

Defence Signal Responsiveness and Fitness in Plants Under Herbivory

Advocacy for the application of the Ising model in ecology

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Abstract

To the end of protecting certain plants for various reasons or fleshing out evolutionary histories, one might wonder if there is an optimal way for a plant population to signal its neighbours about potential herbivory threats. In this paper, the relationship between induced-defence signal responsiveness and fitness under varying herbivory conditions is explored. This is done by modelling a spatially-distributed, nearest-neighbour interacting plant population with an active overlapping population of point-particle herbivores. A slightly modified version of the Ising model from statistical mechanics is employed to simulate the communication between plants. I do so because the Ising Model is designed for spatially separated, 2-state interacting individuals, and also as advocacy for the general implementation of the Ising model in ecology for similar systems. My results show that the correlation between fitness and signal responsiveness changes as a function of the relative costs of an individual activating their defences, and recovering from undefended attacks. Specifically, three distinct correlations are observed depending on these costs: positive, negative, and a combination of correlations depending on herbivory level. The results largely match with the intuition that optimal signal communication depends on the degree of herbivory; Hyper-reactivity is ideal when the threat is extreme, and under-reactivity is useful when the threat is negligible.

1 Introduction

As plants do not generally have much capacity for running away or fighting back, they logically have two primary options for passing on their genes in the face of attackers: spread seeds before or via the attacker, or survive the attack long enough to spread your seeds despite being attacked. It is this, plant defence mechanisms, which are the focus of this project. These defence mechanisms also come in two flavours: constitutive and induced. Constitutive defences are always present, take rose thorns for example, and will not be discussed here. Induced defences are "activated" when a plant is attacked, take radish plants producing chemicals to make themselves less palatable and harder to digest for caterpillars [1]. These induced defence mechanisms are also generally accompanied by an outgoing signal of some sort to warn other nearby members of the population to start activating their defences early so that they can ward off the herbivores without damage being necessary. This signal can take various forms, with airborne pheromones [2] being the method of interest for this project.

The understanding of induced defence mechanisms and the communication strategies by which they are deployed has implications in agriculture, conservation efforts, and evolution. Revealing new information about optimal survival strategies can enlighten us on how to protect crops and endangered plants, or even better, how to help them protect themselves [3][4]. Understanding the communication methods of how these strategies are enacted can likewise be useful for optimizing protection practices, but also potentially putting together how these strategies might have evolved, or how they could continue to evolve in the future.

If one wishes to address how a specific plant species' protection changes depending on circumstance, it would be beneficial to subject that species to various conditions and observe response and efficiency. If one wishes to address more generally how various plant populations might protect themselves under a wide range of circumstances and with high levels of replication, modelling and simulating is the method of choice. Simulating allows us to test many more conditions with higher levels of replication at the cost of system simplicity. Modelling allows us to draw general conclusions about overarching principles and make predictions based on mechanistic reasoning, rather than simple inference. Of course, bolstering the model with biological data is highly advantageous, but nonetheless having the theoretical background is powerful.

The Ising model is a spatially-distributed, neighbour-interacting model, originally designed to model magnetic properties of metals caused by electron spin states [5]. Some interest has appeared in applying this model to other topics of research, from ice formation [6] to neural activity in the brain [7], and more [8]. In 2015, Noble et al. wrote about the potential applications of the Ising model to ecology [9], and then subsequently three years later demonstrated that this proposition was valid [10]. I am likewise interested in the possible applications of the Ising model to ecology. Most generally, I'm interested in how plant synchrony can be understood by applying principles of the Ising model; More specifically, I'm interested in how induced defence mechanisms in plants might be better understood by making use of the Ising model to simulate communication between individuals within a population. To this end, I have written a program in Python which simulates herbivory of a plant population using the Ising model as the mechanism for communication, and then explored the effect of varying signal responsiveness on the fitness of the plant population.

