

## Modelling an ecosystem: The example of agro-ecosystems

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### ABSTRACT

Methods to predict ecosystem responses to changing environmental conditions, including options for mitigation and management, are vital for scientists and policy makers. We propose that modelling ecosystems by grouping species into trophic-functional types has great utility, because it is potentially generic and applicable to any ecosystem.

Here we describe in details a trophic-functional ecosystem model of arable agriculture (the TrophicLINK model), constructed using an individual-based model, and present some supporting sensitivity tests of the model performing according to our expectations for the arable ecosystem. We vary parameters for particular plant and invertebrate trophic-functional types and we show that the model is sensitive to the values chosen.

Though this trophic-functional method for modelling ecosystems will be subject to further sensitivity tests and empirical validation, we argue that the modelling structure is fit for investigating the impact of changes in agro-ecosystems.

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### 1. Introduction

A considerable challenge facing ecologists and decision makers is the prediction of ecosystem responses to changed environmental conditions, such as changes in agricultural management, land use and climate change, as well as appropriate decision making. Will changed ecosystems be sustainable and resilient, and able to continue to supply the services and functions that they currently provide (Elmqvist et al., 2003; Folke et al., 2004; Schröter et al., 2005)?

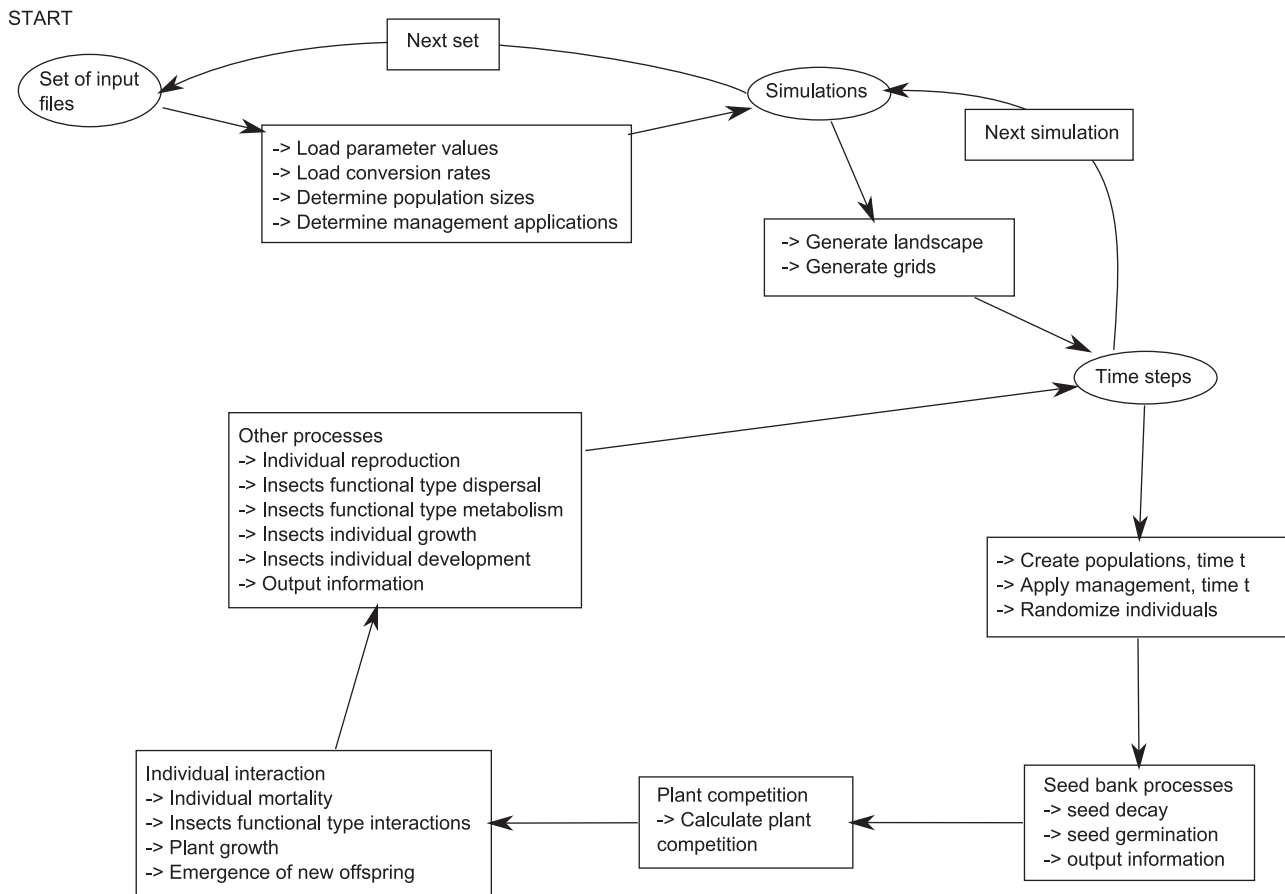
In a recent paper, Caron-Lormier et al. (2009) outlined a novel way of modelling the biotic diversity and productivity of an ecosystem, and thereby predict how management or external disturbances might affect these system properties. The difficulty of building scientifically valid and ecologically realistic models of ecosystems is one of appropriate representation and simplification: how is it possible to reduce the many hundreds of species, and their interactions with one another and the environment (Smith et al., 2008), into a scientifically justifiable and computationally tractable representation that retains the important biological and ecological properties of the ecosystem? Caron-Lormier et al. (2009) advocated a synthesis of approaches from functional ecology, food web net-

work theory and population dynamic theory, elements of which are also advocated by Allesina et al. (2008) and Allesina and Pascual (2009). In Caron-Lormier et al. (2009), species are assigned to “trophic-functional types”. These types are containers for individual organisms that share similar functional properties and trophic behaviour. Types are then linked into a network by the trophic behaviours of the individuals they contain. Population dynamics result from local interactions between individuals, simulated within an individual-based model (IBM), the TrophicLINK model.

The system is defined as considered to be composed of three trophic (or biomass transformation) layers; the primary producers (e.g. plants), and primary and secondary consumers (e.g. invertebrates). This trophic-functional approach has a number of benefits and is not limited to any number of trophic-functional types. It builds upon established theory and it moves the evaluation of an ecosystem away from ecosystem-specific species composition onto the processes we believe might drive ecosystems. Management is considered simply as a form of disturbance to trophic-functional parameter values. The herbicide management of agricultural systems would not, therefore, be modelled differently to insecticide management, or land management, but would differ only in the rate parameters and trophic-functional types are affected. Disturbance of any type or of trophic functional parameter values could have knock-on effects onto other types through trophic cascades (Polis et al., 2000; Schmitz et al., 2000; Borer et al., 2005; Pascual and

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**Fig. 1.** Flow diagram of the model. The diagram starts at the top left corner and ends when all the sets have been done. For any given set, there may be several simulations; for which there may be several time steps.

Dunne, 2006; Schmitz, 2006; Petchey et al., 2008). This modelling structure would allow these cascades to be monitored by tracking biomass flow between trophic layers, and trophic-functional types.

