Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Review

How might we model an ecosystem?

Geoffrey Caron-Lormier[a], David A. Bohan[a,*], Cathy Hawes[b], Alan Raybould[c],
Alison J. Haughton[a], Roger W. Humphry[b,1]

[a] *Rothamsted Research, West Common, Harpenden AL5 2JQ, UK*
[b] *Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK*
[c] *Syngenta, Jealott's Hill International Research Centre, Bracknell RG42 6EY, UK*

ARTICLE INFO

ABSTRACT

Predicting ecosystem effects is of crucial importance in a world at threat from natural and human-mediated change. Here we propose an ecologically defensible representation of an ecosystem that facilitates predictive modelling. The representation has its roots in the early trophic and energetic theory of ecosystem dynamics and more recent functional ecology and network theory. Using the arable ecosystem of the UK as an example, we show that the representation allows simplification from the many interacting plant and invertebrate species, typically present in arable fields, to a more tractable number of trophic-functional types. Our compound hypothesis is that "trophic-functional types of plants and invertebrates can be used to explain the structure, diversity and dynamics of arable ecosystems". The trophic-functional types act as containers for individuals, within an individual-based model, sharing similar trophic behaviour and traits of biomass transformation. Biomass, or energy, flows between the types and this allows the key ecological properties of individual abundance and body mass, at each trophic height, to be followed through simulations. Our preliminary simulation results suggest that the model shows great promise. The simulation output for simple ecosystems, populated with realistic parameter values, is consistent with current laboratory observations and provides exciting indications that it could reproduce field scale phenomena. The model also produces output that links the individual, population and community scales, and may be analysed and tested using community, network (food web) and population dynamic theory. We show that we can include management effects, as perturbations to parameter values, for modelling the effects of change and indicating management responses to change. This model will require robust analysis, testing and validation, and we discuss how we will achieve this in the future.

Contents

* Corresponding author.
  E-mail addresses: carong@bbsrc.ac.uk (G. Caron-Lormier), bohand@bbsrc.ac.uk (D.A. Bohan), cathy.hawes@scri.ac.uk (C. Hawes), alan.raybould@syngenta.com
(A. Raybould), alison.haughton@bbsrc.ac.uk (A.J. Haughton), roger.humphry@sac.ac.uk (R.W. Humphry).
  [1] Current address: Epidemiology Research Unit, SAC, West Mains Road, Edinburgh, EH9 3JG, UK.

1. Introduction

Predicting or forecasting the responses of ecosystems is of considerable interest in a world under threat of human-mediated change. Predictive models could guide the identification of strategies for the mitigation of, and adaptation to, the effects of change on ecosystems. Such models might also be used to suggest management that would yield ecosystems with desirable properties, such as high productivity, or that have particular beneficial functions, such as elevated pollination or natural enemy activity. Probably the most important use for predictive ecosystem models is the analysis of trade-offs with change. Questions such as, 'Is it possible to increase crop yield while maintaining biodiversity?' might be investigated by the model, particularly where there are concerns that increasing productivity has led to loss of biodiversity. Ecosystem models would necessarily incorporate the important biological processes that structure ecosystems and drive their diversity and dynamics, and thus also be of great scientific interest.

Our concept of an ecosystem is similar to that of Odum (1971), and builds on earlier theories of trophic–dynamics in ecosystem ecology (Lindeman, 1942). The *ecological system* consists of a unit of all organisms in a given area interacting with one another and the physical environment so that a flow of energy leads to biotic diversity and dynamic. In principle, ecosystems can be modelled using existing methods that explicitly model interactions between species. However, there may be many hundreds of species to model, in the ecosystem, and potentially many more interactions. Such complexity would likely be prohibitive for the construction of ecosystem models. The models would be mathematically and computationally intractable. Even if such a species model were produced it would take a period of analysis approaching that of the analysis of observed ecosystem data. Indeed, in the nearly 75 or so years since the term 'ecosystem' was conceived by Roy Clapham (Willis, 1997) and discussed by Tansley (1935), we are still trying to analyse and understand these complex systems of species.

Translating ecosystems into models is a problem of appropriate representation and simplification. The representation we adopt here is one frequently used in functional ecology (Loreau et al., 2001), and we hypothesise that it will achieve a scientifically valid, ecological representation of important ecosystem processes. Functional ecology focuses on 'process rather than property' (Calow, 1987). By concentrating on processes, one looks at what drives the ecosystem dynamics; whereas species models only look at specific parts of ecosystems. Following this approach, one can investigate the effect of human activities and environmental changes on the functions of the ecosystem (Dyer et al., 2001; Pakeman, 2004; Liira et al., 2008). Potentially, functional ecology provides a simplification that is mathematically and computationally tractable. Furthermore, a functional model would enable us to build and test theories about the processes that drive ecosystems.

Functional ecological approaches have successfully described and been used to analyse a wide range of ecosystems (McGill et al., 2006) such as grasslands (Pakeman, 2004; Schaffers et al., 2008; Lavorel et al., 2008), arable farmlands (Lavorel et al., 1999; Hawes et al., 2009; Liira et al., 2008) and tropical forests (Slade et al., 2007; Delcamp et al., 2008; Deng et al., 2008; Aguirre and Dirzo, 2008). The functional ecology approach can arguably give a better description of the ecosystem than the analysis of pairwise species interactions that is more commonly used in ecology (McGill et al., 2006). However, although the concept of functional ecology is transferable from one ecosystem to the next, functional traits are typically identified and defined for each ecosystem. For instance, it is unlikely that functional traits defined for an aquatic ecosystem would be applicable to a terrestrial ecosystem. The location of each system (McKie et al., 2008) and the methodology for defining functional traits are important (Lavorel et al., 2008).

In this paper we argue for a novel method of modelling an ecosystem using a functional trait approach, and outline a model based on this concept. We try to achieve the maximum level of simplification that captures the diversity and dynamics that have been measured in real systems and those discussed in the literature. We believe that the simplifications and methodology we follow to make a model of an ecosystem are ecologically defensible. We do not attempt to cover all the ecosystem literature or even the ecosystem modelling done to date. Rather, we limit our discussion of the literature to fields directly relevant to the components of our compound hypotheses. The functional ecology approach we advocate is based upon the feeding, or trophic, interactions (or 'processes' sensu Calow (1987)) that occur between organisms residing within an ecosystem, and we explicitly model the 'flow' of biomass (energy) between different feeding groups. Potentially, this 'flow' is generic and therefore could be applied to any ecosystem. Here, though, we describe the construction of a model parameterised for the arable farmland ecosystem of the UK in order to test our view that "trophic-functional typing can explain the structure, diversity and dynamics of arable ecosystems."

2. Methodology and discussion

2.1. The arable ecosystem

We chose to model arable farmland as there is a pressing need to develop a theoretical framework to analyse the trade-offs between agricultural production and biodiversity (Dunne et al., 2002b; Emmerson et al., 2005; Loreau et al., 2001). In addition, there are several data sets from arable ecosystems suitable for testing our hypothesis.

We represent the arable ecosystem as the plants and invertebrates residing in an agricultural field. The dynamics of individuals outside the field are not modelled explicitly, but are implicitly represented by immigration. Vertebrates, such as mammals and birds, are not considered, but their dynamics could be modelled explicitly using our framework, or inferred from the model's predictions of plant and invertebrate food resources (Gibbons, 2006).

2.2. Functional ecology and food webs as appropriate modelling tools

About 200 species of plants and above-ground invertebrates are commonly present in the arable ecosystem of the UK (Smith et al., 2008). The crop and weeds compete for available resources. The invertebrates compete to feed on the plants and/or on each other. Conceptually, this system consists of primary producers, which transform resources into biomass, and primary consumer invertebrates that feed on this biomass, converting it to invertebrate biomass (Bohan et al., 2005; Hawes et al., 2005, 2009). Higher tiers of secondary consumer invertebrates then feed on and convert this invertebrate biomass (Brooks et al., 2003). Detritivores consume dead organisms from all three trophic layers.

This ecosystem can be represented using ecological network theory (Dunne et al., 2002a). This theory treats the different species as discrete nodes, with particular properties of biomass and abundance, with the links between the nodes representing the interactions between the species. This approach has proved useful for yielding important information on the structure of the system and for evaluating the likelihood of node extinction and network collapse in a changing environment (Pascual and Dunne, 2006). A familiar aspect of ecological networks is a "food web", in which the links in the network are trophic and represent the flow of energy or biomass between the nodes. Food webs have been used successfully to explain structural properties of ecological systems (Dunne et al., 2002a), particularly aquatic systems (Cohen et al., 2003; Emmerson and Raffaelli, 2004; Reuman and Cohen, 2004). Terrestrial food webs have proved less easy to explain (Polis, 1991; Rott and Godfray, 2000; Petchey et al., 2008). Arable farmland food webs have only recently begun to be investigated and this work has concentrated on pollinator and parasitoid webs (Gibson et al., 2006; Van Veen et al., 2008).

Recent theoretical and empirical work has suggested that there might be a simplifying framework underlying food webs. In a seminal study of Tuesday Lake, Michigan, United States, Cohen et al. (2003) established the food web links between 56 phytoplankton, zooplankton and fish species (see also Carpenter and Kitchell, 1988, 1993). In parallel, the authors used a simple energetic theory for how trophic height in a food web might be correlated with abundance and body mass. Put very simply, this theory suggested that a few big things eat many little things (Cohen, 1991; Elton, 1927; Petchey et al., 2008). All other factors being equal, species at similar trophic heights had similar body mass and abundance with very little additional variation. It is possible to infer, from the Tuesday Lake data, that food webs might be simplified by an amalgamation of species-based nodes to nodes that combine the three key biological variables of *trophic height*, *individual abundance* and *body mass* with little loss of explanatory power (see Fig. 3 of Cohen et al. (2003)).

2.2.1. The invertebrate trophic network

Here we present Vortis suction sample data from a large-scale sampling of arable farmland in the UK in support of the thesis that the food web can be simplified to a combination of trophic height, individual abundance and body mass. We note that these invertebrate data, from four arable crops across 265 fields, do not include information on the trophic links between arable species as such data on feeding preference are patchy, at best. We observe a negative relationship between individual abundance and body mass (Fig. 1), and similar patterns were observed across the four crops. These patterns were similar to those observed by Cohen et al. (2003) in the Tuesday Lake data and corroborate the hypothesis that food webs may be simplified to combinations of trophic height, individual abundance and body mass. We also note that there are clear differences between these plots and those of Cohen et al. (2003). In contrast to the Tuesday Lake data, the variation in the farmland data were greater. Some of this variation undoubtedly came about as a consequence of pooling samples of distinct invertebrate populations, and their food webs, across many fields and then summing the samples across the year. However, it is likely that part of this additional variation is a consequence of farmland management, the effects of which must be included in any model.