2 Methods

2.1 Ising model

The Ising model was originally designed to model the magnetic behaviour of metallic materials. The underlying principle is that electrons are themselves tiny magnets. When these tiny magnets are aligned with one another, the material as a whole exhibits magnetic behaviour. When the tiny magnets are misaligned, the whole material is not magnetic at all. The "alignment" of the electrons depends on an intrinsic property called "spin", the details of which are beyond the scope of this paper. The spin of an electron can be in one of two states: spin up, and spin down. The spin of an electron flips somewhat randomly as a function of the whole system's temperature, and also of the spins of the nearest neighbours. The application of the model to plant defence-signal communication is then as follows:

- Individuals are plants instead of electrons.
- States are defence-active and defence-inactive instead of spin up and spin down.
- The system reactivity parameter is defence signal responsiveness instead of temperature.

The components of the model have direct analogies in the biological defence communication system. The application of the model is only justified by this direct analogy and the previous external application of the Ising model to other fields [8]. The results of this study ideally will serve as support for the further application of the model into other systems.

2.2 Plants

The plant model consists of a grid of cells which represent individual plants. These cells are always in one of two states: defence-inactive or defence-active, coloured blue and red, and notated -1 and +1 respectively. These state representations, using -1 and +1 for defence-inactive and defence-active states is quite important, as it allows us to quantify statistics such as whether or not an individual's defence state aligns with those of its neighbours. For each frame of the simulation, an individual is selected at random, and its state is adjusted according to its four nearest neighbours' states. This choice to process one individual at a time is done for two reasons: The first is to simplify the algorithm and computations, thus speeding up the simulation, and the second is to provide another stochastic factor in a effort to better mimic "biological randomness" [11]. As a way to quantify the alignment of an individual with its neighbours, their states can be multiplied. Opposite states (+1, -1) will produce a negative (-1) while like states will produce a positive (+1). E.g. Active-active makes $1 \times 1 = 1$, inactive-inactive makes $(-1) \times (-1) = 1$, and active-inactive makes $1 \times (-1) = -1$. The product for each neighbour can be added together to get a total alignment score for an individual with its neighbours. Higher positive scores indicate several neighbours in the same defence state, while lower negative scores indicate several neighbours in mismatched defence states. However, as this method comes from physics where the convention is to associate lower energy states (as would be the case for better alignments) with negative values, a negative sign is added so that strongly negative values indicate high alignment, and strongly positive values indicate high misalignment. We can then think of this sum as a *misalignment* score. The total misalignment score is thus

$$S = - \sum_{i=1}^4 d_0 d_i, \quad (1)$$

where d_0 is the defence state of the selected individual, and d_i is the defence state of its i th neighbour. This alignment calculation can be extended to all members of the population with a coupling factor determining the weighting of the state of a specific neighbour. In this case, the full misalignment score would be

$$S = - \sum_i J_i d_0 d_i, \quad (2)$$

where i goes over all members of the population, and J_i is the strength of the connection between the individual the score is being calculated for and individual i . In most applications of the Ising model, J_i is set to 0 for all non-nearest-neighbours. It is also often typical to see members of a row have a shared coupling constant, and members of a column also have their own coupling constant, reducing the total possible factors to J_H (horizontal neighbours) and J_V (vertical neighbours). These together greatly speed up computation time and model simplicity, and when $J_H = J_V$, an analytic solution becomes possible [12]. This is done in this project, as well as setting $J_H = J_V = 1$ to produce the simplest case scenario as a starting point. It is not difficult algorithmically to include arbitrary coupling constants, but this increases computation time and makes analysis significantly more complex.

Example. A cell chosen at random is inactive and has three active neighbours, so its misalignment score is $S = -[(-1 \times 1) + (-1 \times 1) + (-1 \times 1) + (-1 \times -1)] = 2$.

This misalignment score is then also calculated as if the selected individual had its defence state flipped. The difference between this score and the original is then taken to observe what the effect would be of flipping the state:

$$\Delta S = [-\sum_{i=1}^4 (-d_0)d_i] - [-\sum_{i=1}^4 d_0d_i] = 2d_0 \sum_{i=1}^4 d_i \quad (3)$$

Subsequently, the probability that the selected individual will flip states is dependent on two factors: the change in energy associated with transition from one state to another, ΔS , and how responsive the individuals are to each other, R . In physics, this value R is written $k_B T$ or simply β , the product of the Boltzmann constant and the temperature of the system. This value is dimensionless and, for reference, the critical value is approximately 2.3 [12]. From the Boltzmann distribution, the probability an individual will flip states is given by

$$P(\text{flip}) = \begin{cases} 1 & \text{if } \Delta S < 0 \\ e^{-\Delta S/R} & \text{otherwise} \end{cases} \quad (4)$$

