et al., 2021; Tay et al., 2023; Zhou et al., 2021). The fall armyworm arrived in China, a major producer of maize, in December 2018, leading agricultural scientists and ecologists to explore different options for controlling the spread and limiting damage to agriculture (Li et al., 2021; Paredes-Sánchez et al., 2021). One of these proposed options was the use of biological control agents, or natural predators of pests, including *E. corollae*, which is known to feed on larvae of *S. frugiperda*. Interestingly, *S. frugiperda* adults feed on *E. corollae* larvae, leading to reciprocal, bidirectional predation with the two species (Li & Wu, 2022).

The Figure Set steps students through critically thinking about the potential use of *E. corollae* as a biological control agent for *S. frugiperda*, while challenging students to consider ethical implications of using biological control agents and thinking about potential ecological impacts. In addition, the Figure Set guides students to learn and explore about Type III functional responses and interpret the significance of functional responses in the context of evaluating the potential of *E. corollae* as a biological control agent.

*Structure of Figure Set*

The Figure Set contains 19 questions grouped into five parts and is designed to be completed within 75-minute class period, though the time can be adjusted depending on students’ pace. Instructors can also modify the activity by removing questions and learning objectives that they do not feel are relevant to their course or adding additional questions to explore certain themes more in depth. The activity does not require much instructor preparation ahead of time other than distributing the handout, including printing the student handout or posting the handout on a course management system (e.g., Canvas, Moodle, Blackboard, etc.). Instructors have several options on how to structure the activity depending on the size of the class and the availability of additional teaching support (e.g., teaching assistants or learning assistants) in the class. For instance, instructors are encouraged to have students work together in small groups to answer the questions. For smaller classes, instructors could ask a different group to share their response with the class for each question, leading to a discussion of the key themes in between each question. Instructors wishing for students to spend more time on the activity could ask students to complete the activity individually first in class prior to working together in small groups, or even assign the activity as homework prior to class discussion. For larger classes, instructors could modify some of the questions into poll questions that they could project and use a poll-response system (e.g., TopHat, PollEverywhere) to gather responses from the entire class.

*Part I: Review of functional responses*

The first three questions of the Figure Set are designed to provide students a chance to review functional responses, given that the Figure Set assumes prior knowledge of Type I and Type II functional responses. The first two questions ask students to define functional responses, which show the relationship between prey density and the rate of predation, and to differentiate between Type I and Type II functional responses. In brief, Type I functional responses show a linear relationship between prey density and the number of prey consumed (i.e., a constant rate of predation). In contrast, type II functional responses show a decreasing rate of predation as the prey density increases, due to limits to predator intake rates as there become too many prey (Holling, 1965). Finally, question 3 asks students to consider why studying functional responses is important. Instructors may wish to highlight that understanding functional responses is critical for studying predator-prey relationships (impacting how ecologists model these dynamics and the impact on other trophic levels as well) and is also important for conservation biology. This latter point will segue well into the rest of the Figure Set, which has students exploring a study involving functional responses of *E. corollae* to evaluate its efficacy as a biological control agent in China.

*Part II: Introduction to study system and evolutionary connections*

In the second part of the Figure Set, students are introduced to the study system. Students are first asked to consider the potential ecological impacts of human agricultural activities, such as the planting of maize. Instructors may also wish to bring up the diversity of other human agricultural activities, which includes the planting of crops, aquaculture, as well as the raising of livestock. Many responses are possible here, and what students respond with may depend on if the class has had any previous discussions on agricultural impacts. Instructors can guide students to think about the impacts of modern agriculture on biodiversity, with agriculture in general decreasing biodiversity due to the loss or modification of natural habitats as well as the depletion of nutrients in the soil, water, or air (McLaughlin & Mineau, 1995; Stoate et al., 2009). In addition, the use of fertilizers and pesticides can have significant negative impacts on natural ecosystems and humans as well (Baweja, Kumar, & Kumar, 2020; Prashar & Shah, 2016). Instructors may wish to make connections to these topics if they have previously discussed these with the class. Students are then asked to consider potential threats to agricultural yield, which include pathogens, climate change, environmental degradation, and invasive species (McDonald & Stukenbrock, 2016; Paini et al., 2016; Sundström et al., 2014). Following this, the Figure Set then introduces the fall armyworm and describes its global spread, asking students to brainstorm potential ecological factors that contribute to its rapid migration to Africa, China, and beyond. Several ecological factors have been highlighted, including its ability to move long distances (thus contributing to higher migratory ability), feed off a variety of agricultural crops (i.e., its status as a generalist), and produce a large number of offspring (De Groote et al., 2020).