Caron-Lormier et al. (2009) argued and showed how it might be possible to construct a model of an ecosystem. In this paper, we show how the concept of a generic ecosystem model based on trophic-functional types can be realised (Section 2), and present supporting sensitivity tests (Section 3). The targeted sensitivity tests presented here vary parameters for the plants (primary producers) and for the invertebrates (primary and secondary consumers). Although we run simulations in which the consumers are invertebrates, it is worth pointing out that there is nothing to prevent the model from being adapted for other types of animal. Our expectation was that the model would produce simulation outputs for plant and invertebrate types that are consistent with observation and other population models. The main difference is that the TrophicLINK model can simultaneously present information on network structure, abundance, biomass and dynamics. We then discuss the performance of the model and whether, in principle, the model is fit for the purpose of testing the compound hypothesis stated by Caron-Lormier et al. (2009) that “trophic-functional types of plants and invertebrates can be used to explain the structure, diversity and dynamics of arable ecosystems”.

## 2. Methods

Here we describe how trophic-functional types and the salient features of the model have been implemented. The description is as exhaustive as possible and follows the standardised ‘Overview, Design concepts and Details’ description developed by Grimm et al.

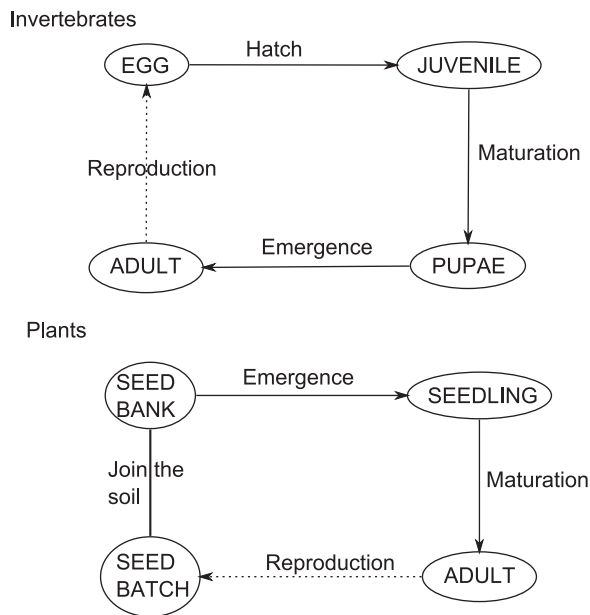
(2006). The model code is available from the authors on request. Design concepts were discussed in Caron-Lormier et al. (2009). Here, we concentrate on the detail of “Sub-models” and give a full description of the model rules and functions, following the general structure shown in Fig. 1. We attempt, where biologically appropriate, to use similar functions for describing the life history of both the plants and the invertebrates.

The model reads in input files to load the parameter values of the different trophic-functional types, their conversion rates (trophic links) and the management information. From the parameter values, the sizes of type populations and their introduction times into the simulations are set. For each parameter set, the model then loops on the appropriate number of simulations. First, the landscape is created with grids of the appropriate dimensions. For each simulation, the model runs for a given number of time steps, within which it goes through different processes from creating populations and applying management at the relevant times, to processing plant and insect functions.

Individuals of plant and invertebrate types follow common life cycles (Fig. 2). Individuals start as egg or seed and hatch at the defined time(s) to become juvenile or seedling. Juvenile individuals develop to become adults, which produce the next generation of eggs or seeds (propagule).

### 2.1. Input files

The program reads the set of input files and loads parameter values for all the trophic-functional types in the model. At this stage, the two parameters of interest are the abundance and the time of first emergence which are used to determine the popu-



**Fig. 2.** Schematic representation of the life cycles of plant and invertebrate individuals simulated in the model. The solid lines represent a individual transformation from one state to another, whereas the dotted lines represent a creation of individuals.

lation size of the different trophic-functional types. Management information is also read in and used to specify the timing of management and its effect on life-history parameters on the affected functional types. A typical management file for application of, say, a chemical spray will contain the name of one or several managements, the date of first spray, the periodicity and the number of sprays, as well as the list of affected types, and the success probabilities of the management applications for each of the affected types. Environmental information is used to create the landscape. A typical file for the environmental parameters contains the start and end of the simulations, the environmental temperature, the dimensions of the simulated patch, the number of simulations and the distance between two rows of crop ( $dx_{crop}$ ). The parameter values for each functional type are loaded from a single file containing information on initial population densities and life history traits (e.g. mortality, reproduction rate, growth, ...). For each parameter, the model is given three different values representing the minimum, maximum and mode of a triangular distribution from which individual characteristics are drawn.

## 2.2. Loop on simulations

At the start of each simulation, the continuous landscape is generated based on specified  $DimX$  and  $DimY$ . Two types of grid

are then created and overlayed on the landscape. One grid, hereafter referred to as the general grid, is used for keeping track of individuals by storing their individual ID in grid cells. The second, the micro-grid, is used for calculating plant competition. The cell dimensions of the general grid are based on the smallest foraging radius of the invertebrate trophic-functional types. This means that any invertebrate will always search across at least one cell for neighbours with which to interact. In the case that there are no invertebrate types included in a simulation, the parameter  $maxGridCell$  is used instead. The general grid is also used to keep track of the seed bank of the various plant functional types. The micro-grid cell dimension is based on the smallest plant zone of influence ( $zoi$ ) used in the simulation. This means that any plant will experience at least one micro-grid cell, at any time. We would note that individuals retain continuous co-ordinates on the space; the grids are simply used to speed up searching for neighbours and the calculation of plant competition. The interactions between individuals are presented further down in the text.

## 2.3. Loop on the time steps

Individuals of particular trophic-functional types are created as specified in the input files. Individuals of the plant (including the crop) and detritus trophic-functional types are created at the  $StartTime$  of the simulations. Other trophic-functional types may emerge within the patch later in the simulation. Crop plant individuals are sown in rows. The crop is introduced with appropriate characteristics (e.g. distance between rows, seed size, emergence pattern, ...) at the start time and its development begins.

Weed trophic-functional types are introduced as seeds in the seed bank. When the model enters a germination period, seeds of particular types may emerge. Individuals of invertebrate trophic-functional types are randomly and uniformly distributed on the simulated patch, and are given values for each of their characteristics from the input files and the list of characteristics in Tables 1–5.

The dynamics of detritus in the system is modelled as a set of 'individuals' each with a given, fixed position during the entire simulation. One detritus individual is created per general grid cell, located in the middle of each cell. The role of these individuals, or local detritus pools, is to act as receptacles for dead matter and make detritus biomass available to detritivore trophic-functional types. This formulation of detritus has the advantage of simplifying the pattern of detritus in the system to a number of individuals created during the simulations, whilst retaining the spatial information about the distribution of detritus across the simulated patch.