This is one common way of numerically simulating the Ising model referred to as the Metropolis-Hastings algorithm [13]. This piecewise probability corresponds to a flip occurring when it results in a better alignment, and only flipping a small percentage of the time when it corresponds to a worse alignment. Furthermore, the less favourable a transition is (i.e. $\Delta S > 0$), the less likely that transition is to occur. An inactive individual who only has one neighbour in an active state, for example, would be more aligned with its neighbours if it remained inactive. Thus, this factor R determines how "willing" an individual is to respond to a nearby signal in lieu of the fact it would be better aligned by ignoring it.

This is a typical algorithm for simulating the Ising model, but I have also introduced two biases aimed at producing a slightly more biologically realistic model. While cells in the normal Ising model are not biased toward either state, I have decided to bias my model towards the defence-inactive state. I have done this by preventing maximally inefficient transitions, and adding a time limit for how long one individual can remain defence-active. Real plants are naturally biased toward being defence-inactive for multiple reasons, and simply as a matter of definition, if they weren't biased toward being defence-inactive, these would not be induced defence mechanisms at all, but rather induced "intermission" mechanisms. The first bias prevents an individual from flipping states if it is aligned with all of its neighbours (four for most, three for edges, two for corners). This prevents spontaneous activation of defences when no attack has occurred. The second bias takes the form of a counter. If an individual chosen at random is in an active defence state, and remains in an active defence state after the flipping process described previously takes place, it has its counter incremented by one. Once this has occurred a number of times, and the counter reaches a certain cutoff value, the individual is forced to deactivate its defences, regardless of its neighbours. This emulates a fatigue in the plants, which prevents them from staying in a defence-active state indefinitely. Otherwise, if there is a lot of activity in the population at once, the entire grid may become defence-active, and according to the regular Ising model, a stable state would be achieved and there would be no return to a defence-inactive population, which is not realistic.

2.3 Herbivores

In addition, to introduce the threat of herbivory, I model a population of herbivores on top of the plant population. I assume the herbivores disperse randomly among the landscape except for avoiding defence-active areas, and can only interact with the plants they are in immediate contact with. As such, I simulate the herbivores as point particles which move around in random walk on top of the plant population, periodically attacking. The herbivores move according to a velocity vector which is (mostly) constant in magnitude, but whose direction is adjusted randomly every simulation step. A small vector addition occurs for each defence-active plant around each herbivore in the direction from the plant to the herbivore. This produces an avoidance mechanism in the random walks of the herbivores. The herbivores have a random attack cooldown chosen between a specified minimum and maximum. Every step in the simulation, every herbivore's attack cooldown is decreased by one. Once a timer reaches zero, the herbivore "attacks" the plant it is currently on, setting the defence state to active (if it isn't already), and setting a new random cooldown to repeat the cycle. I've chosen to make the induced defence mechanism is "fatal", in that if a herbivore happens to attack an individual whose defences are active, the herbivore dies (stops moving and attacking). This choice is made for two reasons: Firstly, it simplifies and thus speeds up the computations; Secondly, it can model multiple circumstances: the herbivore dies, the herbivore leaves permanently, the herbivore's attack mechanism is broken, etc.

2.4 Parameters

I have made the simulation such that many different parameters can be modified easily, allowing for the simulation to be run many times under different conditions to compare results. The parameters which can be modified in the function which starts the simulation are the following:

- the size of the grid
- whether the entire population starts defence-inactive or if the states are randomized
- the number of herbivores
- the movement speed of the herbivores
- the minimum attack cooldown of the herbivores (the maximum is double this)
- the starting value of the system responsiveness (which can be changed with a slider during the simulation)
- the herbivores' level of avoidance to defence-active plants
- the maximum random angle change of the velocity vectors of the herbivores (the minimum is the negative of this)
- the maximum number of times a plant can be selected and remain defence-active before being forced to deactivate
- whether the halt condition is a time limit or a fatality limit

In order to explore the correlation between fitness and signal responsiveness under varying herbivory conditions, many simulations were run varying the signal responsiveness parameter (R) and herbivore parameters speed and attack. As many more parameters can be varied, it would be useful to run many more simulations varying one parameter at a time to observe the effects, time permitting.

