

# Modelling Interaction Networks for Enhanced Ecosystem Services in Agroecosystems

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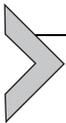
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## Abstract

The development of new methods and approaches for ensuring the sustainability of agriculture and ecosystem services is an important challenge that ecologists, agronomists, and theoreticians must address together. Enhancement of ecosystem services needs to be addressed at different scales and should include the interaction between farmland biodiversity and stakeholders (farmers, managers, policy makers, etc.) to optimize service delivery. Predictions require an understanding of the interactions between numerous management options and components of biodiversity. Here, we argue that interaction networks on a broad sense (from food webs to landscapes networks in which nodes

could be species, trophic groups, fields or farms) can help address this high level of complexity. We examine how tools from mathematics and artificial intelligence, developed for network modelling and reasoning, could be useful for assessing and enhancing ecosystem services. In doing this we highlight the gaps that currently exist between our questions about ecosystem service provision and our ability to answer them with current modelling approaches. We illustrate the use of these tools with three case studies related to 'pest regulation services'. These include food web approaches to assess animal pest regulation services and decisional models to address management strategies for diseases and weeds. Finally, we describe how different types of network models might operate at different scales of management. The future challenge for agroecologists will be to produce models of interactions and emergent ecosystem services, which are sufficiently quantified and validated. We suggest that network ecology is a nascent research topic that is developing a strong and unified empirical and theoretical foundation, which could serve as the central paradigm for a sustainable, intensive agriculture in the future.



## 1. INTRODUCTION

Farmers and other agricultural stakeholders are the dominant managers of the Earth's land surface, and they will continue to shape agricultural ecosystems in the coming decades. The development of new methods and approaches for ensuring the sustainability of agriculture, and the ecosystem services it provides, is one of the most challenging scientific issues faced by ecologists, agronomists, and theoreticians and addressing it will require joint efforts by these different groups (Tilman et al., 2002). Cultivated ecosystems provide a wide range of benefits to people, and these have become known as 'Ecosystem Services' (Millennium Ecosystem Assessment (MA), 2005). After Boyd and Banzhaf (2007), Fischer et al. (2008) proposed that ecosystem services are those aspects of ecological function that are actively or passively used to enhance human well-being. The major role of agriculture is to provide 'provisioning' ecosystem services, as defined in the Millennium Ecosystem Assessment (MA) (2005), mostly through the production of goods and cultural conservation.

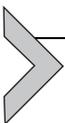
The ecological mechanisms underlying ecosystem services encompass the complexity of numerous possible interactions between species within and among local ecosystems. The effects of biodiversity on mechanisms underlying most ecosystem services are now well established and recognized, both empirically (Letourneau et al., 2011) and theoretically (Isbell et al., 2011). Ideally, all ecosystem services should also be taken into account when resource management decisions are made, and this should be addressed at different spatial and temporal scales, as well as including the

interaction between biodiversity and stakeholders, so as to maximize services and minimize disservices (Tschamtko et al., 2005). Quantifying services and their value has, however, proven difficult (Nelson et al., 2009). In particular, the relationship between agricultural practice and services is poorly understood. One reason is that ecological mechanisms underlying ecosystem services encompass complex interactions not just between species, but also among species, cultural practices, and stakeholder policies. Whereas models tend to be used as exploratory tools for the design of innovative cropping systems, for example, for the spatial arrangement of resources (Kropff et al., 2001; Lo-Pelzer et al., 2010), there is still a lack of mechanistic modelling tools for analysing and exploring the effect of management options on the provision of multiple ecosystem services. These are required for designing innovative cropping systems at field and landscape scales, and at larger scales for planning future options of territory management and policies. Such process- or mechanism-based models also need to incorporate the complexity of the interactions encompassed by ecological and decisional networks.

Agroecosystems are complex systems in which many species interact, with ecological processes that take place at different spatial scales, and with strong interactions between ecological and management processes (Loeuille et al., 2013; Mulder et al., 2013). These diverse types of interactions all fit in the general theoretical framework of 'interaction networks' (e.g. Ings et al., 2009; Woodward et al., 2010a), which is useful for addressing ecological interaction issues including food webs (Bohan et al., 2013; Moya-Larano et al., 2012), interaction networks between hosts and pathogens (Loeuille et al., 2013), and networks of spatial interdependence between localities (Massol and Petit, 2013). The concept of 'interaction networks' allows researchers: (i) to study and comprehend the emergent properties of complex systems and (ii) to develop general rules that link individual stakeholder decisions to broad outcomes of the system. When applied to agroecosystems and ecosystem services, interaction network approaches, and associated methodological tools, could provide insight into the relative influence of natural communities, landscape elements and management decisions on one another, and on the various ecosystem services they provide. The concept could help researchers determine how much of each service is provided across the multiple scales of the networks (field, farm, or landscape) at different organizational levels (species, community, or ecosystems) and decision makers design innovative strategies for ecosystem services management. Interactions at different scales and different organizational levels greatly increase the level of complexity that must be considered, and tools are

needed to design efficient collective and spatially structured strategies to enhance services and reduce disservices of agroecosystems.

In this chapter, we review how network models might be used to address major issues concerning the future of agricultural sustainability and how they can be used in an applied perspective to analyse, compare, and design management strategies of ecosystem services. We consider here network models in a broad sense; from food webs to landscapes networks in which nodes could be species, trophic groups, fields or farms. We highlight the great potential of network models to address global questions because of their ability to integrate properties across complex ecological (e.g. conservation (Montoya et al., 2012)) and management questions (Daugherty et al., 2007), which necessarily involve numerous interactions. We also point out gaps between current modelling possibilities and applied research questions concerning ecosystem services. Although network models can be applied to optimize a wide range of ecosystem services, this chapter focuses on pest regulation services, as these are currently the best understood in this context. Three case studies illustrate the broad uses of these models and demonstrate that network models can be used to address, simultaneously, several services in agroecosystems. Case study 1 concerns the use of food web models to assess the pest regulation services. Case study 2 describes a decisional landscape network model for the design of collective disease management strategies. Case study 3 describes a decisional landscape network model for the sustainable management of weeds. Finally, we propose a comprehensive approach for the linking of networks and services and for answering theoretical and applied agricultural questions with network models.



## **2. WHICH NETWORK MODEL FOR WHICH ECOSYSTEM SERVICE QUESTION?**

Network models encompass a wide variety of mathematical tools that enable researchers to study a broad range of processes linked to interactions between entities/nodes in networks (Bohan et al., 2013). Network models, relevant to agriculture, can represent ecological interactions between organisms, spatial relationships between entities and the exchange of information between stakeholders (farmers, policy makers, etc.). Network models all share some features. Irrespective of the mechanism that they simulate or their spatial extent, the structure of the associated interaction network includes entities that exchange energy or matter or information that shapes the network. Given this common structuring, network models share design

principles, such as metrics (e.g. connectivity and clustering; see [Bohan et al., 2013](#)), and simple building-block motifs that can be analysed similarly whether the network is physical, ecological, informational, or social ([Milo et al., 2002](#)). Several types of network models are suitable for understanding this diversity of network in ecology, in general, and in agroecology, in particular ([Table 7.1](#)). Here, we review three major types of network

**Table 7.1** Examples of modelling (in grey) and applied (in black) issues to be addressed with network models

Ecosystem services	Network models		
	Trophic: material and energy flow (food webs)	Spatialized interactions	Decision interactions
Production	How to link food web and crop models?		How to quantify/model the cost of a strategy?
Pest regulation	How can predation be used as a pest regulation strategy?	How to design management strategies that optimize pest control at the landscape scale? How to incorporate mechanistic dispersal models within decision frameworks?	
Pollination	How to integrate non-trophic interactions in food webs?	Where should we direct conservation efforts to maximize pollination service?	
Biodiversity conservation	How to predict diversity?	How to prioritize conservation of semi-natural habitats?	
	How to estimate a trophic network model from rare and noisy observation data?	How to reconstruct an occurrence/abundance map from rare and noisy observation data?	How to model the trade-off between production and biodiversity conservation?
Mitigation of invasive pests	Which community structure is most resilient to pest invasion?	How to define strategies minimizing the spread of diseases	
		How to reconstruct an occurrence/abundance map from a sample?	How to measure the quality of an estimated occurrence/abundance map?

**Table 7.2** Summary of main characteristics of food web models

Food web model type	Dynamic	Stochastic	Comments
Lotka–Volterra	Yes	No	Dynamic and process-based representation
Structural models	No	No	Comprehensive representation
Bayesian network	No	Yes	Simpler to estimate from data but static

model that allow researchers to address a wide range of questions related to ecosystem services and agroecosystem management. The first two are food web and spatial network models, which are directed at the analysis of network processes and the testing of management strategies. The third type, the decision interaction model, is concerned with understanding stakeholder decisions. Together, these provide a framework for the design, by optimization, of innovative, agricultural management strategies.

