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Food web-based simulation for agroecology

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Abstract Ecosystems are increasingly manipulated for agricultural and conservation goals. Ecosystem functions need to be sustained socially and ecologically. New frameworks must be built to simulate agrosystems based on ecological processes instead of external chemicals. Food web structures of agrosystems highly influence their agronomical performance and stability. Although it has been observed that living communities are ruling the performance of agroecosystems, these living communities are generally ignored by agronomists who focused mainly on abiotic factors. Indeed, agronomists usually focus on the soil–plant–atmosphere continuum. Now, ecological modellers can link food web models with soil–plant models to create innovative frameworks. Here, we advocate that food webs must be included in simulations of production and in studies of emerging properties. We emphasize the role of trophic chains in the regulation of pests. Emerging properties

include aboveground and belowground interactions, pest control, and positive feedbacks on soil properties. We propose a conceptual structure for this framework and discuss how the structure of linked food web/cropping system models can account for the specific properties of agroecosystems. The proposed structure includes a process-based approach to link food webs with crop models. Such comprehensive models address the issue of trade-offs between ecosystem services, including regulation of crop pests by the ecosystem community, nutrient cycling, and crop production.

Keywords Agroecosystems · Biological regulation · Trophic interactions · Agriculture sustainability · Ecosystem services

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1 Introduction

Declining biodiversity can alter ecosystem functioning and performance (Hooper et al. 2005) and thereby greatly affect human well-being (Díaz et al. 2006). Many ecosystems are being increasingly manipulated for agricultural purposes (Tilman et al. 2002), while their functions (e.g. primary production, biodiversity conservation, or water storage) and properties (e.g. stability resulting from resistance to perturbation or recovery after perturbation) (Cardinale et al. 2006) need to be maintained for environmental sustainability. In the age of computational ecological modelling, scientists and decision makers use predictive tools to forecast possible changes in

such ecosystems in order to maintain their services to society (Wright et al. 2006). In that view, scientists and stakeholders will need new frameworks to simulate not only natural but also manipulated agricultural ecosystems.

To meet the challenges that agriculture is facing today, e.g. providing more food and energy while adapting to global climate change and mitigating environmental impacts, scientists are developing new technologies and approaches for growing crops and increasing yields while maintaining ecosystem services. One of the most promising approaches is to design new agroecosystems based on management of ecological processes, e.g. top-down and bottom-up regulation of pests, nutrient capture by intercropping, soil structuration by ecological engineers, rather than on application of fertilizers and pesticides (Tilman et al. 2002). Especially in developing countries, these new agricultural systems attempt to reconcile biodiversity conservation and food security while minimizing social and environmental impacts (Brussaard et al. 2010).

Recent research has shown that food web structure greatly alters ecosystem performance; for instance, the complexity and the stability of food webs increase along a productivity gradient (Neutel et al. 2007). Lin (2011) reviewed how crop diversification alters resilience in agriculture and demonstrated that more diversified basal resources in agroecosystem food webs can enhance ecosystem services by increasing pest and disease suppression, increasing production stability, and buffering the effects of climate change.

One of the widest and latest biodiversity experiments showed that the effects of species richness of one trophic level on others tend to decrease with trophic distance (Scherber et al. 2010). In the case of agroecosystems, these effects are linked to how biodiversity is managed. Intensification of agricultural practices affects the trophic groups differently; larger soil organisms appear to be more influenced by perturbation and intensification than smaller organisms (Laliberté and Tylianakis 2012). Lower intensification as in organic farming methods promotes evenness among larger species including natural enemies, which mitigate altered food webs' structure and communities dominated by few common species, which together contribute to pest outbreaks (Crowder et al. 2010). Crowder et al. also demonstrated that increasing natural enemy evenness triggered a powerful trophic cascade that reduced pest densities by 18 % and increased plant biomass by 35 %.

Compared to natural ecosystems, agroecosystems are characterized by a limited number of plant species and by a high level of human control (Malézieux et al. 2009). Although it has long been recognized that above- and belowground communities affect both agroecosystem functions (carbon recycling, pest regulation, pollination, etc.) and performance (biomass production, yield), agronomic models have usually focused on the soil-plant-atmosphere continuum and have seldom considered communities (Jones et al. 2003). This is probably because the soil-plant-atmosphere continuum was

considered as the main driver of nutrient and water flows. The easiness of soil-plant measures compared to whole community measures has promoted the emergence of large soil-plant databases, with no equivalence for above- or belowground communities' interactions. In the past, the possibility to simplify agroecosystems with pesticides has also participated to poorly consider communities' interactions.

