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Evolution of Chemical Signals in ecological system evoked by the "cry-wolf" plants

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Abstract

We model the tritrophic system composed of plants, herbivores, and carnivores, where plants produce chemical signals when they suffer from feeding damage by herbivores; and this chemical, Herbivore Induced Plant Volatile (HIPV) attracts carnivores, thus plants can indirectly protect themselves from feeding damages caused by herbivores. Carnivores in this system are able to evaluate and learn its usefulness of the chemical signals, therefore plants do not emit the chemical signals until the population of herbivores becomes large enough for carnivores, where in the coupled tritrophic system, it has been confirmed that there are plants called "cry wolf plants" that emit chemical signals even if there are few herbivores. It has been pointed out that if there emerges cry wolf plants in this system, chemical signals may change in order to preserve the quality of information and keep on attracting carnivores. We model the tritrophic system including cry wolf plants, and we confirm that the chemical signal may change through simulations of the model. Further we show the chemical signal may not change when plants grow densely in the field.

1.Introduction

The tritrophic system composed of plants, herbivores, and carnivores has been investigated. In this system, when plants suffer from feeding damage by herbivores, plants produce Herbivore Induced Plant Volatile, HIPV; HIPV attracts carnivores to the plants and the attracted carnivores exclude the herbivores giving feeding damage, hence the plants are able to protect themselves from herbivores indirectly (for example, Takabayashi et al. 1988) and this system has been theoretically investigated (for example, Sabelis et al. 1988, 2002). In the tritrophic system, plants commonly produce HIPV in a dose-dependent manner: the more herbivores, the more volatiles are released.

The volatiles attract predatory carnivores and the amount of produced HIPV determines the probability of predator response. They show that seedlings of a cabbage variety (Brassica oleracea var. capitata, cv Shikidori) also show such a response to the density of cabbage white (Pieris rapae) larvae and attract more (naive) parasitoids *(Cotesia glomerata*) when there are more herbivores on the plant. However, Shiojiri et al. (Shiojiri et al. 2010) discovered when the plant is attacked by diamondback moth (*Plutella xylostella*) larvae, seedlings of the same variety (cv Shikidori) release volatiles of which the total amount is high and constant, and thus independence of the caterpillar density, and naive parasitoids (*Cotesia vestalis*) of diamondback moth larvae fail to discriminate herbivore-rich from herbivore-poor plants. In contrast, seedlings of another cabbage variety of *B. oleracea* (var. acephala: kale) respond to the density of diamondback moth larvae in a dose-dependent manner and attract more parasitoids when there are more herbivores.

Assuming these responses of the cabbage cultivars reflect behaviors of some genotypes of wild plants at least, they provide arguments why the behavior of kale (B. oleracea var acephala) is best interpreted as an honest signaling strategy and that of cabbage cv Shikidori (B. oleracea var capitata) as a "cry wolf" signaling strategy, implying a conflict of interest between the plant and the enemies of its herbivores: the plant profits from the visits of the herbivore's enemies, but the latter would be better for the enemies to visit other plants with more herbivores. If so, evolutionary theory on alarm signaling predicts consequences of major interest to students of plant protection, tritrophic systems, and communications alike.

On the tritrophic system with cry wolf signal, Sabelis et al. (Sabelis et al. 2010) pointed out it may evoke co-evolution of signals; because once plants send the dominant honest signal, new opportunities arise for 'cry wolf' plants that mimic this signal, though they harbor no or few herbivores, if any. Thus, frequency-dependent selection will give rise to alternating waves of plants sending 'honest' or 'cry wolf' signals (Baalen, et al. 2003). This process is likely to increase the complexity of plant signals, and the theory on the evolution of cooperation has shown that the more complex the signal is, the more likely it evolves and perpetuates cooperative alliances (Traulsen et al. 2007). Thus they predict that chemical alarm 'languages' of plants change over generations and become complex due to frequency- dependent selection. Since the perception of odor blends seems not to be a simple sum of responses to individual components, but rather to be based on properties of the odor blend as a whole, small changes in the odor blend may allow the signal to be perceived as new and this may more easily give rise to new signals of plants by mutation and more easily for them to be selected.

The evolution of Herbivore-Induced Plant Volatiles (HIPV) shares common traits with the evolution of language (Baalen et al. 2003, Traulsen et al. 2007). In the evolution of language, a mutation is reflected by the change of symbols, and through natural selection, the mutated symbols become understandable and widely used, they called such a situation as the "tower of Babel." Likewise, in the evolution of HIPV, a mutation brings about a change in Herbivore-Induced Volatile Chemicals, and natural selection enables the mutated HIPV to become understandable and widely used in the ecosystem. A plant changes the response to its feeding damage through mutations.