Food web models (Table 7.2) allow the representation of trophic interactions between species of a given community (Ings et al., 2009). Lotka–Volterra equations (Lotka, 1925; Volterra, 1928) have long been used to represent the dynamics of simple prey–predator systems. However, where there is a need to capture all or most interactions between a large number of species, structural food web models (Dunne et al., 2002a; Williams and Martinez, 2008) can give higher descriptive power, but usually at the cost of a loss of representation of the dynamics of interactions. Bayesian network (BN) models would be preferred where stochasticity is considered to be important (Eklöf et al., 2013; McDonald–Madden et al., 2011), as these also have the advantage of requiring simpler data sets, given that they have no mechanistic underpinning. Their limitation is that they are purely static and therefore lack spatial and temporal dynamics. Spatial interaction models (Table 7.3) explicitly represent the spatial interactions between populations of organisms/pathogens (Massol and Petit, 2013). Within this family, metacommunity models extend dynamic models to spatial interactions (Loeuille et al., 2013; May, 1973), but the representation of space is strictly implicit. Individual dispersion models are played out across a grid space of discrete cells (regular or irregular) in order to build dynamic, spatially explicit interaction networks or ‘grid-based’ models. Markov random fields (MRFs; Li, 2009) can represent stochastic spatial interactions on any structure of spatial interaction network (regular or not). These models are not dynamic, but the dynamics of spatial processes can be handled by extending them by

**Table 7.3** Summary of main characteristics of spatial interaction models: metacommunity models, individual-based models (IBM)/grid-based models, Markov random fields (MRF), dynamic Bayesian networks (DBN)

<b>Spatial interaction models</b>	<b>Dynamic</b>	<b>Stochastic</b>	<b>Comments</b>
Metacommunity	Yes	No	Not spatially explicit
IBM/grid	Yes	No	Can combine local and global dynamics
MRF	No	Yes	Enables uncertainty to be attached to spatial maps
DBN	Yes	Yes	Very flexible modelling framework

**Table 7.4** Summary of main characteristics of decision interaction models: influence diagrams, factored Markov decision processes (FMDP), factored actions factored Markov decision processes (FA-FMDP) and graph-based Markov decision processes (GMDP)

<b>Decision interaction models</b>	<b>Decision structure</b>	<b>Utility structure</b>	<b>Comments</b>
Influence diagrams	Multiple decision variables	Additively structured utility	No explicit notion of time. Exact solution for medium-sized problems
FMDP	A global decision variable	Generally structured global utility	Not relevant to most problems of agricultural network because of the assumption of a unique global decision
FA-FMDP	Multiple decision variables	Generally structured global utility	Very flexible modelling framework
GMDP	Multiple decision variables	Additively structured utility, with respect to the same structure as for decision	Can solve approximately high dimension dynamic problems

using, for instance, the enhanced capabilities of dynamic Bayesian networks (DBNs; Ghahramani, 1998).

Several decision interaction models (Table 7.4) have also been developed, that are suitable for managing interaction networks. They are extensions of BNs and Markov decision processes (MDPs; Puterman, 1994). These can be used to model species management optimization within trophic/spatial interaction networks (ID, Howard and Matheson, 1984;

FMDP, Boutilier et al., 1999; FA-FMDP, Kim and Dean, 2002; GMDP, Sabbadin et al., 2012).

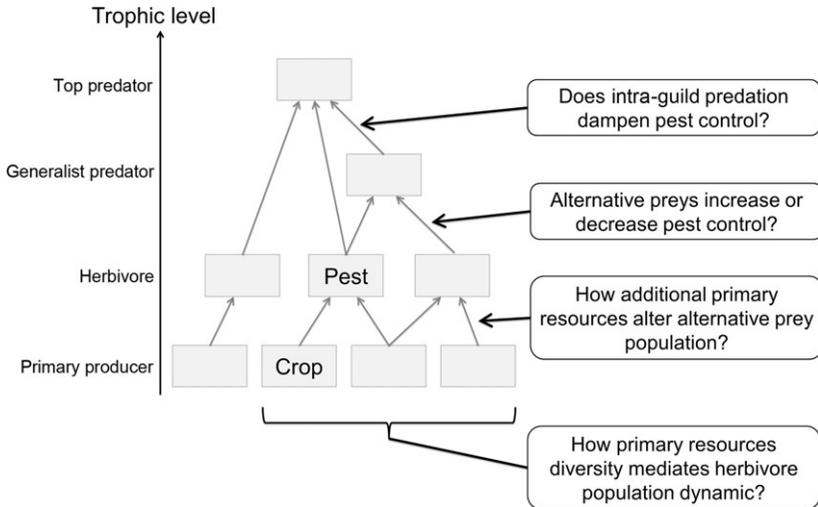
We now examine, in more detail, the potential usefulness of these three families of models for enhancing ecosystem services, and we present some exciting perspectives for their development and use.

## 2.1. Food web models for pest regulation services

Food web structure, or the realized network of trophic links between species of a given community, is a major factor affecting the performance and stability of ecosystems (Layer et al., 2010; Neutel et al., 2007). Food webs are one logical representation for agroecosystems because they describe who-eats-whom, and consequently the flow of biomass through the system. Plant diversification in agriculture is a key tool that farmers can use to structure food webs (Scherber et al., 2010) and to increase pest and disease suppression (Chaplin-Kramer et al., 2011). Increased plant diversity can result in increased pest and disease control as a consequence of habitat effects, dispersal, and bottom-up and top-down effects (Ratnadass et al., 2012), which drive or are driven by trophic interactions (Worm and Duffy, 2003).

While the role of direct trophic interactions in the control of pests has been demonstrated (Cardinale et al., 2003), the biological regulation of pests does not rely on the complete elimination of the pest from the ecosystem, as in chemical-based agriculture (Lewis et al., 1997). Rather, it is believed that a stable and healthy agroecosystem relies on a balance between pests and their predators and parasites in a given community (Hudson et al., 2006) and other biotic modes of regulation, such as mitigation through selection of crops that have non-host status for pests (Desanlis et al., 2013). Among the processes that mediate the success of pest control, predation within the guild of predators is of particular importance (Nóia et al., 2008; Roy et al., 2008) since it is a process that may be enhanced by modification of habitats and primary resources available in agroecosystems (Mollot et al., 2012).

Food web models provide a quantitative framework for combining community structure and population dynamics, to study the functions and services associated with biodiversity processes and ecosystem management options, including a wide range of questions associated with pest control (Fig. 7.1). The use of food web models, which include primary producers, pests and alternative herbivores, and different trophic levels of predators, to address issues applied to agricultural contexts remains relatively scarce. Lotka–Volterra models are, however, particularly suitable for studying the



**Figure 7.1** Major questions associated with pest control inside food webs.

role of intra-guild predation in pest control; for example, by searching for a set of species between which the level of intra-guild predation is sufficiently high to disrupt pest control. These simple models are suitable for studying the role of alternative food resources, whether primary producers or herbivores, which play a significant role in the dynamics of the community (Loeuille et al., 2013). This latter question is crucial in those cropping systems to which an agronomist specifically introduces more diversity, such as in cover cropping or companion planting situations. Case study 1 (see below) illustrates a concrete use of this type of simple model. More complex models, dealing with many species, would allow the study of the role of diversity among trophic groups or of the whole community on the enhancement of pest control; a crucial question in highly diversified cropping systems, such as tropical agro-forestry systems. Indeed, it has long been hypothesized (Elton, 1927) that more pest control might be expected in complex systems (Letourneau et al., 2011; Vockenhuber et al., 2013), but this may occur at the same time as more trophic interactions that could interfere with the regulation service (Straub et al., 2008). Models could help in disentangling how the organization of plant diversity in space and in time might maximize regulation services.

### 2.1.1 Existing models

Lotka–Volterra differential equations (1925; 1928) are the starting point of most dynamic food web models (Allesina and Tang, 2012; Berlow et al., 2004;

De Ruiter et al., 1995; Deangelis et al., 1989; May, 1973; McCann et al., 1998). Recent developments of Lotka–Volterra-based models include stability analysis, under nutrient-limited conditions (Hulot and Loreau, 2006), and the integration of adaptive traits (Sun and Loreau, 2009). Given the possibility of chaotic behaviour of this type of model in systems of when more than three species are included or for particular parameter values (May, 1973), Lotka–Volterra-based models have mostly been used to simulate simplified webs, usually with no more than three trophic levels. In contrast, structural food web models allow the integration of a diversity of feeding links among a large numbers of species (Dunne et al., 2002a; Williams and Martinez, 2008). Although they have detail, structural models use relatively simple rules to predict feeding relationships (Petchey et al., 2008; Woodward et al., 2010b). In the niche model, for example, possible prey can be modelled according to body size or other niche traits (Williams and Martinez, 2000), and more recent models are able to predict where in the web the links will be positioned (Petchey et al., 2008; Woodward et al., 2010b). However, structural models usually do not include population dynamics or demography, and focus on describing the food web structure at a given time in a given condition; their use as tools to test changing management strategies over time is therefore limited.

Researchers who are attempting to understand a system might choose to focus on the broad ecological functions of the organisms rather than attempting to identify, describe, and understand every species (Caron-Lormier et al., 2009, 2011). Functional groups or types are groups of species that share similar ecological properties or traits and that, therefore, perform the same function in a given system (Hawes et al., 2009). Once these groups are identified, the next step is to link them together. In agroecosystems, the aim is to grow crops to obtain a good yield, so any organism or process that removes crop biomass or yield is then treated as a ‘pest’ or disservice. Building functional food webs is challenging, however, because it requires information on the feeding habits of the functional groups. The problem is that it is not always possible to ‘witness’ a feeding link between two species or functional groups (Ings et al., 2009). Innovative methods like machine learning, as exemplified in Bohan et al. (2011), can help solve this problem when applied to species-occurrence data. The type of data available is usually taxonomic but Tamaddoni-Nezhad et al. (2013) describe a method for learning and estimating the explanatory power of food webs using functional groups rather than species. Functional food webs are a static representation of the system and allow for robust connectivity analyses (Dunne et al., 2002b), but would not indicate changes in the density of each functional group over

time. For this, we need to model food webs by including population dynamics as is done in individual-based models or Lotka–Volterra representations (Pascual and Dunne, 2006). Once the dynamics of the system can be simulated, we can investigate whether system perturbations may lead to the loss of function. The function of interest depends on the system being studied, but in the case of agroecosystems, two that are typically considered are crop yield or pest control. System perturbations may be in the form of chemical management leading to the change of some life–history traits (e.g. survival rate). Indeed, the perturbation of one or more functional groups may propagate, or cascade, through the food web and reach other functional groups that are performing important functions (Hawes et al., 2003). Using a simulation model, Raybould et al. (2011) have recently shown that a reduction of one life–history trait of an aphid predator functional group, due to a chemical management, does not necessarily lead to a loss of function (i.e. aphid predation) because of the functional redundancy in the system. When two predator groups perform the same function, the reduction in the performance of any one group may be compensated for by the other. The research of Raybould et al. (2011) involved only a few type species for functional groups, but showed that the combination of functional groups and food web representations, coupled to a simulation approach, might help predict the impact of management on the overall functioning of the system.

