



Research Article

Modeling and Sensitivity Analysis of the Role of Biodiversity to Control Pest Damage in Agroecosystems

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Abstract

The paper provides a mathematical framework for cost-effective and environmentally safe strategies to minimize alfalfa damage from pests in alfalfa agroecosystems with optimal biodiversity levels and to predict outcomes for scenarios not covered by field experiments. Alfalfa is the most important forage legume world-wide and is a valuable source of nutrition for farm animals. The potato leafhopper (PLH) pest damages the alfalfa plant leading to a reduction of the productivity, a loss in nutritional value, and a decrease in milk production. The PLH pest outbreaks are also prone in monocultures. New mathematical models are shown to accurately fit results from field experiments utilizing plant diversity and enemies (pest-predator) hypotheses. The focus is on polyculture as a farming technique and the damsel bug, *Nabis*, a natural predator of the PLH. Mathematical methods include the Shannon diversity index, differential equations, scramble competition approaches, and sensitivity analysis to determine critical parameters.

Keywords: alfalfa, mathematical modeling, sensitivity analysis, Shannon diversity index, plant-herbivore-predator system

1 Introduction

Alfalfa, *Medicago sativa*, is a perennial flowering plant from the Fabaceae family. The alfalfa plant is the most cultivated forage legume in the world. The US is the largest alfalfa producer in the world, and alfalfa is Pennsylvania's second-most important crop. Its primary benefits include a high yield per hectare and a high nutritional value (high protein content and highly digestible fiber) for cows and other farm animals [15, 14]. The Potato Leafhopper (herein after "PLH"), *Empoasca fabae*, is the main pest associated with alfalfa and is known to damage the leaves of the alfalfa plant by injecting its saliva into the plants. This causes the alfalfa's usual green leaflets to turn yellow due to the "hopper burn" (triangular areas pointing inwards), leading to a degradation in crop quality and quantity, interference with the growth of the plant, a loss of nutrition to farm animals, a decrease in milk production from cows [9], and a severe monetary loss for farmers. These highly mobile herbivores cause \$15 million in damage to alfalfa annually in Pennsylvania alone. Under modern agricultural practices, alfalfa is planted in monoculture, and the PLH regularly exhibits population outbreaks for pure alfalfa stands. Pesticides used present both serious ecological and monetary costs in addition to potential health risks and a decrease in a product's market value, such as milk, compared to a pesticide-free product [8].

Alternative techniques to minimize pest damage that have shown success in other agroecosystems [6, 12, 17], include combinations of approaches based on plant diversity and

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predator-enemies hypotheses. The diversity hypothesis [3, 12] states that a greater biological diversity of a community of organisms leads to a greater stability of that community. The diversity hypothesis suggests that increased diversity in crop fields can prevent outbreaks of herbivorous pests by interfering with the pest colonization of crop plants, enhance natural enemy populations, or both [4]. Increasing plant diversity can directly reduce herbivorous pests by reducing their ability to locate and remain on host plants [3]. So, planting grasses within an alfalfa field may reduce the number of the PLH since they are not able to reproduce or rear nymphs on grasses [10]. Alfalfa and grass mixed fields, also known as polycultures, may better protect alfalfa from the PLH and lower the PLH abundance compared to a pure alfalfa field or monoculture, and therefore less alfalfa damage is expected. Moreover, polyculture fields, commonly found in nature, are not prone to pest outbreaks. Farmers, however, prefer monoculture fields because they yield more product than that of the polyculture fields due to the extraneous plants intermingled with the main crop.

The enemies hypothesis states that predatory insects are more effective at controlling populations of herbivores in diverse systems of vegetation than in simple ones [13]. Thus, it claims that predatory insects are more abundant and effective at reducing populations of herbivorous insects in diverse vegetation systems [13]. In other words, predators kill herbivorous pests at higher rates in polycultures than in monocultures, thus significantly reducing herbivore populations. The damsel bug, Nabis, is the main natural predator of the PLH, and it is used in this project as the predator to control the population of the PLH and thus control the damage to the alfalfa. The Nabis lives on low-growing plants and is especially common in agricultural habitats, such as alfalfa [11]. It feeds on several economically important pests. In fact, the Nabis is believed to be a beneficial insect.

