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Abstract

Promoting plant diversity through crop mixtures is a mainstay of the agroecological transition. Modelling this transition requires considering both plant-plant interactions and plants' interactions with abiotic and biotic environments. Modelling crop mixtures enables designing ways to use plant diversity to provide ecosystem services, as long as they include crop management as input. A single modelling approach is not sufficient, however, and complementarities between models may be critical to consider the multiple processes and system components involved at different and relevant spatial and temporal scales. In this article, we present different modelling solutions implemented in a variety of examples to upscale models from local interactions to ecosystem services. We highlight that modelling solutions (i.e. coupling, metamodelling, inverse or hybrid modelling) are built according to modelling objectives (e.g. understand the relative contributions of primary ecological processes to crop mixtures, quantify impacts of the environment and agricultural practices, assess the resulting ecosystem services) rather than to the scales of integration. Many outcomes of multispecies agroecosystems remain to be explored, both experimentally and through the heuristic use of modelling. Combining models to address plant diversity and predict ecosystem services at different scales remains rare but is critical to support the spatial and temporal prediction of the many systems that could be designed.

Keywords: crop mixtures, process-based models, crop models, individual-based models, modelling synergies, pest regulation

1. Introduction

New models are frequently developed for specialists in a field to answer specific scientific questions, without much interaction with other disciplines in the initial stages. During the past decade, however, modellers have integrated knowledge from multiple disciplines (e.g. micro-meteorology, environmental physics, ecophysiology, ecology, soil science) to better represent interactions between processes within plants, between plants, and between plants and their environment (e.g. Gauthier *et al.* 2020). The result is a distinct diversity of modelling approaches that can be used to benefit the complementary properties and strengths of models (see e.g. Colbach *et al.* 2021; Pointurier *et al.* 2021). This knowledge and model sharing requires certain upstream steps that are necessary to render models more accessible, such as free licenses, open-source code, accessible software products, improved usability, extensive documentation and training sessions. These steps are especially important when setting up close collaboration between teams of modellers that include in-depth work on exchanges between models, such as the international modelling communities working on crop models, such as AgMip ("Agricultural Model Intercomparison and Improvement Project"; Rosenzweig et al. 2013) and MACSUR ("Modelling European Agriculture with Climate Change"; https://macsur.eu/). A good example of this desire to share and standardize practices is the study of Midingoyi *et al.* (2021) on the development of a meta-language to facilitate the exchange and reuse of crop-model components between modelling platforms.

The need to combine several modelling approaches, each with trade-offs in accuracy and generality, is crucial in all scientific disciplines and assumes that each model may improve understanding and predictions of ecosystem functioning. For instance, Evans *et al.* (2016) highlighted that the global models used to predict the geographic distribution of plant species throughout the world have low predictive power if they are not improved with process-based range models that predict impacts of environmental changes. Therefore, the need exists for accurate predictions of processes and more global and qualitative modelling approaches to understand an ecosystem, while also considering the feedback between different approaches, especially as the factors involved in ecosystem functioning are not necessarily the same for the spatial scales considered (Pearson and Dawson 2003; Xu *et al.*, 2021).

Building connections between modelling approaches is particularly crucial in the context of the current agroecological transition, which involves in-depth changes to agricultural practices, with more complex and diversified agroecosystems and a multifunctional view of agriculture (Caron *et al.* 2014; Duru *et al.* 2015; Gaba *et al.* 2015). Increasing plant diversity is a mainstay of the agroecological transition and the cornerstone for "biodiversity-based agriculture" (Duru *et al.* 2015), which depends on agrobiodiversity at field, farm and landscape scales (Kremen and Miles 2012;

Prieto *et al.* 2015; Tscharntke *et al.* 2021). In these types of agriculture, ecological processes are fundamental to agricultural production, which requires particular focus on production-ecology trade-offs (Sabatier and Mouysset 2018). More than ever, modelling synergies must be identified to enable upscaling from plant functioning (i.e. ecophysiological processes and plant-plant interactions) to ecosystem services to support the agroecological transition (Tixier *et al.* 2013).