Management derived disturbance is applied uniformly to the entire patch, and all individuals have the potential to be affected. The grid is scanned and individuals of affected trophic-functional types have their characteristics modified. The characteristics of

**Table 1**  
List of individual characteristics and their description of the generic traits.

| Individual characteristics            | Description   |
|---------------------------------------|---|
| Age                                   | Age of the individual, in days (or time step)   |
| Development state                     | Individual development. Values between 0.0 and 1 mean that individuals are juveniles; values over 1.0 individuals are adults  |
| Base temperature                      | Individual base temperature (°C)  |
| Functional type                       | Individuals belong to only one functional type during their life time   |
| Individual ID                         | Individual identification number which is fixed throughout individuals' life time   |
| Alive status                          | States whether individuals are dead or alive  |
| Individual status                     | States whether individuals are individuals or batches of seeds/eggs   |
| Food competitors                      | This is the ratio of herbivore biomass currently carried by plants to the upper limit of herbivore biomass that plants can carry. Values around 1.0 mean that plants have reached their maximum carrying capacities |
| Starvation index (invertebrates only) | States how hungry are individuals. Values around 1.0 mean that individuals are very hungry  |

**Table 2**

List of individual characteristics and their description of the position, mortality and weight traits.

| Individual characteristics | Description   |
|----------------------------|---|
| X and Y                    | X and Y individual continuous coordinates (in space units)                                  |
| Previous X and Y           | X and Y individual continuous coordinates of the previous time step (in space units)        |
| Juvenile mortality         | Juvenile individual mortality rate  |
| Adult mortality            | Adult individual mortality rate   |
| Senescent mortality        | Senescent individual mortality rate   |
| Base weight                | Individual base, or structural, weight (in g)   |
| Free store weight          | Individual free store, or reserve, weight; it is used to meet daily individual costs (in g) |
| Propagule weight           | Individual propagule weight; it is used to produce offspring (in g)                         |

**Table 3**

List of individual characteristics and their description of the foraging, and reproduction traits.

| Individual characteristics         | Description  |
|------------------------------------|--|
| Foraging radius                    | Invertebrates use the individual foraging radius to create their neighbour list. Plants use this as a surrogate to convert their zone of influence to plant biomass (in space units) |
| Relative growth rate (plants only) | Relative growth rate used for plant growth   |
| Competition weight (plants only)   | Individual competition weight is used to calculate the amount of resources shared between plants covering the same area  |
| Single propagule weight            | Single propagule weight is used to calculate how many offspring are created from one propagule batch (in g)  |
| Reproductive ratio                 | Individual reproductive ratio is the ratio individual propagule weight to individual total weight over which individuals can release the propagules and create new offspring         |

managed individuals are modified according to management specifications.

The order of processing active individuals is randomised to ensure that there is no bias towards any individual or trophic-functional type.

**Table 4**

List of individual characteristics and their description of the growth trait.

| Individual characteristics         | Description   |
|------------------------------------|---|
| Age at maturation                  | Age at maturation is the age (in days) at which plant individuals reach maturation. Invertebrate individuals reach maturation when their development state reaches 1.0 (no dimension) |
| Proportion free store to base      | Individual proportion of free store to base is the proportion of individual free store weight juvenile individuals attribute to individual base weight (i.e. growth)                  |
| Proportion free store to propagule | Individual proportion of free store to propagule is the proportion of individual free store adult individuals attribute to individual propagule weight (i.e. reproduction)            |
| Maximum weight (plants only)       | Individual maximum weight that plants can reach (in g)  |
| Time as pupae                      | Invertebrates only, number of days individuals spend in pupae form before becoming adults (in days)   |
| Proportion after pupae             | Invertebrates only, proportion of individual total weight remaining after the pupae form  |

**Table 5**

List of individual characteristics and their description of the food demand, respiration and development traits.

| Individual characteristics                        | Description   |
|---|---|
| Base daily food demand                            | Base daily food demand is the daily food demand when at base temperature (proportion of own weight, in g)       |
| Daily food demand increase                        | This is the increase with temperature of the daily food demand  |
| Base respiration cost                             | This is the respiration (metabolism) cost at base temperature (proportion of own weight, in g)                  |
| Respiration cost increase                         | This is the increase, with temperature, of the respiration cost   |
| Time to full development at $T=0^{\circ}\text{C}$ | This is the time needed to reach full development at a hypothetical $0.0^{\circ}\text{C}$ temperature           |
| Time to full development decrease                 | This is the decrease (negative values) with temperature of the time needed to reach full individual development |

### 2.3.1. Seed bank processes

The model scans the general grid and for each cell retrieves the number of seeds in each weed type. Each seed in turn is tested for survival and germination. The information on the remaining seeds is exported into a data file for analysis. For each weed type there may be one or two germination periods across the growing season, each defined by three dates: a start, end and modal. If the current simulation day is between the start and the end dates, the probability of germinating is calculated using a triangular distribution using the four parameters: current day, start, end and modal dates; and a type-specific annual germination rate. Each seed has in turn a chance of germinating, based on this probability, and successful seeds are introduced as seedlings into the population with a random position within the general grid cell. Seedlings then start to compete with other plants.

### 2.3.2. Plant competition

In the second loop on individuals, the model determines the spatial variation in plant competition over the patch. This process fills the micro-grid up with competition information so that individual plants will experience appropriate levels of competition for shared resources. Each plant individual has an allometric constant, *allometricC*, and a base weight, *baseweight* from which the radius of its zone of influence (hereafter *Zol*) is calculated:

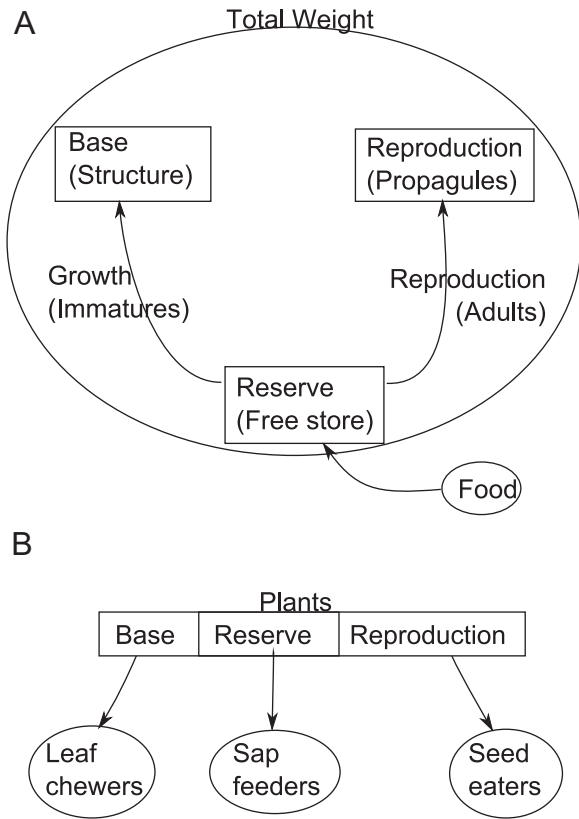
$$\text{radius} = \left( \frac{\text{baseweight}}{\text{allometricC}} \right)^{1/3} \quad (1)$$

Eq. 1 assumes that a plant's *Zol* depends on its base weight (equivalent to structural weight) corrected by an allometric constant for when the plant is short and squat or tall and thin. Each individual has a competitive strength (or coefficient) which is added to the micro-grid cells within its *Zol*. This tracks how competitive the different plant individuals are and is used for sharing resources between plants.