Another approach, as proposed by McDonald–Madden et al. (2011) and Eklöf et al. (2013), is the use of the BN framework (Jensen and Nielsen, 2007) to model food webs. BNs represent the trophic relations between species graphically, with conditional probabilities for the presence of predators given the presence of prey, differing from Lotka–Volterra and structural food web models that are based on material fluxes. As a result, the BN framework allows researchers to explicitly model the inherent uncertainty of species persistence without explicitly modelling the dynamics of extinctions. This explicit modelling of uncertainty will allow researchers to evaluate for the first time network resilience based on species–persistence probabilities, rather than on structure alone, but to the best of our knowledge this has not yet been attempted. Furthermore, because conservation management typically deals with species persistence, and likelihood, rather than web structure, BN approaches could be extremely useful for designing and evaluating management strategies for increased system resilience. Finally, because models using a BN framework are based on correlated probabilities of species presence, rather than biological processes such as predation, they can be built from simple ‘on–field’ observations of individual presence/

absence, enabling simpler experimental set-ups than required for computing the parameters and structure of Lotka–Volterra or structural models. Unlike these two later types of models, the BN approach is static in nature, focusing on species persistence probabilities in a hypothetical equilibrium state. The approach has also been extended to incorporate species dynamics (Probert et al., 2012), using a DBN model in a way similar to that used for decision interactions models, which are described in Section 2.3.

### **2.1.2 Application to the improvement of ecosystem services**

Lotka–Volterra-based models and structural models are applicable to pest regulation in agroecosystems, and particularly for studying the dynamics of the interactions between pests and their predators, when basal resources and alternative prey availability vary over time. Lotka–Volterra-based models are also useful for studying how the traits of pests, predators and alternative prey change the potential for pest control and the long-term system stability. Recent progress in agroecology has come about through linking food web and agronomic models. The concept of food web-cropping system models proposed by Tixier et al. (2013b) is an example of the linking of two types of model normally used by two distinct scientific communities. In this coupling, the crop models detail the soil–plant relationships, with regard to water and nutrient consumption, while the trophic-web models describe interactions between the invertebrate communities associated with the crop. This process-based approach allows the trade-offs between ecosystems services, including biotic regulation of crop pests, nutrient cycling and crop production to be examined in simulation.

In contrast to dynamic food web models, structural models allow a comprehensive representation of food webs, accounting for all the species and interactions within the community. Comprehensive representation becomes especially important in agroecosystems that have higher levels of biodiversity than intensively managed systems (Malézieux, 2012). While these models are not generally dynamic, the complex structure of networks can be linked to community functions and emerging properties by the detection of motifs (Milo et al., 2002). Motif analyses enable to reveal particular organization of a small set of species interactions (usually three or four) that occur more frequently than expected from observation of random networks. Such motif analysis is particularly useful because three- or four-species motifs (Bascompte and Melian, 2005; Stouffer et al., 2007) might be linked to ecological functions, in particular intra-guild predation and apparent competition. Motif analysis fills the gap between food web models

and more theoretical dynamic models. Size-3 motifs have received in-depth attention from ecologists, and as an example exploitative competition and apparent competition motifs have been studied theoretically in-depth for many years (Holt and Polis, 1997; Polis and Holt, 1992). Understanding of the behaviour of motifs (Schoener, 1983) and their occurrence has permitted a wide range of hypothesis to be tested, from the basic ‘green world hypothesis’ that states that terrestrial herbivores consume relatively little plant biomass because they are controlled by predators ( Hairston et al., 1960) to applied questions such as conditions of pest regulation in agroecosystems (Liu et al., 2005; Mills and Getz, 1996). Such simultaneous use of structural analysis and dynamic modelling of simplified motifs will surely have great relevance for linking food web structure with associated functions, especially where species of interest may be clearly identified and for which it is necessary to understand both the species–species interactions and the implications for other interactions within the community.

The BN approach has been recently applied to model and optimize the management of species interacting through food web relations (McDonald-Madden et al., 2011). This approach, and the dynamical extension to DBN, are potentially very promising as they could provide powerful reasoning/management tools for a cost-effective level of experimental effort.

### **2.1.3 Trends and future challenges**

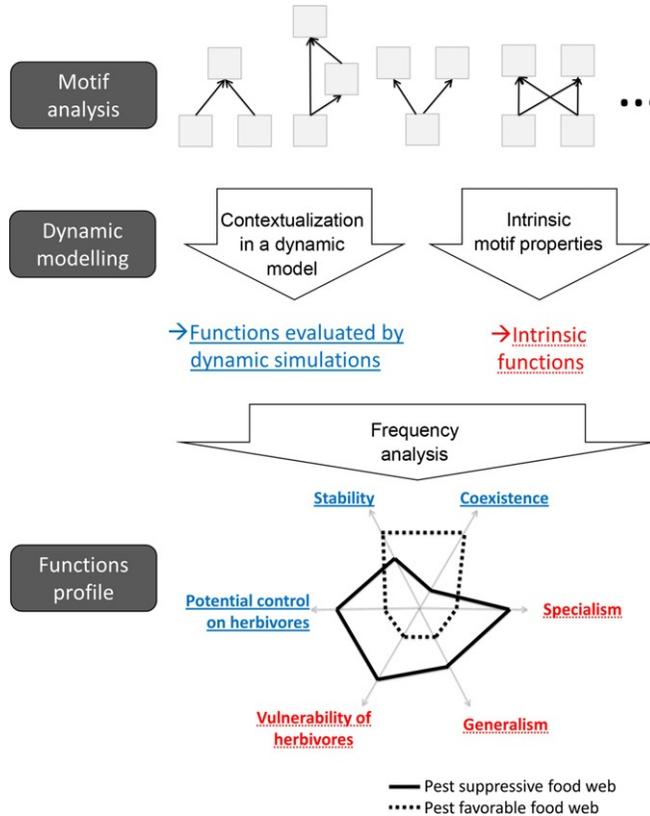
There is a growing effort to unify community models and ecosystem functioning into a comprehensive food web ecology that takes into account both: (i) the spatial and temporal variability of individuals, populations, and species of community ecology and (ii) the stocks, flows and dynamics of energy, biomass and nutrients considered in ecosystem ecology (Thompson et al., 2012). However, this effort is limited by the substantial effort required to construct and analyse food webs and by the lack of models with testable, mechanistic foundations. We believe that new, more comprehensive methods could be used to address one of the most logistically challenging tasks in the modelling of agroecosystem food webs; the identification of all consumer–resource interactions—who is eating whom. These novel methods combine stable isotope analysis, in natural or enrichment experiments that manipulate abundance, and the tools provided by molecular biology (Carreon-Martinez and Heath, 2010). Stable isotopes can provide an integrative measure of the diet of species (Ponsard and Arditì, 2000). Next-generation DNA sequencing provides the most comprehensive and accurate measure of trophic links in ecosystems by enabling

researchers to match DNA barcode sequences amplified from the gut content to large DNA sequences databases (Pompanon et al., 2011; Traugott et al., 2013). With these data, modellers should be able to develop models that detail current theory and understanding. Designing dynamic models that account for such newly revealed complexity is major issue for being able to predict food web responses to management options. One direction is to account for the multitude of interactions using structural models and studying the dynamical behaviour of the system at a smaller scale, for instance at the motif scale (three to four species in interaction). In such prospective models, food webs may be represented by stochastic–dynamic models, where each motif (and its associated functions) has a probability of occurrence in a given food web. The probability dynamics of each specified motif, accounting for life–history traits of the species involved in the motif, would then lead to the evaluation of indicators of functions such as the stability or the coexistence of species in the motif at equilibrium. These indicators could be completed by indicators of functions directly deduced from the intrinsic structure of motifs (e.g. generalism and vulnerability). Both the model derived and the intrinsic indicators of structure could then be tailored to specific question, such as the roles played by particular species of interest like pests and predators. The resulting profile of functions could be used to characterize those ecosystem services necessary to address a given issue (Fig. 7.2).