Historically, disturbances such as the introduction of natural enemies, implementation of vegetation diversity, and the use of traditional pesticides when each has been considered independently [1] have proved inadequate as a single control of herbivorous insect populations [1]. It is important to convey both mathematically and via actual field experiments the economical and ecological benefits associated with a successful strategy that combines plant diversity and enemies hypotheses. These benefits go beyond the annual alfalfa's quantity yield and limited use of pesticide. This paper provides evidence of selecting such a successful strategy.

This project uses recent data from field experiments, by Straub et al., that investigated a merge of diversity and enemies hypotheses. Mathematical models and computer simulations are then developed for cost-effective and environmentally-safe strategies to minimize alfalfa damage from pests and to maximize farmers' profit with optimal biodiversity levels. The data and other relevant results on enemies and diversity hypotheses were also used to determine parameter ranges and to validate the models. Parameters were adjusted to predict outcomes for scenarios not covered by field experiments. Sensitivity analysis was used to determine the impact of each parameter on the system and to detect critical parameters. Modeling techniques included the creation of a system of differential equations that incorporates the Shannon Diversity Index, implicit age structures, scramble competition and other modeling approaches. By creating mathematical models, shown to be accurate, it was possible to identify management strategies to best control alfalfa damage while taking many simultaneous factors into consideration. The models were also used to produce results consistent with the various field experiments and to inform future field experiments using insights on the relationships between the alfalfa damage, the PLH, the Nabis and pesticides.

2 Overview of Field Experiments

This section gives an overview of the field experiments conducted to produce data used in this paper. The field experiments by Straub et al. [15] consisted of enclosed field and open field experiments, each with four different settings: monoculture with the Nabis absent, monoculture with the Nabis present, polyculture with the Nabis absent, and polyculture

with the Nabis present.

The enclosures in the enclosed field experiments were composed of 20 plots, each of 0.56 m² in size. The twelve that were used for the actual experimentation, included the PLH and the predatory insect Nabis, and variable levels of plant diversity. In addition, four monoculture and four polyculture plots were used for the experimental control group and contained no PLH. The control group was used to keep track of the damage done to the alfalfa due to environmental factors other than the pest. Monoculture fields held thirty-two alfalfa stems while polyculture fields held sixteen alfalfa stems intermixed with orchard grass for equal densities of plant life. Orchard grass does not affect the growth of alfalfa, and is also not a source of food for the PLH. Thus the orchard grass did not directly affect the damage done to the alfalfa as it neither shared resources nor was an alternative source of food for the pest. Each treatment was stocked with thirty PLH adults and four Nabis adults. Thirty days were initially considered for the experiment; this is the growth period of alfalfa before it is cut for the first time, to see if any cycles occurred ([18], [15]). However, the experiments lasted for fourteen days due to unfavorable conditions that summer, including high temperatures and limited precipitations unsuitable for insect life. Data was collected in two different ways;

1. by observation: standing outside of the enclosures and counting all of the insects that were seen inside of the enclosures;
2. by density data: the biologists went inside the enclosures and disturbed the alfalfa, and then counted all of the insects that flew from the stems.

Since the density data is more accurate, this is the data used for the model.

The open field experiments [16] consisted of twelve larger open-field plots (8 meters by 10 meters each). These plots were planted alternating monoculture and polyculture fields. In the monoculture plots broadleaf weeds were manually removed and a selective herbicide, Poast, was used to remove grasses. All broadleaf weeds and grasses were left in the polyculture treatments. To control for bare ground produced from plant removal in monoculture plots, an approximately equal proportion of bare ground was produced in polyculture plots through indiscriminate removal of plants. Plots were sampled weekly to determine insect and alfalfa densities as well as alfalfa damage caused by the PLH. Insect samples were collected through sweep sampling and ten sweeps were performed per plot at a standard depth from the center. Twenty stems of alfalfa were randomly chosen and removed from each plot per week, and were analyzed to determine number of the PLH and predator. Damage to alfalfa caused by the PLH was ranked per stem on a scale from 0 to 10; 0 corresponding to 0% of leaflets showing hopper burn; 1 corresponding to 1–10% of leaflets hopper burn; etc. Two 1-meter-by-1-meter squares were haphazardly selected within each plot on a weekly basis. Percentages of alfalfa, broadleaf weed, grass, and bare ground were estimated within each of these squares for vegetation analysis. Stem counts were performed within each square to determine stem density of alfalfa and other plants. Sticky traps were collected on a weekly basis and caught insects were identified and counted.