The final two questions of this part tie in evolutionary principles. Question 7 asks students to consider which evolutionary force is likely going to decrease in influence in a population that is expanding. Students should be familiar with the major evolutionary mechanisms of random genetic drift, selection, gene flow, and mutation and should identify that the influence of drift will decrease as a population increases in size, given that the influence of drift is inversely proportion to a population’s size (Ohta, 1973). Students should identify that since drift removes genetic variation, the population will maintain its genetic variation better following the increase in population size, and that genetic variation is important for a species’ resiliency. Similarly, question 8 guides students to think about the influence of gene flow on genetic variation. Gene flow (i.e., movement of individuals between populations that then reproduce in the new population) tends to homogenize populations and increase genetic variation given the potential of migrating individuals to bring new alleles into other populations. Indeed, past work on *S. frugiperda* have identified high levels of admixture between different populations (Arias et al., 2019).

*Part III: Impacts of fall armyworm and potential solutions*

In the next part, students are asked to consider the potential ecological impacts after the emergence of the invasive fall armyworm in China as well as potential solutions to mitigate the threat to maize and other agricultural crops. Students are first asked to predict the impact of *S. frugiperda*’s emergence in China on the common cutworm (*S. litura*), a native predator of maize. Instructors can highlight how species with similar ecological niches will compete for access to resources, and how the interspecific competition between the common cutworm and fall armyworm could potentially lead to decreases in the common cutworm’s population if the fall armyworm outcompetes it for access to food (Song et al., 2021). This competitive advantage has been demonstrated in both the lab and the field, and intriguingly, there is evidence that the fall armyworm preys upon immature stages of the common cutworm, accelerating the displacement and potential extirpation of the common cutworm (Song et al., 2021). Students may draw a variety of graphs to illustrate their prediction here; many students will likely draw a bar graph with two groups (before and after the fall armyworm invasion) on the x-axis and population size of the common cutworm (*S. litura*) on the y-axis. Students should show a lower population size for the common cutworm after the emergence of the fall armyworm.

Next, students are asked to consider the broader ecological impacts of *S. frugiperda*’s emergence in China by thinking about the impacts on natural predators of the common cutworm, which includes wasps and other insects (Ranga Rao, Wightman, & Ranga Rao, 1993). Students should reason that if the fall armyworm outcompetes the common cutworm, then the population sizes of common cutworms would decrease, thus leading to negative consequences for wasps and other insects that prey on the common cutworm. In addition, instructors may wish to highlight how such trophic interactions may be more complex if the wasps and other insects are generalists and do not depend on eating the common cutworm or are able to feed on the fall armyworm as well. Similarly, assuming that the population of wasps and other insects that feed on the common cutworm decreases, this means that the trophic level above these species may see a decrease in population size if their primary prey population diminishes. Instructors should again highlight the complex nature of such trophic interactions. Instructors may also note that there may be apparent competition between *S. frugiperda* and *S. litura*, if wasps and other insects can prey on both species. This term refers to the indirect interaction between two prey species who share a predator, where an increase in one prey’s population size can lead to increases in the predator population size and thus corresponding decreases in the other prey’s population (Holt & Bonsall, 2017). Like the previous question, students may draw a diversity of graphs to illustrate their prediction. Many students will again have a bar graph where the x-axis has groups for before and after the *S. frugiperda* invasion, and the y-axis is labelled with population size. Students should show a lower number of wasps and other insects that feed on *S. litura*, as well as a lower number of the natural predators of wasps and other insects, after the invasion.