2.5 Fitness

To find the correlation between fitness and signal responsiveness, a proxy for fitness must be created as it is not so straightforwardly observable. One simple but effective proxy is the energy expenditure. If an individual spends too much energy and resources on defences, it will not be able to reproduce; However, if it spends too little on defences, it is more likely to be damaged, possibly repeatedly, meaning it has to spend more energy on repair or may even be damaged beyond repair, and also will likely not be able to reproduce. Therefore higher energy expenditure indicates lower fitness and vice versa. The total energy expenditure of a population at the end of a simulation will be

$$E_T = -(c_a A + c_u U), \quad (5)$$

where A is the number of times defences were activated, U is the number of undefended attacks (damage), and c_i is the associated energy cost to count i . This can be rewritten in vector notation using $\vec{c} = (c_a, c_u)$ and $\vec{D} = (A, U)$. So we have

$$\tilde{E}_T = \vec{c} \cdot \vec{D}. \quad (6)$$

The values of \vec{D} will simply be tallied during the simulation and recorded at the end. The values of \vec{c} cannot so easily be determined. To this end, I have implemented a feature in the data visualization script which allows the user to select a point on the X-Y plane determining the values of \vec{c} and immediately updating the data accordingly.

Time, Uptake, and Reserve

It is also quite reasonable to include in the fitness calculation the time the simulation lasts until meeting its halting condition, how much energy uptake might occur during this period, and some initial resource/energy value. These however are only insightful in the interest of absolute comparisons, rather than relative. E.g. If population 1 spends half the energy of population 2, it makes no difference within the scope of this paper whether the absolute values were 5:10 or 5,000:10,000, just that population 1 was more efficient. If one were interested in this calculation though, the figure of interest would be

$$E_T = E_0 + E_r t - \vec{c} \cdot \vec{D}, \quad (7)$$

where the new values E_0 , E_r and t are the initial energy reserve, energy uptake rate, and time elapsed, respectively.

2.6 Simulation

The simulation is coded in Python and is fully available at <https://github.com/Jake314/EcoIsing>. The simulation is run with the above algorithms for plant and herbivore processing, with the responsiveness parameter ranging from 1.25 to 3.25 at intervals of 0.25. This is done on a 10x10 grid fifteen times for each value of responsiveness: five times for each of three levels of herbivory: low, medium, high. The level of herbivory corresponds to changes a doubling in speed and aggression (minimum bite cooldown) for each new level.

The correlation between energy usage and signal responsiveness (i.e. the shape of the data) depends on the relative costs of undefended attacks and costs of activating defences, \vec{c} . There seem to be just a handful of regions for which any cost vectors within result in roughly the same shape/correlation in the data. Thus a single representative cost vector is chosen for each region. The resulting Energy Usage vs. Responsiveness plots are presented with their corresponding cost vectors shown in an adjacent cost phase-space plot.

3 Results

After simulating the defence response of herbivory on a plant population, I find that the correlation between fitness and signal responsiveness depends heavily on the relative costs of defence activation and damages incurred. There are roughly three regions in cost phase space for which a representative of each is chosen: positive correlation, negative correlation, and mixed correlation. Choosing different values for $\vec{c} = (c_a, c_u)$ within the same region only appears to magnify or minimize the absolute differences between data points without changing the general shape. Therefore, a single representative is chosen for each region to be presented here. Approximate boundaries between the regions have been plotted and are described below in terms of c_u , the relative energy cost on a plant for an undefended attack, and c_a , the relative energy cost on a plant for activating its defences.

A positive correlation between fitness and signal responsiveness occurs when $c_u > 800c_a^2$ (Figure 1), with representative $\vec{c} = (0.05, 7)$, and $\bar{R}^2 \doteq 0.56$. There is a difference between groups even though all are positively correlated: The low level herbivory population seems to have a relatively weak positive correlation ($m = 80\frac{J}{r}$ where r represents an increase of 1 in the signal responsiveness), whereas the high herbivory population has a much stronger positive correlation ($m = 906\frac{J}{r}$).