Because the paradigm based on a soil-plant-atmosphere continuum explained the crop growth only through flows of water, nitrogen, and phosphorous (Hartemink 2005), it resulted in the development of crop models dedicated to the optimization of these resources. In these models, plant growth and development depend on radiation interception, temperature, and nitrogen use. Consequently, the effects of communities on pest control and soil physical and chemical properties have been widely ignored until very recently in generic crop models (Jones et al. 2003; Affholder et al. 2012), even though evidence indicates that most of the long-term properties of agroecosystems are considerably modified by communities, e.g. soil structure by earthworms (Cock et al. 2012).

Recently, food web modelling frameworks have allowed significant progress in modelling interactions between communities in ecosystems (Allesina and Pascual 2009; Caron-Lormier et al. 2009). Van Der Putten et al. (2009) asked for the model that includes linkage between above- and belowground food webs. The first use of these models will be to better understand and simulate ecological processes in agroecosystems. One of the main issues to be addressed by food web-crop models is trade-offs between regulation, conservation, and production ecosystem services. Indeed, the effect of innovative or conservation cultural practices (e.g. enhancement of plant and arthropod diversity (Fig. 1), zero tillage...) on trade-offs between regulation of crop pests



Fig. 1 Cover cropping in banana systems (Martinique, French West Indies), as most innovative cultural practices, alters the overall ecological functioning of the ecosystem including soil-plant interactions (Ripoche et al. 2012), aboveground pest regulation (Duyck et al. 2011; Mollot et al. 2012), and belowground pest regulation (Djigal et al. 2012) (Photo Ph. Tixier)

by the ecosystem community, nutrient cycling, and crop production remains hard to quantify with actual modelling tools. By linking processes involved in these services, it will be possible to build a process-based assessment of these trade-offs. In managed ecosystems, services result from interactions between community processes and crop growth. These interactions need to be simulated on a dynamic way to assess how community structure alters plant growth (e.g. regulation of pest, soil function enhancement) and vice versa how plant growth alters community (e.g. dynamic of production of basal resource: living biomass or crop residues). The dynamic evaluation of conservation (biodiversity and soil functions), regulation (pest regulation), and production services (primary production and yield) resulting from food web–crop model simulations opens the field of optimizing agroecosystems for multiple ecosystem services simultaneously. Ultimately, such models would constitute important tools for agroecologists who design innovative cropping systems, including, for example, the management of plant diversity associated to the crop or the enhancement of some trophic groups through the organisation of ecosystem habitats. Linking models that simulate flows of material and energy (crop models) with food web models hence remains a challenge for modellers.

In designing innovative cropping systems that account for both yield and sustainability (i.e. no externalities to other ecosystems and natural resources), modellers should now recognize that food webs are acting as drivers of production and emerging system properties, including pest regulation, nutrient cycling, biodiversity conservation, or simply primary production and yield that results from abiotic factors and community interactions. These properties include communities' interactions and especially pest regulation and feedbacks to soil properties. We attempt here to reconcile ecological and agronomical approaches by proposing the concept of “food web-based cropping system models”. This concept emphasizes the effects of communities' interactions, plant growth, soil properties, and farmer actions on both primary production and the overall sustainability of agroecosystems in terms of food production, environmental quality, and social well-being. Ecological and agronomical approaches have seldom been combined because agronomists and ecologists usually inhabit different scientific communities and because soil–plant–atmosphere models were clearly focused on modelling crop productivity and not simulating agroecosystems.

In “food web-based cropping system models” as proposed in this paper, crop models (Jones et al. 2003; Keating et al. 2003), which accurately describe the soil–plant relations regarding water and nutrients, are linked with trophic-web models, which adequately describe interactions between communities associated with the crop (De Ruiter et al. 1994; Moore et al. 2005). A theoretical and practical framework for this linkage is summarized in Fig. 2. We first recall the trends in soil–plant modelling and the importance of communities on

the agroecosystem functioning. We then propose a unified simulation framework that accounts for both approaches.