To illustrate how these modelling synergies and complementarities are essential to better characterize biodiversity-based agriculture, we focus on modelling species and cultivar crop mixtures along the continuum of plant (and plant-plant interactions), field and farm scales. Each scale requires representing specific abiotic and biotic factors (Pearson and Dawson 2003; Peng *et al*. 2020), as well as ecosystem functions that support ecosystem services, including production and regulating services (Haines-Young and Potschin 2013). The nature, importance and level of expression of ecosystem functions also depend on the scale considered. While experiments have identified agronomic advantages of these diversified systems (e.g. Kiaer *et al.* 2012; Beillouin *et al.* 2021), better understanding is needed about their agricultural management and especially about how to integrate them into cropping systems to attain the ecosystem services targeted. The diversity of ecosystem services targeted and the extent of the temporal and spatial scales at which these services are developed make modelling choices complex. Issues to consider include which processes the model should simulate and at what resolution, as well as which temporal scale (e.g. instantaneous, daily, crop-cycle, rotation or long-term) and spatial resolution (e.g. plant, field or landscape, along with its multiple cultivated and uncultivated components) to use to represent the multiple interactions of interest. These considerations suggest that a single modelling approach is not sufficient to meet these legitimate expectations. Moreover, how these issues are addressed depends on which stakeholders use the models.

In this opinion article, we advocate that complementarities and coupling of different modelling approaches are critical to consider the complex and diversified agroecosystems involved in the agroecological transition, as well as to upscale from the plant and/or field scales to the ecosystem services targeted in diversified agroecosystems. Using several examples, we demonstrate that the complementarity between individual-based models (including functional-structural plant models (FSPMs)), crop models and physical or more qualitative or statistical models, improves understanding and facilitates simulating the functioning of crop mixtures and the ecosystem services for which they are designed. These modelling complementarities are discussed through the lens of crop mixtures or are integrated at larger scales to address three important modelling challenges: to i) quantify and understand plant-plant interactions and their underlying processes, ii) represent impacts of the environment and agricultural practices on the functioning of crop mixtures and iii) assess the ecosystem services provided by these heterogeneous covers (Figure 1).

2. Modelling plant-plant interactions in crop mixtures to assess ecosystem services at fine scales (plant and field)

Plant-plant interactions in crop mixtures are the foundation for the ecosystem services provided by diversified agroecosystems. Although these interactions can provide large-scale ecosystem services, for most processes they usually occur at a fine scale due to interactions between neighbouring plants or between plants and microorganisms. To illustrate this, we focus on complementarities between existing modelling approaches to simulate production and regulating services quantified at the plant and/or field scales.

2.1. Modelling plant-plant interactions to quantify underlying processes for production services

One widely known advantage of crop mixtures is their potential to achieve higher yields due to more efficient and complementary use of abiotic resources compared to that of sole crops, especially in a low-input context (Banik *et al.* 2006; Dhima *et al.* 2007; Gaudio *et al.* 2021; Hauggaard-Nielsen *et al.* 2008). Predicting effects of plant-plant interactions on the capture and use of abiotic resources is therefore crucial to assess the production services provided by crop mixtures.

From an ecophysiological viewpoint, some processes are particularly determinant in crop mixtures because they strongly influence functioning and performance, especially related to competition (for light, water and nutrients), complementarity (spatio-temporal and niche processes) and facilitation (Malézieux *et al.* 2009; Brooker *et al.* 2015). The main modelling approaches developed to study plant-plant interactions within crop mixtures are process-based models at plant and crop scales (Gaudio *et al.* 2019). We do not provide a detailed description here of how process-based modelling approaches simulate the processes that underlie these plant-plant interactions, as several recent reviews and integrated studies have done so and have described their strengths and weaknesses (e.g. Gaudio *et al.* (2019) for crop or individual process-based models, Evers *et al.* (2019) and Louarn and Song (2020) for FSPMs). When downscaling to quantify and understand the relative contributions of primary ecological processes in crop mixtures, individual-based models, especially FSPMs, are usually required, as the phenotype of individual plants emerges from interactions between the local environment they perceive and their functioning (Evers *et al.* 2019). Thus, some FSPMs can quantify ecological processes (Zhu *et al.* 2015; Faverjon *et al.* 2019) or assess the role of given traits involved in the performance or resource-use efficiency of crops (usually light or nitrogen; Barillot *et al.* 2014; Louarn *et al.* 2020). For instance, Zhu *et al.* (2015) used an FSPM to simulate wheat-maize relay-intercropping and highlighted that plasticity is the main process involved in the higher light-use efficiency in intercrops than in sole crops.