3 Plant Diversity Index

This section introduces the plant diversity index as a mathematical measure of plant diversity. This index is subsequently used to develop functions that measure the impact of that index on the interactions between the PLH pest, the predator Nabis, and the plants in the ecological systems of alfalfa fields. A diversity index should provide more information about community composition than simply the number of species present, and should take the relative abundances of different species into account. The Shannon-Weiner Diversity Index H is used in this paper. The measure of the diversity is based on species richness, the number present, species evenness, and the distribution of the number of organisms per

species [2]. The index H is then defined by

$$H = - \sum_{i=1}^S p_i \ln p_i,$$

where S is the total number of species in the community, and p_i is the proportion of S made up of the i^{th} species [5]. Values for H in this paper are found for monoculture and various polyculture fields. Since $S = 1$ for monoculture, H is zero. With $S = 2$ for our polyculture plot, alfalfa and “other plants” (its composition does not matter although it is essentially orchard grass), with the minimum of 50% of alfalfa, $H = \ln 2$. Thus in the mathematical models, the parameter H is between zero (complete monoculture) and $\ln 2$ (fifty-percent polyculture).

How should we translate H in the modeling process to accurately represent the impact of plant diversity in the alfalfa-PLH-Nabis interactions? Based on the data and the hypotheses, an increase in the diversity index H causes a decrease in alfalfa damage through the decrease in the PLH population. In addition, this decrease in alfalfa damage is bounded between an exponential curve and a linear curve. The impact of H is reflected in the mathematical models via a function, noted $f(H)$, that implicitly impacts the gain to the PLH adult population from the PLH nymphs. Two separate functions were drawn out, a linear form and an exponential form:

$$f(H) = 1 - k_l H \quad \text{or} \quad f(H) = e^{-k_e H}. \quad (1)$$

Both functions satisfy $f(0) = 1$; thus there is no reduction factor on the alfalfa damage in a monoculture setting. They should also satisfy the plant diversity impact found in the data from the field experiments with $H = 50\%$. This will be used to determine the values of k_l and k_e in equations (1) for both enclosed and open field experiments. The values of k_l and k_e were found by considering the change in the PLH nymphs from monoculture to polyculture (at the 50% level). The percentage that remained was used as the value of $f(H)$ when $H = \ln(2)$ (50% plant diversity), then solved for k_l and k_e . For the open field experiments, in average only 89.286% of the PLH nymphs remained in polyculture versus monoculture fields. Thus the corresponding values of k_l and k_e are:

$$k_l = 0.1546 \quad \text{and} \quad k_e = 0.1635. \quad (2)$$

For the data from the enclosed field experiments, it was found that only 70% of nymphs remained. Thus

$$k_l = 0.43280 \quad \text{and} \quad k_e = 0.51457. \quad (3)$$

4 Mathematical Modeling

In this paper, two models are considered: one for the enclosed field experiments and one for the open field experiments. Initially, a standard age-structure approach was used with three explicit compartments for the insects’ life cycle (eggs, nymphs and adults) for both the PLH and the Nabis, where all possible interactions within the same species as well as across species and alfalfa were considered. However, the model was too complex, it was not considered of interest to ecologists, and most parameters were impossible to evaluate through the field experiments or through search in literature. An alternative and creative modeling approach focusing mainly on the adult stage of the insects was then used. It implicitly incorporates age-structure, and was ultimately more practical for this project and favored by ecologist colleagues. This implicit age structure incorporated the impact of plant diversity on the life cycles for both the predator Nabis and the herbivore prey PLH, especially through the impact of the function $f(H)$ described above. Other modeling techniques used to create systems of differential equations, included logistic, scramble competition and

the Allee effect. The scramble competition states that the survival and reproduction of individual organisms declines as the density of the population rises. The Allee effect defines the positive correlation between population density and individual fitness. The logistic approach takes in consideration the limited resources and the impacts of the interactions on changes of each population class. These modeling approaches allowed the models to accurately represent the dynamics between populations of the PLH and the Nabis as well as the Alfalfa damage and plant diversity effect. For the models created, it is assumed that the only way to leave the system is through death. No migration was considered in particular because it was not a factor for the enclosed field experiments and sampling was used in the middle of the open field experiments; thus, insects only leave the system through death. For the PLH life cycle, only death due to predator consumption is considered (because the shorter experiment time period).