The next two questions (questions 11 and 12) ask students to consider ethical implications of using pesticides and biological control agents. This question does not presume any previous knowledge about pesticides or biological control. Instead, the question asks students to brainstorm possible ethical arguments for or against the use of pesticides and biological control agents, and instructors can encourage students to bring in knowledge from other contexts (e.g., news articles, etc.) Some students may not be familiar with any of these advantages or disadvantages, and instructors may wish to spark a whole class discussion by listing some of these potential impacts. There are a wide range of positives and negatives for both approaches. For instance, pesticides are often initially very effective at controlling pest populations and may be cost effective, but can also harm a wide range of non-target native species as well and have negative impacts on human health (Kim, Kabir, & Jahan, 2017; Pimentel & Hart, 2001). Biological control agents, in contrast, are often seen as a ‘natural’ alternative to the use of pesticides and may be more cost-effective than pesticides depending on where the biological control agent is being obtained from. However, there are risks and ethical concerns associated with releasing non-native species into an ecosystem, which may cause negative consequences on non-target organisms or disrupt the ecosystem (Bentley & O’Neil, 1997; Delfosse, 2005; Lockwood, 2001). Similarly, there have been cases, such as with the release of the Asian ladybeetle, where the biological control agent has become a pest itself (Koch, 2003). Instructors who wish to spend more time on these topics may wish to facilitate a class wide discussion or debate on the use of these potential approaches to control pests.

The final question in this part (question 13) asks students to consider the reciprocal predation between the fall armyworm and the hoverfly, where adults of each species will prey on larvae of the other species. Instructors can use this bidirectional predation to emphasize the complex nature of ecological interactions and how such bidirectional predation may limit the population growth of both species, depending on the strength of the predation of each species on the other. Such bidirectional predation may complicate the use of *E. corollae* as a biological control agent by decreasing its effectiveness, particularly if the invasive *S. frugiperda* has a greater rate of predation on *E. corollae* than vice versa. If this is the case, it is possible that an introduction of *E. corollae* may potentially even increase the *S. frugiperda* population.

*Part IV: Exploring functional responses*

Part IV of the Figure Set now challenges students to think about designing experiments and interpreting data from such experiments. The first question (question 14) asks students to outline an experiment to test the functional response of the hoverfly on fall armyworm and vice versa. Students may design either lab- or field-based experiments; in either case, students should recognize that the independent variable should be the prey density, while the dependent variable is the predation rate (i.e., number of prey consumed by each predator). For instance, many lab-based experiments place prey in a petri dish and then introduce a predator before counting the number of prey eaten in a given amount of time. This experiment is then repeated with different number of prey in the petri dish (i.e., different prey densities) to generate a functional response. Experiments in the field would take similar approaches, though in a more natural environment. For instance, such a study could be conducted in the field with field cages placed over a natural habitat of the predator and prey (Xia, Rabbinge, & Van Der Werf, 2003). Instructors may wish to check with students about their experimental designs prior to moving on to question 15, which asks students to interpret authentic results from a study conducted with *S. frugiperda* and *E. corollae* (Li et al., 2021).

Question 15 presents students with published data of the functional response of *E. corollae* feeding on *S. frugiperda* and vice versa. Instructors should note that the two graphs have different scales on both the x- and y-axes, and that the first graph provides raw values while the second graph provides mean values. Thus, the first graph plots multiple points for each prey density, while the second graph only depicts one point for each prey density per developmental stage of predator and shows error bars. Here, depending on the size of the class and the pace of the activity, instructors may wish to perform a jigsaw where half of the groups are asked to interpret the results of *E. corollae* feeding on *S. frugiperda* larvae (the ‘hoverfly predator’ group), while the other half are asked to interpret the results of *S. frugiperda* feeding on *E. corollae* larvae (the ‘fall armyworm predator’ group). Following this, students can re-form groups that contain individuals from both hoverfly predator and fall armyworm predator groups. Such use of a jigsaw can lead to cooperative learning, where students in the second set of groups share their ideas and results from the initial group, leading to potentially richer discussion (Karacop, 2017). However, if instructors are short on time, they can opt to skip the second part of the jigsaw and instead ask for volunteers from both the fall armyworm predator and hoverfly predator groups to share out their ideas with the class. Alternatively, instructors may also assign each group to work with both sets of data.