A negative correlation between fitness and signal responsiveness occurs when $c_u < -8c_a^2 + 16c_a$ (Figure 2), with representative $\vec{c} = (0.4, 0.3)$ and $\bar{R}^2 \doteq 0.53$. Here, there is no significant difference between groups, as all populations with varying levels of herbivory seem to display a relatively equal negative correlation between fitness and signal responsiveness ($m = -387\frac{J}{r}$ to $m = -583\frac{J}{r}$).

Between these two regions, when $800c_a^2 > c_u > -8c_a^2 + 16c_a$, the correlation between fitness and signal responsiveness varies depending on the degree of herbivory (low, medium, high) (Figure 3). The plant population under high herbivory shows a positive correlation ($m = 589\frac{J}{r}$, $R^2 = 0.54$) while the population under low herbivory shows a negative correlation ($m = -118\frac{J}{r}$, $R^2 = 0.27$). A special case of the mixed correlation pattern occurs near $\vec{c} = (0.2, 3)$ whereby there is almost no correlation between fitness and signal responsiveness regardless of herbivory level.

Close to $\vec{c} = 0$, the mixed correlation region vanishes and the boundary divides the positive and negative correlation regions. It is important to note that the change in correlation from one region to the next is gradual. Near the region boundaries there is much uncertainty as to which shape the data are assuming.

Cost Vector	Correlation Group	Herbivory Level	Slope	R^2	P-value
(0.05, 7)	Positive	Low	80	0.26	0.00028
(0.05, 7)	Positive	Medium	393	0.66	1.1e-11
(0.05, 7)	Positive	High	906	0.77	1.5e-15
(0.4, 0.3)	Negative	Low	-387	0.49	5.0e-08
(0.4, 0.3)	Negative	Medium	-518	0.61	2.1e-10
(0.4, 0.3)	Negative	High	-583	0.48	1.2e-07
(0.25, 7)	Mixed	Low	-118	0.27	0.00019
(0.25, 7)	Mixed	Medium	120	0.16	0.0055
(0.25, 7)	Mixed	High	589	0.54	4.8e-09

Table 1: Statistics of Fitness vs. Responsiveness Plots

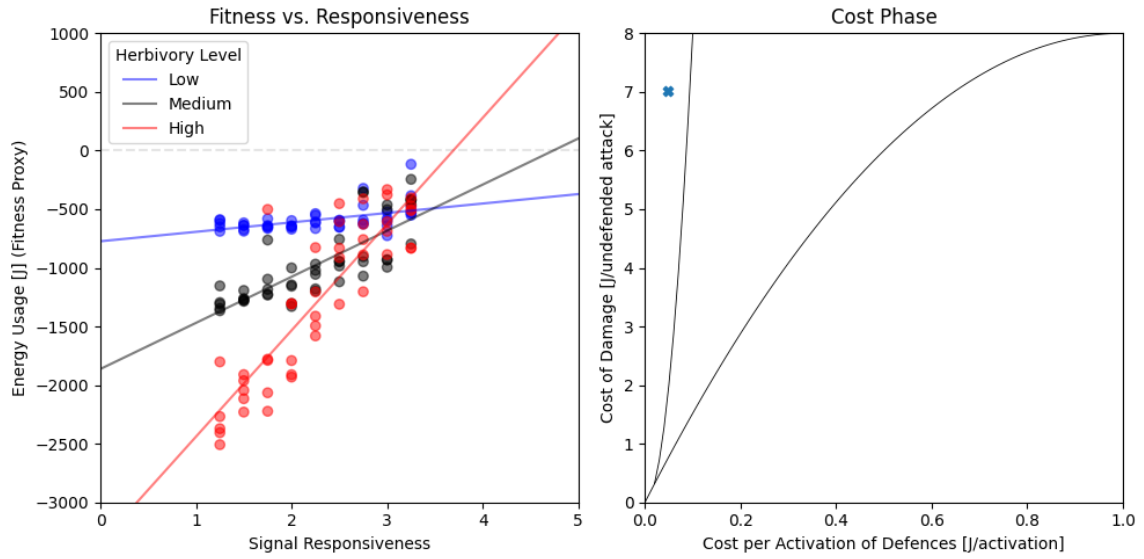


Figure 1: Positive Fitness vs. Responsiveness Correlation. The left plot shows the energy expended for each simulated plant population against its responsiveness. The blue, black, and red points indicate low, medium, and high levels of herbivory respectively. The right plot shows the selected cost vector which is in a region producing the positive correlation seen in the left plot.