2 From plant-based models to agroecosystem models

Since the early 1980s, researchers have developed robust crop models based on energy balance, where the plant is modelled based on thermodynamic exchange with its surrounding environment, i.e. with the soil and atmosphere. Recently, soil models linked to crop models have been developed to simulate the dynamics of element fluxes in soils (Keating et al. 2003; Zhang et al. 2009). While useful for agricultural management, these models focus on the photosynthesis of the main crop and on soil–plant relationships and ignore biological interactions between plants (including weeds) and between plants, animals, and microorganisms living in agroecosystems. Recent models now account for the interactions between different plant species in mixed cropping systems (Malézieux et al. 2009). Such interactions are especially important in diversified cropping systems.

Although cropping system models sometimes account for the impacts of pests on yield (Willoquet et al. 2008), the effects of pests are often included as forcing parameters, and interactions between crop growth and pest dynamics are hardly taken into account. In many cases, this makes crop models applicable by agronomist only when pests are fully controlled, except for some particular cases such as the WHEATPEST model (Willoquet et al. 2008) or in other approaches such as integrative models as proposed by Rabbinge and van Laar (1989). Agroecosystem models will be more useful in the context of ecological intensification if they include additional top–down effects, represented by predator–prey systems such as biological control and intra-guild predation.

The main modelling issues for elaborating complex predictive tools rely on the level of detail that should be included in the model. In food web–crop models, the precision of the community structure can vary from simple trophic groups as proposed by Caron-Lormier et al. (2009) to species levels as performed in the marine ecosystem with the ECOPATH model (Pauly et al. 2000). Similarly, the precision of the plant community can be defined with a different precision as reviewed by Malézieux et al. (2009). Finally, the level of precision of interactions between food web and soil–plant compartment could be processed based as proposed in Fig. 3 or could be simplified using statistical relationships. The calibration of food web–crop models is the other challenge that the modeller will face. Recent advances in food web description make possible a better calibration of trophic links. However, the calibration of community–plant and community–soil interactions remains a hard task that can actually be correctly achieved only in well-studied agroecosystems. Future field studies will certainly need to focus on these interactions.

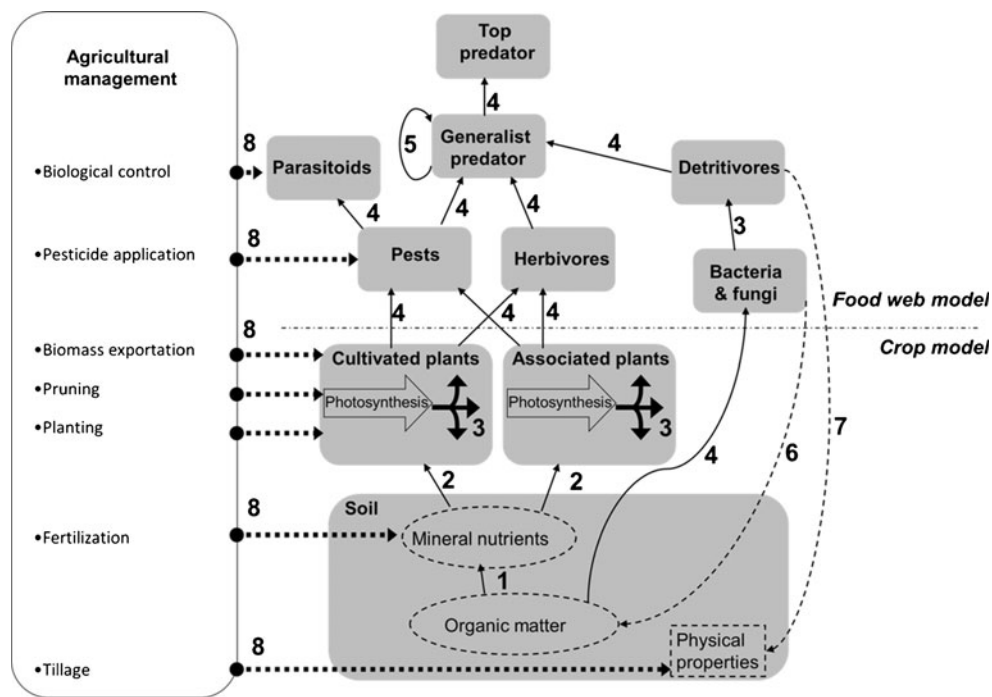


Fig. 2 Conceptual framework of the linkage between soil, plants, and food web processes in agroecosystems. This conceptual framework describes the interactions between components in agroecosystems. *Solid lines* represent the flows of materials and energy, *thin dotted lines* represent the feedback of food web communities on the soil and plants, and *bold dotted lines* represent the effects of agricultural management practices on the system. 1 soil organic matter mineralization, 2 uptake of nutrients by plants, 3 biomass allocation to different plant

organs, 4 direct consumption link, 5 intra-guild predation, 6 chemical feedbacks on soil properties, 7 physical feedbacks on soil properties, 8 effect of agricultural practices on the system. This model is not a closed system: in addition to the exportation of nutrients by humans (harvest) and by natural processes (e.g. leaching), human actions and especially agricultural practices directly and indirectly affect the functioning of the soil–plant system and, to a lesser degree, the functioning of the food web communities