### 2.3.3. Individual interactions

The third loop on individuals deals with processes such as individual mortality, invertebrate interactions and plant growth, and emergence of new offspring. Each individual has an age or a development state and this is used to determine a survival probability. At death, individuals are removed from the grid and from the list of active interacting individuals. Dead individuals with non null weight are converted into detritus and their total weight is transferred to the local detritus pool. Detritus biomass decays with time using a daily decay rate.





**Fig. 3.** Illustration of individual weight and feeding preferences. (A) Distribution of the individual total weight in the three weight compartments: base (or structure), reserve (or free store) and reproduction (or propagules). Juvenile individuals grow by allocating some reserve weight to base weight, while adults allocate some reserve weight to reproduction. (B) Feeding preferences of herbivore trophic types based on the three weight compartments of plant individuals.

For each invertebrate individual, a list of neighbours is created, with which it can interact. The individual has a foraging radius from which the search area is calculated and any grid cell in this area is scanned for interacting individuals, such as food items. All relevant neighbours are added to the neighbour list; once the process is completed the list is shuffled. Processes controlling the bioenergy of individuals are based on the work of Crowl et al. (2000); Gutierrez (1996) and Rudstam (1989). Invertebrate individuals have a base daily food demand,  $d_b$ , a daily food demand increase with temperature,  $d_t$ , a base temperature,  $T_b$ , and a total weight,  $weight$ . The daily food demand,  $d$ , is the amount food individuals could ingest within a time step:

$$d = d_b \exp(d_t(T - T_b)) \text{weight} \quad (2)$$

The starvation state,  $starv = d - \text{freeStoreWeight}$ , represents how hungry an individual is and will determine the amount food required before satiation. Individuals only feed when hungry; once fully satiated, they stop feeding. Herbivore trophic-functional types only feed on their preferred plant weight compartment whereas predator trophic-functional types can eat the whole prey (Fig. 3B). Food mass is converted into the consumer's mass using a conversion rate held at the trophic-functional type level. This means that all individuals of a given trophic-functional type convert their food with the same efficiency,  $\text{intake} = \text{fooditem} * \text{convrate}$ . When the intake value is greater than the food required, individuals only take what they need. When the intake value is smaller than the food required by the consumers, the food item is eaten whole. In the case of herbivores feeding on plants, a plant loses the amount of weight that the herbivore takes. Invertebrate prey die even if they

have only been partially consumed, and become unavailable for future interactions.

A conversion rate matrix is also used for the feeding preferences of the different functional types. If a functional type can feed on different food sources, the conversion rates will be used as probability of feeding on each food sources, relative to the maximum conversion rate. Consider, for example, a predator type capable of feeding on two different prey types. The first is converted at 0.45 and the second at 0.30. The feeding probabilities for each type are  $0.45/0.45 = 1$  and  $0.30/0.45 = 2/3$ , respectively. These probabilities are used at each interaction. Plants can only carry a (daily) given herbivore biomass which is based on their own individual biomass. As herbivores feed on plants, they contribute to the daily herbivore biomass until a maximum is reached. In this case, plants become crowded and repulsive. Under these conditions, no further herbivore individuals can be accommodated on the particular plant, and herbivores begin to disperse to other plants.

Individual plant growth is based on the radius of the ZoI,  $radius$ , and the competitive weight,  $compw$ , of the plant, and follows the work of Weiner et al. (2001) and references therein. A focus plant examines all the micro-grid cells within the ZoI and calculates the fraction of micro-grid cells it can 'claim' for energy capture,  $fraction$ . Plants have a relative growth rate,  $rgr$ , and we assume that published  $rgr$  values are suitable when plants are very small and far from their maximum weight. A proportion of mass at fixed point, when plants are young,  $RGR_{\text{applied}}$ , is used to calculate what would be the radius at this fixed point,  $radius_{\text{young}}$ :

$$radius_{\text{young}} = \left( \frac{RGR_{\text{applied}} * \text{MaxWeight}}{\text{allometricC}} \right)^{1/3} \quad (3)$$

The energy captured:

$$E_{\text{capt}} = \frac{rgr * \text{allometricC} * radius_{\text{young}}}{\pi * (1 - RGR_{\text{applied}})} \quad (4)$$

The total energy this plant receives from the fraction of its ZoI is

$$E_{\text{tot}} = E_{\text{capt}} * \text{fraction} * \pi * radius^2 \quad (5)$$

Plants maintain a fixed proportion of their base weight,  $weight_{\text{propn}}$ , in the sap weight compartment. Therefore, they may need to adjust this amount at every time step using the proportion of free store to base parameter:

$$sap_{\text{adjust}} = weight_{\text{propn}} * \text{baseweight} - \text{sapweight} \quad (6)$$

The sap weight is adjusted based on the proportion and the base weight and the remainder of the total energy can be used for growth or seed production,  $E'_{\text{tot}} = E_{\text{tot}} - sap_{\text{adjust}}$ . When the plants are mature and have energy to allocate to seed production, a proportion of the total energy is transferred to reproductive weight compartment. The remainder of the total energy is used for growth

$$\text{baseweight}' = \text{baseweight} + E'_{\text{tot}} * \left( 1 - \frac{\text{baseweight}}{\text{maxbaseweight}} \right) \quad (7)$$

The model ensures that the amount of biomass added to the base weight does not exceed the maximum base weight allowed for this individual,  $\text{maxbaseweight}$ .

Batches of invertebrate propagules are stored within the population as individuals. Once the propagules are ready to hatch, they are released in the environment. New individuals are created, at their current position, and introduced into the population using the same process as presented above. New individuals are given starting values for their weight compartments. The total weight of a new individual is determined from the initial distribution (i.e. at trophic-functional type level), but the repartition of the total weight between base weight and free store is calculated from the parental repartition when the propagule batch was created. Batches of seeds

are stored for a given length of time during which seeds are available to seed predators. After this time, the remaining seeds join the local seed bank and may emerge later in the season depending on the germination profile for that functional type.

### 2.3.4. Other processes

The fourth loop on individuals deals with individual reproduction, dispersal, growth, and development, and the specifics of metabolism in invertebrate. Each adult individual may create a batch of new offspring if the ratio of “reproductive weight to total weight” is above a given threshold (this threshold is held at functional type level). Only enough reproductive weight to create exact numbers of propagules is used; the remainder is left in the reproductive weight compartment. For each batch, the number of propagules, the weight of one propagule, the partitioning of total weight between base weight and reserve weight at hatching/germination and the number of time steps before hatching/germination is stored. Seed batches are stored at the general grid cell level as opposed to an exact position. Seeds are dispersed around the parental plant. As individual seeds touch the ground they join the local batch created that day by the parental plant. Seeds created by the same plant on a different day will form a new batch. This ensures that the number of individuals created during the simulation is not computationally excessive while approximating the spatial and temporal distribution of seeds for each functional type. Note that reproduction is implicit in the current version of the model in the sense that individuals have no gender and do not need to interact to produce offspring.