Important processes highlighted by FSPMs can be summarized using functional relationships to include them in crop models (Escobar-Gutièrrez *et al.* 2009), which would enable understanding of plant-plant interactions and thus achieve upscaling. However, few studies have highlighted complementarities between these two modelling approaches. For instance, FSPMs can be used to evaluate simplified assumptions applied in upscaled crop models. Crop models can simulate light interception and partitioning differently, but the common way to represent light interception is to use the "turbid-medium approach" and Beer-Lambert law. However, the question remains as to whether this simplified approach is sufficiently accurate to simulate light partitioning among plants in crop mixtures. Barillot *et al.* (2011) addressed this question for three grass-legume mixtures (wheat-pea, fescue-alfalfa and fescue-clover) and compared light partitioning between the component species. They simulated detailed 3D representations of plants, coupled with a solar radiation model that followed the turbid-medium approach, with the plant canopy represented by one, two or ten layers. The results indicated that more detailed representation of the canopy (several layers or in 3D) improved the prediction of light partitioning in mixtures only slightly, thus validating the turbid-medium approach for estimating light competition at the canopy scale in crop models. Similarly, Pao et al. (2021) transformed a 1D light model using Beer-Lambert equation by estimating empirically the light extinction coefficient from the canopy geometry formalised by plant and row distances. The performance of this approach in combination with hourly-step time resolution of simulation was equivalent to a 3D light model using ray tracing, in a dynamic plant model predicting leaf-level photosynthetic acclimation and plant-level dry matter accumulation. This smart solution provided efficient estimation for long-term processes integrated over weeks. Another example exhibiting how emerging results can be simplified using FSPM demonstrated that a model input that is time-consuming to assess, the red: far-red ratio, was successfully replaced by a proxy computed from the leaf area of the upper ten leaves and the plant density (Kahlen and Stützel 2011).

The complex integration of local plant responses to light competition and plant structure considered in FSPMs is largely incompatible with the simple representation of plants in crop models. However, indirect connections can be identified using inverse modelling and the adaptive calibration of input parameters in crop models. For instance, these models frequently use the response function of crops to plant density to represent the competitive effect of neighbours in mixtures by calibrating a dominance ratio or an equivalent-density parameter (Brisson *et al.* 2008; Confalonieri 2014). These parameters depend strongly on environmental conditions and the identity of neighbouring species in the mixture (Van Oijen *et al.* 2020). Their variations can be derived from simulated data produced by more detailed FSPMs, such as the relative-density responses of species (e.g. as illustrated by Louarn and Faverjon (2018) for contrasting legume species).

Interactions for belowground resources are not reflected to this extent in modelling platforms (Evers *et al.* 2019). Because the spatial distribution of resources and physiological characteristics of species drive the growth and plasticity of roots, they are important factors that influence the response to water or nutrient changes in intercropping (Yin *et al.* 2020). Results of intercropping studies that focus on how to regulate root systems through spatio-temporal variation in the water or nutrient supply are rarely reported. However, studies have focused on species-specific responses of root morphological plasticity as influenced by nutrient availability, showing greater plasticity in graminaceous species (e.g. maize) than in leguminous species (e.g. faba bean, chickpea) (Li *et al.* 2014). Other studies compared mixed cropping to segregated strip-intercropping, showing that using strip-intercropping to concentrate low C:N species increased N mineralization potential in the planting zone for the subsequent crop (Lowry and Brainard 2016). Finally, benefits of legume-based intercrops have been shown through direct plant-to-plant N transfer, depending on the physical co-location of the root systems and thus on the spatial arrangement of the two species (Johansen and Jensen 1996; He *et al.* 2009; Chapagain and Riseman 2014). These results indicate the need to model phenotypic plasticity of roots as a function of the distribution of resources in a predefined spatial arrangement of intercrops. However, simple and generic approaches that focus on belowground resources already exist. For instance, Bertrand *et al.* (2018) developed BISWAT, a crop model that simulates dynamics of water stress in plants in sole crops and crop mixtures. The model integrates and combines simple approaches to simulate the main processes in the system with a 2D representation of the plants and soil, radiation-use efficiency, total transpirable soil water content and a simple representation of root dynamics. The resulting model requires few data for parametrization and yet remains robust for simulating water-stress dynamics in a wide range of systems.

Compared to these ecophysiological approaches, ecological approaches are particularly relevant for studying and understanding the functioning of systems in which multiple heterogeneous populations, such as crop mixtures, interact. However, representing mechanistically the processes that interact within these systems and quantifying the resulting ecosystem services requires knowledge and conceptual frameworks that are well theorized in ecophysiology and agronomy. Thus, dialogue between these different disciplines – environmental physics, ecophysiology, agronomy and ecology – is crucial for modelling these agroecological systems (Evans *et al.* 2016; Brooker *et al.* 2021). In particular, the concept of "functional trait" commonly used in ecology and recently used to characterize agrobiodiversity and ecosystem services (Wood *et al.* 2015) can be related to the parameters and variables in process-based models using the distinction between pattern and process traits developed by Volaire *et al.* (2020). Unlike the strict definition of functional traits, which are measured independent of the environment (Violle *et al.* 2007), the authors argue that process traits (*a trait measured under environmental conditions fluctuating in time, which characterizes processes, that is, flows of material and energy in a given environment during a defined period of time*, e.g. growth rate or phenological stage duration) are also functional and crucial for parameterizing models. This distinction may provide a bridge between ecology and crop science, partly because it allows to discuss upon a common semantics linking pattern and process traits with input parameters and state variables which are used in process-based models.