Hawes et al. (2003, 2009) and Bohan et al. (2007) evaluated the variation explained in this suction sampled data-set by amalgamating species abundances into trophic/functional groups. This work showed that typically about 30% of the variation could be explained by regression relationships between invertebrate trophic groups and between the trophic groups and the plants. This was considered to be quite high, given the variety of sources of variability in the data-set, and allowed Bohan et al. (2007) to propose a schematic trophic structure for the arable food web. The work of Hawes et al. (2003) and Bohan et al. (2007) provided further tests and corroboration of the hypothesis that ecosystems can be simplified to a combination of trophic height and abundance, at least for the arable ecosystem. However, this schematic structure of the arable food web did not explicitly include body mass. Neither did the structure realistically link the invertebrates to their plant food resources.

These issues were resolved by Hawes et al. (2009) with the inclusion of body size classes and specific herbivore and predator feeding groups. Four categories for the trait of individual body size were defined based upon the readily observed length classes in the field: small (size < 4 mm), medium ($4 \leq$ size < 6 mm), medium–large ($6 \leq$ size < 8 mm) and large (8 mm $\leq$ size). Herbivores can feed upon the sap (phloem), structural matter (e.g. leaves) and reproductive parts (e.g. flowers and seeds) of the plant. These three categories were therefore used to describe the food preference traits of herbivores: sap, leaves and seeds. Detritivores, which we treat here as modified herbivores and have the same trophic height, feed on detritus made from all trophic heights, and potentially contribute enormously to the biomass flow in the food web. Unassimilated food, such as dead individual plants, or dead individual invertebrates (in the case of non-predatory mortality) is converted into detritus. Analyses of the invertebrate communities from arable fields, based on these classifications, showed significant changes in functional composition in response to management and crop type, suggesting that the groupings presented are sensitive to environmental conditions (Hawes et al., 2009).

This expansion of simple trophic types to include other aspects of invertebrate functioning, termed here trophic-functional types, is summarised in Table 1. Characteristic arable species that reside within these trophic-functional types are shown, along with the body size category and plant resource for each. It should be noted that not of all the combinations exist across the two functional
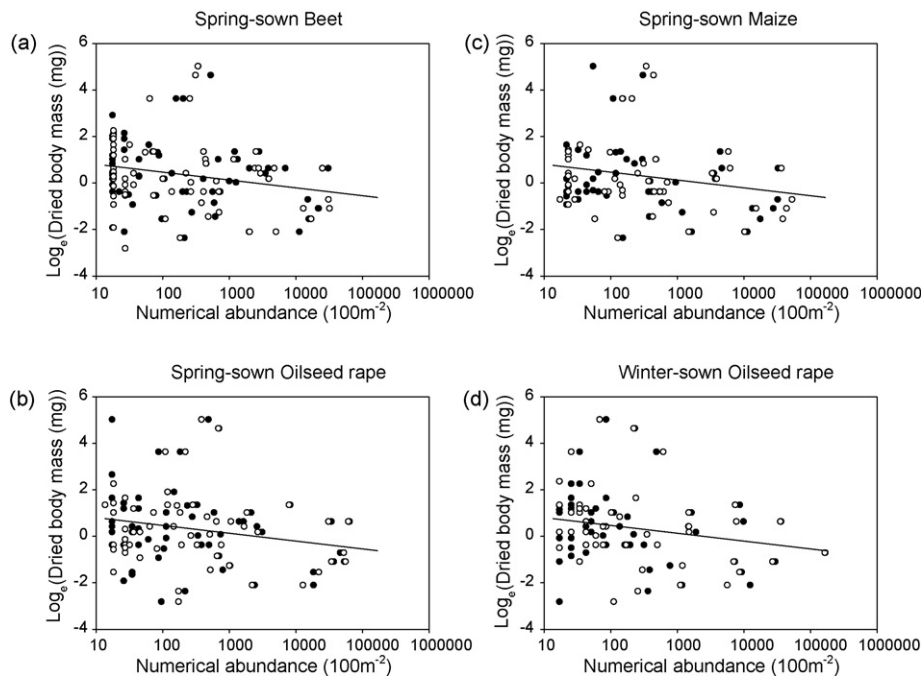
Fig. 1. Fitted relationship between individual body mass and the total abundance of individual invertebrate species sampled by Vortis suction sampling from 265 halved-fields, of four arable crops, across the U.K. Closed circles denote species sampled in field-halves managed using current conventional herbicide management regimes. The open circles are species sampled from half-fields managed according to genetically modified, herbicide-tolerant guidelines. The significant relationship was fitted using a generalised linear model ($F_{1,451} = 22.16$, $p < 0.001$, $r^2 = 4.5\%$), in Genstat, and no effect of crop or herbicide management was found. (a) Spring-sown beet, (b) spring-sown oilseed rape, (c) spring-sown maize and (d) winter-sown oilseed rape.

traits. We thus achieve 14 trophic-functional types for the invertebrate community in arable farmland.

2.2.2. Plants as biomass producers

The classification of plant species into functional groups is a common approach that allows simplification of a complex community into categories of plant types that respond to or affect their environment in similar ways (e.g. Lavorel et al., 1997; Storkey, 2006). The classification adopted here follows that proposed by Hawes et al. (2009). Briefly, the first split amongst the plants is between crop and weeds; a distinction important to make for the purpose of evaluating the trade-off between crop productivity and weed biodiversity. Weeds are then further subdivided by traits that affect growth, resource quality, architecture and resource availability to insect herbivores. These traits include: cotyledon number, splitting the monocotyledon and dicotyledon plants that present different resource qualities to insect herbivores and respond differently to herbicide treatments; annuality, where annual forms are favoured over perennials under annual disturbance; development rate, which determines the relative performance of different species under winter and spring sown crops and where herbicides are applied at different times during the growing season; perennial form, where herbaceous, woody and rhizomatous perennials are distinguished due to their differential response to management; and canopy architecture, which is estimated from plant height within a crop canopy and determines the ability of a plant to compete and tolerate competition within a crop. This formulation of traits yields 28 plant trophic-functional types that together have been shown to capture the main characteristics that determine the persistence and abundance of weeds within cropped, arable fields (Hawes et al., 2009).

2.2.3. The simplified arable food web

Simplification to this trophic-functional representation gives 42 plant and invertebrate functional types, which is far fewer than the 200+ species that would have to be modelled and analysed for a full description of the plants and invertebrates in the arable ecosystem. Linking these different trophic-functional types together, using their feeding preferences, yields the simplified food web that in principle might be modelled (Fig. 2).

We represent the food web of the arable ecosystem as a suite of trophic-functional nodes that are connected by trophic links. However, although networks and network theory are useful for representing object nodes and their interactions, networks are static snapshots of a system. Our simplified arable web does not elaborate the dynamics of the agricultural ecosystem. It is necessary to

Table 1

Representative invertebrate taxa for each trophic-functional type generated from the identified functional traits for body size and feeding preference. Aphids, by example, are considered typical 'small sap-suckers'.

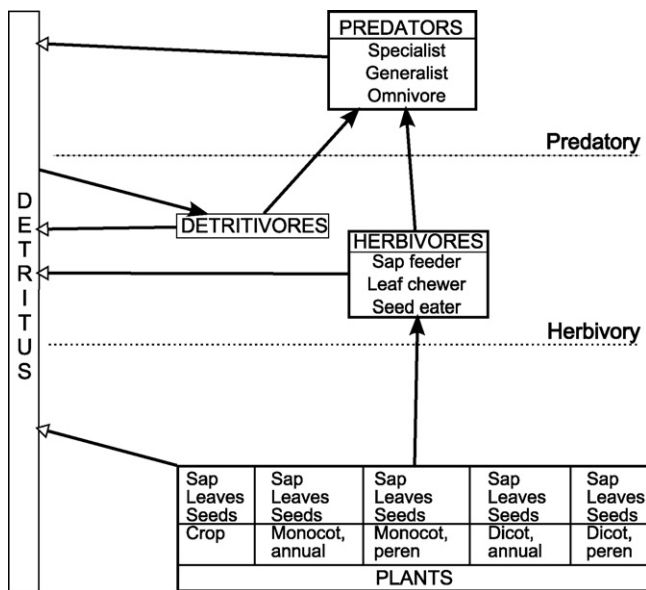| Feeding trait	Small	Medium	Medium–large	Large
Herbivores				
Sap	Aphids(l)	Auchenorrhyncha (2)		
Leaves			Weevils (3)	Lepidoptera larvae (4)
Seeds			*Amara* spp. (5)	*Harpalus* spp. (6)
Detritus	Collembola (7)			
Predators				
Generalist	Spiders (8)	*Bembidion* spp. (9)	*Agonum dorsale* (10)	*Pterostichus madidus* (11)
Specialist			*Coccinella* spp. (12) and *Loricera pilicornis* (13)	Neuroptera larvae (14)

Fig. 2. Schematic representation of the arable ecosystem based on trophic-functional types. For simplicity, we only represent the main types in the system. The plants are divided into crop, monocotyledon annual and perennial, and dicotyledon annual and perennial weed groupings that are then further divided into invertebrate food categories: phloem (sap), structural parts (stems and leaves) and reproductive parts (flowers and seeds). The next trophic level is composed of sap-sucking, leaf-chewing and seed-eating herbivores, which feed on the crop and the weeds. The third trophic level includes the generalist and specialist predators of the herbivores. Mortality transforms invertebrate and plant biomass into detritus, which is then fed back into the system through detritivory. We represent the detritivores, in the system, as modified herbivores.

synthesise food webs with population dynamic theory to include these dynamics. There is a need, therefore, to identify appropriate approaches for representing the dynamics of this agro-ecosystem, trophic-functional network.

2.3. Modelling functional ecology for a dynamic ecosystem

Ordinary differential equations (ODEs) have been widely used by biologists and ecologists to describe the dynamics of interacting species (Turchin, 2003). ODEs have well characterised properties (Brown and Rothery, 1993). Particularly, for relatively simple systems with a low number of interacting species or groups, ODEs have analytical solutions that allow researchers to represent all the potential dynamics of the system. However, with increasing complexity of interacting species or groups, ODEs can often only be solved numerically, with the properties of the system being depicted through simulation; as would certainly be the case for a model with the number of trophic-functional types we propose here.