Invertebrate trophic-functional type individuals can disperse during the simulation and their motivation (probability of movement and distance moved), *motiv*, is based on food competition, *food<sub>comp</sub>*, and their individual starvation level, *starv*.

$$motiv = \max(food_{comp}, starv) \quad (8)$$

Either starvation or competition for food can trigger dispersal. *motiv* is kept under 1.0 and is corrected by the development state of the individual. *motiv* is used as a probability of dispersal and an individual may disperse a distance, *disp*, between *d<sub>min</sub>* and *d<sub>max</sub>*:

$$disp = (d_{max} - d_{min})motiv - d_{min} \quad (9)$$

In the current model, the direction of dispersal is random, individuals adopt a random walk. New individual positions are established from the parameter *disp*, a randomly generated angle and the previous position. When individuals disperse over the boundaries of the simulated patch, they reflect back into the patch with a given probability. Dispersal incurs a weight cost, *cost*, to the individual which depends on individual weight, the cost of dispersing per unit distance per total unit weight, *disp<sub>cost</sub>*, and the distance travelled, *disp*:

$$cost = totweight \cdot disp_{cost} \cdot disp \quad (10)$$

This weight cost of dispersal is subtracted from the reserve weight of the dispersing individual.

Individual metabolism of invertebrate trophic-functional types, *r*, is calculated using the individual base respiration, *r<sub>b</sub>*, the individual respiration increase with temperature, *r<sub>t</sub>*, the individual base temperature, *T<sub>b</sub>*, and the environmental temperature, *T*, such that:

$$r = r_b \cdot \exp(r_t(T - T_b)) \cdot weight \quad (11)$$

This cost of metabolism is then subtracted from the reserve individual weight.

Individuals with negative value weight compartments die from starvation. Growth of live individuals is based on development state, with juveniles allocating a proportion of their free store to their base weight, whereas adults allocate a free store proportion to their reproductive weight (Fig. 3A). Individual development

**Table 6**

Life history traits used for the sensitivity analysis for plants and invertebrates.

| Taxa    | Parameter name               | Description   |
|---------|------------------------------|---|
| Plants  | Competitive coefficient      | Plant capacity for “claiming” shared resources  |
|         | Juvenile mortality           | Daily mortality rate of juvenile plants   |
| Inverts | Foraging radius              | Radius of a circle centred on an individual invert from which food can be accessed                |
|         | Herbivore feeding preference | Value between 0.0 and 1.0 for each of the potential food items representing the chance of feeding |

is based on the individual starvation index and the environmental temperature. It is generally assumed that satiated individuals develop faster than hungry individuals, where *coef* =  $1 - starv/d$  represents the effect of satiation on development rate in a given time step.

Individual daily development is *devel* =  $a + bT$ , with *T* the environmental temperature, *a*, a constant daily development and, *b*, the slope of the linear regression. Typical values for small sap-feeders (e.g. aphids) are  $a = 0.75e^{-02}$  and  $b = -3.75e^{-02}$ , which at  $T = 20^\circ C$  and optimum food conditions gives a duration of around 10 days from birth to maximum adult weight.

## 3. Results

### 3.1. Generalities

Before using any model, it is necessary to build confidence in the model outputs by providing a detailed description and by performing sensitivity tests and validation. Sensitivity testing is important because it illustrates how the model reacts to parameter changes. The approach takes a defined set of input parameters and runs several simulations for different values for each parameter. It is usually not possible to test for all parameters of the model. The sensitivity simulation output can then be analysed, to provide some confidence in the model (Saltelli et al., 2004; Grimm and Railsback, 2005). Where the model is found to be insensitive to a given parameter, the model may be simplified by removing the parameter or fixing the parameter at a constant value.

### 3.2. Parameters explained

For the targeted sensitivity analysis presented here we varied the values of two important plant and invertebrate parameters (Table 6) and conducted replicated simulations runs. Outputs were extracted from the simulation runs to investigate the sensitivity of the model system.

General model parameters were fixed so that *DimX*=*DimY*=10 m, the plants (weed and crop types) were introduced as seeds near the beginning of the simulations, at around day 94, and were left to emerge. The values were taken to illustrate part of the TrophicLINK model performance and do not represent a specific situation in farmland systems.

#### 3.2.1. Plant parameters

The sensitivity testing of plant interactions were performed with simulations of a cereal crop and one of three different weed functional types. The weed types used were a spring-germinating weed (sgw, FT11), an autumn-germinating weed (agw, FT22), and a spring- and autumn-germinating weed (sagw, FT10). The crop density was approximately 300 plants/m<sup>2</sup>, the crop row spacing was set to 0.15 m and the *RGR<sub>applied</sub>* was set at 0.15. The simulations were repeated ten times for each parameter value change. The weed seed

**Table 7**  
Parameter values used for the weed competitive weight.

| % relative to the default value | 50%   | 75%   | 100%  | 125%  | 150%  |
|---------------------------------|-------|-------|-------|-------|-------|
| Weed                            | 0.150 | 0.225 | 0.300 | 0.375 | 0.450 |
| Crop                            |       |       | 0.500 |       |       |

Five values were used, representing 50%, 75%, 100%, 125% and 150% of the default values (100%). For the simulations the competition weight of the crop was set to 0.5.

**Table 8**  
Parameter values used for the weed juvenile mortality.

| % relative to the default value | 50%    | 75%     | 100%  | 125%    | 150%   |
|---------------------------------|--------|---------|-------|---------|--------|
| Weed                            | 0.0075 | 0.01125 | 0.015 | 0.01875 | 0.0225 |
| Crop                            |        |         | 0.001 |         |        |

Five values were used representing 50%, 75%, 100%, 125% and 150% of the default values (100%). For the simulations the juvenile mortality of the crop was set to 0.001.

**Table 9**  
Parameter values used for the herbivore and predator foraging radii, in meters.

| % relative to the default value | 50%  | 75%  | 100% | 125% | 150% |
|---------------------------------|------|------|------|------|------|
| Herbivore                       | 0.10 | 0.15 | 0.20 | 0.25 | 0.30 |
| Predator                        | 0.25 | 0.38 | 0.50 | 0.62 | 0.75 |

Five values were used representing 50%, 75%, 100%, 125% and 150% of the default values (100%).

bank was initially set to 2000 seeds/m<sup>2</sup> in all of the simulations. The plants were grown without management or invertebrates.

**3.2.1.1. Competitive coefficient.** The competitive coefficient of a plant, *compw*, can introduce asymmetry in the competition between plants and plant functional types for resources. The different values taken for sensitivity test of this parameter are shown in Table 7.

**3.2.1.2. Juvenile mortality.** The natural juvenile mortality (*jm*) of plants represents the probability of an individual dying at each time step. These parameter values can be used to approximate self-thinning in plant populations. Table 8 shows the different values used for this sensitivity test.