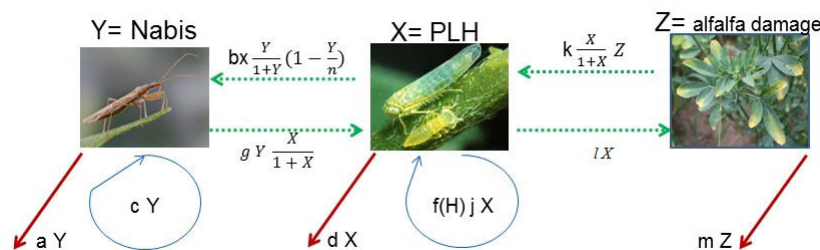


Figure 1: Open Field Experiment Model – Flow Diagram

Table 1: Open-Field Experiment Parameters

Parameter	Description
a	predator adult mortality rate
b	predator adult consumption rate of PLH adults
c	predator adult population gain from nymphs
d	PLH adult mortality rate
g	PLH adult mortality rate by adult Nabis harm
j	PLH adult population gain from nymphs
k	PLH adult benefit from alfalfa
l	PLH adult consumption rate of alfalfa
H	diversity index
m	recovery coefficient of alfalfa in absence of damage
n	carrying capacity

The model in Figure 1 for the open field experiments shows the interaction between the three variables: adult predator (Y), adult pest (X), and plant damage (Z). The associated eleven parameters are included below in Table 1. The corresponding differential equations are

$$\begin{aligned} \frac{dY}{dt} &= -aY + bX \left(\frac{Y}{1+Y} \right) \left(1 - \frac{Y}{n} \right) + cY, \\ \frac{dX}{dt} &= -dX - gY \left(\frac{X}{1+X} \right) + f(H)jX + k \left(X \frac{Z}{1+X} \right), \\ \frac{dZ}{dt} &= lX - mZ. \end{aligned}$$

For the enclosed field experiments, the model and the system of differential equations are similar to those for the open field with the exception that the recovery coefficient of alfalfa in absence of damage m is set to 0.

5 Simulations, Analysis, and Comparison to Field Experiments

For the simulations of the models, parameters were derived and adjusted from the experimental data to produce the best fit between the graphs given by the models and the actual data. It was shown that the exponential forms of the functions $f(H)$ defined in equations (2) and (3) give a better fit. Simulations were performed for various scenarios: open and enclosed fields, monoculture and polyculture, with or without the predator Nabis, and with exponential and linear forms of $f(H)$. It was clear that the simulations fit the data from the experiments well. Figure 2 shows two examples of simulations for the open field experiments in a polyculture setting with the Nabis. In each figure, the green curve represents the predator Nabis, the blue curve represents the pest PLH, and the red curve represents the damage to the alfalfa. The dashed curves represent the trend curves (best fit) obtained from the actual data points from the field experiments, and the colors of the dashed curves match the colors of the corresponding simulation curves. This strongly validated the models, especially that similar accuracies between the simulations and the actual experimental data were also observed in other tested scenarios. The models can then be used to make predictions, develop strategies and inform decisions about new field experiments to minimize the alfalfa damage while efficiently maximizing alfalfa production with the optimal combination of plant diversity and predator insect abundance.

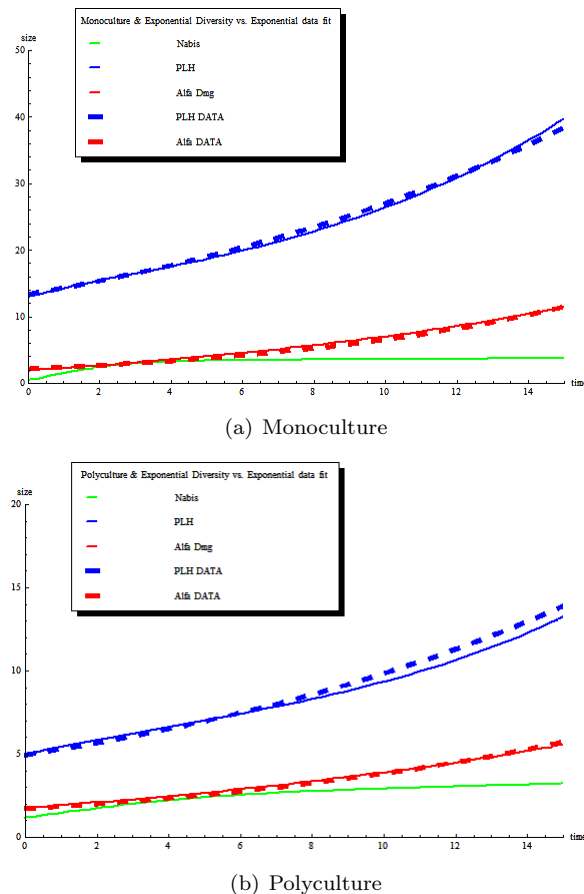


Figure 2: With adjusted parameters, the simulations accurately fit the data trend graphs from the open field experiments for both monoculture and polyculture fields.