In turn, differential systems represent whole populations of species or groups, and do not model the variability between individuals or heterogeneities in interaction. Here, we argue that individual body weight and variability are fundamental variables and trophic interactions are fundamental processes that drive ecosystem dynamics. To test this hypothesis, we particularly need to document changes in key biological variables for explaining food web structure: body weight, abundance and height. In the trophic-functional formulation, each type represents numerous individuals of several species, each with slightly different values for the same traits. For ODEs, however, only the average value for any trait is represented. For instance, the body weight of individuals within a given trophic-functional type would be summarised to the average weight of the whole trophic-functional type in an ODE, losing

information on variability within the trophic-functional type. For our hypothesis, this information is important and should be modelled. A particular individual's feeding behaviour, and the rules that embody these behaviours, will depend on the weight or size of the individual. It is, therefore, inappropriate to average across the variation between individuals (Kindlmann and Dixon, 1996), as is done with ODEs.

We propose that the most appropriate way of representing the population dynamics of plants and invertebrates in the agricultural ecosystem is by using simulation models that allow the explicit definition of individuals and their particular properties and characteristics. Individual-based models (IBMs) allow us to document changes in the key biological variables of body weight, abundance and trophic height for explaining the food web structure of ecosystems. IBMs allow flexibility in modelling how the properties of individuals, which have exchanged energy or biomass following a trophic interaction, are updated. Most importantly, IBMs allow the imposition of relatively simple rules at the level of the individual. Often population and community patterns of dynamics are emergent properties of individual interactions rather than built-in modelling assumptions. The use of IBMs is now widespread in ecology (Grimm and Railsback, 2005; Breckling et al., 2006) and has matured to produce standards for model description (Grimm et al., 2006).

In a recent paper, Caron-Lormier et al. (2008) showed that different methods of updating energy flow along trophic links, following an interaction, could lead to markedly different output. Using a simple IBM, the authors examined the differences between asynchronous and synchronous updating methods. They showed that the total energy in a system was dependent upon the updating method used. Systems with synchronous updating had higher total energy, particularly when the number of individuals simulated increased. These findings are important because both synchronous and asynchronous updating is possible in modelling natural phenomena (Caron-Lormier et al., 2008). There are, however, consequences of adopting IBMs over ODEs. As already mentioned, the mathematics on which ODEs are based and are well understood. Despite the use of IBMs being widespread in Ecology (Grimm and Railsback, 2005), and other areas of applied science (Axelrod, 1997; Gilbert and Troitzsch, 2005), the theoretical and philosophical underpinning of IBMs are not as well established. IBMs are also not as readily analysed as ODEs, requiring extensive sensitivity and validation. Even so, the standards of testing of simulation models do not meet the rigour expected by many biological mathematicians (Maynard Smith, 1974). Finally, IBMs are not readily extendible or generalisable. In contrast to ODEs that can readily be compared between systems, IBMs are written for specific systems and situations. We argue that the important point is that if the IBM works, it corroborates an expectation about how ecosystems function, which is far more profound than whether we can make a particular calculating tool produce a useful description of an ecosystem.

2.4. The trophic-functional individual-based model

Here we give a synopsis of the structure of our individual-based model. The description illustrates how trophic-functional types are implemented, and the salient features of the model that will assure it achieves the aims set in this paper. The description is not exhaustive but follows the standardised 'Overview, Design concepts and Details' description developed by Grimm et al. (2006).

2.4.1. Purpose of the model

Our IBM is designed to test the hypothesis that trophic-functional ecology can describe the diversity and dynamics of

arable ecosystems. The model embodies expectations that individual and local variation are important, and that local, trophic interactions drive ecosystem dynamics.

2.4.2. State variables and scales

The model is spatially explicit, with each individual having an exact position in the continuous space of a simulated patch. Individuals in each trophic-functional type are explicitly represented with individual trait characteristics. A non-exhaustive list of individual characteristics (or state variables) includes whether they are dead or alive, and their body mass, age and developmental state. Individuals with similar trait characteristics belong to particular trophic-functional types; each of these embodies a feeding preference, on other trophic-functional types, and a distribution of body mass. Individuals within each type may either inherit these characteristics or are generated from the properties of the type. The model uses a discrete daily time step, and simulations are usually run for 200 time steps. A typical simulated patch measures 10 m × 10 m. Several patches may be simulated independently, to represent several patches within a field, or even several fields.

2.4.3. Process overview and scheduling

The primary producer plants consist of a crop and associated weed trophic-functional types. Crop and weed individuals compete locally for resources. These resources are not explicitly modelled. Rather, we presume that the availability of resources is proportional to an area of the patch being covered by each individual. Where the zones of a set of plants overlap, these plants share resources. Plants have an individual competitive weight that dictates how efficient they are at competing for resources. The energy value of resource that a plant receives is weighted by these competitive coefficients allowing some individuals to garner more of the available resource than others. The weight of each individual plant is split into three compartments on which herbivores may feed: structure, sap and reproductive.

Individual invertebrates move across the continuous patch in response to food availability and their individual dispersal parameter values. Herbivores feed on their preferred, primary producer food plant types and predators feed on their preferred primary consumers. Juvenile individuals put their energy intake into growth whilst adult individuals allocate it to reproduction. Adults of all trophic-functional types, plant and invertebrate, can reproduce. Energy allocated to reproduction is used to create new offspring, which enter the simulated trophic-functional type as new individuals. All individuals of all trophic-functional types are subject to 'natural' mortality, which depends on a daily survival probability, and mortality from predation. Plants and invertebrates that die may become detritus, which is the primary food source for detritivores. Detritus locally accumulates as individuals die and is removed following a decay rate.

For the individual invertebrates, state variables are modified following interactions using asynchronous updating, where the state variables are modified, updated and new values are made available immediately for the next interaction (Caron-Lormier et al., 2008). Most state variables of the plants are also asynchronously updated, but plant competition is a synchronous process (Caron-Lormier et al., 2008). Management is incorporated in the model as a disturbance at the trophic-functional type level. Disturbed individuals within a functional type have modified behavioural characteristics, such as lower rates of survival, dispersal and interaction. Management characteristics such as date of first application, affected functional types and number of applications are read from input files. Different files with different characteristics can be used to represent diverse management practices or environmental conditions.

2.4.4. Design concepts

At the core of the design concept for the IBM is individual variation. For any particular characteristic, individuals within a trophic-functional type vary, with the distribution of the characteristic reflecting the natural variation across all individuals, of whatever species, ordinarily present in the trophic-functional type. Minimum, maximum and modal values are specified for each characteristic. At creation each individual is assigned a value from these unimodal, triangular distributions. Clearly, though, some characteristics may be multi-modal, particularly where individuals from a large number of species were amalgamated to a single trophic-functional type. With further development multi-modality may be incorporated into the model, if necessary, but for the present it will be interesting to see whether the unimodal situation is adequate.

All individual interactions are local. Individuals 'sense', within their local environment, using a foraging radius or zone of influence. From this zone, a neighbour list is created to determine possible feeding interactions, amongst the consumers, and competitive interactions, amongst the plants. Each consumer feeding-event is modelled explicitly. However, there is no handling time as predators are assumed to process their prey in a much shorter time than the daily time step of the model. Once a prey individual is killed by a predator, it becomes unavailable for the other predators. Individual growth and performance are therefore strongly related to trophic and competitive interactions and it is expected that spatial and temporal dynamics would emerge from local interactions between competitors and between consumer and food.

The 'objectives' of any individual are to survive and reproduce; fitness is an emergent property of the model and is not explicitly modelled. Adaptation is currently excluded from the model. Newly created individuals assume values for their traits from the fixed trait distributions for their trophic-functional type. However, the values for particular characters that tend to survive and reproduce are an interesting outcome of the model. Variation in individual characteristics ensures some stochasticity in the model output. There is also stochasticity in the processes of the model. In particular, the dispersal of individuals is based on a random walk (Turchin, 1988) and individual survival is contingent upon a randomly chosen, daily survival probability. All state variables for individuals are periodically written to a raw data file, during simulation, so that individual information can be tracked. From these raw files, database operations can be performed to produce summary statistics. Raw data files are kept intact and a full analysis can be performed as needed.

2.4.5. Initialisation

We typically simulate a 10 m × 10 m area, representing a patch within a field. Individual crop plants are sown in the regular rows found in arable fields. Weed and invertebrate individuals are distributed, according to specified random, aggregated or uniform distributions, across the patch. Each individual is created in turn and is allocated values for each state variable, appropriate to the distribution for the trophic-functional type. For a given set of state variables simulations are run. Although the values always come from the same distribution, for any given set, individuals will assume slightly different values between runs, and this stochasticity should represent the natural variability found in the field.

2.4.6. Input

Several input files are used in the model to parameterise the environment and individuals. The environment is set using a spatial definition of the dimension ($X \times Y$ m rectangular shape), a start and end date for the simulation, an ambient temperature, which is currently set to be constant throughout the season, and the number of simulations to perform for each set of parameters.

Individuals are created from an input file storing minimum, maximum and modal values for each state parameter, by trophic-

functional type. Individuals may also assume modified parameter values, from a table in a management file, where management has been imposed. The management file details the date of first application, the periodicity and the total number of applications. It also lists, for affected trophic-functional types, changes to state variables. For instance, some weed types may have reduced survival distributions following herbicide application.

2.4.7. Submodels

A full description of the model is beyond the scope of this paper. We present below a brief summary of the different rules implemented in the IBM. We attempt, where biologically appropriate, to use similar functions for describing the life history of both the plants and invertebrates.

2.4.7.1. Emergence. Individuals of particular trophic-functional types are introduced into the simulation at different times, measured in number of days after the start of the simulation. Plants have a germination time, in days after the start, while invertebrates have an incubation time for their eggs, in days.

2.4.7.2. Mortality. Individuals have three distinct life stages from juvenile through adult to senescent. Each period has a unique survival rate and the stages are reached as individuals exceed specified age or development state thresholds.

2.4.7.3. Initial weight. Individual weight is structured into three different compartments: a base compartment that is the structural components of each individual; a reserve that serves as a store of biomass that individuals can draw upon; and a reproductive weight into which each individual contributes in order to form offspring. All of these compartments are initialised when individuals are introduced into the simulation. Depending on the initial conditions, for the scenario tested, individuals may have different parameter values from one parameter set to another.

2.4.7.4. Foraging. Foraging uses several parameters that are plant or invertebrate specific. Plants have an allometric constant to represent how individuals of a given trophic-functional type spread over the ground. For large values the plant is short and squat, while tall and thin plants have small values. This constant is used to calculate the zone of influence around each plant. Individual energy capture depends on the zone of influence and trophic-functional type-specific parameters of energy capture per unit area and competition. Invertebrate individuals have a similar daily foraging radius within which a list of potential prey resources is created.