2.Method

We model the tritrophic system on the two dimensional grid (torus) and each grid point has eight neighbors (the Moore neighbor), each grid spot has a plant or empty space; herbivores invade each plant and eat the plant. When a plant suffers from feeding damage, and if the amount of damaged biomass is large, then the plant starts to produce Herbivore Induced Plant Volatile, HIPV; produced HIPV diffuses on the space isotropically; carnivores search herbivores by tracking HIPV, if a carnivore can sense the gradient of HIPV, then it tracks the gradient, otherwise searches the HIPV randomly; each carnivore possesses “energy” and it is expensed through searching and if the carnivore find herbivores then it removes all herbivores in the plant and gains the energy in proportion to the number of herbivores in the plant; if a carnivore cannot find herbivores and spends all energy, it dies and is eliminated from the space.

2.1. The details of the model

Plants: In the simulation in this paper, all plants are in the same condition where they complete their growth for simplicity. The biomass of a plant is expressed as the given value, in the initial state it is set to 100 and decreases 2 because of feeding damage by a herbivore and when the biomass is below 98 because of feeding damage, it increases 2 by growth; the maximal value of biomass is 100 and it does not grow beyond 100; if the value of biomass is equal to zero, it dies and is eliminated from the space.

If there are herbivores or carnivores in the eliminated plant, they are moved to the nearest plants randomly; the use of the parameter indicates biomass which has the fixed maximal value and the maximal population of the plant is the total number of grids in the space, which means that the total size of biomass of plants is finite and limited. The growth of a plant is expressed as the increment of its biomass by 2 and when a plant grows and reaches 50% of the maximal biomass (in this paper, it is 500, when the plant has a descendant, then a descendant plant is placed in the neighbor of its parent plant and if there is no neighboring empty place, it is placed in the nearest empty place.

The initial biomass of the descendant is 100 and the descendant changes the type of HIPV according to the mutation rate of the type of HIPV; when a descendant plant does not mutate, it produces the same type of HIPV as its parent plant; the characteristics of plants such as “honest” or “cry wolf” can be only changed during the generation change. Each plant has the threshold value on generating HIPV (in this paper, the threshold value is 15); if the number of herbivores exceeds the threshold value, the plant starts generating

HIPV; HIPV is expressed as the non-negative natural number, the characteristics of each plant is “honest” or “cry wolf”; the threshold value of a honest plant is high and of a cry wolf plant, low. In the initial state of the simulation, every plant has the same HIPV: plants in a certain percentage to the total population change the type of HIPV. Herbivores; Herbivores invade a plant randomly; a plant is selected randomly from the field and a herbivore is put inside it; they grow up by reducing the biomass of the plant, and the maximal number of herbivores in a plant is limited. When the population of herbivores reaches the maximum, herbivores move to the nearest plants that have not the maximal population of herbivores. If there are no neighboring plants they can move to, then they move to the nearest plant.

Carnivores; a carnivore moves 1 grid point by each step; it moves to the plant which produces the target HIPV. If there are no neighboring target plants, it searches the target HIPV and tracks the gradient of the HIPV concentration; when there is no neighboring target HIPV, it searches the same HIPV until it moves 5 steps among the neighboring 8 grids. If it is still unable to reach the target plant, it randomly selects a plant around the 8 grids. Each of carnivores has a memory and the memory affects the preference of HIPV, a carnivore evaluates the usefulness of HIPV and changes the preferences of HIPV; if a carnivore tracks a certain HIPV and it cannot obtain enough herbivores, then the carnivore devaluates the usefulness of HIPV and memorizes it.

The memory is realized as the First In First Out, FIFO queue of the type of HIPV which attracts a carnivore, where the number of memories of the HIPV type represents the preferences of HIPV and the maximal length of the queue expresses the characteristic of learning activity of a carnivore; if the maximal length is short, such a carnivore is likely to change its preference frequently, vice versa. For example, the memory of a carnivore is the queue of “1,1,1,2,3”, where the each natural number represents the type of HIPV. If the length of the queue exceeds the maximal length, the oldest element is removed and the newest element is put in (such operation is called First In First Out manner). In this simulation, the maximal length of the queue is set to 100 and there is the same type of HIPV in the initial state. A carnivore selects the type of HIPV randomly from the queue and tries to track the HIPV in the space and if the usefulness of the HIPV is high, the selected type of HIPV is put in the queue and the oldest information is removed from the queue.