Students should identify for both sets of data that the functional response is neither a type I nor type II functional response. These functional responses are not type I since they do not show a linear relationship between prey density and the rate of predation; instead, there is a sigmoid (S-shaped) curve. Similarly, while students may initially identify the graph as having similarities with type II functional responses, they are not type II, which show a decreasing amount of predation as the prey density increases. Instead, these functional responses initially show an increasing rate of predation as prey density increases, prior to this rate of predation gradually plateauing. Students should thus recognize that the data shown represents a new type of functional response that they have not previously learned, called a type III functional response. Instructors may wish to guide students to think about these functional responses at low, medium, and high prey densities, and ask students to examine the graphs at each of these intervals. For instance, at low densities the rate of predation should be increasing as the prey density increases. However, at medium densities this rate of predation begins to slow, before finally plateauing at high densities. Instructors should also note that this sigmoidal relationship may be challenging to see given the density of data points in the first graph and is clearer in the second graph. Instructors who wish to extend the activity can also point out to students that the graphs depict different developmental stages of *E. corollae* and *S. frugiperda,* which are depicted by the different symbols in the graph, and challenge students to think about why different developmental stages may have different rates of predation, and why there may be greater variation for some of these data.

Next, students are asked to interpret these data. Students should identify that *E. corollae* likely has a higher rate of predation than *S. frugiperda*, given that the hoverfly reaches a higher number of prey consumed than the fall armyworm does at maximum predation rates (i.e., the hoverfly reaches a higher asymptote for the number of prey consumed than the fall armyworm does, and would thus likely consume a higher number of prey). The instructor should highlight to students how the researchers used different prey densities in their experiments, leading to the two graphs having different values for the axes. Despite this greater rate of predation for *E. corollae*, instructors may wish to highlight the limitations here, including the fact that lab-based approaches (as seen in the experiment here) may not capture the true complexities of ecological interactions that are seen in the field, and that many factors may influence the true rate of predation in the wild. Similarly, natural ecosystems may not be able to sustain the prey densities tested in such lab-based experiments. Despite these limitations, students should recognize that if *E. corollae* has a significantly higher rate of predation on *S. frugiperda* than the other way around, then this would support the use of *E. corollae* as a biological control agent given its potential to consume more *S. frugiperda* than the other way around. Instructors may wish to guide students here given that the two graphs show different values on the x-axes by asking students to compare how many of each prey is eaten at an equal level of prey density. For example, instructors could ask students to consider a scenario where prey density is equivalent to 50 larvae per Petri dish; students should then be more easily able to compare the absolute rate of predation among the two predators at this same density.

*Part V: Drawing conclusions*

The final part of the Figure Set contains two concluding questions. First, question 18 introduces type III functional responses. Students should identify that unlike type I functional responses, there is no linear relationship between prey density and the rate of predation. However, similar to type II functional responses, type III functional responses also show a gradual decrease in the rate of predation as the prey density reaches saturation. In contrast to type II functional responses, though, organisms with type III functional responses will initially increase their rate of predation as the prey density increases. Students are challenged to consider what could explain this functional response in the final question. Students should identify that in type III functional responses, predators will initially search for prey more frequently as the prey density increases. For instance, it is possible that the predator here may identify clusters of prey based on pheromones or may learn to identify the prey after consuming a small amount, thus increasing its predatory searching and consumption. However, like with Type II functional responses, eventually the predator reaches saturation and cannot increase its rate of predation, thus leading to the sigmoidal curve seen in type III functional responses. If students struggle with coming up with these ideas, instructors may wish to spark a broader conversation with the entire class or provide hints, e.g., asking students to think about what happens if a predator identifies a prey cluster or learns how to identify the prey.