3 Food web models for simulation of community feedbacks to soil properties and pest regulation

To obtain a mechanistic understanding of crop–communities interactions, we need to consider the network of both direct (trophic) and indirect (non-trophic) interactions in an agroecosystem. Indirect interactions include processes such as soil structure enhancement by earthworms (Jouquet et al. 2006) and pollination by bees and other organisms (Fontaine et al. 2006). More generally, in above- and belowground ecology, there has been a recent surge of interest in the use of “interaction networks” (Loreau and Holt 2004; Schröter et al. 2004; Moore et al. 2005; Holyoak and Loreau 2006) for understanding the consequences of trophic and indirect interactions on food web stability (De Ruiter et al. 1998; Neutel et al. 2007; Tylianakis et al. 2008).

Most food web models are based on equations derived from the simple Lotka–Volterra equations, either for population approaches (Sun and Loreau 2009) or stoichiometric (biomass) ones (Daufresne and Loreau 2001). To deal with more complex systems that often include many links between species or trophic groups, researchers often use an adjacency matrix that describes all of the consumer–resource interactions (Allesina and Pascual 2009). This

adjacency matrix is not measured in theoretical studies but is sometimes measured in case studies (De Ruiter et al. 1995), although doing so is difficult because of the low accessibility of this kind of data. Quantifying the adjacency matrix is easier for agroecosystems than for natural systems because agroecosystems have fewer species.

One of the most challenging tasks in modelling food webs in agroecosystems is determining the consumer–resource interactions (i.e. determining who is eating whom). For this, stable isotopes are useful because they provide an integrative measure of the diet of species (Ponsard and Arditi 2000), especially if they are used jointly with experiments in which the abundance of prey or predators is manipulated (Wise et al. 2006). To determine source contributions of each trophic group, researchers can use stable isotopes and software tools such as Isosource (Benstead et al. 2006). The tremendous development of next-generation DNA sequencing will surely provide the most comprehensive and accurate measure of trophic links in ecosystems, regardless of the size of organisms and without a priori on the species consumed by a given organism, by matching sequences amplified from the gut content to wide gene databases (Pompanon et al. 2011). With these data, modellers will be able to go beyond theoretical studies and