Plants	
Initial population:	65% of the total number of grid points
Generation rate of a new plant:	0.65 (This generation rate means the generation rate of a new plant but not a descendant).
Feeding damage:	2
Carnivores	
Generation rate of a bug:	0.03 / step
Natural enemy	
Growth rate:	0.04 (the growth rate of the enemy’s population)
Initial energy value:	500
Traveling cost:	5 (a carnivore spends 5 energies at every step).
The maximum possible travel distance:	5 (a carnivore can move up to 5 steps at 1 travel.)

Table 1. Parameters used in the simulations

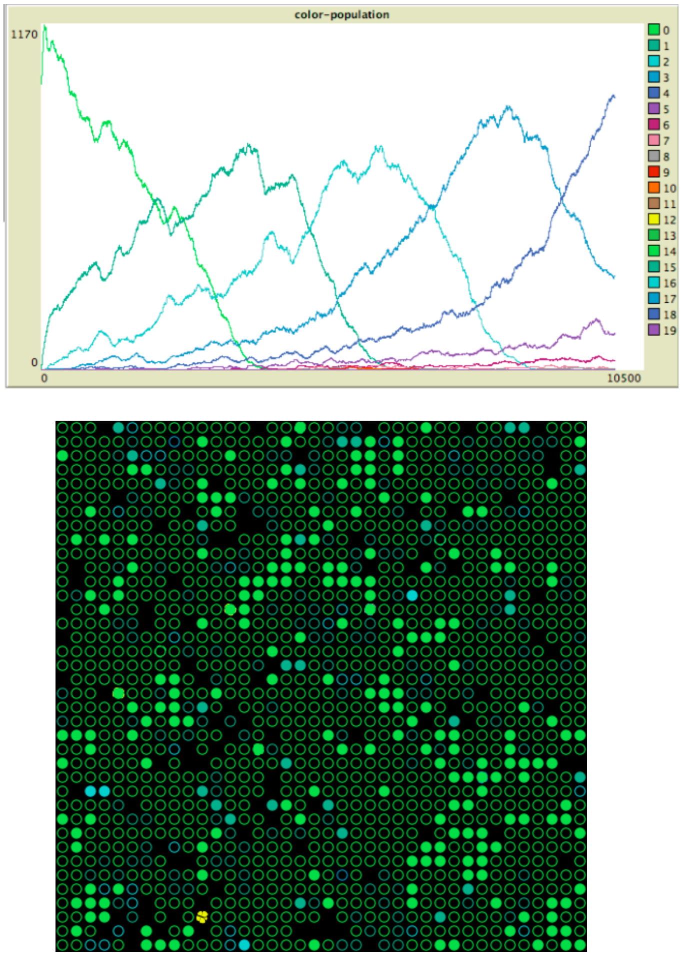

Figure 1. Sparsely distributed plants in the initial state: (above) the population dynamics of plants, where each line denotes the number of plants that generate the same type of HIPV; the vertical axis illustrates the number of plants and horizontal axis illustrates the step time. (below) The circles show the distribution of plants in the space at the 10,000 step times, the colored circle illustrates the HIPV produced by a cry wolf plant and the difference of the HIPV type is represented by a different color.

In the case when a carnivore does not find the target HIPV or cannot reach the patch of herbivores, the carnivore stops finding or tracking the HIPV and tries to track a different type of HIPV. A carnivore evaluates the usefulness of HIPV as the ratio of the number of herbivores in the patch to the total travel distance to the patch; the carnivore gains this ratio as "energy". The number of the type of HIPV to be put in the queue is the proportion to the result of the evaluation. If the evaluation of the HIPV is high, relatively large numbers of the type of HIPV are put in and the same numbers of information are removed from the memory.

3.Results

When there are no cry wolf plants, carnivores do not have to track a different type of HIPV other than the dominant type of HIPV, therefore carnivores do not visit plants that produce non-dominant HIPV, hence such plants go extinct (Figure 1). When there emerges cry wolf plants since the dominant HIPV is mimicked by emerged cry wolf plants, honest plants have to produce different types of HIPV in order to keep on attracting carnivores; such a change of HIPV is regarded as a "mutation" and if the changed HIPV can attract many carnivores, the plants that produce such HIPV are able to increase its population, which can be regarded as "selection"; it is noticed that we use the terms, "evolution", "mutation", and "selection" for analogical describing of the HIPV changes.

The evolution of HIPV is affected by the rate of HIPV change, we call the rate as mutation rate; when the mutation rate is high, there may emerge many types of HIPV, as we addressed in the previous section, the total biomass of plants is limited, so as the number of HIPV types is large, the population of plants that produce each type of HIPV becomes relatively small; hence in such a case, it is likely to be difficult for the carnivores to track and find the target HIPV, then plants are likely to go extinct; which is "the tower of Babel" addressed in the previous section.

3.1 Cry wolf plants can be honest plants

In the previous every simulation, we set plants sparsely on the space, next we only change the distribution of plants by placing them densely on the field, while all the other parameters and settings are the same.