**ADDITIONAL** **RESOURCES**

There are several additional resources that may be helpful for instructors. First, I highlight the original Figure Set in *Teaching Issues and Experiments in Ecology* that introduces type I and type II functional responses as well as biological control agents (Hsu, 2018). Second, I direct the instructor to a helpful review of type III functional responses that includes an overview of articles that have identified type III functional responses and provides a discussion of why type III functional responses remain much rarer than type I or type II functional responses (Kalinkat, Rall, Uiterwaal, & Uszko, 2023). Other research and review articles describe type III functional responses in more detail (Beardsell et al., 2021; Krebs, 2022). Finally, instructors may wish to consult this recent review article on the ecology, evolution, and management options of *S. frugiperda*, which provides an overview of this invasive species, its ecology, its evolutionary history, and the various approaches taken to mitigate its spread (Tay et al., 2023).‬‬‬‬‬‬‬‬‬‬‬‬‬‬

**LITERATURE CITED**

Arias, O., E. Cordeiro, E., A. S. Corrêa, F. A. Domingues, A. S. Guidolin, and C. Omoto. 2019. Population genetic structure and demographic history of *Spodoptera frugiperda* (Lepidoptera: Noctuidae): implications for insect resistance management programs. Pest Management Science 75:2948–2957. doi: 10.1002/ps.5407

Barros, E. M., J. B. Torres, J. R. Ruberson, and M. D. Oliveira. 2010. Development of *Spodoptera frugiperda* on different hosts and damage to reproductive structures in cotton. Entomologia Experimentalis et Applicata 137:237–245. doi: 10.1111/j.1570-7458.2010.01058.x

Baweja, P., S. Kumar, and G. Kumar. 2020. Fertilizers and Pesticides: Their Impact on Soil Health and Environment. In B. Giri & A. Varma (Eds.), *Soil Health* (pp. 265–285). Cham: Springer International Publishing. doi: 10.1007/978-3-030-44364-1\_15

Arias, O., E. Cordeiro, A. S. Corrêa, F. A. Domingues, A. S. Guidolin, and C. Omoto. 2019. Population genetic structure and demographic history of *Spodoptera frugiperda* (Lepidoptera: Noctuidae): implications for insect resistance management programs. Pest Management Science, 75:2948–2957. doi: 10.1002/ps.5407

Barros, E. M., J. B. Torres, J. R. Ruberson, and M. D. Oliveira. 2010. Development of *Spodoptera frugiperda* on different hosts and damage to reproductive structures in cotton. Entomologia Experimentalis et Applicata 137:237–245. doi: 10.1111/j.1570-7458.2010.01058.x

Baweja, P., S. Kumar, and G. Kumar. 2020. Fertilizers and Pesticides: Their Impact on Soil Health and Environment. In B. Giri & A. Varma (Eds.), *Soil Health* (pp. 265–285). Cham: Springer International Publishing. doi: 10.1007/978-3-030-44364-1\_15

Beardsell, A., D. Gravel, D. Berteaux, G. Gauthier, J. Clermont, V. Careau, N. Lecomte, C.-C. Juhasz, P. Royer-Boutin, and J. Bêty. 2021. Derivation of predator functional responses using a mechanistic approach in a natural system. Frontiers in Ecology and Evolution 9:10.3389/fevo.2021.630944

Bentley, J. W. and R. J. O’Neil. 1997. On the ethics of biological control of insect pests. Agriculture and Human Values 14:283–289. doi: 10.1023/A:1007477300339

De Groote, H., S. C. Kimenju, B. Munyua, S. Palmas, M. Kassie, and A. Bruce. 2020. Spread and impact of fall armyworm (*Spodoptera frugiperda* J.E. Smith) in maize production areas of Kenya. Agriculture, Ecosystems & Environment 292:106804. doi: 10.1016/j.agee.2019.106804

Delfosse, E. S. (2005). Risk and ethics in biological control. *Biological Control*, *35*(3), 319–329. doi: 10.1016/j.biocontrol.2005.09.009