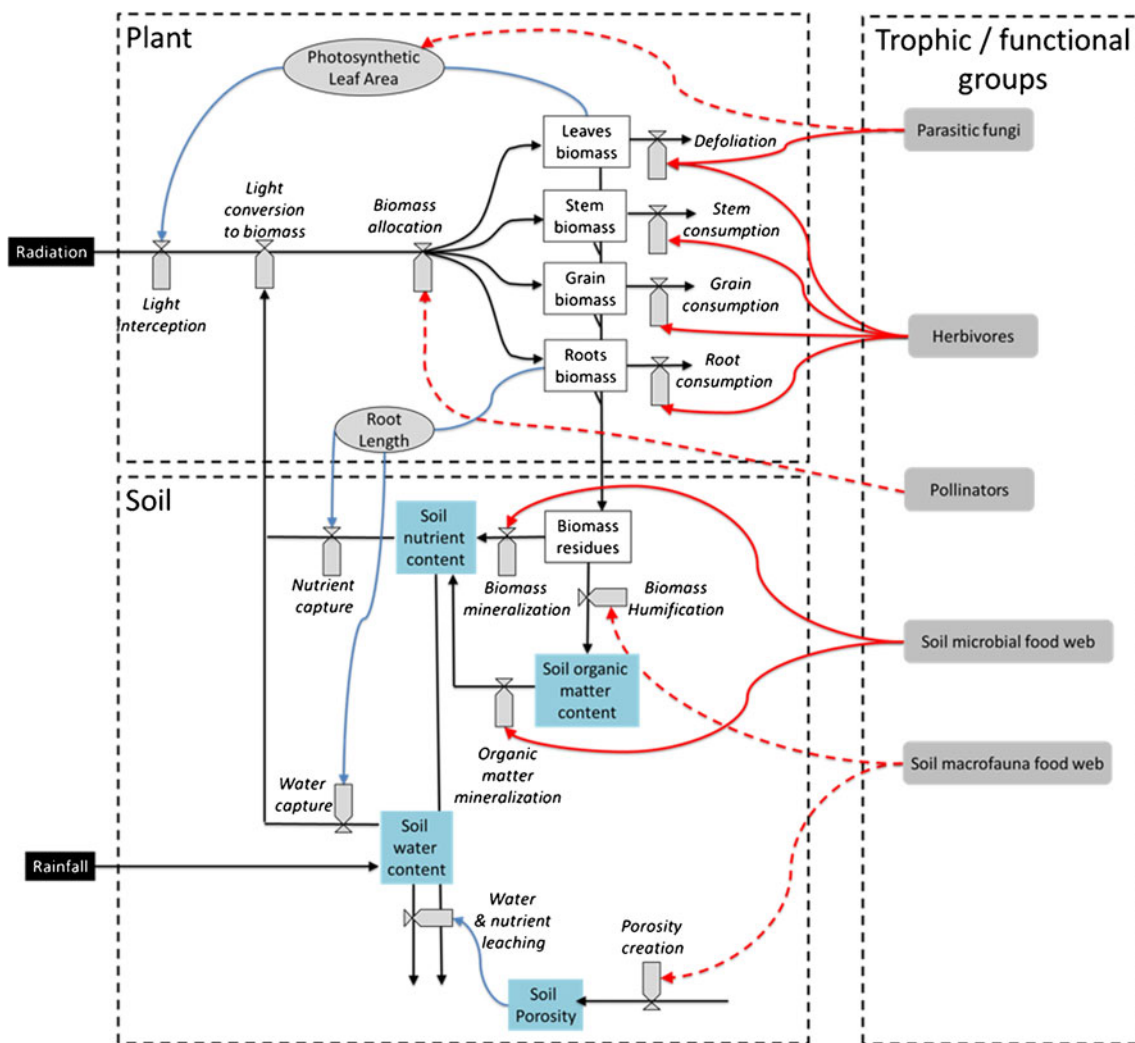


Fig. 3 Summary of soil–plant processes and how they are altered by trophic groups. *Black arrows* show flows of material or energy. *Blue arrows* show the relation between state variables and processes. *Red arrows* show the direct (*solid*) and indirect (*dashed*) effect of trophic groups on soil and plant processes

develop specific models (those that include specific characteristics of particular ecosystems) to address the complexity of future challenges of agriculture. Because the validation of such models can be difficult, it necessarily begins with a simplified approach in which trophic groups are considered instead of each species (Caron-Lormier et al. 2009).

Food web and soil–plant models can interact in two ways: (a) from soil–plant to food web, with direct effect of the dynamics of basal resources, and (b) from food web to soil–plant, with direct effects of the consumption of plant biomass, plant residues or soil organic matter, and indirect effects of pollination or soil porosity creation. The direct effect of the dynamics of basal resources can be taken into account in the Lotka–Volterra-based food web model by altering the carrying capacity of the system according to the resource availability, as proposed in the plant–pest model SIMBA-NEM (Tixier et al. 2006). Taking into account food web effects on soil–plant processes require the alteration of a wider range of processes (Fig. 3). Resource exploitation and indirect effects may be

computed according to the abundance of each species or trophic groups involved in the process and the state of the system (resource available or state variable). For instance, at time step t , the effect on a process altered by i trophic groups could be defined as: $\sum_{i=1}^{n} (\text{abundance of trophic group}_i \times \text{consumption rate}_i \times \text{state variable})$. Accounting for variation of state variables over time is a major benefit of linking soil–plant to food web models. Some trophic groups can have both trophic and non-trophic effects, e.g. plant parasitic fungi that consume carbohydrates in leaves and that also alter their photosynthetic ability (Fig. 3).