2.4.7.5. Dispersal. Only invertebrates are mobile. The minimum and maximum distances determines the range of distances individuals can travel in a daily time step. Movement is density dependent and governed by a 'sensitivity to crowding' that reflects the intolerance of individuals to others of the same trophic height. Movement has a cost in grams of body weight per metre dispersed. The boundary conditions are determined by a probability for individuals to reflect back into the patch, so emigration is possible.

2.4.7.6. Immigration. Net daily immigration is determined from a daily immigration parameter for each trophic-functional type.

2.4.7.7. Reproduction. New individuals also enter the patch through reproduction driven by a combination of the average of seed or egg weight for each trophic-functional type and the individual reproductive weight threshold needed for releasing seeds or eggs.

2.4.7.8. Growth. The growth of individuals is governed by four parameters that determine when biomass is allocated between the base, reserve or reproductive weight compartment. Juvenile individuals put a proportion of their reserve weight towards growth whereas adults allocate a different proportion to reproductive parts. Plants grow until their base weight reaches a limit.

2.4.7.9. Bioenergetic model. Processes controlling the bioenergy of individuals are based on the work of Crowl et al. (2000); Gutierrez (1996) and Rudstam (1989). Invertebrate reserve weight is a balance between daily food demand (D), or consumption, and daily respiration (R), or metabolism. The daily food demand is calculated using the relation:

$$D = D_b * exp(D_t(T - T_b)), \tag{1}$$

where D_b is the base daily food demand, D_t is the daily food demand increase rate with temperature (T) and T_b is the base temperature. The product of D and the total weight of the individual is the amount of biomass an individual needs for satiation. The cost of respiration is calculated using the expression:

$$R = R_b * exp(R_t(T - T_b)), \tag{2}$$

where R_b is the base respiration cost, R_t is the respiration cost increase rate with temperature (T) and T_b is the base temperature. Similarly, R multiplied by the total weight of the individual gives the amount of biomass the individual loses, naturally, during one time step. We would note that for constant temperature conditions, these functions yield values for R and D that are constant and specific to each trophic-functional type. In this version of the model, the parameters of these two equations are kept constant throughout the simulations. Test and validation of these relations will be part of later work.

2.4.7.10. Development. Invertebrate development is linearly related to temperature and food availability. As food availability increases and intake approaches satiation, individuals develop faster.

2.5. Incorporating management

Change, such as environmental change or management, is included in the model as a perturbation that acts upon some processes that particular individuals undergo. Perturbations may reduce the probability of an individual surviving, and this can be limited to the individuals of a particular trophic-functional type, a suite of types or all types, depending on the change being simulated. This means that, in our formulation, there is nothing special about the effects of different perturbations. For example, insecticide perturbations are included in the model in precisely the same way as herbicides; the effects differ just in the target trophic-functional types and processes. Although all individuals within a trophic-functional type will respond in the same way to the perturbation, no change is completely efficient and some individuals will escape the effect.

Initially we are concerned with modelling the changes associated with herbicide management. Herbicide is sprayed on the simulated patch and the individuals of the different trophic-functional types targeted by the spray respond accordingly. It is possible to test this perturbation approach using published data on the differences between the effects of broad-spectrum herbicides, which affect most weed trophic-functional types and the crop, and specific herbicides that target particular weed types.

2.6. Model structure and diversity

42 trophic-functional types remains a large number to model. Analyses of the plants and invertebrates in arable fields shows that between 10 and 15 trophic-functional types, depending on the locality and cropping situation, are necessary to account for more than 97% of the abundance and 95% of the biomass in the system (Unpublished data). We therefore propose, initially, to limit our modelling to these abundant trophic-functional types. However, we are aware that in excluding the rare trophic-functional types we are deliberately removing diversity from the system.

The different processes implemented in this model have been made as generic as possible. Where possible, they are applied to all trophic-functional types. Only the parameter values that drive the behaviour differ systematically between types. The exception to this is the difference between the producer plants and consumer invertebrates that differ in the way they acquire resources. This general repetition of process throughout the model framework is very important. It facilitates testing and analysis. Once a process or function or rule has been sensitivity tested and validated for one trophic-functional type, the sensitivity testing for other types only requires corroborative checks and validation using biological data. Biologically, it may be argued, this approach also has some philosophical merit. We believe that natural selection would tend to select for new parameter values, to maximise fitness, under changed circumstances. The natural history of a set of individuals, which under selection had switched between two trophic-functional types, would therefore be an evolution of the natural history of the progenitor set, as is implemented in our IBM. It would not require distinct model processes for the two sets of individuals.

Diversity, both of input and output, is a characteristic of our model framework. For each trophic-functional type, the natural variation in parameter values is represented by stylized, triangular distributions, allowing output that even for a simple food chain is diverse (Fig. 3 a–c). Representing the food chains that stem from each plant weight compartment further increases the complexity and diversity of the modelled system (Fig. 3d). Further layers of plant types, and the invertebrates types dependent upon them, shows that potentially quite complex and diverse output can be generated using relatively generic, repeated processes (Fig. 3e).

3. Test, validation and model analysis

We propose to test and validate the model as complexity increases. The first version of the model only contains a few functional types, including the crop type, a pest type and an associated natural enemy predator type. Practically, this ecosystem models an Oilseed Rape (Canola) crop, aphid pests and predatory ladybirds. Our aim in this section is to present some preliminary output from the model and to progress this output through an illustrative test and validation exercise. For this testing, we will consider the model output at both the individual and trophic-functional type, and population levels.

3.1. Model inputs

We have found the search for parameter values more difficult. As each trophic-functional type is composed of many different species, with distinct values, each trophic-functional type requires a considerable list of parameter values if it is to reflect the variation and diversity found in nature. The dis-
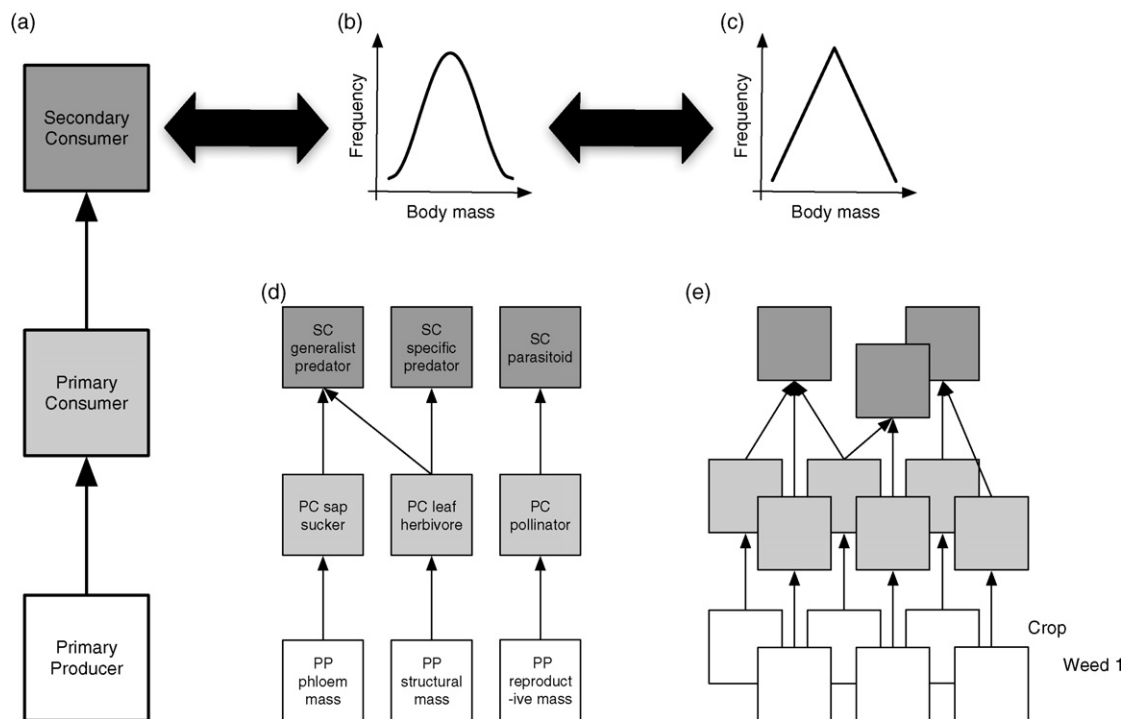

Fig. 3. Illustrative diagram of the input and output diversity and complexity within the trophic-functional IBM: (a) simple food chain of primary producer, primary consumer and secondary consumer trophic-functional types, with arrows illustrating the direction of flow of biomass between the types; (b) the frequency distribution of parameter values present across individuals of all species within a trophic-functional type, here represented by the distribution of body mass; (c) the stylized, triangular distribution formed from estimated minimum, maximum and modal values to represent the distribution of parameter values within a trophic-functional type; (d) a series of food chains, dependent upon particular primary producer weight compartments, that form the food web dependent upon one primary producer plant type; (e) further food web layers for each plant type and the invertebrates types dependent upon the plants—it should be noted that some invertebrate trophic-functional types may exist, or be shared, across a number of plant type layers.

Table 2
Parameter values used in the simulations for the plant trophic-functional type. Some values are from references, others may be assumed for the purpose of this work but will be tested and validated at a later date.

Parameters	Crop	References/notes
Juvenile mortality - m1	0.00	Simulation assumption
Adult mortality - m2	0.00	Simulation assumption
Senescent mortality - m3	0.00	Simulation assumption
Switch to adult - s1	1 g	Simulation assumption
Switch to senescent - s2	500 g	Simulation assumption
First emergence	Day 0	For simulation
Second emergence	Day 300	Simulation assumption
Initial base weight	1 mg	Simulation assumption
Initial free weight	0.1 mg	Simulation assumption
Initial reproductive weight	0.0	Simulation assumption
Immigration	0.0	Assumed closed system
Seed weight	450 mg	Simulation assumption
Weight ratio for reproducing	0.45	Simulation assumption
Switch to adult	40 days	Simulation assumption
Ratio base weight/free weight	0.1	Simulation assumption
Energy allocated to seed production	30%	Simulation assumption
Weight limit	1000 g	Simulation assumption
Biological type	1	For simulation

tribution of functional traits will be based on estimates from existing datasets and the published literature for representative species within each functional group such as the Farm Scale Evaluations (FSEs) (Brooks et al., 2003; Champion et al., 2003; Hawes et al., 2003; Heard et al., 2003; Haughton et al., 2003; Bohan et al., 2005). However, we have found that these sources are limited and many of our parameter values are assumed values based on unpublished data or the biological and ecological experience of colleagues and collaborators. In Tables 2–4,

we present individual parameter values employed here in this schematic test of the first version of the trophic-functional IBM.

