Production and diversity in multi-trophic systems

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A scheme is presented for studying the interactions between three trophic layers in arable ecosystems. Every living member of an ecosystem seeks to acquire resource from the trophic layer below and convert this resource to self, or to offspring. Trophic interactions between organisms have a major impact on the structure of a given community, and specifically on its contribution to food production and to biodiversity. The trajectory of any individual in trait space is, as was considered in the previous article, a function of its genetic traits, and the external influences on it. Just as plants occupy, at any given time, a position in trait space, so do other components of an ecosystem such as pests, natural enemies, and members of other trophic levels.

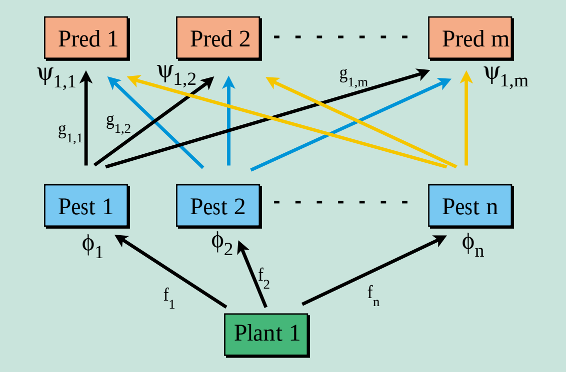
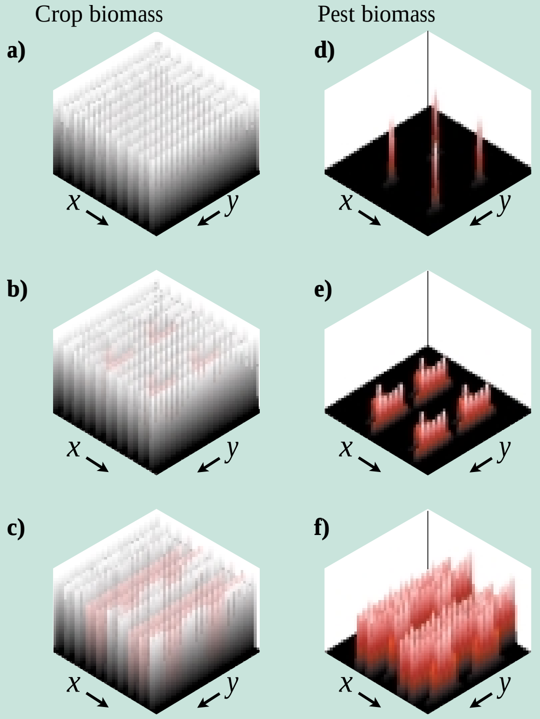


Figure 1 Representation of a tri-trophic system. Text describes the symbols.

Due to the complexities of the trophic, competitive and spatial interactions between organisms in a given habitat, any change in management is likely to propagate through the system with effects that are difficult to predict. This uncertainty is particularly important when considering the impact of, say, the introduction of a new insecticide or a new crop variety which has been bred or genetically modified for insect resistance or herbicide tolerance. It also limits Integrated Pest Management strategies in which, for example, natural enemies are used as a biotic factor to suppress a pest population. The work described is the first step towards defining and quantifying the components of the arable tri-trophic systems, including aspects of spatial grouping and dispersal.

The basic scheme The tri-trophic system is examined through a linked mathematical and experimental approach. The first aim has been to develop a modelling framework that both draws in existing experimental knowledge and enables precise hypotheses to be set and tested in the laboratory, glasshouse and field. The scheme in Figure 1 shows a single plant type interacting with several herbivore types, and these in turn with several predators of the herbivore. Following earlier workers, the many potential interactions between these layers are simplified to two functions, linking each layer. That between crop and pest depends on the function, f, defining the rate at which crop is eaten, and ϕ,defining the amount of pest biomass produced per unit crop eaten. The values of f and ϕ are specific to the crop-pest combination. The symbols, g and ψ, define the corresponding functions linking predator to pest. The scheme allows for generalist herbivores and predators, for which the two functions take values greater than zero for all interactions, and for specialists, for which the functions may take values greater than zero for only one or a few specific combinations. Adding other plants types (not shown), such as weeds or different crop varieties in a mixture, increases the potential number of pests and predators brought into the scheme, but does not alter its basic structure. The inclusion of the dimension of time allows for feedback among the three layers, and will allow for f, ϕ, etc. changing with the phenology of the plant, though still within the scheme shown. Expressed in time, each plant type in the absence of a pest can be represented by a seasonal growth curve (e.g. logistic or expo-linear), which itself can be split into radiation interception (surface) and conversion (photosynthetic efficiency) to allow discrimination between herbivores that, say, bite and chew leaves, e.g. the Lepidopterans, and those that suck plant sap, e.g. Homopterans. However, the salient point is that this simplification directs our attention to measurable variates that discriminate between plants.