3.1 Communities' feedbacks on pest regulation

Although substantial information exists on the role of direct trophic interactions in the control of pests (Cardinale et al. 2003), the availability of a comprehensive simulation framework (see Fig. 2) should help agronomists and pest control specialists (plant pathologists, entomologists, biological

control researchers, etc.) to clarify and quantify these interactions. This is especially true for physiologically based multitrophic population dynamics models which have the highest potential for examining the complex issues that are at the heart of crop production, integrated pest management, and biological control (Gutierrez and Baumgärtner 2007). No discussion of ecological feedbacks would be complete without considering trophic interactions (Lewis et al. 1997), which represent perhaps the most important class of feedback phenomena in ecosystems and thus in agroecosystems (Worm and Duffy 2003). By definition, multitrophic models include these feedbacks on pest population. They can notably deal with intra-guild predation processes that are increasingly cited as interfering with the control of plant pests (Nóia et al. 2008; Roy et al. 2008).

The communities' interactions may also influence herbivores and parasitoids when belowground organisms affect aboveground organisms (Bezemer et al. 2005) and vice versa (Soler et al. 2005; De Deyn et al. 2007). Although root–shoot interactions should often be more developed in crop models, these models are a good basis to bridge above- and belowground compartments on a process-based perspective. It is especially important in pest regulation processes (a) when one compartment controls the plant community structure that then alters the pest dynamic in the other compartments or (b) when one compartment alters plant health that can thus modify the pest dynamic in the other one (modification in resource availability for the pest). Additionally to the bridge constituted by crop models, interactions between above- and belowground communities may be implemented in interaction-web models as proposed by Goudard and Loreau (2008); this concept of the model includes both trophic and non-trophic interactions, in which each species can modify the trophic interaction between any two species. The simultaneous use of interaction networks and crop models for soil and plant processes is probably the key for linking above- and belowground communities.

3.2 Communities' feedbacks to soil properties

ABC influence each other through a variety of direct, e.g. consumption of roots and soil organic matter, and indirect interactions, e.g. creation of soil porosity (Wardle et al. 2004). There is a strong link between plants and fungi, e.g. the flow of nutrients between plants via fungi is a significant feature of the “wood-wide web” (Whitfield 2007). In agroecosystems, soil basal resources are strongly modified by farmer-induced perturbations such as tillage, plant selection, and pesticide applications. According to these perturbations, the quantity and quality of detritus created in the ecosystem can favour plant, bacterial, or fungal pathways (Powell 2007). The stability of food webs increases when pathways are more diversified (De Ruiter et

al. 1998, 2005; Moore et al. 2005), and stability can be simulated by food web models that deal with multiple basal sources (Moore et al. 2005).

Like the cultivated crop, which alters soil structure by root growth and litter production, soil macrofauna also contribute to soil structure formation. Brussaard et al. (2007) emphasized the need to develop models that simulate soil porosity and soil organic matter dynamics in relation to the soil food web. For instance, earthworms are involved in positive feedbacks to the soil–plant system (Postma-Blaauw et al. 2006), i.e. by increasing soil porosity and plant nutrition, they increase their food resource, which is largely litter and soil organic matter. Models would help clarify the significance and nature of these feedbacks. For example, population dynamics of earthworms can be modelled like other detritivores as a function of available soil organic matter (Huang et al. 2010), and their non-trophic feedback to soil structure and soil chemistry can be simulated following existing equations, e.g. WORMDYN (Pelosi et al. 2008) or SWORM model (Blanchart et al. 2009). It will thus be possible to link the abundance of this functional group with their effect on specific processes (Fig. 3).

4 Conclusion

Modelling complex and dynamic food webs is a major challenge in ecology. Food web models are valuable because they can be used to understand system stability and the related concepts of robustness and resilience and therefore can be used to predict how the system will respond to perturbations affecting agroecosystem productivity and sustainability. The concept of linkage between food web and crop models represents the next step to address the issues of ecological intensification of agricultural systems and trade-offs between ecosystem services. Additionally, to bring together two types of modelling tools, it will help to bridge the gap between the communities of agronomists and ecologists. This concept will help the rise of innovative strategies based on the manipulation of the biodiversity of agroecosystems.

The concept of model linkage proposed here will participate to address ecological issues in natural ecosystems. Indeed, given global climate change and the rapid changes in agriculture, the structure and composition of food webs might also change quickly. It follows that a dynamic view of food webs becomes essential, which becomes possible with precise modelling of primary producers. On a larger scale, comprehensive approaches that aim at linking ecology, economics, and social models will be facilitated by selecting models that already include both ecological processes (such as food web interactions and biogeochemical cycles) and human-driven factors (social networks and decision models). We believe that as researchers continue to develop tools that

link ecological and agronomical processes, they will contribute to the development of new management strategies for both natural and agricultural ecosystems.

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