3.2. Testing and validation

We will use sensitivity testing and simulation experiments to simplify, test and validate the model. The theory and practice of sensitivity testing simulation models is well established (Brown and Rothery, 1993; Grimm and Railsback, 2005; Law and Kelton, 2000), and we do not reprise these here. The simulation experiments are constructed using biological scenarios that are well characterised from observational data, and here we present example simulation output in support of our arguments.

3.2.1. Individual level dynamics

The growth rates of the oilseed rape crops, aphids and ladybirds have characteristics that are well documented (Dean, 1974; Dixon, 2000; van Emden and Harrington, 2007). Output for the individual weight of plants and invertebrates can be analysed from the model and should match these biological characteristics. What is interesting is that many of the characteristics of body mass are not explicitly stated as rules in the model but emerge out of other coded rules and trophic interactions. In Fig. 4, the growth of crop plants is followed through time for an experiment with different treatment levels of crop plant density. The plants grow, reaching average individual weights with time that are consistent with those seen for oilseed rape plants. We find that with increasing crop plant density, the average individual weight declines, again as expected for individuals competing for resources.

We show in Fig. 5 average growth curves for 5 aphids that were randomly distributed in the patch and were initialised as juveniles

Table 3
Parameter values used in the simulations for the herbivore trophic-functional type. Some values are from references, others may be assumed for the purpose of this work but will be tested and validated at a later date.

Parameters	Herbivore	References/notes
Juvenile mortality - m1	$1.38\,e^{-02}$	Dean (1974) and Dixon (2000)
Adult mortality - m2	$9.00\,e^{-03}$	Dean (1974)
Senescent mortality - m3	$6.00\,e^{-01}$	1% of senescent individuals will survive 5 days
Development stage at adulthood - s1	1.0	Sensible value
Switch to senescent - s2	27 days	Dean (1974)
First emergence	Day 10	For simulation
Incubation time	0 day	During season, aphids do not produce eggs
Initial base weight	0.042 mg	Total init weight of 0.06 mg Dixon (2000) split 70/30
Initial free weight	0.018 mg	
Initial reproductive weight	0.0	Juveniles do not have any reproductive weight at birth
Dispersal: Min distance	0.0 m	Simulation assumption
Dispersal: Max distance	2.0 m	Simulation assumption
Crowding: Min Nb of Individual	0.0	Simulation assumption
Crowding: Max Nb of Individual	20.0	Simulation assumption
Cost of dispersal	$1.00\,e^{-03}\,\text{m}^{-1}$	Simulation assumption
Immigration	0.0	Assumed closed system
Egg weight	0.06 mg	Sunderland et al. (1986)
Weight ratio for reproducing	0.12	van Emden and Harrington (2007) and Timms and Leather (2007)
Development state to adulthood	1.0	Sensible value
Energy allocated to growth	90%	Simulation assumption, individuals are matured in around 10 days
Energy allocated to egg production	50%	Simulation assumption
Food demand, D	40%	Schoonhoven et al. (2005), Slansky and Rodriguez (1987) and Peters (1983)
Respiration cost, R	2.8%	Schoonhoven et al. (2005), Slansky and Rodriguez (1987) and Peters (1983)
Biological type	2	Computing purpose
Development constant	$7.50e^{-03}$	Dean (1974) and Dixon (2000)
Development rate	$-3.75e^{-02}$	Dean (1974) and Dixon (2000)

Table 4
Parameter values used in the simulations for the predator trophic-functional type. Some values are from references, others may be assumed for the purpose of this work but will be tested and validated at a later date.

Temperature	Predator	References/notes
Juvenile mortality - m1	$7.50e^{-02}$	Dean (1974) and Dixon (2000)
Adult mortality - m2	$1.00e^{-01}$	Simulation assumption, 55% of adults survive until day 75
Senescent mortality - m3	$4.00e^{-01}$	1% of senescent adults peach the age 84 days
Development stage at adulthood - s1	1.0	Sensible value
Switch to senescent - s2	75 days	Dixon (2000)
First emergence	Day 40	For simulation
Egg incubation time	5 days	Dixon (2000)
Initial base weight	0.14 mg	Total init weight of 0.2 mg Dixon (2000) is split 70/30
Initial free weight	0.06 mg	
Initial reproductive weight	0.0	No reproductive weight for new born individuals
Dispersal: Min distance	0.0 m	Simulation assumption
Dispersal: Max distance	3.0 m	Simulation assumption
Crowding: Min Nb of individual	0.0	Simulation assumption
Crowding: Max Nb of individual	10.0	Simulation assumption
Cost of dispersal	$1.00\,e^{-03}\,\mathrm{m}^{-1}$	Simulation assumption
Immigration	0.0	Assumed closed system
Egg weight	0.20 mg	Sunderland et al. (1986)
Weight ratio for reproducing	0.10	van Emden and Harrington (2007) and Timms and Leather (2007)
Development stage at adulthood	1.0	Sensible value
Energy allocated to growth	82%	Simulation assumption, individuals are matured in around 20 days
Energy allocated to egg production	18%	Simulation assumption
Food demand, D	35%	Schoonhoven et al. (2005), Slansky and Rodriguez (1987) and Peters (1983)
Respiration cost, R	2.56%	Schoonhoven et al. (2005), Slansky and Rodriguez (1987) and Peters (1983)
Biological type	2	For simulation
Development constant	$4.69e^{-03}$	Dean (1974), Dixon (2000)
Development rate	$4.69e^{-02}$	Dean (1974), Dixon (2000)

with a total weight of 0.06 mg. They grow and develop until they reach their adult state at day 10 and then start producing juveniles. Minimum simulated weight of juveniles, at about 0.06 mg, and maximum adult weight at $0.8 - 1.0$ mg accord well with observed growth patterns. Overlapping bouts of growth and reproduction then produces a series of damped cycles in the average individual weight of aphids.
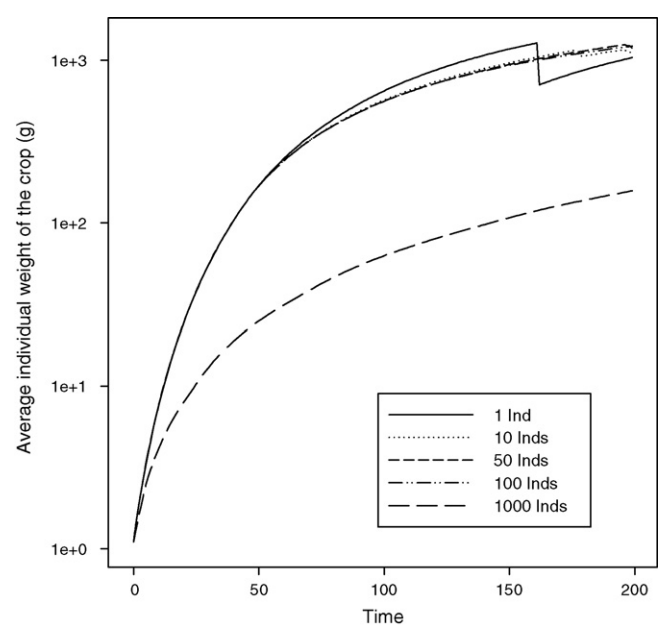
Fig. 6 shows the average individual weight of a number of ladybirds that were randomly distributed over the patch at day 10. Individuals grow from day 10 until about day 30, at which point they reach their adult state, where they start producing and then releasing eggs. The next generation of ladybirds appears just after
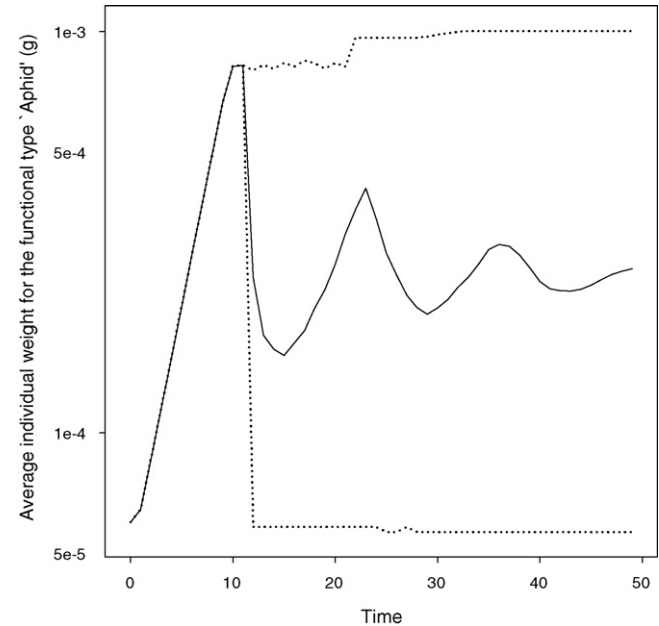

Fig. 4. Simulated crop plant growth, over 200 days, at different abundances of plant individuals within a patch. The curves are the average weights, across the individuals in the patch, for one simulation.

Fig. 5. Simulated individual growth of primary consumer aphids with respect to time. The solid line is the aphid average weight over the total number of aphids present in the patch from one simulation run. The dotted lines indicate the minimum and maximum range of individual weight. Five aphids were initialised as juveniles, with a weight of 0.06 mg, and introduced into a simulated patch of 1000 crop plants.
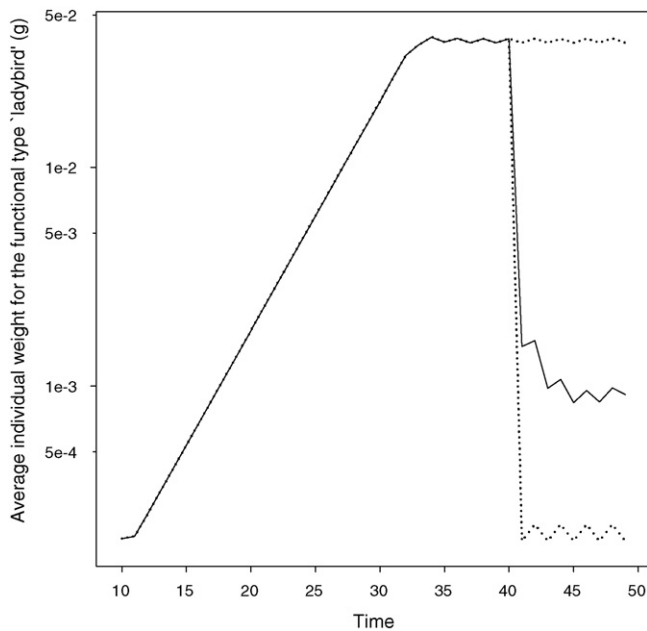
Fig. 6. The simulated growth of secondary consumer ladybirds with respect to time, from one simulation run. The solid line is the ladybird average weight over the total number of ladybirds present in the patch. The dotted lines represent the minimum and maximum range of the individual weight. At day 10, 2 ladybirds, with a weight of 0.2 mg, were introduced to the patch that had been previously been initialised with 500 aphids and 1000 crop plants.

day 40, at which point the average individual weight falls. The maximum weight of these ladybirds is about 40 mg and the minimum is ~0.2 mg, within the range expected.