Erenstein, O., M. Jaleta, K. Sonder, K. Mottaleb, and B. M. Prasanna. 2022. Global maize production, consumption and trade: Trends and R&D implications. Food Security, 14:1295–1319. doi: 10.1007/s12571-022-01288-7

Feldmann, F., U. Rieckmann, and S. Winter. 2019. The spread of the fall armyworm *Spodoptera frugiperda* in Africa—What should be done next? Journal of Plant Diseases and Protection 126:97–101. doi: 10.1007/s41348-019-00204-0

Goergen, G., P. L. Kumar, S. B. Sankung, A. Togola, and M. Tamò. 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. PLoS ONE 11:e0165632. doi: 10.1371/journal.pone.0165632

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. The Memoirs of the Entomological Society of Canada 97:5–60. doi: 10.4039/entm9745fv

Holt, R. D. and M. B. Bonsall. 2017. Apparent competition. Annual Review of Ecology, Evolution, and Systematics 48:447–471. doi: 10.1146/annurev-ecolsys-110316-022628

Hou, P., Y. Liu, W. Liu, G. Liu, R. Xie, K. Wang, B. Ming, Y. Wang, R. Zhao, W. Zhang, Y. Wang, S. Bian, H. Ren, X. Zhao, P. Liu, J. Chang, G. Zhang, J. Liu, L. Yuan, H. Zhao, L. Shi, L. Zhang, L. Yu, J. Gao, X. Yu, L. Shen, S. Yang, Z. Zhang, J. Xue, X. Ma, X. Wang, T. Lu, B. Dong, G. Li, B. Ma, J. Li, X. Deng, Y. Liu, Q. Yang, H. Fu, X. Liu, X. Chen, C. Huang and S. Li. 2020. How to increase maize production without extra nitrogen input. Resources, Conservation and Recycling 160:104913. doi: 10.1016/j.resconrec.2020.104913

Hsu, J. L. 2018.

Hubert, B., M. Rosegrant, M. A. J. S. van Boekel, and R. Ortiz. 2010. The future of food: Scenarios for 2050. Crop Science 50:S33-S50. doi: 10.2135/cropsci2009.09.0530

Kalinkat, G., B. C. Rall, S. F. Uiterwaal, and W. Uszko. 2023. Empirical evidence of type III functional responses and why it remains rare. Frontiers in Ecology and Evolution 11:1033818. doi: 10.3389/fevo.2023.1033818

Karacop, A. 2017. The effects of using jigsaw method based on cooperative learning model in the undergraduate science laboratory practices. Universal Journal of Educational Research 5:420–434.

Kim, K.-H., E. Kabir, and S. A. Jahan. 2017. Exposure to pesticides and the associated human health effects. Science of The Total Environment 575:525–535. doi: 10.1016/j.scitotenv.2016.09.009

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science 3:32. doi: 10.1093/jis/3.1.32

Krebs, C. J. 2022. Some historical thoughts on the functional responses of predators to prey density. Frontiers in Ecology and Evolution 10:1052289. doi: 10.3389/fevo.2022.1052289

Li, H., S. Jiang, H. Zhang, T. Geng, K. A. G. Wyckhuys, and K. Wu. 2021. Two-way predation between immature stages of the hoverfly *Eupeodes corollae* and the invasive fall armyworm (*Spodoptera frugiperda* J. E. Smith). Journal of Integrative Agriculture 20:829–839. doi: 10.1016/S2095-3119(20)63291-9

Li, H. and K. Wu. 2022. Bidirectional predation between larvae of the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) and the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Journal of Economic Entomology 115:545–555. doi: 10.1093/jee/toab268

Lockwood, J. A. 2001. The Ethics of “Classical” Biological Control and the Value of *Place*. In *Balancing Nature: Assessing the Impact of Importing Non-Native Biological Control Agents (An International Perspective)*. Entomological Society of America. doi: 10.4182/RMVT4781.2001.100

McDonald, B. A. and E. H. Stukenbrock, 2016. Rapid emergence of pathogens in agro-ecosystems: Global threats to agricultural sustainability and food security. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20160026. doi: 10.1098/rstb.2016.0026