### **2.1.4 Case study 1—modelling arthropod food webs to test pest regulation strategies**

#### **2.1.4.1 The system under study and the services targeted**

The relatively simple food webs and flexible management of banana plantation agroecosystems are suitable for studying how the management of alternative basal resources, such as weeds and cover crops, changes the top-down suppression of crop pests and the productivity of banana plants. The banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae), which is the most serious insect pest of this crop (Gold et al., 2001), has been found to be regulated more efficiently by generalist ant and earwig predators when in the presence of a cover crop (Mollot et al., 2012). The management of the weeds or cover crops mediates the structure of the arthropod food web by modifying the resources available to herbivores (Duyck et al., 2011; Tixier et al., 2013a), and modulates the intensity of competition between the living cover and banana plants for mineral resources in the soil (Ripoche et al., 2012). Here, we have used a process-based model to understand how the frequency of mowing, which is the main cover crop management option, alters the provision of production (yield),

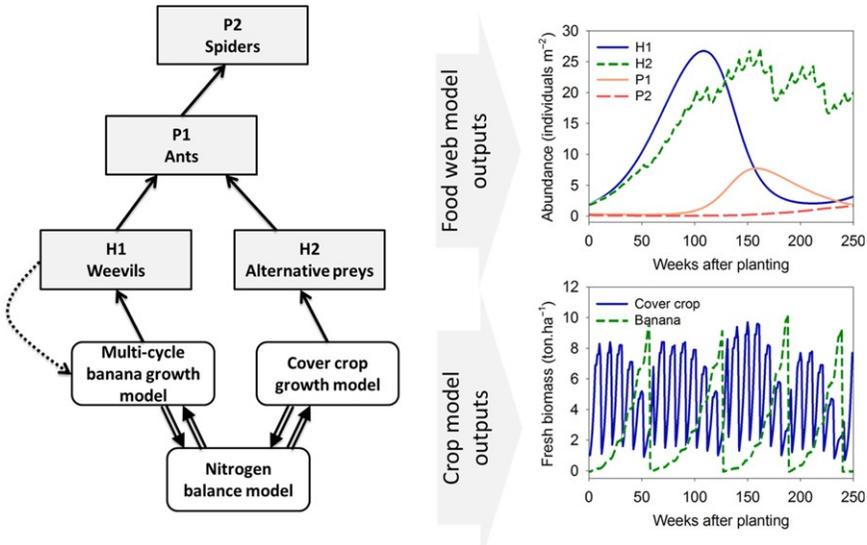


**Figure 7.2** Perspective of linking motif analysis and dynamic simulation to assess functions of highly resolved food webs. Functions evaluated by dynamic models could be the stability including the amplitude of variations, the coexistence of the species of the motif, and the potential to control herbivore (could be evaluated by herbivores abundance at equilibrium). Intrinsic functions are resulting from the inherent structure of each motif, it could be notes given by experts to each module assessing the levels of specialism, generalism, and vulnerability. Functions evaluated by dynamic models and intrinsic functions should be modulated according to the functions to be evaluated (e.g. focussing the indicator on pest control, maintenance of predator community, or minimizing intra-guild predation). We illustrate what could be the functions profile of a pest-suppressive food web and a pest-favourable food web.

regulation (pest control) and conservation (arthropod diversity) services in banana ecosystems.

#### 2.1.4.2 The modelling approach

Tixier et al. (2013b) proposed a linked crop model and a food web model for banana agroecosystems (Fig. 7.3). We follow this proposition by using a



**Figure 7.3** Diagram and outputs of the banana agroecosystem modelling framework (case study 1). The diagram on the left shows the structure of the model. The model includes banana and the cover crop, which compete for soil nitrogen, and four trophic groups. Double-line arrows indicate flows of nitrogen, single-line arrows indicate trophic links, and the dotted-line arrow indicates the feedback of the pest on crop functioning. On the right, the two graphs show dynamic outputs of soil–plant modules (biomass of banana and cover crop) (bottom) and food-web modules (population dynamics of each trophic group) (top).

simple crop model, derived from the SIMBA cropping system model (Tixier et al., 2008), to simulate the growth of banana plants over successive cropping cycles; growth is based on the interception of light, which drives photosynthesis and therefore growth, and daily temperature, which governs plant phenology. Banana and a cover crop species (*Brachiaria decumbens*) partition light resources and compete for nitrogen in the SIMBA-N module (Dorel et al., 2008). Growth of the cover crop is described by the SIMBA-CC module (Tixier et al., 2011). We link this soil–crop plant model to a Lotka–Volterra food web model, analogous to the one developed by Takimoto et al. (2007). This food web model includes the major pest of banana plants (banana weevils, H1), a herbivore that feeds on the cover crop (crickets, H2), a predator that feeds on both herbivores according to their relative abundance (ants, P1) and an intra-guild predator that can feed on H2 and P1 according to their relative abundance (spiders, P2).

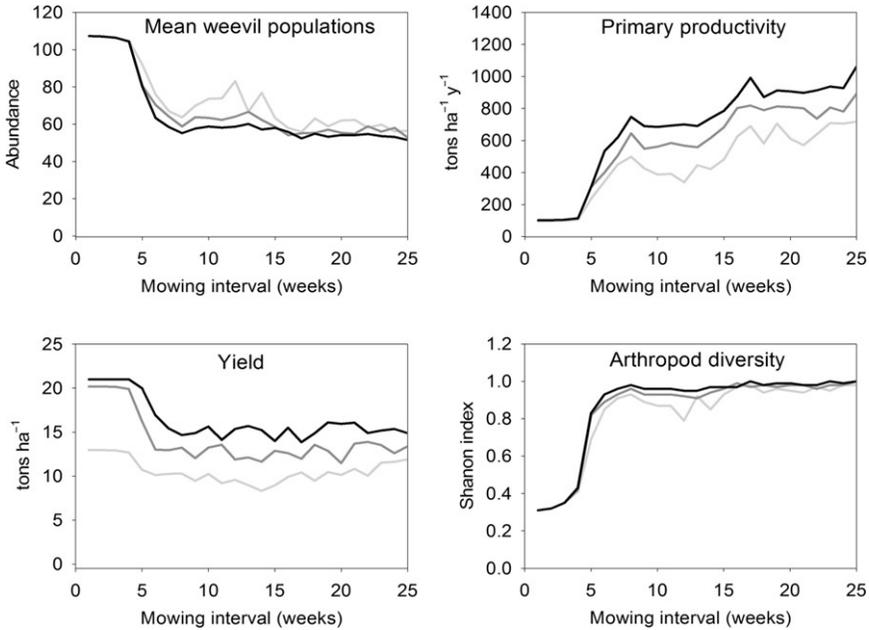
This food web appears to reproduce the structure observed in banana agroecosystems (Duyck et al., 2011; Mollet et al., 2012). The increase in herbivore populations follows logistic growth, as was also seen for the COSMOS model (Vinatier et al., 2009) that we have adapted. We assumed that the carrying capacity of H2 varies with cover crop biomass (simulated by the SIMBA model). Predation rates of P1 and P2 have been parameterized using measurements made in commercial banana fields (Abera-Kalibata et al., 2008). Banana growth is affected by banana weevil herbivory, in the SIMBA model, following a damage function (Ayuke et al., 2011; Vinatier et al., 2009).

#### 2.1.4.3 Main outputs

We used this framework to simulate agronomic performance (yield and pest abundance) and ecological performance (diversity of the arthropod community and total primary production). The model allowed us to test how an additional resource and its management alter the soil, the plants, the arthropod community and their interactions. When mowing was more frequent, banana yield increased because of reduced competition for nitrogen, while biological control of the insect pest by the generalist predators decreased (Fig. 7.4). The model can, therefore, be used as a tool to explore the trade-offs between these two ecosystem services. The tool allowed us to disentangle the relationship between cropping practices (frequency of mowing) and ecological metrics, such as arthropod diversity (the Shannon index) in the food web. The model output indicated that mowing intervals of less than 7 weeks would dramatically decrease diversity. These simulations also showed that increasing fertilization would increase yield and biological control. The latter result is consistent with general ecological theories predicting that the strength of trophic cascades increases with ecosystem productivity (Polis et al., 2000).

## 2.2. Spatial network models for describing spatial and spatio-temporal agroecosystem dynamics

Spatial interactions take place across many spatial scales, from intra-field scale to the scale of a landscape. These spatial interactions weave together various sub-networks that determine whole-ecosystem functioning (see Massol and Petit, 2013). The spatial management of biodiversity and of cultural practices are levers that could be used to optimize agriculture sustainability and the provision of ecosystem services using spatial network models. Typically, spatial network models consider nodes (see Glossary in Bohan et al., 2013),



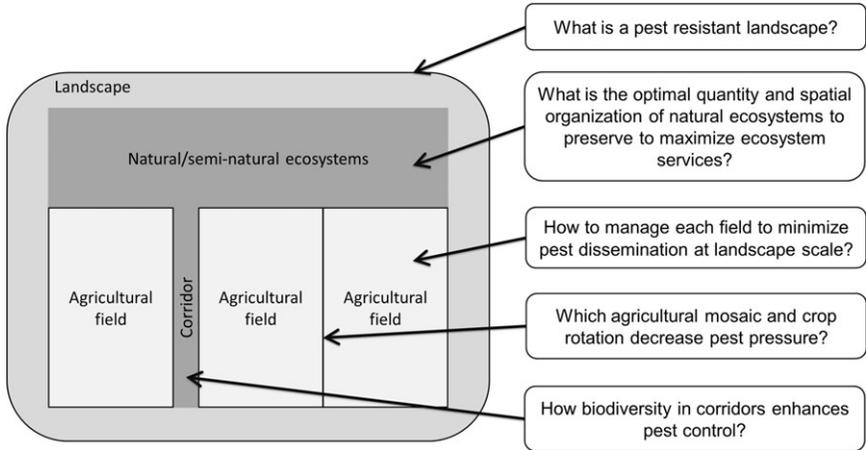
**Figure 7.4** Simulated agronomic performance (yield and weevil populations) and ecological performance (primary productivity and arthropod diversity) of a banana agroecosystem as affected by cover crop management (interval between consecutive mowing) and fertilization level (— 0.6, — 1.0, and — 1.4 times the recommended dose of nitrogen) (case study 1).

which may be plants or patches or locales or fields that interact by exchanging organisms, pathogens, etc. The aim of spatial network modelling is then to understand the spatial pattern of occupation or the spatial dynamics of those organisms, over the spatial network.