This simulation output demonstrates that the trophic-functional IBM can reproduce expected individual patterns of growth for the trophic-functional types to which the crop, aphids and ladybirds belong. It also suggests that our model description capture the important trophic interactions that drive growth dynamics.
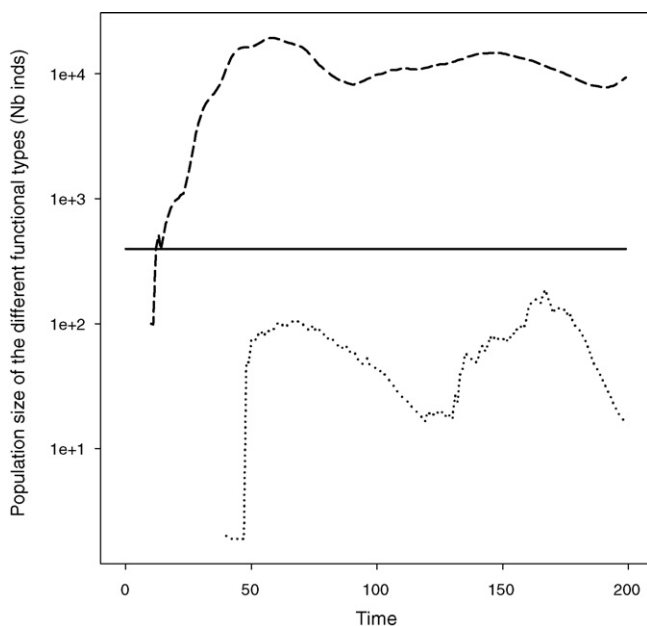

Fig. 7. The simulated population size, over 200 time steps, of the crop, solid line, the herbivore, dashed line, and the predator, the dotted line. The curves are the average population size over the ten simulations run for this experiment. The crop population was initialised with 400 individuals at day 0; 100 herbivores were created at day 10 and 2 predators were introduced at day 40.
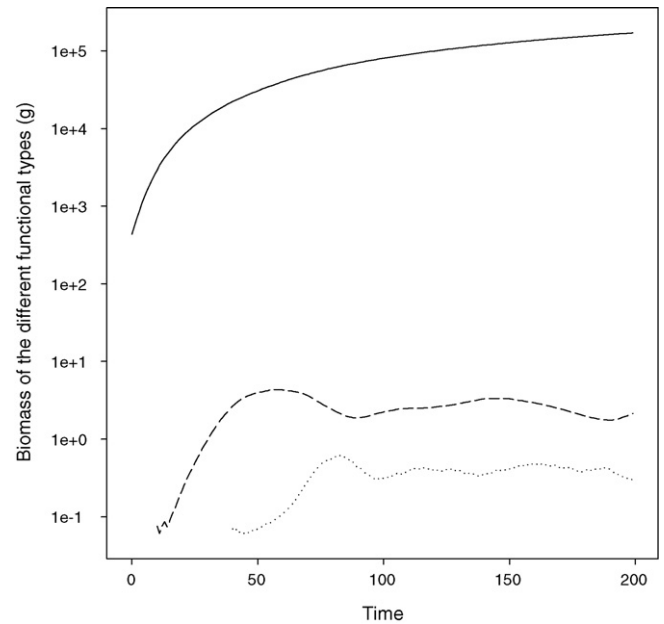

Fig. 8. Simulated biomass of the crop, solid line, herbivore, dashed line, and predator, dotted line, trophic-functional types over time. The curves are the average biomass values over the ten simulations run for this experiment. The crop population was initialised with 400 individuals at day 0; 100 herbivores were created at day 10 and 2 predators were introduced at day 40.

3.2.2. Trophic-functional type or population level dynamics

In Fig. 7, the population size of each trophic-functional type is shown over 200 time steps. The crop population size remains constant through time as the crop did not reproduce and no plants died, because we set a 100% survival rate. The herbivore population increased in size to day 50 and then slowly oscillated for the remainder of the time at a population size of ~16,000 individuals. Following introduction, the predator population quickly increased in size, reaching a maximum of ~100 individuals, before oscillating between ~20 and ~100 individuals.

We find that the crop biomass increased with time in these simulations, and tended to a plateau at ~170 kg. The herbivore and predator biomass oscillated around 3.3 and 0.4 g, respectively (Fig. 8).

In Fig. 9 the phase plane for predator and herbivore biomass is plotted. This figure shows that the predator biomass follows the herbivore, seemingly on a limit cycle. The phase-plane cycle turns anti-clockwise, which might suggest that the predator regulates the herbivore's population (Britton, 2003).

When we plot trophic-functional type abundance and body mass, on common axes, unexpected output was apparent (Fig. 10). These trajectory-plots, through time, were strongly reminiscent of the relationships found by Cohen et al. (2003), in the Tuesday Lake food web, and the data presented in Fig. 1. This suggests that the model produces simulation output that is consistent with food web ecology. However, whether these plots are consistent with the energetic models and analysis of Cohen et al. (2003) will require further experimentation and analysis.

These simple simulation experimental results give us great confidence that a trophic-functional representation can reproduce ecosystem dynamics. Although the systems we model, currently, are extremely simple, the output at the population level demonstrates that the trophic-functional IBM model can reproduce expected results. Individuals interact as expected. We find cycles in abundance and biomass that are consistent with the regulation observed experimental populations of aphids and ladybirds in the
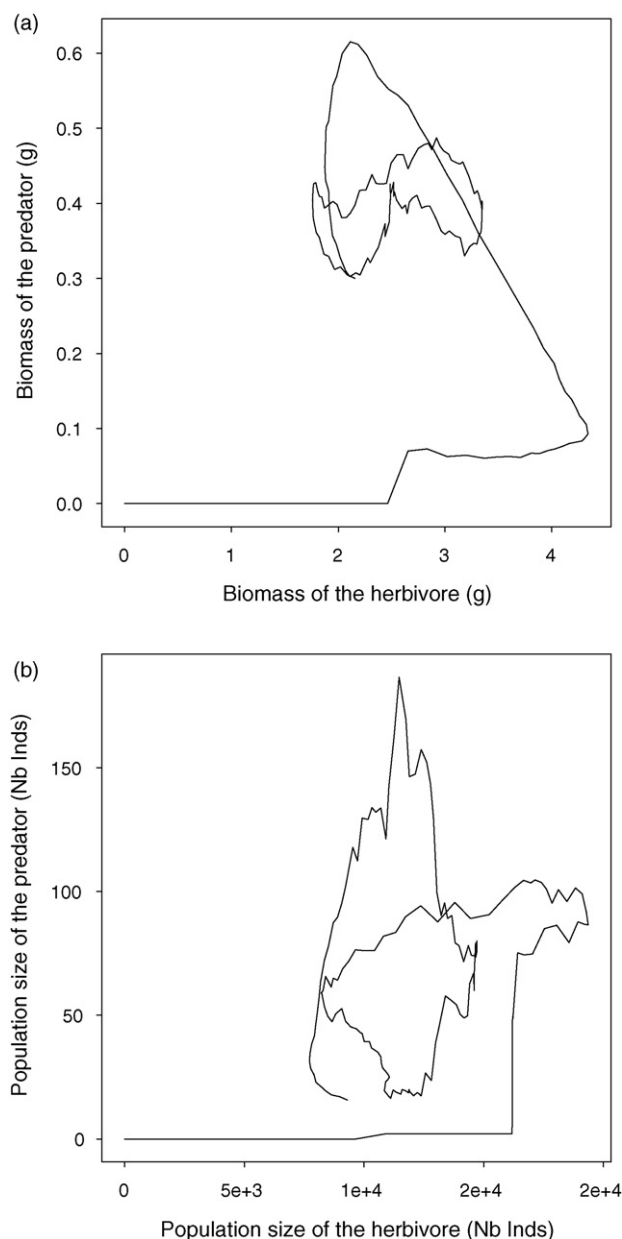
Fig. 9. Phase planes for: (a) predator and herbivore biomass; and (b) predator and herbivore population size. The curves are the average values over the 10 simulations run for this experiment. The crop population was initialised with 400 individuals at day 0; 100 herbivores were created at day 10 and 2 predators were introduced at day 40.

Fig. 10. Simulated trajectories of average individual weights, for the herbivore (solid circle) and predator (open circle) trophic-functional types. The data points are the average weight values over the 10 simulations run for this experiment.

trophic-functional types. The crop and the weed functional types compete for resources, as previously described. The herbivores feed on the crop and the weed with equal preference, and the predators feed on the herbivores. We evaluated the herbicide management impacts by applying two herbicide sprays at days 80 and 120 over the entire patch. Weed individuals had increased mortality rates ($p = 0.2$) when subjected to herbicide sprays; the crop was not affected. Six different configurations of this system were examined (Fig. 11), some with herbicide management.

Relative crop biomass at the last time step of the simulations, which we treat as a correlate of crop productivity, was found to change significantly with the configuration of the model system and the presence of herbicide management (Fig. 12). Where weeds were not present in the model, in configuration sets 1, 2 and 3, high crop biomass was achieved. There were slight, but significant differences between these sets with the presence of herbivores and the impact of their feeding on the crop and the ranking was set 1 > set 3 > set 2. As expected, the lowest biomass was observed in sets 4, 5 and 6 due to the presence of weeds and weed competition with the crop. The introduction of herbivores in sets 5 and 6 reduced weed competition significantly over that seen in set 4. However, the effect of this herbivore related reduction in weed competition on crop

laboratory. Moreover, we also see unexpected output as we had not expected to observe the trajectory-plots. Although it is not certain that these plots are consistent with the energetic models and analysis of Cohen et al. (2003), it suggests that the IBM can reproduce valid output that is consistent with findings from food web and population dynamic ecology.