McLaughlin, A. and P. Mineau. 1995. The impact of agricultural practices on biodiversity. Agriculture, Ecosystems & Environment 55:201–212. doi: 10.1016/0167-8809(95)00609-V

Ohta, T. 1973. Slightly deleterious mutant substitutions in evolution. Nature 246:96–98. doi: 10.1038/246096a0

Paini, D. R., A. W. Sheppard, D. C. Cook, P. J. De Barro, S. P. Worner, and M. B. Thomas. 2016. Global threat to agriculture from invasive species. Proceedings of the National Academy of Sciences 113:7575–7579. doi: 10.1073/pnas.1602205113

Paredes-Sánchez, F. A., G. Rivera, V. Bocanegra-García, H. Y. Martínez-Padrón, M. Berrones-Morales, N. Niño-García, and V. Herrera-Mayorga, (2021). Advances in control strategies against *Spodoptera frugiperda*. A Review. Molecules 26:5587. doi: 10.3390/molecules26185587

Pimentel, D. and K. Hart. 2001. Pesticide Use: Ethical, Environmental, and Public Health Implications. In A. W. Galston & E. G. Shurr (Eds.), *New Dimensions in Bioethics: Science, Ethics and the Formulation of Public Policy* (pp. 79–108). Boston, MA: Springer US. doi: 10.1007/978-1-4615-1591-3\_6

Prashar, P. and S. Shah. 2016. Impact of Fertilizers and Pesticides on Soil Microflora in Agriculture. In E. Lichtfouse (Ed.), *Sustainable Agriculture Reviews: Volume 19* (pp. 331–361). Cham: Springer International Publishing. doi: 10.1007/978-3-319-26777-7\_8

Ranga Rao, G. V., J. A. Wightman, and D. V. Ranga Rao. 1993. World review of the natural enemies and diseases of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae). International Journal of Tropical Insect Science 14:273–284. doi: 10.1017/S1742758400014764

Ranum, P., J. P. Peña-Rosas, and M. N. Garcia-Casal. 2014. Global maize production, utilization, and consumption. Annals of the New York Academy of Sciences 1312:105–112. doi: 10.1111/nyas.12396

Song, Y., X. Yang, H. Zhang, D. Zhang, W. He, K. A. G. Wyckhuys, and K. Wu. 2021. Interference competition and predation between invasive and native herbivores in maize. Journal of Pest Science 94:1053–1063. doi: 10.1007/s10340-021-01347-6

Stoate, C., A. Báldi, P. Beja, N. D. Boatman, I. Herzon, A. van Doorn, G. R. de Snoo, L. Rakosy, and C. Ramwell. 2009. Ecological impacts of early 21st century agricultural change in Europe – A review. Journal of Environmental Management 91:22–46. doi: 10.1016/j.jenvman.2009.07.005

Sundström, J. F., A. Albihn, S. Boqvist, K. Ljungvall, H. Marstorp, C. Martiin, K. Nyberg, I. Vågsholm, J. Yuen , and U. Magnusson. 2014. Future threats to agricultural food production posed by environmental degradation, climate change, and animal and plant diseases – a risk analysis in three economic and climate settings. Food Security 6*:*201–215. doi: 10.1007/s12571-014-0331-y

Tay, W. T., R. L. Meagher, C. Czepak, and A. T. Groot. 2023. *Spodoptera frugiperda*: Ecology, evolution, and management options of an invasive species. Annual Review of Entomology 68:299–317. doi: 10.1146/annurev-ento-120220-102548

Xia, J. Y., R. Rabbinge, and W. van der Werf. 2003. Multistage functional responses in a ladybeetle-aphid system: Scaling up from the laboratory to the field. Environmental Entomology 32:151–162. doi: 10.1603/0046-225X-32.1.151

Zhou, Y., Q. Wu, H. Zhang, and K. Wu. 2021. Spread of invasive migratory pest *Spodoptera frugiperda* and management practices throughout China. Journal of Integrative Agriculture 20:637–645. doi: 10.1016/S2095-3119(21)63621-3