For the case of enhancing pest control, spatial network models might help disentangle the role of the spatial organization of natural, semi-natural and agricultural ecosystems in driving landscape–ecological mechanisms. These mechanisms can comprise regulation, through the management of pest dispersion, and the enhancement of biological control (Fig. 7.5).

### 2.2.1 Existing models

We introduce several families of spatial network models here, all of which are built on the hypothesis that the current state of one particular node in the interaction network depends only on the states of neighbouring nodes. Deterministic metacommunity models were probably the first models developed by ecologists (May, 1973) to represent communities organized



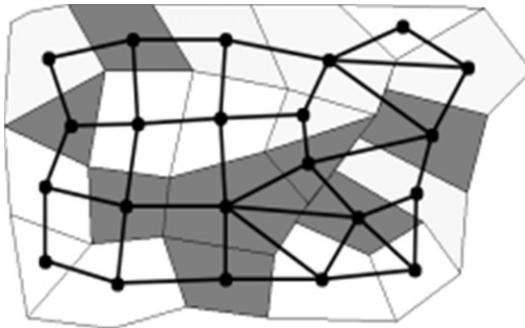
**Figure 7.5** Major questions associated with the spatial management of pests at different scales.

spatially on patches of habitats (the nodes of the network). Each community is spatially distinct (a patch) but dispersal to other communities is possible. These models are primarily spatially implicit and composed of two explicit dynamical scales: a local one at the patch scale (usually non-spatial and not individual-based), and a global one that corresponds to exchanges between patches (Leibold et al., 2004). Recently, this type of metacommunity model has been combined with spatially explicit models so that the exact location of each habitat patch can be described. Two factors, in particular, have contributed to the increased interest in, and development of, spatially explicit models: (i) a better understanding and appreciation of the spatial dynamics of land cover (provided by geographical information systems and satellite images) and (ii) the increased calculation power of computers.

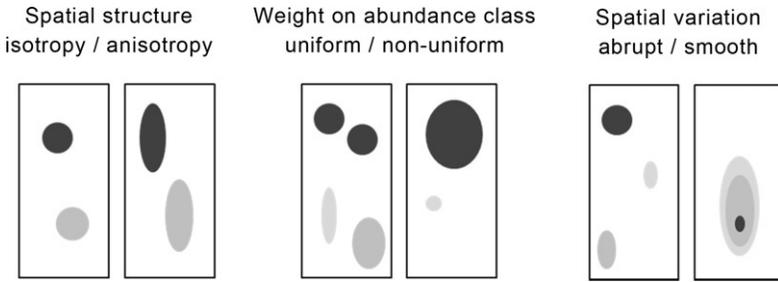
The landscape scale is often more suitable than the field scale for analysing the spatial distribution of pests, as dispersal typically occurs across supra-field scales (Chave, 2013). Landscapes, which are composed of a network of interconnected management units, exhibit a high level of landscape element heterogeneity (fields and inter-field habitats) (Loeuille et al., 2013). Space discretization in landscape models is generally based on regular grids that discriminate landscape elements. Irregular grids have been considered (Colbach et al., 2005b), but solely to model single-species dynamics. The cells of the grids become the spatial entity within which species interact. Spatial redistribution of species from one cell to another is modelled using dispersal kernels, which describe both long-distance dispersal (Nathan, 2006)

and local dispersal (Wiegand et al., 1999). Interactions within cells can be formalized by Lotka–Volterra models, depending on the interaction type.

Stochastic models of spatial interactions in a network include MRFs that enable a static representation of spatial correlations between variables (Li, 2009). An MRF describes the joint probability distribution of a set of random variables at each spatial location. This may be a crop field in an agricultural region or a quadrat in a particular field, for instance depending on the landscape scale of the study. The state of a location can be, for example, a measure of weed abundance or a disease severity index. Graphically, a node is assigned to each location of the landscape of interest, and edges link any two neighbouring nodes (Fig. 7.6). As was the case for the BN model, the MRF model allows researchers to specify a joint probability distribution over global maps of spatial phenomena, using only local interaction functions. These functions specify which local patterns are more likely than others. The full description requires only site-specific abundance measures and neighbourhood correlation measures. Even though the number of parameters in an MRF is reduced, the framework can be used to model complex, large-scale spatial processes (Fig. 7.7). Anisotropy of the process can be modelled by using different interaction functions on different edges of the network. Similarly, smooth or abrupt spatial variations of the process can be modelled through selection of particular interaction functions. Density repartitions of the process, associated with differences from the average weed abundance or average disease severity over the entire study area, can be modelled by using particular local, site-specific functions.



**Figure 7.6** Graph associated with a Markov random field model of a spatial network of locations: there is one node per location and an edge between two locations that share a common border. In a disease management context, the set of locations can be, for instance, a set of crop fields in a landscape. Grey areas are infected fields, and white areas are healthy fields.



**Figure 7.7** Example of spatial patterns that can be modelled and compared using an MRF model. Grey levels represent the abundances of the mapped process (weed, pathogen, etc.). Left: The process maybe isotropic (disc pattern) or anisotropic (disc pattern stretched in preferential directions). Centre: The different density classes may be evenly represented or some density classes may be over-represented in space. Right: Density variation in space can be abrupt, or smooth.

When the spatial process has important temporal dynamics, DBNs can be used to extend MRF to the modelling of spatio-temporal dynamics (Ghahramani, 1998). By combining spatial and temporal components, DBNs provide a rich modelling framework. As with MRFs, random variables in DBNs are attached to all locations but the state of each variable in a DBN is followed at successive (discrete) time steps.

### 2.2.2 Application to the improvement of ecosystem services

Metacommunity models can be used to examine how different spatial arrangements of land use modifies interactions between multiple species assemblages (Vinatier et al., 2012b). Vinatier et al., 2012a, used a grid-based model as a virtual laboratory to explore the effects of management practices, such as crop rotation, on a tri-trophic system including a host plant, and insect herbivore and a parasitoid. Such model represents one of the first concrete tools to orient the crop management at a landscape scale to maximize biological control.

When field observations are limited, MRFs help to reconstruct the most likely maps of pest abundance. It was successfully applied to weeds population at the field scale to provide marginal probability distributions of weed abundance: to accomplish this, an MRF was constructed, using neighbourhood correlation coefficients obtained from experts or learned from limited field observation. However, map reconstruction from limited observations was only part of the problem. The quality of the reconstructed map depended on the locations of the observations. Peyrard et al. (2013) and Bonneau (2012) have developed decision-theoretic models, combining

MRF and MDPs (Puterman, 1994, see Section 2.3), and simple heuristics for choosing sample locations and number to optimize the quality of the reconstructed map. The corresponding sampling strategies are adaptive: as soon as new observations become available, they are used to choose the next sampling location. The authors showed that these adaptive strategies produced better quality maps than static sampling strategies in which the sampled locations were set at the beginning of the survey. In particular, the adaptive strategies outperform standard sampling strategies (regular sampling, star-shaped sampling, random sampling, etc.). Such MRF-based approaches will be very useful for spatial-process map reconstruction and sampling-design. They should also enable researchers and managers to compare the structure of maps resulting from different decisions, providing a powerful tool for analysing the effect of candidate management decisions on ecosystem services.

### **2.2.3 Trends and future challenges**

All of these spatial models share common methodological issues: (i) choice of a modelling structure (What are the network elements? Which elements are correlated?), (ii) choice of the model parameters (How many parameters are used to represent spatial correlations?), and (iii) parameter estimation based on limited observations (Li, 2009). If the model is stochastic, as with MRFs, the imperfect and noisy nature of observations needs to be taken into account. Observations may only indirectly represent the process to be mapped (e.g. weeds density may be only approximately measured, or weed species may be confused). Hidden MRFs, which generalize MRFs can be used in this context, as in Peyrard et al. (2013). Finally, the construction of sampling cost models is a specific task in designing sampling strategies. Cost may be difficult to define, and data are not always available. The cost can be monetary or have a different nature. In Bonneau (2012), for example, the cost model represented the time required to sample a quadrat and to move from one to the next.

### **2.2.4 Case study 2—designing networks of crop fields for the collective management of disease**

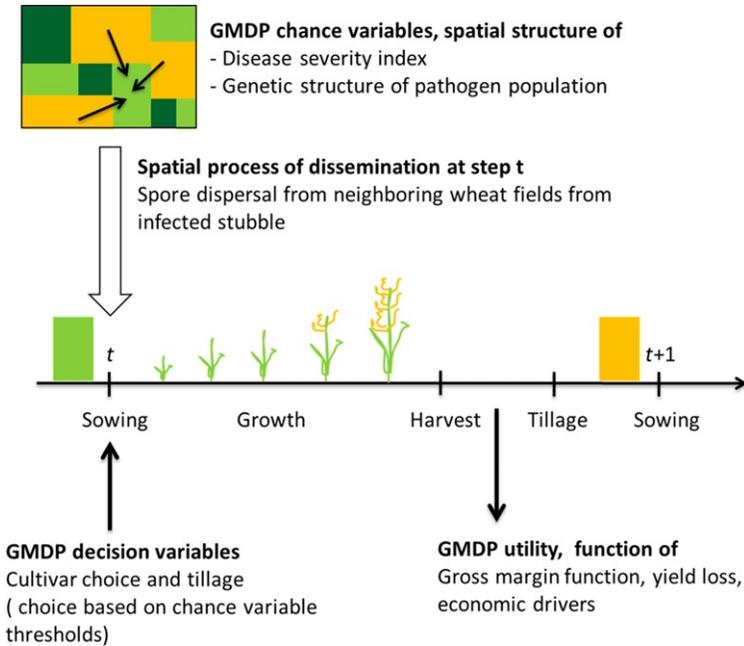
#### **2.2.4.1 The system and targeted services**

Long-term management of phoma stem canker on oilseed rape, caused by the species complex *Leptosphaeria maculans*/*L. biglobosa*, was chosen as a case study because of the economic importance of the disease and the substantial scientific knowledge available on the pathosystem (Aubertot et al., 2006). Epidemics of phoma stem canker are initiated by infected stubbles that

remain on the soil surface after harvest of oilseed rape. These are the source of ascospores that are wind-dispersed after a period of maturation. Ploughing can therefore be effective for reducing inoculum production at the field scale (Schneider et al., 2006). These wind-dispersed spores infect seedlings and young plants. Once the fungus has infected a leaf, it systemically colonizes the plant and produces a canker located at the basal stem and the crown. Because the efficacy of chemical control is uncertain, the control of phoma stem canker on oilseed rape relies on the use of cultivars with specific and/or quantitative resistances and cultural control. However, resistance can break-down within a few years (Daverdin et al., 2012), and collective resistance management at the territory level is needed for effective disease control (Aubertot et al., 2006). Whenever possible, tillage should be adapted to reduce the quantity of primary inoculum produced on infected stubble. Because of ascospore dispersal, designing genetic and cultural control at the field level is not optimal. Collective strategies at a regional level could lead to a more efficient and more sustainable management of the disease.