3.2.3. Management impact

Predicting the effects of management is a key use for this model. Weed management using herbicide has been adopted for testing the model, although the effects of insecticide application and other pest and agronomic management can be modelled as perturbations in the development of particular trophic-functional types. To illustrate the effects of herbicide application, we created a limited version of the model including crop, weed, herbivore and predator
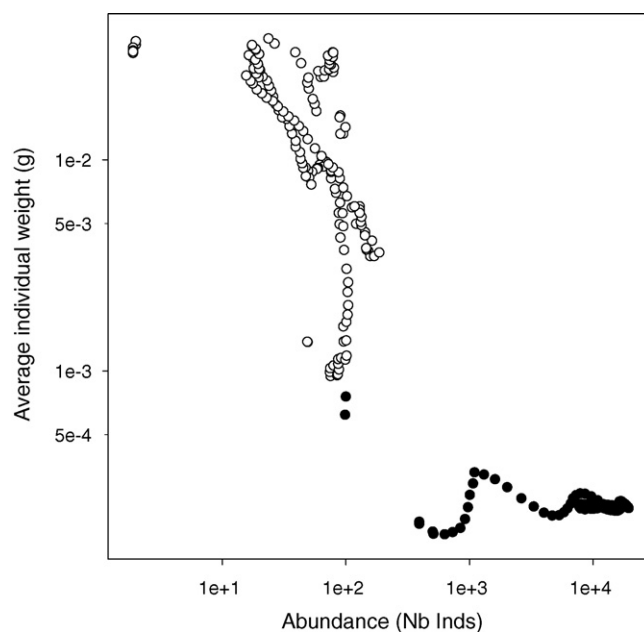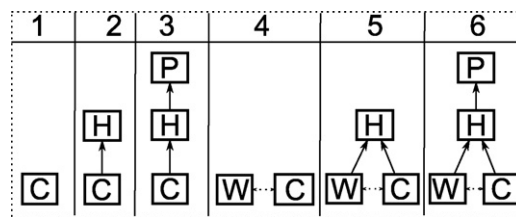

Fig. 11. Schematic representation of the 6 different configurations of the system simulated for the experimental results shown in Fig. 12. Crop (C), Weed (W), Herbivore (H) and Predator (P) trophic-functional types were simulated. Where weeds are present in configurations 4-6, sets of simulations were run with and without herbicide management to manipulate weed competition with the crop. 200 crop plants were introduced at day 0. When applicable, 200 weed type and 100 herbivore type individuals were introduced at day 10, and 2 predator type individuals were introduced at day 40. 10 simulations were run over 200 time steps.
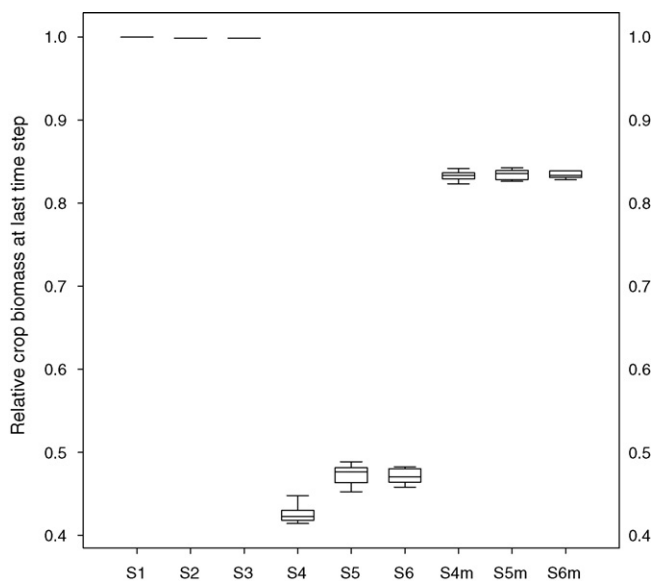
Fig. 12. Box-whiskers plot for the simulated crop biomass at the last time step relative to the crop biomass of set 1. The statistics are calculated from ten simulations for each configuration presented in Fig. 11 and *m* means that management was applied at days 80 and 120.

biomass was small when compared to the increase in crop biomass with herbicide management found in sets 4*M*, 5*M* and 6*M*. The herbicide applications significantly improve crop biomass, although as expected the simulated biomass was not as high as in the sets without weeds.

These results for management are encouraging. We find that our model produces agronomically sensible output alongside credible population dynamics data.

3.2.4. Uncertainty and sensitivity analysis

Some parameters of this model will have to be estimated from the experience of colleagues and collaborators as biological data may not be available. This may have consequences for the certainty that can be placed on the model output. A full sensitivity analysis to evaluate and analyse model uncertainty is likely to be difficult, given the number of input parameters. We therefore suggest that only a select part of the life history traits be considered, and allow them to take different values from a distribution. Several simulations for each of the configurations will be run and the output analysed. This approach, as outlined in Saltelli et al. (2004), will provide sensitivity measures for each input parameter. From there, we will have a good idea of the confidence we can place on the model output, and what input parameters may require deeper investigation (Grimm and Railsback, 2005). One of the main aims of the sensitivity analysis will also be to identify those parameters that are insensitive to scaling, thereby allowing us to derive appropriate aggregation methods/scenarios for scaling-up the model.

3.2.5. Validation

That the model output is similar to expectation provides supportive evidence that our model has validity. The current version of the model, though limited, is able to produce expected and sensible individual behaviours, population dynamics and individual interactions. Seemingly, the individual interactions between the different trophic-functional types are shown to be relevant and appropriate as the ecosystem behaves as expected. However, while valuable, this approach is limited and we also propose to validate the output against observed data. We are currently conducting a field scale experiment on the influence of herbicide spray timing on both the plant and invertebrate communities. The experimental herbicide treatments have been applied in 10 fields of winter wheat, over 2 years, at two geographically distinct research institutes. Weed and invertebrates communities have been sampled over the 2 years using experimental protocols that are complementary to those of the FSEs (Firbank et al., 2003; Bohan et al., 2005; Champion et al., 2003), which have been used for parameterisation. Herbicide management scenarios for validation are also being developed in conjunction with Syngenta Ltd.

4. Conclusion

Here we present a method of constructing an ecosystem model. We describe a trophic-functional simplification of plant and invertebrate individuals, and their interactions, in the arable ecosystem, following Hawes et al. (2009). This representation facilitates modelling of the arable ecosystem and tests the hypothesis that trophic-functional ecology can explain the structure, diversity and dynamics of arable ecosystems. The trophic-functional types in our 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. In this manuscript we illustrate some points of our argument using 4 functional types with indicative output for testing.

The simulation output for simple ecosystems, populated with realistic parameter values, is consistent with current laboratory observations, and the effects of agricultural management as illustrated by herbicide application. In its current state, the model is capable of reporting simultaneously on population size, individual traits, and crop yield. As the model develops, we aim to investigate more complex problems such as devising management to optimise the trade-off between agricultural productivity and functional biodiversity. These predictions will help guide which management strategies are best given a particular ecosystem (e.g. one particular crop). This advice could be of great interest to pesticide developers, farmers and local decision makers, but might also be used to guide national scale decision making.

Future work will address the role of distinct network, or food web, configurations to test ecological theory. We will evaluate the influence of omnivory on ecosystem dynamics, and will further extend the IBM to other food web structures and trophic-functional type behaviours. Empirical and theoretical studies have suggested that ecosystems consist of a few weak trophic links and many stronger ones (Emmerson et al., 2005; Wootton and Emmerson, 2005), and that weak omnivore links and complexity of linkage may stabilise ecosystems (May, 1974). More recently, (Christianou and Kokkoris, 2008) have argued that many of these putative food webs would not exist in reality. Given our model is based on ecological principles, and so will only model realistic situations relevant to agricultural systems, we will be able to test these hypotheses.

References

Aguirre, A., Dirzo, R., 2008. Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a mexican tropical forest. Biol. Conserv. 141 (2), 375–384.
Axelrod, R., 1997. The Complexity of Cooperation: Agent-Based Models of Competition and Collaboration. Princeton University Press, Princeton.

Bohan, D.A., Boffey, C.W., Brooks, D.R., Clark, S.J., Dewar, A.M., Firbank, L.G., Haughton, A.J., Hawes, C., Heard, M.S., May, M.J., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Squire, G.R., Woiwod, I.P., Champion, G.T., 2005. Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape. Proc. Roy. Sco. B: Biol. Sci. 272 (1562), 463–474.

Bohan, D.A., Hawes, C., Haughton, A.J., Denholm, I., Champion, G.T., Perry, J.N., Clark, S.J., 2007. Statistical models to evaluate invertebrate-plant trophic interactions in arable systems. Bull. Entomol. Res. 97 (1), 1–16.

Breckling, B., Middelhoff, U., Reuter, H., 2006. Individual-based models as tools for ecological theory and application: understanding the emergence of organisational properties in ecological systems. Ecol. Model. 194 (1–3), 102.

Britton, N.F., 2003. Essential Mathematical Biology. Springer.

Brooks, D.R., Bohan, D.A., Champion, G.T., Haughton, A.J., Hawes, C., Heard, M.S., Clark, S.J., Dewar, A.M., Firbank, L.G., Perry, J.N., Rothery, P., Scott, R.J., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J.H., Baker, P., Bell, D., Browne, E.L., Dewar, A.J., Fairfax, C.M., Garner, B.H., Haylock, L.A., Horne, S.L., Hulmes, S.E., Mason, N.S., Norton, L.R., Nuttall, P., Randle, Z., Rossall, M.J., Sands, R.J., Singer, E.J., Walker, M.J., 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil–surface-active invertebrates. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1439), 1847–1862.

Brown, D., Rothery, P., 1993. Models in Biology. Wiley New York, New York.

Calow, P., 1987. Towards a definition of functional ecology. Funct. Ecol. 1 (1), 57–61.

Caron-Lormier, G., Humphry, R.W., Bohan, D.A., Hawes, C., Thorbek, P., 2008. Asynchronous and synchronous updating in individual-based models. Ecol. Model. 212 (3–4), 522–527.

Carpenter, S.R., Kitchell, J.F., 1988. Consumer control of lake productivity. Bioscience 38, 764–769.

Carpenter, S.R., Kitchell, J.F., 1993. The Trophic Cascade in Lakes. Cambridge Univ. Press, Cambridge, UK.