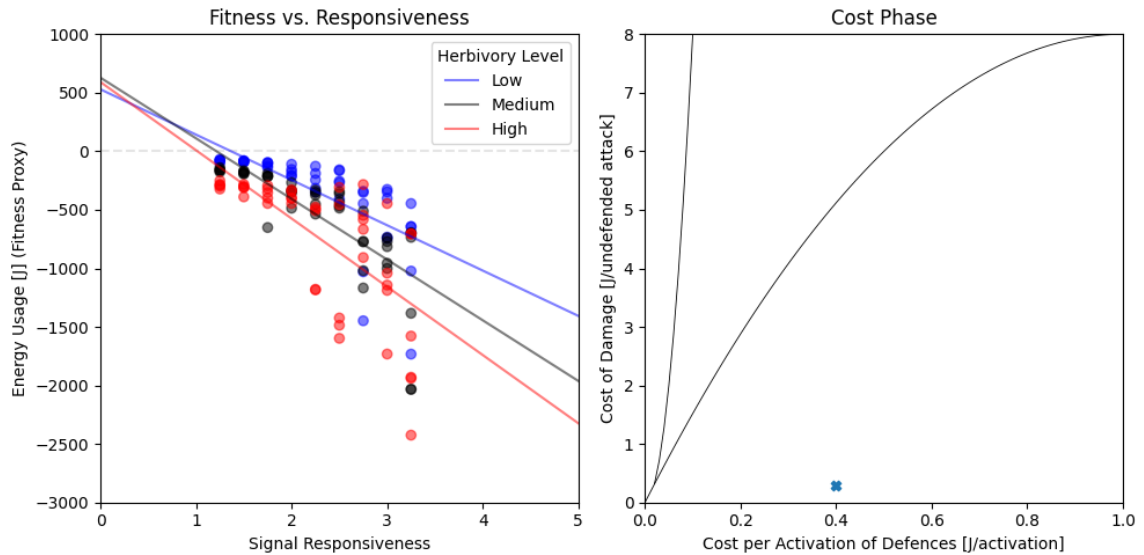


Figure 2: Negative Fitness vs. Responsiveness Correlation. This is almost identical to Figure 1, except the selected cost vector is in the region which gives rise to a negative correlation.

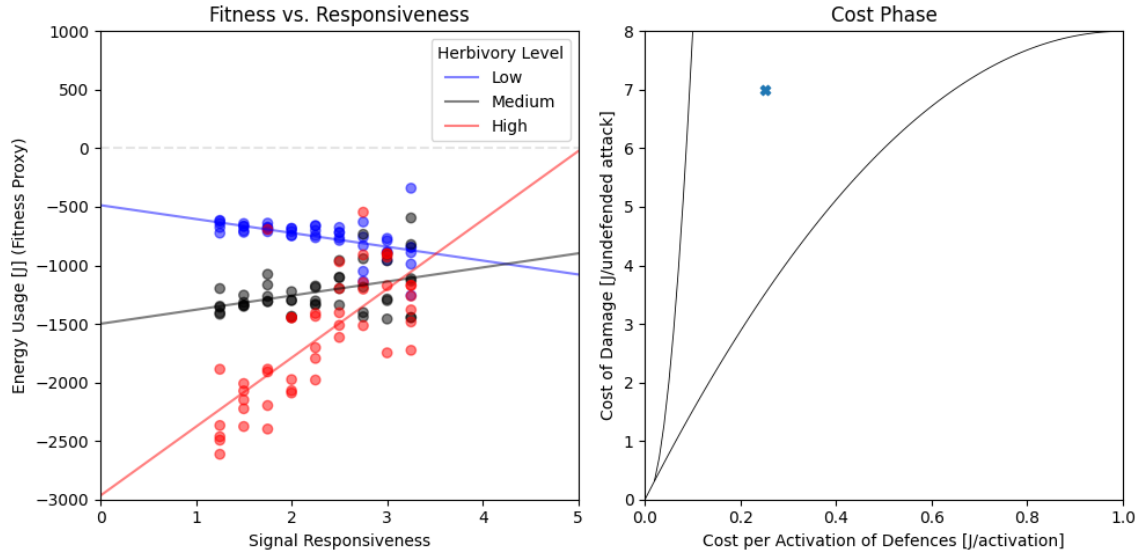


Figure 3: Mixed Fitness vs. Responsiveness Correlation. Identical to Figures 1 and 2, with a different cost vector showing there exists a region of mixed correlations.