#### 2.2.4.2 The modelling approach

We used a GMDP framework to represent interactions between patches with local dynamics, across a network. A repeated 3-year rotation (oilseed rape–wheat–barley) was investigated. The GMDP model represented the relationships between neighbouring fields, in terms of spore dispersal from wheat fields with infected stubble to oilseed rape fields. The local predicted variables assigned to each field were the crop, disease severity, and the proportion of virulent pathogens (i.e. pathogens that have lost their virulence to host–plant resistance). The local cultural practices variables assigned to each field were the cultivar choice (resistant vs. susceptible) and the decision to plough or not to plough as a function of a disease severity threshold. Actions have no effect on dispersion but can limit infection as well as inoculum production for the following year. Local utility functions combine local yields, and control action costs. Local transition probabilities represent disease severity and pathogen population evolution between two time steps, taking into account pathogen dispersal from the infected stubble in neighbouring fields as affected by cropping practices (i.e. cultivar choice and tillage). Figure 7.8 provides a schematic representation of the drivers of the crop and disease changes within one time step (1 year). As an optimization model, this GMDP is linked to a disease dynamic model that is far less detailed than the epidemiological or crop models usually used by agronomists and pathologists. The transition probability was therefore divided into three successive

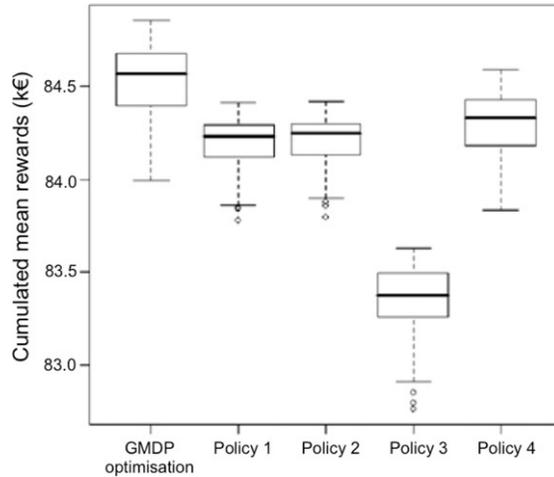


**Figure 7.8** Schematic representation of spore dispersal and crop management of winter oil seed rape fields under a 3-year rotation, as modelled in a simple GMDP (case study 2). Orange, light green, and dark green fields are wheat, winter oil seed rape, and barley fields, respectively. At the beginning of cultural season  $t$ , spores of phoma stem canker are wind-dispersed from stubble remaining in wheat fields, and the wind-dispersed spores infect oil seed rape fields. The choice for control decisions (cultivar choice and tillage) is made at time  $t$ , and their effects occur between  $t$  and  $t + 1$ . Rewards are estimated after harvest and are used to build the utility function. Solving the GMDP model involves computing the strategy that optimizes the expected cumulated sum of utilities.

modules: inoculum production, dispersal, and infection and stubble burial. The parameters for each module have been derived from simulations of the much more detailed SIPPOM-WOSR model (Lo-Pelzer et al., 2010). They correspond to a discretization of the original variables for infection and pathogen population in each field, given by SIPPOM-WOSR. The proportion of virulent pathogens was discretized into five classes, while only three disease severity classes were considered for computational reasons.

#### 2.2.4.3 Main outputs

A simulation analysis was conducted to compare the strategy provided by the GMDP model, representing disease epidemics and the adaptation of the



**Figure 7.9** Box and whiskers plot of the value (cumulative mean rewards for farmers) for five strategies of phoma stem canker control of phoma stem canker in winter oilseed rape–wheat–barley rotations in a given agricultural region (case study 2). The results were obtained from two spatial distributions of cropping systems  $\times$  50 initial states  $\times$  100 runs over 30 years. The largest value was obtained by solving a GMDP model that simulated epidemics and the adaptation of the pathogen population to specific host–plant resistances. The other four strategies were defined using expert knowledge.

pathogen population to specific levels of resistance at the landscape level, and four other strategies (local and global) that were defined by a set of decision rules designed using expert knowledge (Fig. 7.9). In this case, the predicted cumulated reward (gross margins minus control costs, cumulated over years, at the landscape scale) based on the strategy provided by the GMDP model was significantly higher than those of strategies designed from expert knowledge. With increasingly complex spatial decision problems, the GMDP model solution leads to more efficient solutions than those based on expert knowledge (Forsell et al., 2011).

## 2.3. Decision interaction models for the design of management strategies

### 2.3.1 Existing models

Network models are used not only for modelling ecological processes but also for modelling problems of decision under uncertainty and for optimizing those decisions. When network models are used for guiding decisions, the goal is to optimize the value of a strategy according to utility functions. Utility functions incorporate both rewards and costs resulting from particular

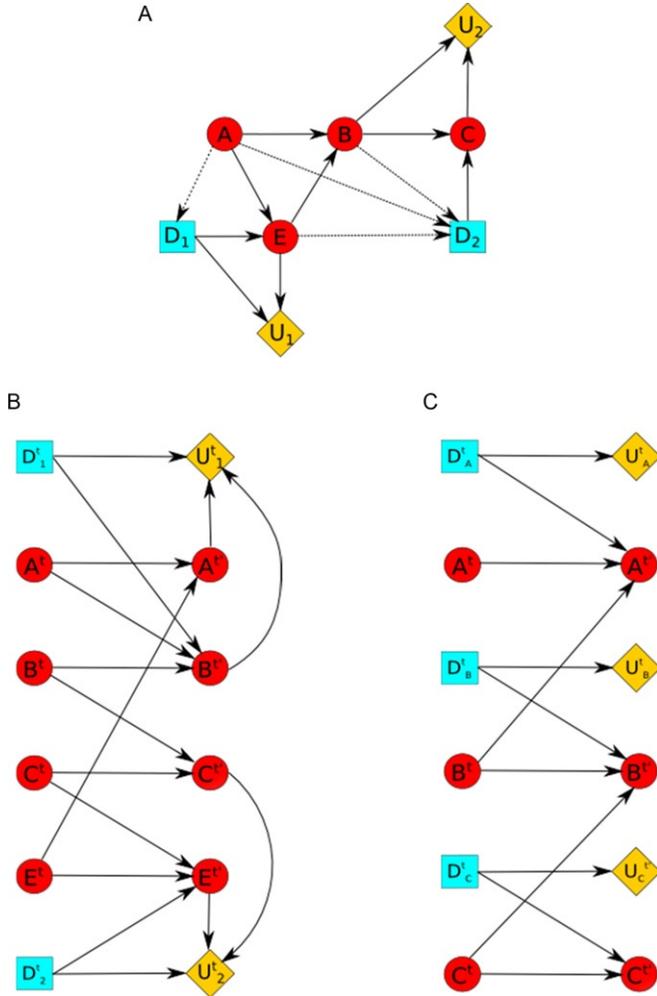
decisions or strategies. The value of a strategy represents the expected cumulated sum of rewards (less costs) that may be incurred when following the strategy from some fixed starting state. Such decision-oriented models may be based on: (i) the extension of the BN framework to decision and (ii) the extension of MDPs to multiple correlated variables.

The influence diagram (ID) framework (Howard and Matheson, 1984), shown in Fig. 7.10a, is an extension of BN that allows researchers to model stochastic interactions between state variables (as in BNs) and between state variables and decision variables. IDs also include utility nodes, representing the functional dependency of local utilities on state and decision variables. The ID framework allows the modelling of decision problems, and the output consists of automatically designed strategies in the form of decision rules: the designed strategies are those with optimal values.

The MDP framework has long been used for optimizing sequential decisions under uncertainty (Puterman, 1994). In an MDP, time is discrete, and there is one utility function per time step. Furthermore, MDPs usually involve a single state variable and a single decision variable (evolving over time). The MDP framework was originally used to model sequential decision problems, but not decision problems in networks. Recently, the framework has been combined with several network-based representations of probabilistic transition functions and utility functions to model structured decision problems. Unlike MDPs, structured decision problems may involve several state and decision variables that jointly evolve over time. They are termed factored MDPs (FMDPs) when the problem involves several state variables and a single decision variable (Boutilier et al., 1999) or factored action FMDPs (FA-FMDPs) when the problem involves multiple decision variables (Kim and Dean, 2002; Fig. 7.10b). Graph-based Markov Decision Processes or GMDPs (Sabbadin et al., 2012; Fig. 7.10c) are a particular kind of FA-FMDP that are particularly well suited to spatial management problems because they involve pairs of local state/decision variables for each decision unit, as well as additive utility functions (one per decision unit).