A comparison of the alfalfa damage across both types of simulations (using linear “Linear” and exponential “Exp” forms of $f(H)$) compared with data “Data” from the actual field experiment is shown in Figure 3. The differences between the actual data and the simulated data are indeed minimal.

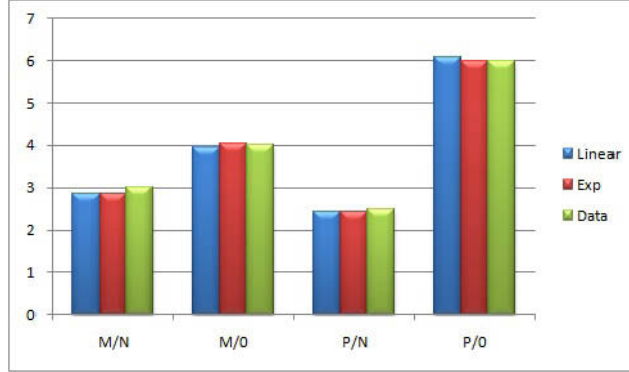


Figure 3: Bar Graph of Alfalfa Damage from the Linear Model, Exponential Model, and the Data. M→monoculture, P→polyculture, N→with predator Nabis, 0→without predator

6 Steady State and Sensitivity Analysis

One of the immediate goals of the analysis of the steady states of the system is the long-term control of the alfalfa damage. There are three possible steady state solutions, but only one makes sense in our context. The others have values that are either negative or zero. The state of interest, with positive values, is described with the equations

$$\bar{Y} = \frac{mn(f(H)j-d)(a+b-c)+mb(d-f(H)j)+nkl(a-c)}{(mn(f(H)j-d)+nkl)(c-a)+mbg(n-1)},$$

$$\bar{X} = \frac{nm(g-d+f(H)j)(a-c)}{(mn(f(H)j-d)+nkl)(c-a)+mbg(n-1)},$$

$$\bar{Z} = \frac{nl(g-d+df(H)j)(a-c)}{(mn(f(H)j-d)+nkl)(c-a)+mbg(n-1)}.$$

A visualization of the corresponding numerical values, for the open field experiments in

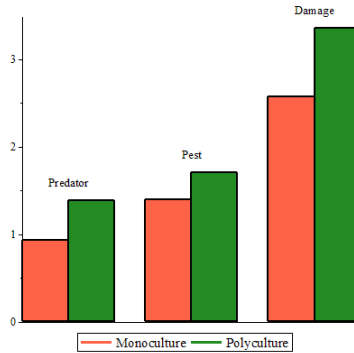


Figure 4: Monoculture and Polyculture Comparison of Steady States

polyculture and with the Nabis, is given in Figure 4. It is unexpected that the damage is greater in polyculture than in monoculture caused by the increase in predators. However,

when the results in Figure 4 are standardized, there is a 6% decrease in alfalfa damage per pest from monoculture to polyculture, thus a slight advantage to reduce damage with the use of a polyculture agriculture approach. Moreover, there is a 17% decrease in alfalfa damage per predator from monoculture to polyculture. Thus, from monoculture to polyculture fields, the impact of the predator Nabis in reducing the alfalfa damage is significantly more important and greater (about 3 times) compared to the PLH pest. In other words, the enemies hypothesis is more efficient and a better strategy for polyculture agroecosystems.

Sensitivity analysis aims at establishing the relative importance of the input factors (and in their ranges) involved in the model [7]. A local sensitivity analysis approach was utilized in this project. The effect of the variation on the long-term level of the plant damage is estimated while keeping all the others fixed at their nominal values. By introducing a small change on one parameter, we want to measure the change of the alfalfa damage, then normalize these measures. The results are shown in Figure 5.