4 Discussion

4.1 Costs and Correlations

There are three principal patterns which are of interest when concerning the relationship between signal responsiveness and fitness: positive correlation, negative correlation, and mixed correlation (exhibiting both positive and negative for different groups). Which pattern a population exhibits is a function of $\vec{c} = (c_a, c_u)$, the costs of undefended damages and defence activation. A positive correlation appears when the cost of damage is significantly higher than the cost of defence activation (Figure 1). In this scenario, it is simply too costly to let herbivory go unchecked, and so hyper-reactive signal propagation results in the least overall energy expenditure. A negative correlation appears when the cost of damage is instead significantly lower than the cost of defence activation (Figure 2). In this situation, the damages caused by herbivory are almost negligible, and thus can essentially be ignored. Therefore low signal responsiveness results in higher fitness, as frequently activating defences costs more than it saves from defending the imminent attacks. Between these two extremes of lies a region of variable correlation. Some cost vectors result in almost no correlation between signal responsiveness and fitness. This suggests that when the costs achieve a certain balance, there is no benefit to neither over- nor under-reacting to threat signals. In this case, there is no preferred strategy, and fitness does *not* depend on the signal responsiveness of the population, even under varying herbivory conditions. Other cost vectors within the mixed region exhibit negative correlation for low herbivory, zero correlation for medium herbivory, and positive correlation for high herbivory (Figure 3). This indicates that a population may exhibit high or low fitness depending on the degree of herbivory. Specifically, under low herbivory conditions, lower signal responsiveness is preferred, while under high herbivory conditions, high responsiveness is advantageous. (Of course a corollary of this is that there is a level of herbivory in between for which, once again, there is no correlation between fitness and signal responsiveness.) A population with a balance of costs such as this would find that its optimal survival strategy would be to adapt its defence-signal responsiveness based on the level of aggression the herbivores display.

4.2 Strategies

A plant population, like most other populations of living organisms, will survive best when it adapts to its environment and the threats within. Of course, plants are not generally privy to the capabilities of relocation and retaliation, and so must rely on defence adaptation rather than escape or offence adaptation. One way a plant population may adapt its defences is to alter the potency of its communication pheromones. That is, the more dangerous of a threat an herbivore is, the more easily communicated the threat should be. If an herbivore causes catastrophic damage (Figure 1), or if the attacks are sufficiently aggressive (Figure 4, group: high), the plants would benefit from activating defences rapidly and in a widespread manner. Conversely, if the herbivore causes negligible damage (Figure 2) or is sufficiently placid (Figure 4, group: low), the plants would benefit from almost ignoring the threat altogether. These adaptations could be made in various ways. Several

hypothetical methods include releasing more pheromones on a stronger/more aggressive attack as well as upon receiving more pheromones, thereby compounding the effect; releasing different chemical pheromones based on the strength and aggression of the attack, meaning different signals facilitate different responses; or altering the frequency at which the pheromones are released, meaning threat information might be communicated through timing.