2.2. Modelling plant-plant interactions to quantify the underlying processes for regulating services

Crop mixtures should promote regulating services as well as production services (Haines-Young and Potschin 2013). For instance, vegetation diversity at all spatial scales (intra- vs. inter-field) improves pest regulation in several ways. It increases the matrix of unfavourable habitats and thus limits pest dispersal (Fabre *et al.* 2012; Papaïx *et al.* 2014). The spatial heterogeneity of host plants can also restrict pest population dynamics, which slows the specialization process (Plantagenest *et al*. 2007). In the next modelling example, a splash dispersal model was coupled with a snapshot of virtual 3D canopies provided by an FSPM to understand fine processes involved in controlling rain-borne diseases in wheat-cultivar mixtures (Vidal *et al.* 2018, Figure 2).

By mixing susceptible and resistant cultivars, the habitat favourable to a pathogen is spatially fragmented, thus generating i) a "barrier" effect, related to the presence of resistant cultivars, and ii) a "dilution" effect, as the probability of an individual finding a favourable habitat is reduced proportionally to the reduction in density of the susceptible cultivar (Finckh *et al.* 2000). This latter effect can be reinforced by a difference in height between cultivars when the pathogen spreads from the bottom to the top of the plant. Vidal *et al.* (2018) showed that a wheat-cultivar mixture composed of a short resistant cultivar and a taller susceptible cultivar would result in a lower layer that mixes susceptible and resistant leaves, which may provide a strong barrier effect (Figure 2). In contrast, the upper part of the canopy would be less dense (containing only the taller susceptible cultivar), and the upper leaves would be protected by their increased distance from the inoculum source at the bottom (height effect) and the presence of resistant leaves in the lower part of the canopy (barrier effect). In this example, the coupled model clarified understanding of the mechanisms involved and identified height as a relevant architectural trait to reduce spore dispersal when mixing cultivars. However, manipulating such models is extremely time-consuming. The idea again is to identify emerging results − response functions to plant architecture and cultivar resistance − and then introduce them in a simplified manner into models that simulate other important factors in epidemics, such as the microclimate in the canopy. The next step is to quantify the influence of these associations on regulating pest populations and limiting crop yield losses. Consequently, coupling process-based modelling approaches and food-web modelling could provide a promising path for upscaling (Tixier *et al.* 2013; Malard *et al.* 2020).

3. Representing impacts of the environment and agricultural practices when assessing ecosystem services provided by crop mixtures at the cropping-system scale

3.1. Representing impacts of external drivers on plant-plant interactions

As described in previous sections, understanding mechanisms of plant-plant interactions requires describing the plant environment in detail. Promoting the use of crop mixtures at the cropping-system scale (e.g. rotation, farm) requires considering effects of agricultural practices and environmental factors that influence plant-plant interactions when building and evaluating the ability of crop mixtures to provide one or more ecosystem services. Current FSPMs often do not consider this particular point as extensively as crop models due to their complex structure and the associated modelling costs (Louarn and Song 2020). This could be mitigated by borrowing the strengths of different approaches and developing hybrid modelling. However, the level of precision and degree of simplification required to consider plant-plant interactions are not necessarily the same and depend on the outputs targeted by the simulation study. Colas *et al.* (2021) illustrated this point by simplifying a complex individual-based model at the cropping-system scale to design effective strategies for weed control. They simplified light partitioning – which is usually represented with a 3D voxelized canopy in their mechanistic model (FlorSys, Colbach *et al.* 2014) – using a random-forest-based metamodelling approach to accelerate the simulations and enable interactive testing of many complex cropping systems with end users.

In crop models, agricultural practices influence the crop environment, such as soil fertility and water availability, which modifies the soil-climate context in which crop mixtures may adapt as a function of their complementarity and/or plasticity properties (Stöckle and Kemanian 2020). Crop models are thus able to supply inputs for FSPMs, i.e. quantified and dynamic descriptions of abiotic constraints under which a crop mixture grows. For instance, the STICS crop model was used to simulate impacts of delayed sowing dates on plant-plant competition for light (Launay *et al.* 2009) and impacts of different levels of nitrogen fertilization on relative dominance (Corre-Hellou *et al.* 2009) in barley-pea intercrops.