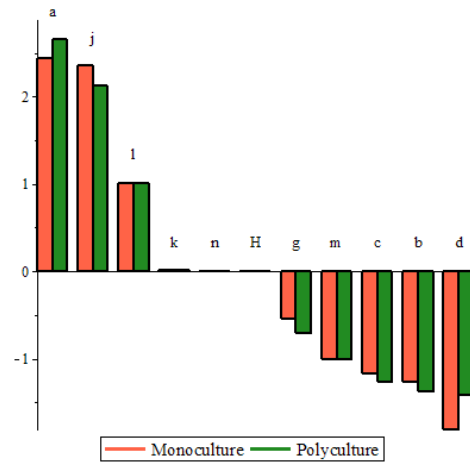


Figure 5: Sensitivity Analysis: monoculture and polyculture comparison of the impact of the parameters on the plant damage at the steady state.

Based upon the sensitivity analysis, we conclude that d , the PLH adult mortality rate; b , the Nabis adult consumption rate of the PLH adults; and c , the Nabis adult population gain from nymphs have the largest positive effect when all of the parameters are at their mean values. It makes sense that the high PLH mortality rate, d , and the high Nabis consumption rate of the PLH, b , would cause a positive change in the system. Obviously, if the PLH are dying due to the Nabis consumption, there will be a decrease in alfalfa damage. The other parameter, c , the Nabis adult population gain from nymphs is a little less trivial. When more adult Nabis mature, there will be more Nabis to consume the PLH. Since more of the PLH will be consumed, there will be less damage.

On the opposite side, a , the Nabis adult mortality rate and j , the PLH adult population gain from nymphs have the largest negative effects on the system. It is clear that as the Nabis die, a , there will be fewer to consume the PLH, resulting in an increase in alfalfa damage. Finally, the PLH adult gain from nymphs, j , indicates that a growth in the PLH population will lead to more plant damage.

A clear result of this analysis is the counterproductive role of the use of pesticides. Indeed, on one hand the pesticides may kill both the PLH and the predator. On the other hand, the impact on the mortality rate of the predator is higher than the impact on the mortality rate of the PLH. Denote by A the increase in alfalfa damage for a slight increase in predator adult mortality rate a . Denote by D the decrease in alfalfa damage for a slight increase in the PLH adult mortality rate d . It is clear from Figure 5 that A is significantly

larger than D . Therefore, there will be a rather a greater increase in alfalfa damage if pesticides are used.

Moreover, a comparison of the changes in sensitivity of the parameters between monoculture and polyculture, shows a higher sensitivity for the parameter a in polyculture fields. This means that for a similar increase in the predator adult mortality rate a (for example via pesticides), the alfalfa damage increase is worse in polyculture compared to monoculture fields. On the other hand, an increase of the mortality rate of the PLH d leads to a smaller decrease in alfalfa damage for polyculture versus monoculture fields. There is then more evidence indicating that the impact of the pesticides on alfalfa damage is worse for polyculture compared to monoculture fields.

In addition to the monetary, environmental and health costs and risks associated with pesticides, these counterproductive aspects of pesticide usage in alfalfa fields represent significant incentives for farmers to avoid or to reduce the use of pesticides. In a future work, field experiments could be conducted to confirm these findings.

7 Conclusion

The paper provides a framework for designing cost-effective and environmentally-safe strategies to minimize alfalfa damage, determine critical parameters, and utilize the enemies hypothesis and polyculture diversity. The methods in this paper can also be applied to different agroecosystems, especially when accurate simulations of an agroecosystem and specific data are available.

Since the models were shown to accurately fit the experimental data, they can be used to simulate scenarios not covered by the field experiments, at a significantly lower cost, shorter time and with no risks potentially associated with field experiments. The models also provide effective strategies to design targeted field experiments and accurate predications on the optimal level utilizing both diversity and enemies hypotheses.

These mathematical models can be improved as more accurate data is collected. Moreover, future work can consist of using optimal control theory in order to make decisions that involve minimizing the overall costs and maximizing the overall revenues associated with alfalfa and milk productions with the use of plant diversity, a natural predator and limited pesticides. The goal is to transform a set of the parameters into adjustable control functions in order to either maximize or minimize a given objective function. Objective functions can be investigated with emphasis on lowering costs associated with growing alfalfa (less weeding, less pesticides, more fibers from naturally grown grasses) and more income through increase in the milk value from cows feeding on pesticide free crops (even if there is a decrease in the milk quantity).

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