Extending the model spatially The ability of an individual to capture resource is strongly influenced by spatial factors. The structure of the vegetation level can have a large impact on the searching and dispersal behaviour of a pest and its natural enemies. Spatial



The mathematical model is the 2-dimensional analog of the following.

$$\frac{\partial C}{\partial t} = \theta(x)C\left(1-\frac{C}{K}\right)-fCH$$

$$\frac{\partial H}{\partial t} = \phi fCH-\mu H+\frac{\partial}{\partial x}\left(D(x)\frac{\partial}{\partial x}H\right)$$

Where:

C	is crop density
H	is herbivore density
θ	is the crop growth rate
K	is the crop carrying capacity
f	is the *per unit herbivore per unit crop* consumption rate
ϕ	is the conversion efficiency
μ	is the *per unit herbivore* mortality rate
D	is the diffusion coefficient.

In a 2-D grid, $\theta(x)$ is set to 0 in regions where there is no crop (i.e. nothing grows). In this way, spatial arrangements of crops are simulated. D is also allowed to vary spatially to simulate variations in the surface on which the pest moves.

References: Shigesada & Kawasaki (1997); Murray (1989, Chapter 12).

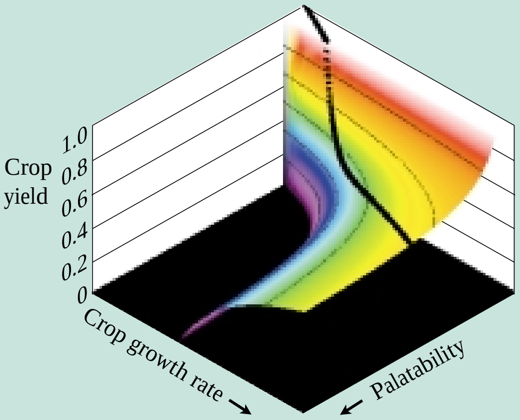
Figure 2 A spatially explicit 2-D crop-pest model showing crop biomass (a, b, c) at increasing time after invasion and pest biomass (d, e, f) at corresponding times. Height of bars represents biomass at individual plants.

grouping, dispersal and migration can have great effects on the behaviour of the systems in Figure 1. In a simple example, a population of a herbivore type feeding on a plant type increases over time, but also spreads out as result of density-dependent or random movement. If flightless, the herbivore's spread depends on the way its own characteristics interact with factors of the plant, notably its architectural features – the angling and connectivity of its surfaces, the distribution of food sources over its structure and wider aspects of stand density and spatial arrangement. It is necessary, therefore, to determine how pests and predators will move in response to their genetic programming and to environmental stimuli. Again, simulation has been used first to aid synthesis of existing data and to set measurable goals in experimentation.

A simple example of a small, plot-scale simulation model with two trophic levels is shown in Figure 2. Parts a, b, and c represent the biomass of a crop at three different times during the growing season, and parts d, e, and f represent the biomass of the herbivore at corresponding times. The crop is planted in rows, such that the herbivore can move more easily from plant to plant along than across rows. Each vertical rod shows the biomass of the crop and pest within one unit of the crop, for example, a single plant. Observe the non-uniform spread of the pest, which arises from the greater ease of movement along rows than across them.

The spatial spread model in Figure 2 has a small set of parameters, which can be quantified from existing information where available, or measured experimentally. The crucial botanical parameters affecting spread of flightless herbivores exist in three dimensions (not two as in Figure 2) and include features of the vertical architecture and physiology of plant stands. Work is in progress to define the salient aspects of vertical and horizontal connectivity in crop-weed stands by image analysis of photographic slices of the stand at different times during the season. Experimental systems are being tested that will enable the links to be made between architecture and rate of insect spread within and between crop fields.

The complication of plant energy trade-offs One of the practical aims of this work is to offer optimal designs for both plant breeding of new genotypes and the construction of multi-purpose stands. The work here links to the individual-based approach to diversity described in the preceding article. Within the plant level in Figure 1, individuals can partition the



The mathematical model is a system of 2 Ordinary Differential Equations.

$$\frac{\partial C}{\partial t} = \theta C\left(1-\frac{C}{K}\right)\frac{-fCH}{H+fhC}$$

$$\frac{\partial H}{\partial t} = \frac{\phi fCH}{H+fhC}-\mu H$$

Reference: Jost *et al.* 1999.

We impose a constraint on the crop C so that the following holds

$$\frac{\theta h}{\phi f} = q$$

where q is constant. This imposes an energy trade-off. For instance, additional investment in growth (increase in θ) leads to one of the following:

1) increase in ϕ (the food quality or palatability).
2) decrease in h (the "handling time". This can be thought of as the time it takes a unit of pest to process a unit of crop).
3) increase in f (the maximum crop consumption rate).

In the example presented in the dialogue the first of these is assumed, giving us that $\theta = Q\phi$ with $Q=qf/h$ representing the "strength" of the trade-off. This is the equation of the line cutting across the yield surface .