A keen herbivore population will, however, also adapt its strategy based on the strategies of the plants. If the level of herbivory is low enough, the optimal strategy for the plants is to lower signal responsiveness, thereby reducing overall defences. This means that, by the petty thief approach, if an herbivore population can sustain itself while causing minimal damage, its attacks would likely go unhindered. The disadvantage of this strategy is that for the attacks to go undefended, they would likely have to be such minimal impact that they would be of little benefit. The advantage however is the plant population is largely unaffected, meaning the process is sustainable. The more boxing match like approach would instead be to deliver substantial blows infrequently, so as to trigger the defence mechanism response, and then waiting for it to subside. This combination of unpredictability and threat of high damage would force the plant population to fatigue itself, overreacting to the potential threat, leaving it unable to defend itself at a later point at which the herbivores could increase aggression while the plants are weak or in a latent undefended state. The disadvantage to this strategy is that in the early phase, while certain individuals gain from their devastating strikes, the rest of the population would be left with nothing in waiting. The advantage however is that in the late phase, when the plants are largely unable to defend themselves, the herbivores have much more to gain as a whole. A corollary downside, however, is that the strategy is likely unsustainable as it would leave the plant population in ruin. With all this in mind, the data suggests for smaller, slower, more cooperative species, the petty thief strategy would likely be better, whereas for larger, faster, more pillage-and-feast species, the boxing match strategy would likely reign.

4.3 Further Inquiry

The central proposition of this paper is that the Ising model, with some slight modifications, is a valid method of modelling communication within plants. This is corroborated by the findings of Noble et al. [10] and further buttressed by the results presented here. As a next step, it would be highly beneficial to collect data to confirm the relationship between the defence cost vector and the correlation of fitness and signal responsiveness. This would of course require measuring signal responsiveness, a dimensionless, abstract figure. One potential method would be to measure how much of a specific pheromone is required to trigger a response [14]. E.g. If species A produces a reaction to 5 ng of a pheromone, and species B needs at least 10 ng of the same pheromone to trigger the response, then species B is half as responsive as species A. If this could be confirmed, it would lend more credence to the application of the Ising model in ecology. This would further open the door for the new ways of modelling and advancing the understanding of other communication-based phenomena in plants, such as mass seeding events, abiotic stressor preparation, and general cooperation strategies. It is possible that previous similar modelling methods, such as that of cellular automata, will be outclassed by the Ising model as it relies (generally) on fewer strict rules, instead favouring emergent behaviour, and yet still allowing for much more dynamic interactions as each cell, as its own individual, can have its own unique characteristics.

The next generation of this model, so to say, would involve an evolutionary component. There are several possible strategies for both the defending plants, and the attacking herbivores, as discussed in section 4.2. These strategies could be implemented into the model directly, or even better, observed as emergent as the model is allowed to evolve. This would further provide a wealth of insight into the dynamic interactions between plants and herbivores, and how adaptive defence strategies can lead to better survival.

Another route this model can take is generalization and expansion. The premise presented is that the Ising model is suitable and easily implementable to model induced defence-signalling in plant populations. This is carried out in this project with many restrictions and arbitrary parameter choices. The next obvious step is to start varying these parameters one by one to qualify and quantify their effects, and relaxing some of these in-built restrictions. The details of the route this process would take are outlined in the following section, section 4.4. Beyond this, I strongly believe the Ising model can be used to model many more biological phenomena. I believe it to likely be useful in almost any situation in which a network of individuals are switching states based on some cooperation strategy. This has the potential to shed light on many synchrony phenomena observed in nature.

4.4 Further Improvements

There are a number of steps which can be taken to continue developing this project, time permitting:

- Extend workflow to R for the the handling of data.
- Streamline the process from simulation to data presentation and statistical analysis, including automatic dynamic file naming and handling, and more user friendly presentation of the data.

- 322 • Run higher count simulations with a wider range of parameters and larger grids to better bolster the
323 findings and explore the current boundaries.
 - 324 • Fit better models to the data than simple linear regressions.
 - 325 • Automatically recording correlation for a range of cost vectors, pinning down the region shapes more
326 precisely.
 - 327 • Search for analytic solutions to the region boundaries based on methods of the Metropolis-Hastings algo-
328 rithm.
 - 329 • Explore effects of altering different parameters independently (herbivore avoidance angle, fatigue timer,
330 etc.)
 - 331 • Expand application of the Ising model to explore the effects of non-isotropic coupling constants, long-range
332 communication, removal or addition of biases, periodic boundary conditions, and dead-zones ($J_i = 0$ for
333 all i for an individual)
- 334 Implementing these changes would further increase the predictive potential and likely increase the accuracy by
335 making it more realistic and exploring a wider variety of configurations. The streamlining would make it easier
336 to adjust and improve the model, as well as making new predictions faster and more consistent.

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