The density of Cry Wolf plants expressed as the mutation rate between cry wolf plants and honest plants; in the preliminary simulations, we empirically found that if the mutation rate from honest plants to cry wolf plants is twice as much as the mutation rate from cry wolf plants to honest plants, cry wolf plants grow in clumps. Then, we use this parameter to make cry wolf plants grow in clumps, on the other hand, we double the mutation rate from cry wolf plants to honest plants to make honest plants grow in clumps. In this case, the HIPV does not evolve (Figure 2).

This is because the carnivores evaluate the HIPV produced by cry wolf plants as "honest signal"; otherwise if the carnivores evaluate such HIPV as cry wolf signal, they explore and change its preference and the evolution of HIPV should emerge; it was confirmed that the carnivore's preference of HIPV does not change through checking the time developments of the memory queue of the carnivore (Figure 2).

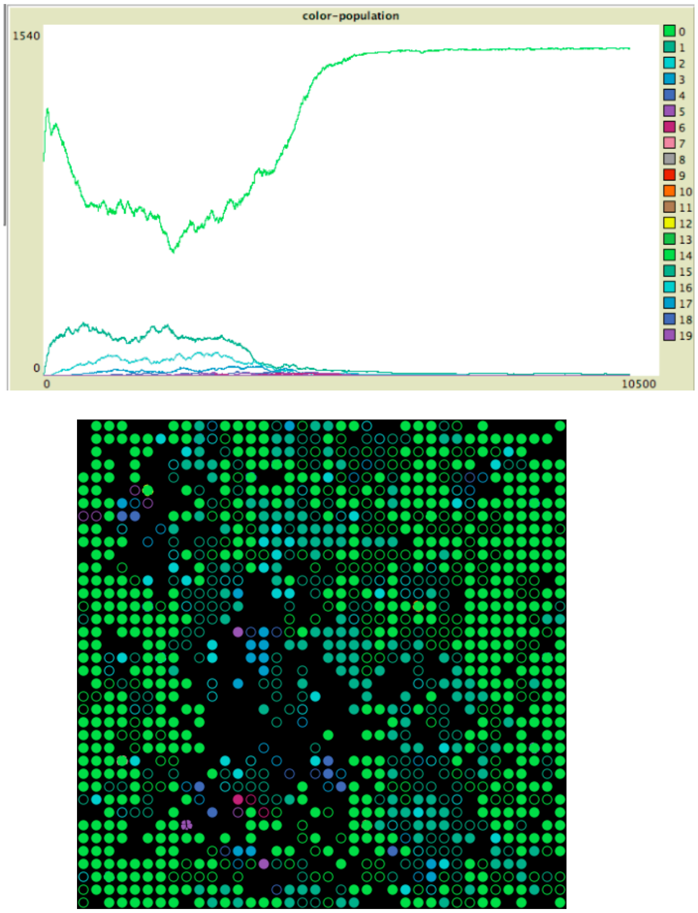

Figure 2. Densely distributed plants in the initial state: (left) the population dynamics of plants, where each line denotes the number of plants that generate the same type of HIPV; the vertical axis illustrates the number of plants and horizontal axis illustrates the step time. (Right) The circles show the distribution of plants in the space at the 10,000 step times, the colored circle illustrates the HIPV produced by a cry wolf plant and the difference of the HIPV type is represented by a different color.

4.Discussion

In this simulation, a carnivore evaluates the usefulness of HIPV as the ratio of the number of herbivores in the patch it reached to the total travel distance to the patch; hence comparing the travel distances between sparsely and densely distributed plants, when the distribution of plants is dense, the travel distances are likely to be shorter, thus, even if carnivores are attracted to the cry wolf producing HIPV and obtain few herbivores, the evaluation of the usefulness of HIPV may not be low, while if the distribution of cry wolf and honest plants is sparse, carnivores may devaluate the usefulness of such HIPV. On the contrary, if honest plants are densely distributed and cry wolf plants are sparsely distributed, the carnivore's travel distance to the cry wolf plants increases, then the evaluation of the HIPV by the carnivore is low, and a new HIPV produced only by honest plants will be dominant and the HIPV will develop. However if cry wolf plants are sparsely distributed among densely distributed honest plants, the carnivore's travel distance is short, and then we consider it is unlikely that the new HIPV will be dominant.

As previous studies showed, when the spatial distribution of Cry wolf plants and honest plants is homogeneous, HIPV may become diverse because of the emergence of Cry wolf plants. However, for example in a field, when one type of plants grows in clumps, HIPV may not become diverse even though there are Cry wolf plants as this study showed.

Acknowledgements

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