### **2.3.2 Application to the improvement of ecosystem services**

The MDP framework and its network-based extensions have the advantage of including the cost of a strategy and the associated budget constraints, which enables the consideration of the constraints on the behaviour of farmers. For example, MDP models have been used to represent and solve numerous decision problems in agriculture and natural resources management (Kennedy, 1986). The GMDP framework has also been used to model



**Figure 7.10** Network-based stochastic decision models. (a) Influence diagram model. (b) Factored action space factored Markov decision process model. (c) Graph-based Markov decision process model. For all models, state variables are represented by red circular nodes and labelled from A to E, utilities are represented by yellow diamond-shaped nodes and labelled U, and decision variables are represented by blue square nodes and labelled D. Arrows indicate interactions. In the influence diagram model, time is not explicit, as opposed to the two other models, in which the graphical representation corresponds to a single transition between time  $t$  and  $t'$ .

and solve problems of forest management under the risk of storm (Forsell et al., 2011) and of disease management within a network of fields (Peyrard et al., 2007). We briefly describe the first application here. The second application will be described in more detail in Section 2.2.4.

Forsell et al. (2011) modelled the problem of including the risk of wind damage in long-term forestry management within the GMDP framework, in order to design efficient silvicultural management policies. The model took stochastic wind events (storms) into account and was applied to forest estates containing a large number of stands. The GMDP framework allowed modelling the impact of ‘edge-effects’ between stands (a stand with old-growth trees neighbouring a newly replanted stand is more likely to be damaged by storms).

The performance of the model was demonstrated for a forest estate in Björnstorp, southern Sweden, including more than 600 interconnected forest stands (Fig. 7.11). The treatment of the stands, using a management policy optimized by the GMDP model was compared to a management policy computed by ignoring the edge-effects, which allowed for considerable simplification of the policy computation, as it treated all stands as being independent.



**Figure 7.11** The Björnstorp estate. The grey areas represent the forest stands and the white areas represent the non-forest areas.

The study revealed an increase in the expected net present value of the whole forest of less than 2%, under different wind-risk assumptions and when applying the GMDP policy. Most of the stands were managed in the same manner as when the stands are considered independent. However, for the stands that were identified for different management regimes, the expected net present value increased by 3–8%, which would constitute a significant improvement for forestry managers.

### ***2.3.3 Trends and future challenges***

The main technical issue of applying FA-FMDPs or GMDPs to the management of agricultural services lies in the modelling of the spatio-temporal dynamics. Given the computational constraints and limited data available, only simple models can be explored at present. These are not as detailed as some mechanistic models used for analysing the dynamics of diseases or animal pests or weeds. However, a decision model does not require high detail because management units are rarely defined at the plant or animal level but more usually at the field or farm level. Thus, it is reasonable to describe the model dynamics and the decision model at a shared level of detail (the field or farm). Second, there is the issue of an agreed definition of the value of a strategy, and therefore the definition of utility functions. For some problems, ecologists, agronomists and stakeholders do not agree on the criteria to be used to determine whether a system is sustainable or whether ecosystem services have been provided. These criteria often vary among researchers, farmers, managers, and policy makers. From a modelling perspective, it remains extremely challenging to account for different spatio-temporal scales in models designed to optimize ecosystem services.

### ***2.3.4 Case study 3—*which agricultural landscape network provides sustainable management of weeds?****

#### ***2.3.4.1 The system and targeted services***

Weed species have different functions and potentially, therefore, provide different ecosystem services (Marshall et al., 2003). Current recommendations for weed management are directed towards conserving farmland biodiversity and reducing herbicide use. These will require the design of alternative weed management strategies that enhance the sustainability of agricultural landscapes through greater reliance on ecological goods and services. The main challenge in designing alternative management of weeds is the resolution of the trade-off between their dual function, that is, the trade-off between their negative effects on crop production and their positive

effects on biodiversity. Although the field is the appropriate scale for weed management, dispersal processes act at supra-field scales (Chave, 2013). Here, we assume that this trade-off can be more efficiently resolved at the landscape scale. Given this, one way to support both crop production and the maintenance of weed species and their ecological functions is, therefore, to propose weed management strategies that build sustainable and multifunctional landscapes (O'Farrell and Anderson, 2010). Researchers have proposed two opposing management principles for this landscape-scale management (Green et al., 2005; O'Farrell and Anderson, 2010). According to the land-sparing principle, high yields should be maintained on most farms but some land should be managed specifically to preserve biodiversity. According to the land-sharing principle, more land should be cultivated but at a lower yield level so as to preserve biodiversity on both cultivated and uncultivated lands. Neither of these strategies has been shown to outperform the other (Loeuille et al., 2013) and their efficiency is context-dependent (Fischer et al., 2008; Hodgson et al., 2010). Furthermore, the principles are categorical, and we could imagine dynamic strategies.

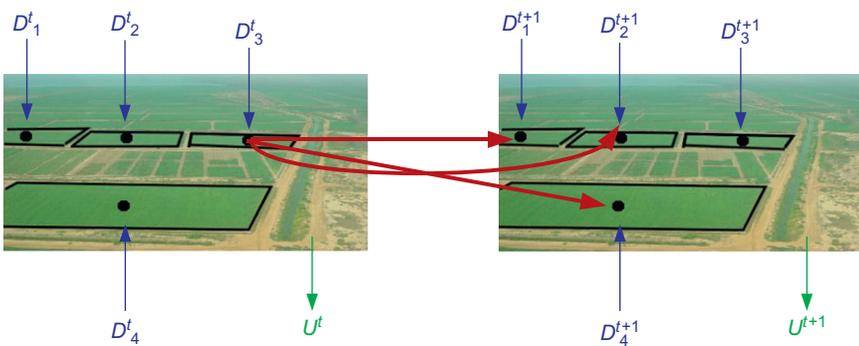
Generally, the efficiency of a management solution is highly dependent on the stakeholder perspective (i.e. on the perspective of farmers, policy makers, ecologists, etc.), and different definitions of a sustainable solution can be envisaged. Therefore, to be able to design stakeholder-dependent strategies and discuss their potential convergence, intermediate and possibly optimal strategies between land-sparing and land-sharing should be explored. Furthermore, to avoid any *a priori* bias in selecting the optimal landscape structure, we should consider exploratory rather than exploitative strategies, targeting approaches that do not rely only on existing knowledge (Martin et al., 2013). This means that the optimal landscape structure would be selected without any socio-economic constraints, that is, the farm type, local agricultural market, or pedoclimatic constraints even though they modulate the potential crop yield.

#### 2.3.4.2 Factored MDPs for designing sustainable weed management strategies in a landscape network

Designing explorative weed management strategies can be treated as a problem of spatial, sequential decision-making under uncertainty, in a factored version of the MDP framework (Section 2.3). The problem is sequential in that management decisions are taken at discrete time steps within a year. The problem is also spatial because of weed dispersal and local agricultural practice influences weed community structure in the

neighbourhood. In addition, uncertainty is naturally present in weed dynamics and in the effects of management practices on weed populations. Were we able to define strategy quality, this factored version of the MDP model-based approach would enable the design of a spatially structured strategy by optimization.

The landscape can be interpreted as a network of spatial locations where nodes are cultivated fields, pastures, or edges, and links between nodes indicate possible weed dispersal. Quite naturally, in each management unit, the predicted variables could represent weed diversity, and the action variables could correspond to the cropping systems used (Fig. 7.12). Because of this network structure, and of the locality of management, the AF-FMDP framework extension to the MDP framework has most utility (see Section 2.3). This choice raises some non-trivial modelling questions, however, such as the definition of a strategy value (linked to the notion of utility in an MDP), the modelling of weed spatio-temporal dynamics and the modelling of the relationship between weed community composition over the network and global functionalities (potential services). This also raises the question of finding efficient methods for solving large state and action space FA-FMDP.



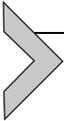
**Figure 7.12** Schematic representation of the problem of designing weed management strategies at the landscape network scale. Each node of the network is a landscape element (cultivated field, pasture, edge). Correlations between nodes are temporal (red arrows), they depend on weeds dispersion and local actions (cropping systems,  $D$  variables) applied at each node. At each time step, a global utility  $U^t$  is defined which depends on the current configuration of functionalities at the landscape scale and on the management actions applied.

### 2.3.4.3 Modelling weed community spatio-temporal dynamics in a landscape network

For a FMDP, it has been shown that the optimal model of process dynamics for a fixed strategy is a DBN model (Boutilier et al., 1999) (Section 2.2). To our knowledge, DBN models have not been used for weeds, where the focus is generally put on the simulation and analysis of weeds dynamics under different agricultural practices and environmental conditions. Several simulation models have been developed for weeds (Holst et al., 2007), where agricultural practices are included either explicitly (Colbach et al., 2005a) or implicitly, through crop-specific values of weed demographic parameters (Gerowitt and Bodendorfer, 2001; Zwerger and Hurlle, 1989). These models are generally built to explore the response of a particular weed, such as *Alopecurus myosuroides*, to management factors (Colbach et al., 2005a). However, a given arable field shelters an average of 20–30 weed species, among hundreds of potential species compositions (Gaba et al., 2010). As a consequence, developing a detailed mechanistic model that explores the response of the entire weed community is impractical, given current knowledge, although some studies have attempted to do so (Munier-Jolain et al., 2013). Nevertheless, it should be kept in mind that a model of decision is not a model for prediction or understanding; the goal of the predictive models may not be the development of good management solutions. Moreover, predictive models usually address the field scale and rarely consider the landscape. Rather, weed management actions are usually chosen by decision makers through decision policies, as functions of rough indicators of the ecosystem's state. The difficulty of optimizing these decision policies (in the FMDP framework and many other decision frameworks) increases exponentially as a function of the number of state variables/indicators (Boutilier et al., 1999). This explains why management optimization needs to be more reasonably performed in 'simplified' models.