Champion, G.T., May, M.J., Bennett, S., Brooks, D.R., Clark, S.J., Daniels, R.E., Firbank, L.G., Haughton, A.J., Hawes, C., Heard, M.S., Perry, J.N., Randle, Z., Rossall, M.J., Rothery, P., Skellern, M.P., Scott, R.J., Squire, G.R., Thomas, M.R., 2003. Crop management and agronomic context of the farm scale evaluations of genetically modified herbicide-tolerant crops. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1439), 1801–1818.

Christianou, M., Kokkoris, G.D., 2008. Complexity does not affect stability in feasible model communities. J. Theor. Biol. 253 (1), 162–169.

Cohen, J.E., 1991. Food webs as a focus for unifying ecological theory. Ecol. Int. 19, 1–13.

Cohen, J.E., Jonsson, T., Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. Proc. Natl. Acad. Sci. U.S.A. 100 (4), 1781–1786.

Crowl, T., Bouwes, N., Townsend, M., Covich, A., Scatena, F., 2000. Estimating the potential role of freshwater shrimp on an aquatic insect assemblage in a tropical headwater stream: a bioenergetics approach. Verh. Internat. Verein. Limnol. 27, 1–5.

Dean, G., 1974. Effect of temperature on the cereal aphids metopolophium dirhodum (wlk.), rhopalosiphum padi (l.) and macrosiphum-avenae (f) (hem aphididae). Bull. Entomol. Res. 63 (3), 401–409.

Delcamp, G., Gourlet, F.S., Flores, O., Garnier, E., 2008. Can functional classification of tropical trees predict population dynamics after disturbance? J. Veg. Sci. 19 (2), 209–211.

Deng, F., Zang, R., Chen, B., 2008. Identification of functional groups in an old-growth tropical montane rain forest on hainan island, china. Forest Ecol. Manag. 255 (5–6), 1820–1830.

Dixon, A., 2000. Ladybird Beetles and Biological Control. Insect Predator–Prey Dynamics. Cambridge University Press, Cambridge.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002a. Food-web structure and network theory: the role of connectance and size. Proc. Natl. Acad. Sci. U.S.A. 99 (20), 12917.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. 5 (4), 558.

Dyer, A.R., Goldberg, D.E., Turkington, R., Sayre, C., 2001. Effects of growing conditions and source habitat on plant traits and functional group definition. Funct. Ecol. 15 (1), 85–95.

Elton, C., 1927. Animal Ecology. Sidgwick & Jackson, London.

Emmerson, M.C., Bezemer, M., Hunter, M.D., Jones, T.H., 2005. Global change alters the stability of food webs. Glob. Change Biol. 11 (3), 490–501.

Emmerson, M.C., Raffaelli, D., 2004. Predator-prey body size, interaction strength and the stability of a real food web. J. Anim. Ecol. 73 (3), 399.

Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Haughton, A.J., Champion, G.T., Scott, R.J., Hill, M.O., Dewar, A.M., Squire, G.R., May, M.J., Brooks, D.R., Bohan, D.A., Daniels, R.E., Osborne, J.L., Roy, D.B., Black, H.I.J., Rothery, P., Perry, J.N., 2003. An introduction to the farm-scale evaluations of genetically modified herbicide-tolerant crops. J. Appl. Ecol. 40 (1), 2.

Gibbons, D.W., Bohan, D.A., et al. (2006). Weed seed resources for birds in fields with constrating conventional and genetically modified herbicide-tolerant crops. Proceedings of the Royal Society B: Biol. Sci. 273(1596), 1921–1928.

Gibson, R.H., Nelson, I.L., Hopkins, G.W., Hamlett, B.J., Memmott, J., 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. J. Appl. Ecol. 43 (2), 246–257.

Gilbert, N., Troitzsch, K., 2005. Simulation for the Social Scientist, 2nd Edition. Open University Press.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198 (1–2), 115–126.

Grimm, V., Railsback, S.F., 2005. Individual-based Modeling and Ecology. Princeton Series in Theoretical and Computational Biology. Princeton University Press, Princeton.

Gutierrez, A.P., 1996. Applied Population Ecology: A Supply-demand Approach. John Wiley & Sons, New York.

Haughton, A.J., Champion, G.T., Hawes, C., Heard, M.S., Brooks, D.R., Bohan, D.A., Clark, S.J., Dewar, A.M., Firbank, L.G., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J.H., Baker, P., Browne, E.L., Dewar, A.J., Garner, B.H., Haylock, L.A., Horne, S.L., Mason, N.S., Sands, R.J., Walker, M.J., 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1439), 1863–1877.

Hawes, C., Begg, G.S., Squire, G.R., Iannetta, P.P.M., 2005. Individuals as the basic accounting unit in studies of ecosystem function: functional diversity in shepherd's purse, capsella. Oikos 109 (3), 521–534.

Hawes, C., Haughton, A., Bohan, D., Squire, G., 2009. Functional approaches for assessing plant and invertebrate abundance patterns in arable systems. Basic Appl. Ecol. 10 (1), 34–42.

Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S.J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., Dewar, A.M., Heard, M.S., Woiwod, I.P., Daniels, R.E., Young, M.W., Parish, A.M., Scott, R.J., Firbank, L.G., Squire, G.R., 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the farm scale evaluations of genetically modified herbicide-tolerant crops. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1439), 1899–1913.

Heard, M.S., Hawes, C., Champion, G.T., Clark, S.J., Firbank, L.G., Haughton, A.J., Parish, A.M., Perry, J.N., Rothery, P., Scott, R.J., Skellern, M.P., Squire, G.R., Hill, M.O., 2003. Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. I. Effects on abundance and diversity. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1439), 1819–1832.

Kindlmann, P., Dixon, A.F.G., 1996. Population dynamics of a tree-dwelling aphid: individuals to populations. Ecol. Model. 89 (1–3), 23–30.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quetier, F., Thebault, A., Bonis, A., 2008. Assessing functional diversity in the field—methodology matters! Funct. Ecol. 22 (1), 134–147.

Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol. E 12 (12), 474–478.

Lavorel, S., Rochette, C., Lebreton, J.D., 1999. Functional groups for response to disturbance in mediterranean old fields. Oikos 84 (3), 480–498.

Law, A., Kelton, W., 2000. Simulation Modeling and Analysis, 3rd Edition. McGraw-Hill, New York.

Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., Billeter, R., Bukacek, R., Burel, F., De Blust, G., De Cock, R., Dirksen, J., Edwards, P.J., Hamersky, R., Herzog, F., Klotz, S., Kuhn, I., Le Coeur, D., Miklova, P., Roubalova, M., Schweiger, O., Smulders, M.J.M., Van Wingerden, W.K.R.E., Bugter, R., Zobel, M., 2008. Plant functional group composition and large-scale species richness in European agricultural landscapes. J. Veg. Sci. 19 (1), 3–14.

Lindeman, R., 1942. The trophic–dynamic aspect of ecology. Ecology 23, 399–418.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology: biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294 (5543), 804.

May, R.M., 1974. Stability and Complexity in Model Ecosystems, 2nd Edition. Princeton University Press, Princeton.

Maynard Smith, J., 1974. Models in Ecology. Cambridge University Press, London.

McGill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21 (4).

McKie, B.G., Woodward, G., Hladyz, S., Nistorescu, M., Preda, E., Popescu, C., Giller, P.S., Malmqvist, B., 2008. Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. J. Anim. Ecol. 77 (3), 495–504.

Odum, E., 1971. Fundamentals of Ecology, 3rd Edition. Saunders, New York.

Pakeman, R.J., 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. J. Ecol. 92 (5), 893–905.

Pascual, M., Dunne, J.A., 2006. Ecological Networks. Oxford University Press, Oxford.

Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. From the cover: size, foraging, and food web structure. Proc. Natl. Acad. Sci. U.S.A. 105 (11), 4191–4196.

Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Polis, G.A., 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. Am. Nat. 138 (1), 123–155.

Reuman, D.C., Cohen, J.E., 2004. Trophic links' length and slope in the Tuesday Lake food web with species' body mass and numerical abundance. J. Anim. Ecol. 73 (5), 852.

Rott, A., Godfray, H., 2000. The structure of a leafminer-parasitoid community. J. Anim. Ecol. 69 (2), 274–289.

Rudstam, L.G., 1989. A bioenergetic model for mysis growth and consumption applied to a Baltic population of mysis mixta. J. Plankton Res. 11 (5), 971–983.

Saltelli, A., Tarantola, S., Campolongo, F., Ratto, M., 2004. Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models. Wiley–IEEE.

Schaffers, A.P., Raemakers, I.P., Sykora, K.V., Ter Braak, C.J.F., 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89 (3), 782–794.

Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., 2005. Insect–Plant Biology. Oxford University Press, Oxford.

Slade, E.M., Mann, D.J., Villanueva, J.F., Lewis, O.T., 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. J. Anim. Ecol. 76 (6), 1094–1104.

Slansky, F.J., Rodriguez, J., 1987. Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates. Wiley-Interscience, New York.

Smith, V., Bohan, D.A., Clark, S.J., Haughton, A.J., Bell, J.R., Heard, M.S., 2008. Weed and invertebrate community compositions in arable farmland. Arthropod - Plant Interact. 2 (1), 21–30.

Storkey, J., 2006. A functional group approach to the management of UK arable weeds to support biological diversity. Weed Res. 46 (6), 513–522.

Sunderland, K.D., Fraser, A.M., Dixon, A.F.G., 1986. Field and laboratory studies on money spiders (linyphiidae) as predators of cereal aphids. J. Appl. Ecol. 23 (2), 433–447.

Tansley, A., 1935. The use and abuse of vegetational concepts and terms. Ecology 16 (3), 284–307.

Timms, J.E.L., Leather, S.R., 2007. Ladybird egg cluster size: relationships between species, oviposition substrate and cannibalism. Bull. Entomol. Res. 97 (6), 613–618.

Turchin, P., 1988. Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution in Animals and Plants. Sinauer Associates Inc., Sunderland, MA.

Turchin, P., 2003. Complex Population Dynamics: A Theoretical/Empirical Synthesis. Princeton University Press, Princeton.

van Emden, H., Harrington, R. (Eds.), 2007. Aphids as Crop Pests. CABI.

Van Veen, F.J.F., Muller, C.B., Pell, J.K., Godfray, H.C.J., 2008. Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids. J. Anim. Ecol. 77 (1), 191–200.

Willis, A., 1997. The ecosystem: an evolving concept viewed historically. Funct. Ecol. 11 (2), 268–271.

Wootton, J.T., Emmerson, M.C., 2005. Measurement of interaction strength in nature. Annu. Rev. Ecol. Evolut. Syst. 36 (1), 419–444.