### 3.2.2. Invertebrate parameters

Where appropriate the sensitivity tests for the invertebrates used the same parameter values as were used in the sensitivity tests for the plants. The values were taken to illustrate part of the TrophicLINK model performance and do not represent a particular situation in farmland systems. One spring-germinating weed type was used at 100 seeds/m<sup>2</sup>. The distance between two crop rows was set to 0.9 m and the crop density was 100 plants/m<sup>2</sup>, and the *RGR*<sub>applied</sub> was set to 0.04. Plants were introduced at day 94 and the herbivores and predators were introduced 30 days and 55 days later, respectively. No management was applied.

**3.2.2.1. Foraging radius.** The foraging radius is used to calculate the area individuals can forage per day and can be used to simulate changes in individual mobility. Table 9 shows the assumed values for these simulations.

**3.2.2.2. Herbivore feeding preferences.** The feeding preferences (*hfpref*) are used to determine the chance of one individual feeding on a prey food item of a particular functional type. Table 10 shows the assumed values for these simulations.

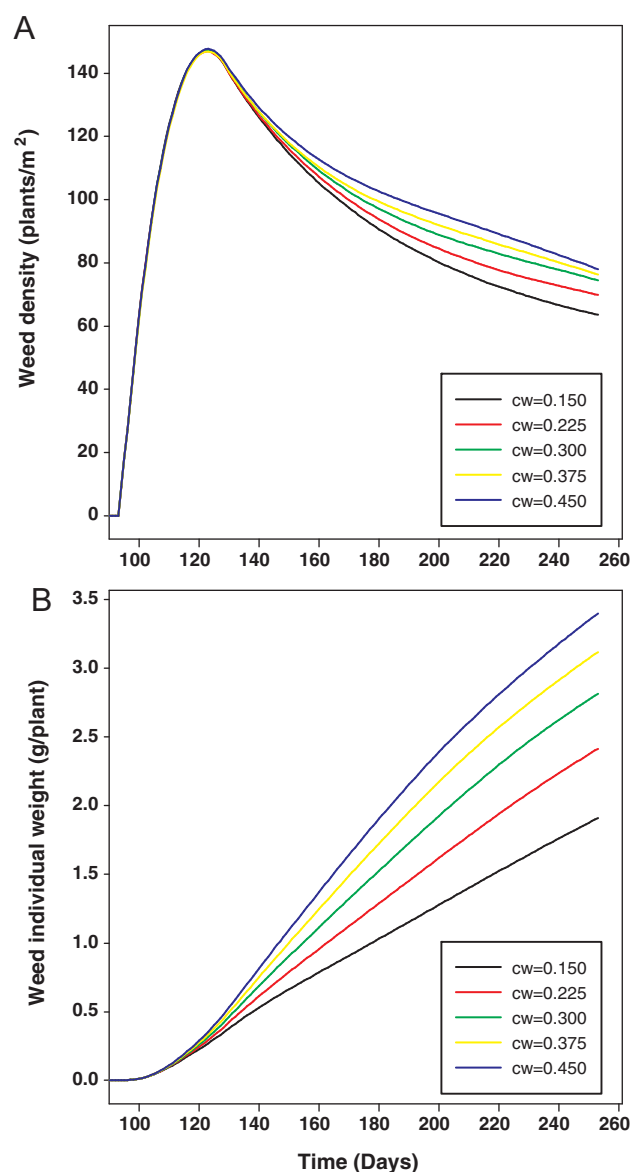
**Table 10**  
Parameter values used for the trait feeding preference of the herbivore functional type.

| % relative to the default value | 50%      | 75%       | 100%    | 125%      | 150%      |
|---------------------------------|----------|-----------|---------|-----------|-----------|
| Conversion rates                | 0.05:0.1 | 0.075:0.1 | 0.1:0.1 | 0.125:0.1 | 0.150:0.1 |
| Feeding preferences             | 0.50:1   | 0.75:1    | 1:1     | 1:0.80    | 1:0.67    |

The conversion rates are the exact values for converting plant biomass to herbivore biomass. The feeding preferences are derived from these values, using the maximum rate as the most preferred item (i.e. 100% of eating if found). Values used are relative to the default value (100%).

### 3.3. Sensitivity tests

For spring-germinating weeds, increases in weed competition coefficient lead to higher weed density and individual weight (Fig. 4). The weeds with higher competitive capacity grow and develop faster spending less time in the juvenile stage, when mortality rate



**Fig. 4.** Influence of plant competition. Influence of competition coefficient (cw) of a spring germinating weed on weed density (A) and weed individual weight (B) with time.

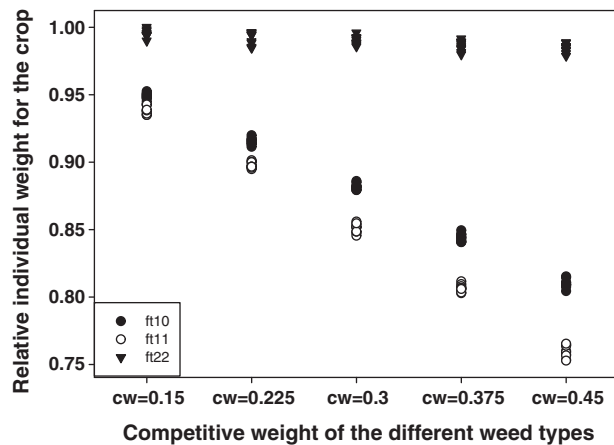


Fig. 5. Influence of weed competition on crop yield. Individual weight of the crop, relative to the maximum, at the last time step of the simulation, for the five values of *compw* and the three different weed functional types (FT11, FT10 and FT22).

is higher than that of the adult stage. Similar behaviours are found for agw and sagw (not shown).

The autumn-germinating weed competitive coefficient (closed triangles) has little effect on the crop individual mass just before harvest (Fig. 5). However, both the spring- and autumn-germinating weeds competitive coefficients (respectively, open circles and closed circles) negatively affect the crop individual mass. This effect is most pronounced for the spring-germinating weed, leading to a loss of approximately 25% of crop biomass for high *compw*.

An increase of the weed juvenile mortality decreases the weed density, for a spring-germinating weed, and triggers an increase in the weed individual weight by up to 25% (Fig. 6). The behaviours shown for agw and sagw are similar, except that the individual weight of agw decreases when the individual mortality increases (not shown).

The autumn-germinating weed has little effect on the crop individual weight, regardless of the weed juvenile mortality (Fig. 7). The two weeds capable of germinating in spring have an effect on the crop individual weight, particularly when *juvmort* is low and for the spring-germinating weed.

For both weed types capable of germinating in spring, an increase of the juvenile mortality decreases the number of individuals which makes the environment less competitive and helps plant individuals to grow bigger, including the crop, by increasing the resources available to the remaining individuals. However, for the autumn-germinating weed, an increase in juvenile mortality decreases both the population size and the individual weight, and has little overall effect on the crop individual weight. Weeds germinating in autumn were facing strong competition against fully grown crop individuals, hence their relatively low success (Fig. 8).

The herbivore to plant biomass ratio increases with the herbivore foraging radius, a larger foraging radius helps individuals to find food and helps sustaining the population (Fig. 9A). As the herbivore foraging radius increases, in the absence of the predators, the average individual plant weight decreases (solid circles) (Fig. 9B). The presence of the predator alleviates this, but the trend is still present (open circles). An increase in the predator foraging radius leads to an increase in individual plant weight as the predator is more effective at controlling the herbivore population with larger foraging radius (closed triangles).