Conceptually, one way to combine a network structure and the spatio-temporal dynamics of weed diversity would be to develop a DBN model in which the state of each field at time  $t+1$  (representing weed diversity) depends on the states (i.e. weed diversity) and the actions (i.e. the agricultural practices) of surrounding fields at time  $t$ . Fields can be interpreted as patches, connected by weed dispersal. The patches are the nodes of a network in which local weed dynamics and management arise, and the links between nodes would be formalized by weed spatial dispersal. In that sense, such a DBN model can be seen as a metacommunity model (Leibold et al., 2004). Being at the landscape scale, this DBN modelling approach would

allow researchers to evaluate patterns of weed species diversity across space and to evaluate underlying mechanisms. We could, therefore, ask ‘how does dispersal of weeds between communities alter local dynamics and then influence community structure locally and regionally?’ To focus on key functional relationships and service delivery (e.g. pollination), we could aggregate species into groupings of responses to environmental changes (*sensu lato*) and their effects on ecosystem functioning, using a trait-based approach (Booth and Swanton, 2002; Lavorel and Garnier, 2002). Species with similar response-trait attributes would likely share similar patches, while species with similar effect-trait attributes would mainly express similar efficiency of resource use, such as competition with the crop or similar resource quality for predators or pollinators. Thus, the combination of a metacommunity model with a trait-based approach, within a DBN framework, would facilitate evaluation of the effects of management at the landscape scale on weed diversity and the rate of services that this diversity delivers. Such knowledge will be crucial for developing sustainable cropping systems that maintain crop production while preserving or augmenting ecosystem services.

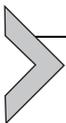


### **3. TOWARD A COMPREHENSIVE APPROACH THAT LINKS NETWORKS AND SERVICES**

The appropriate application of network ecology would allow agro-ecological issues that are often addressed separately to be reconciled. Food web ecology, for example, allows the reconciliation of biodiversity structure and function (O’Gorman et al., 2012; Thompson et al., 2012) and facilitates the investigation of ecosystem services and other emergent ecosystem properties. Because ecosystem services in agroecosystems result from complex interactions between wildlife and stakeholders across different scales (from intra-field to landscape), modelling tools to test management strategies must account for this diversity. However, the ecosystem services of production, conservation, and regulation must be addressed jointly (Nelson et al., 2009). This is especially important because different ecological networks (food webs, parasitoid webs, seed dispersal networks, and pollination networks) do not exhibit similar robustness and ecological restoration of one type of network will not inevitably benefit others (Pocock et al., 2012). In this chapter, we have presented an initial analysis of the trade-off between production and regulation services. Future agricultural sustainability will depend, therefore, on additional integration of all scales of management, from intra-field

cultural practices to landscape policies. The challenge is not only to scale up models in space (Stuart and Gillon, 2013), but also to account for trade-offs that may result from interactions occurring simultaneously at different scales and under different management regimes, driven by farmers at local scales and policy makers at broader scales.

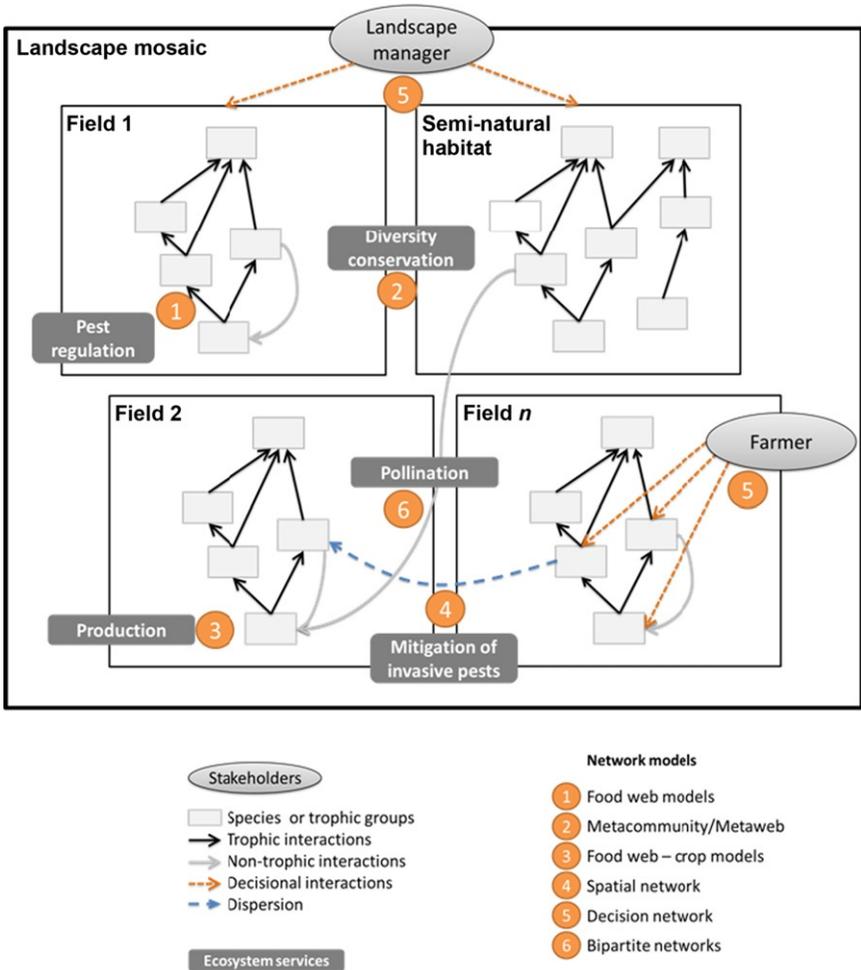
The case of pest regulation demonstrates the simultaneous influences of farming practices at the field and landscape scales (Chaplin-Kramer et al., 2011). The merging or linking of models to allow multi-scale simulations represents a great challenge for modellers (Pascual, 2005), but this could be accomplished with network models because they are sufficiently flexible to account for flows of matter or information. Different types of network models are available for testing scenarios of how management affects ecosystem services. Figure 7.13 illustrates how these different types operate at different scales of management (objectives will not be to link all these models but rather use the most appropriated type at each scale or issue) and it also includes network models not discussed here, such as the bipartite models successfully applied to plant–pollinator interactions to represent pollination service (Thebault and Fontaine, 2010). Recognizing the links between food webs and landscape ecology, as proposed by Polis et al. (1997) and (re) emphasized increasingly in the literature (Hagen et al., 2012) is a first step in this integration. We emphasize that ecosystems that may seem or be assumed to be distinct are often closely linked to one another and recently the theory required for the linking of multi-scale ecology has been addressed by meta-ecosystem ecology and by metacommunity/metaweb concepts (Massol et al., 2011; Pillai et al., 2011). Linking such purely ecological models with decision networks is a complex, but stimulating challenge for modellers. The models that we have also presented are logical candidates for dealing with this challenge.



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## 4. CONCLUSIONS AND FUTURE DIRECTIONS

Agroecosystems encompass ecological and decision networks that are connected to one another and that perform different functions leading to the provision of a wide range of ecosystem services. They are also connected to one another at the landscape scale, which renders their management difficult. These complex interactions, however, can be formalized within the general concepts of interaction networks, and these can be used to explicitly elaborate the interactions within and between ecology and management.



**Figure 7.13** Illustration of multi-scale uses of network models to assess ecosystem services and to design and evaluate management strategies.

We have argued that network models can help address the high level of complexity that is needed to design strategies that promote pest regulation in agroecosystems. Food web models are just one type of network model, but they are particularly efficient at capturing the complex interactions between species or trophic groups and can be used to predict how agroecosystem productivity and sustainability will respond to perturbations. The linking of food web models with other types of models, such as crop models, decision models, and spatial models, represents the next step forward. Using an

example of the linkage between a food web and crop model, we have shown that the former is a valuable tool for answering questions associated with the ecological intensification of agricultural systems and the trade-offs between ecosystem services. In addition to linking ecological and decision processes, network models bridge the gap between agronomists, ecologists, and mathematicians. While some computational limits persist, decision models such as FA-FMDP and GMDP models have great potential for evaluating complex strategies of pest and disease management at the landscape scale. Because they can be used with both quantitative and qualitative data, these models are particularly promising to be used in interaction with stakeholders to design optimized management strategies from field to landscape scale.

The challenge, now, is for agroecologists to produce models that are quantified in terms of interactions and emerging ecosystem services, and for theoreticians to develop new network models that will enable comprehensive approaches to the management of ecosystem services provided by agroecosystems. To be relevant, network models designed for management purposes should include those elements that determine ecological structures and trends and interact with management decisions. For this purpose, network models need to be tested against observational data sets and should be supported by appropriate modelling techniques. Furthermore, the effects of interactions between species and management decisions on each component of the simulated network remain insufficiently studied in the field and inadequately formalized within a strong theoretical background. The link between biotic and abiotic factors in network models requires further study, such as between water and plant development (Wiens, 2002) and between wind and flying insects or pollen (Kuparinen et al., 2007). Currently, it is largely ignored. It is also necessary to consider a unified formalism for space, time and entities to model these interactions in a network approach. Once network models are constructed and validated using observation, modellers optimizing the set of competing ecosystem services will face three challenges, related to the mismatches between temporal and spatial scales governing each landscape service.

In spite of these challenges, we believe that network ecology now has a solid foundation and could serve as the central paradigm for predictive agriculture management.

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