Figure 3 Modelled variation in yield with change in plant growth rate and palatability to herbivores. Contours show lines of equal yield. The black line shows the yield of a single plant type having a defined trade-off between growth rate and palatability (see text).

available resource in a number of areas, important among them being (i) plant growth, (ii), toxins for defence against pest attack (lowering the food quality to the pest), and (iii), structural defence which inhibits attack or hinders spread. Since a plant has only a finite rate of energy acquisition, being limited in the amount of sunlight it can intercept and convert, there must be large regions of the trait space which are unavailable to it. If a plant invests a larger part of its energy into growth, then it has to put correspondingly less into defence, i.e. it produces less toxin or invests less in structural defence. A plant can't be a lettuce and a cactus. This complicates the issue of plant improvement, since breeding for increased growth, with which we would anticipate increased yield, may be offset by a decrease in plant defence which makes the crop more susceptible to attack by pests or more desirable as a food source for a pest, thereby negating or producing the opposite of the desired agronomic trait.

As illustration, the example in Figure 3 shows a 'yield surface', which defines how yield might be expected to vary with changes in the palatability and growth rate of the crop. The surface is derived by using simple functions of the type described previously. Maximum yield in the presence of a pest would be reached at maximum growth rate and minimum palatability to herbivores; this is the area of trait space that plant breeding aims for, but in reality is impossible to inhabit. The contours in the figure indicate lines of equal yield, the different points on which are necessarily achieved by different combinations of growth rate and palatability.

The wider challenge is to place the individual in this scheme. As a first step, we accept the existence of a 'trade-off' between plant growth and defence, and so quantify individuals by the strength of the trade-off (a growth/palatability function), which is the rate of loss of growth per unit decrease in palatability (or how much slower plants grow if they use a unit of their resource to produce toxin). Plants that lose little intrinsic growth while making themselves highly unpalatable to pests might be desirable in crop breeding lines. The black line cutting across the contours in Figure 3 shows one such growth/palatability type, and might represent a crop genotype in a breeding programme or a weed ecotype in an arable field. Any number of other types could be added, but are excluded for clarity. The line (= plant genotype) traverses the yield surface in an interesting way. As we follow the line from the back of the graph (low growth, low palatability), the yield first declines: the surface decreases too steeply since the gain from increased growth rate is overpowered by the loss from increased palatablity. Nearer the front of the graph, the effects are reversed, such that the gain from increased plant growth rate is greater than the loss from increased palatability. Whether the individual gains or loses depends as much on the context - the system parameters - as its physiological traits.

Biodiversity and integrated management The argument can now return to the matter of increasing invertebrate diversity. Many intensive improvement programmes are concerned with the interactions between one plant type (the crop variety) and one herbivore (the main target pest). Intentionally or not, one or both of f and ϕ are altered by plant breeding to reduce the effect of the herbivore on the crop. Even if chemical formulations are not used to augment the genetic change, the alteration has ramifications for other herbivores that might eat the plant and possibly predators that consume herbivores made ‘toxic’ by eating the plant. Additionally, the decline of one herbivore might be matched by the rise in others through change in competitive advantage. Such tri-trophic effects have received particular attention in risk assessment studies on GM crops that have enhanced anti-pest properties. However, our scheme can be used to examine the impact of GM crops in the same way as corresponding effects of conventional crops and of weeds that produce toxic, anti-insect chemicals.

If the intention is to increase biodiversity, however, tri-trophic effects have to be managed rather than avoided. Means have to be found of increasing the number of different values of f and ϕ and then g and ψ in a system, and also of the traits that alter the survival and movement of the herbivores and predators. Increasing the number of plant types potentially increases the complexity of the interactions in Figure 1, but a systematic approach to balancing the traits among individual plants should be preferable to simply increasing the number of plant species. With reference to the arguments around Figure 3, plant types should be mixed that cover a range of growth/palatability lines for the environment in question. The result would be to optimise the trade-off at a broader scale than the individual plant or genotype.

The inclusion of other species in the model results in continual feedback between the different components of the system. For instance, each herbivore type has the potential to affect others through its influence on the amount and quality of plant mass. In principle, the complexity can be examined by techniques similar to those used to probe vegetation communities. Provided the tri-trophic system can be parameterised - and there is no reason why it should not - then searches of the type outlined in Figure 5 of the preceding article should be able to point to the fittest community of plants, herbivores and predators.

Conclusions The aim of this report was to introduce a new area of work at SCRI, which has taken the approach of synthesising the existing mathematical theory and empirical knowledge as a means of defining the salient questions, before embarking on experimentation. Additional subjects tackled in this way, not mentioned above, include the evolution of resistance in the pest population to the genetic change introduced to the plant. As in the comparable research on trait space and interactions in plant communities, a particular function of the models is to condense a complex set of potential traits and variates to a manageable number that are common across organisms and ecosystems. The emphasis will now be on measuring the appropriate traits of crops, pests and natural enemies in field experiments, the prototypes of which were tested during 2000.

References

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