The crop to weed biomass ratio decreases for the first 50 time steps in the simulation and then increases until the rest of the simulation (Fig. 10A). The feeding preferences seem to have little effect on the curves. In absence of predators (solid circles) the plant mass

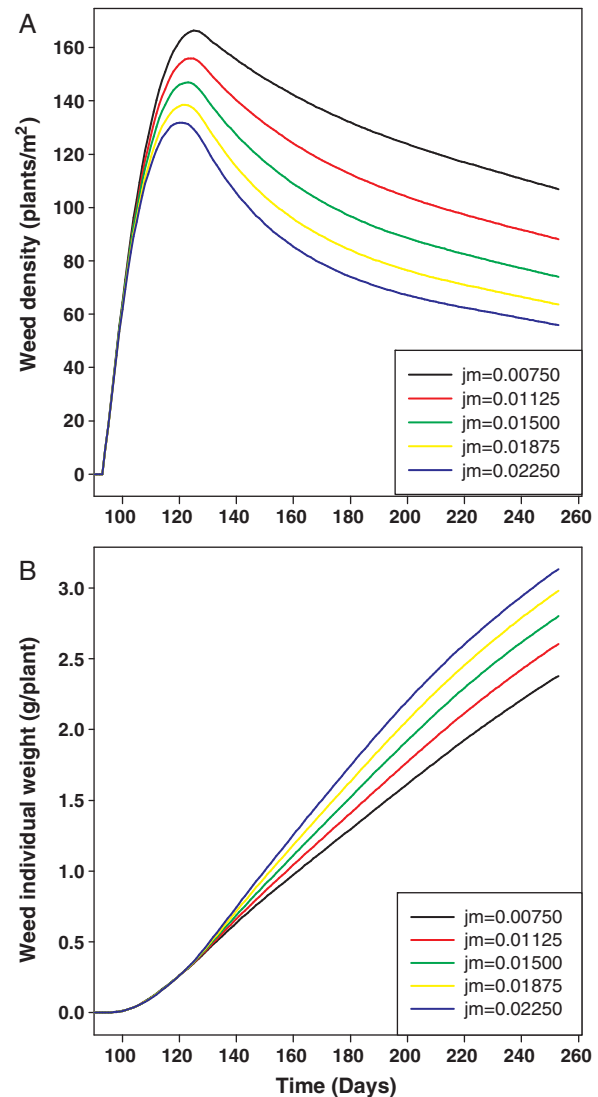


Fig. 6. Influence of plant mortality. Influence of the juvenile mortality of a spring germinating weed on weed density (A) and weed individual weight (B) with time.

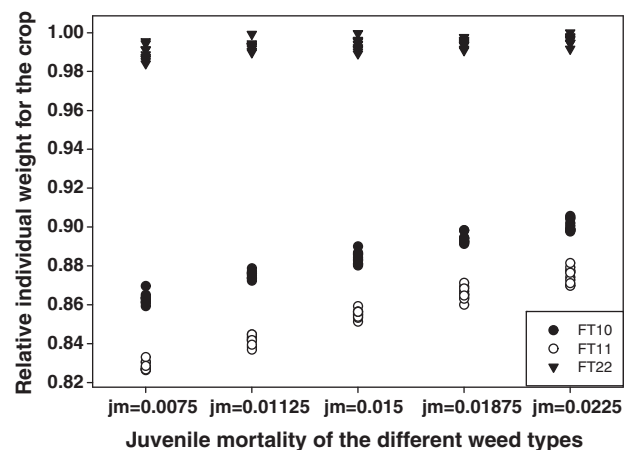


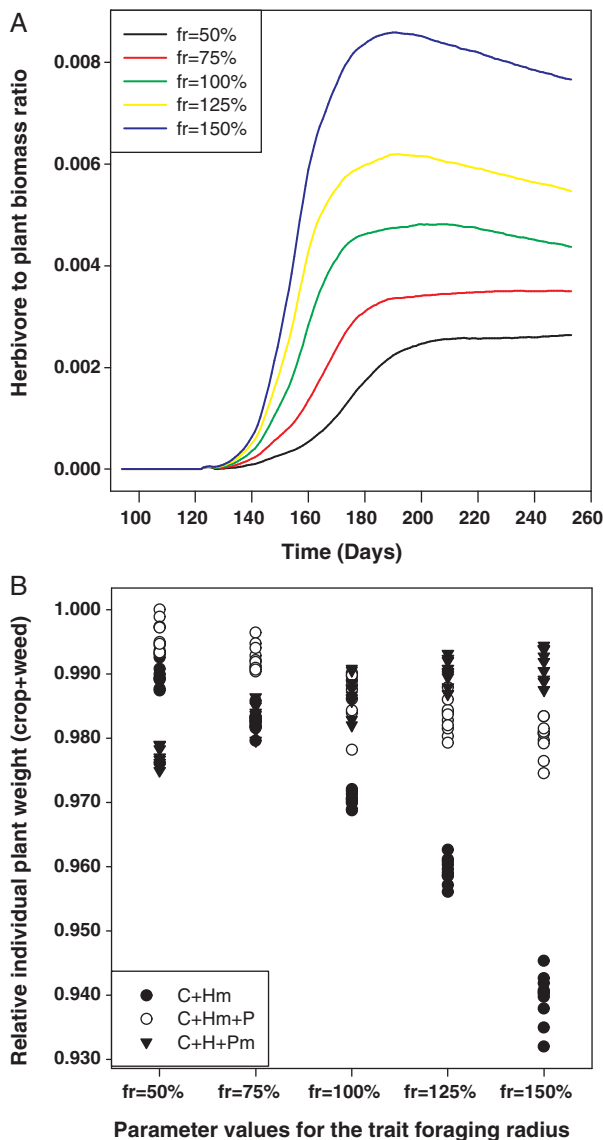
Fig. 7. Influence of plant mortality on crop yield. Individual weight of the crop, relative to the maximum, at the last time step of the simulation, for the five values of *jm* and the three different weed functional types (FT11, FT10 and FT22).



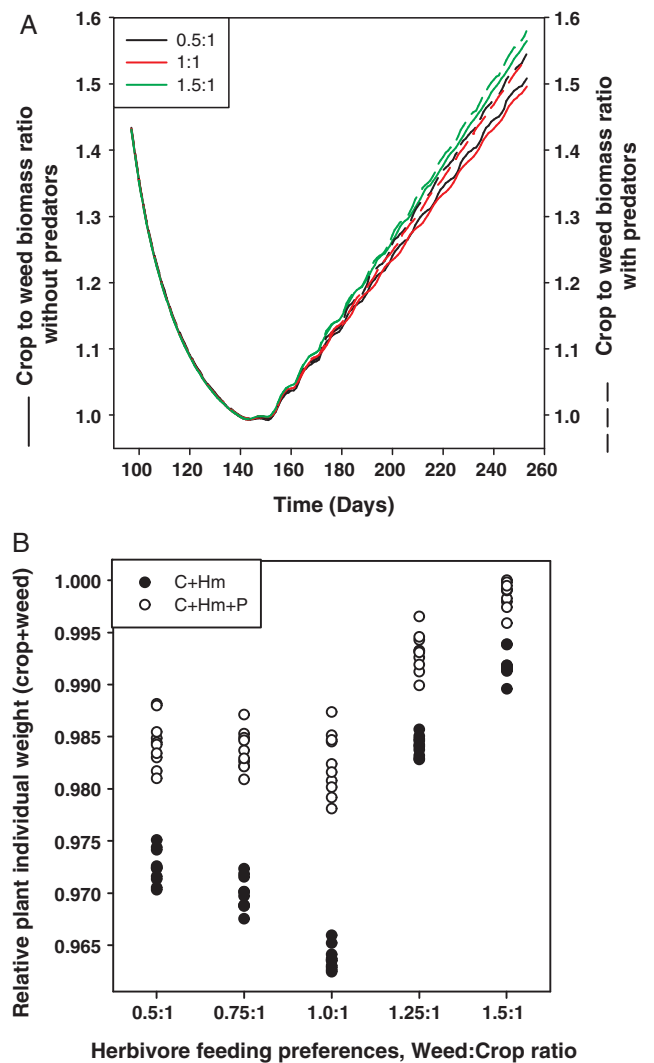


**Fig. 8.** Illustration of the timeline followed in these simulations. The year goes from day one to day 365. Spring sowing occurs around day 94 and harvest happens around the beginning of autumn.

(crop and weed) declines as the herbivore feeding preference shifts towards the weed (but the crop remains the most preferred) (Fig. 10B). As soon as the weed becomes the most preferred food item the plant individual mass increases. This appears counter-intuitive, but may be explained as follows. As  $hfpref$  goes from 0.5:1 to 1:1, the herbivore population can access more food as the probability of feeding on any plant type increases. But, as the crop is the most preferred plant, this configuration is detrimental to the crop. When  $hfpref$  is 1.25:1 or 1.5:1 the weed is now the most preferred plant type and herbivores have access to less food compared to  $hfpref$  = 1:1. A configuration that is relatively profitable to the crop.



**Fig. 9.** Influence of invertebrate foraging radii. Influence of the herbivore foraging radius on the herbivore to plant biomass ratio in absence of predator (A) and the influence of both foraging radii on the relative individual plant weight (the crop and the weed were added together, B). Hm and Pm denotes, respectively, that the foraging radius of the herbivore or the predator was modified.



**Fig. 10.** Influence of the herbivore feeding preference on the crop to weed biomass ratio, with or without predators (A). The relative plant biomass at the last time step for the different values of the herbivore feeding preference (B). The first set included a crop and the herbivore and the second set included the extra predator. For both sets, only the herbivore feeding preference was modified. Ten simulations were run for each set.

#### 4. Discussion

Here we provide a full description of the TrophicLINK model. This model is an individually based simulation model of ecological rules constructed using the trophic-functional framework proposed by Caron-Lormier et al. (2009). The model is a trophic-functional simplification of plant and invertebrate individuals, and their interactions, in the arable ecosystem, following the work by Hawes et al. (2009). The trophic-functional types in this individual-based model are linked by feeding relationships to produce a dynamic food web across which the abundance, body mass and trophic height of individuals is followed. This innovative framework can, in principle, be applied to any ecosystem, or part of an ecosystem with any number of functional types.

We found, through simulation sensitivity testing of a limited number of parameters that the model performed as expected. Varying the level of weed plant competition, by increasing the competition weight, had the effect of reducing crop productivity. At low weed plant densities, where the crop and weed plant zones of influence overlapped less, competitive interactions were

much reduced and crop biomass was unaffected by the competition weight of the weeds, as has previously been shown by Roush et al. (1989). Elevated levels of juvenile weed plant mortality, and the self-thinning that results, resulted in lower weed plant density as might be expected. Varying the food preference parameter of the herbivores feeding on the crop and weed plants had a marked effect on plant performance. A change in preference for the crop or for the weeds reduces the amount of plants available for the herbivores to eat, reducing the number of herbivores, and this consequently increases both the ratio of crop to weed biomass ratio and the individual crop plant weight. The introduction of predators that feed on herbivores to the simulations further increases the crop to weed ratio and the individual weight of the crop plants. An increase in the foraging radius for the herbivores leads to increased herbivore biomass relative to the plants and a decline in overall plant biomass. Introducing predators to the simulations can suppress this herbivore effect and, indeed, an increase in the predator foraging radius can lead to increases in plant productivity. This interplay between predator and prey foraging radii is consistent with the findings of Okuyama (2009), who argued that current models of functional response in animals might need modification because their assumptions are highly dependent upon the dimensions of what the author termed the 'perception range'.

The TrophicLINK model elaborates the effects of changes in parameters and interactions at one trophic level on individuals at other trophic levels. We find such 'knock-on' effects, and these are consistent with the trophic cascades observed in real ecosystems (Moran and Hurd, 1998; Shurin et al., 2002; Petchey et al., 2008; Otto et al., 2008; O'Gorman et al., 2008; Bukovinszky et al., 2008). For example, see the effects of changing the invertebrate foraging radius on plant productivity.

We also found that the model output is consistent with expectations for the performance of the arable agricultural ecosystem, suggesting that the TrophicLINK model is well specified. However, the results also caution that the parameter values that are adopted will be extremely important for the model output we achieve, and we will need to choose parameter values with care. The development of this model will require thorough calibration and validation (Brown and Rothery, 1993; Law and Kelton, 2000; Grimm and Railsback, 2005) against large-scale farmland datasets such as the Farm Scale Evaluations datasets (Firbank et al., 2003; Perry et al., 2003). The variation in model output that is currently observed contains no environmental variation. External heterogeneities due to spatial differences in resources or temporal changes in meteorology, for example, are not included in the model. Such sources in variation are likely to amplify the variation in effect, particularly within an individual-based model. This model framework can readily incorporate such sources of variation, and future studies will examine the consequence of environmental driving.

## 5. Conclusion

We have shown that the model is sensitive to parameter changes, but behaves as expected for the simultaneously output population dynamic, crop productivity and trophic-functional diversity results presented here. This approach explicitly places management, and ecotoxicological measurements of management effect, into the wider context of ecological theories of environmental disturbance. With this model, one would be able to test the influence of management changes on crop productivity and on biodiversity. Management changes may include removal of a specific list of chemicals, or a change in application timings. With this model, results from lab experiments measuring the toxicity of chemical products at the individual level can be used to predict

the impacts of such product at the population level, but also on functional aspects of agro-ecosystems (e.g. crop productivity, pest control).

Our belief is that the TrophicLINK model is a valid representation of an ecosystem and is fit for the purpose of testing the compound hypothesis stated by Caron-Lormier et al. (2009) that "trophic-functional types of plants and invertebrates can be used to explain the structure, diversity and dynamics of arable ecosystems".

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