3.2. Assessment of a given ecosystem service: pest regulation

Pests in agroecological cropping systems can be regulated by significantly increasing plant diversity in the field or landscape using arable crops and semi-natural or natural elements (Sirami *et al.* 2019). However, the effectiveness of these systems depends greatly on their spatial organization at the field scale (Landis *et al.* 2000). Collard *et al.* (2018) transposed the spatial concepts of landscape ecology to the field scale, assuming that proximity, edge length or aggregation could improve understanding of how the spatial organization of non-crop habitats might alter the predator effect and thus increase crop health. They used an individual-based and spatially explicit model to simulate individual behaviours of predators, such as the duration and frequency of visits to orchard crops. They tested several spatial organizations that varied in the clumping of non-crop habitats, the distance between crop and non-crop habitats, and the number of alternative favourable neighbouring non-crop habitats around the crop habitat. To assess pest regulation, however, this modelling approach now needs to include the dynamics of pests and their interactions with predators. The current version partly meets this aim using proxies such as visit duration and frequency, as well as the duration of the predator's absence from the crop.

A good example of a modelling solution that uses complementarities between models and that can represent heterogeneous canopies was built by coupling the individual-based model FlorSys (Colbach *et al.* 2014) with RSCone, a metamodel produced using the architectural root model ArchiSimple (Pagès *et al.* 2020), and the soil submodel of the STICS crop model (Brisson *et al.* 2008). While FlorSys simulates aboveground crop-weed canopies, the ArchiSimple metamodel represents the trophic connection between above- and belowground growth, and the STICS soil submodels represent soil structure and climate and their effects on root growth (Figure 3). Illustrating the issues faced by coupling models or modules with different time or space scales, conversions had to be done to make optimal days of RSCone compatible with thermal time in FlorSys. This smart solution thus generates outputs and proxies that can be used to assess contrasting ecosystem services such as crop grain yield; weed-caused yield loss; weed seed production (as a proxy for future yield loss) and weed-based trophic resources for domestic bees (as one example of weed benefits), resource uptake or striga risk (Pointurier *et al.* 2021). It was necessary to develop working and modelling assumptions as the aim of this multi-faceted model was to cover a wide range of flora (including many contrasting annual species) and address multiple ecosystem services (Colbach *et al.* 2021). Simpler, empirical relationships were preferred for processes for which mechanistic representation would have required downscaling to the cellular or molecular scale. Because representation of individual plants had to be compatible with multi-annual and multi-field simulations of thousands of plants per field, detailed representations, such as used in FSPMs, were rejected in favour of individual-based modelling.

This research model was then used to identify agroecological mechanisms and provide decision support for farmers. This mechanistic and individual-based approach induces considerable algorithmic complexity and slow simulations; thus, using it in decision-support systems is time consuming, as it requires assigning many input variables and calibrating many parameters, particularly when simulating many diverse crops simultaneously. This is solved by aspects of metamodelling (Colas *et al.* 2020) that can identify potential changes to cropping systems that might improve their performance. However, a biophysical parent model is still required to provide biophysical explanations that farmers will accept (Colbach *et al.* 2021).

The authors reconstructed the functioning of a diversified agroecosystem by coupling models that could represent systems (the plant and its aerial and root structure, seeds, soil layers and their structure and microclimate) and mechanisms at similar scales. In particular, they integrated two aspects that are essential to understand and manage these types of agroecological systems: consideration of long-term processes (e.g. evolution of a seed bank) and impacts of management decisions on these processes and the targeted ecosystem services, with consequences that could occur over several years.

<u>3.3. Assessment of a bundle of ecosystem services at the farm scale</u>

Assessing the ecosystem services provided by diverse crop mixtures is challenging due to the many ecosystem services targeted by farmers and the diversity of crops to be investigated (Verret *et al.* 2020). Coupling models may be a promising solution to understand this complexity and diversity because it benefits from the strengths of diverse modelling approaches. However, predicting how management activities and changing future conditions will alter ecosystem services is rendered more complex by interactions (e.g. trade-offs, synergies) among multiple ecosystem services (Agudelo *et al.* 2020). More widespread use of process-based models to estimate ecosystem services could identify physiological processes, or even the traits, that influence interactions between ecosystem services. However, simulating the ecosystem services provided by crop mixtures requires representing their inclusion in crop rotations and long-term effects of the environment. This could be achieved by combining the knowledge provided by process-based models and using more qualitative models based on farmers' expertise.

In agreement with this idea, Meunier *et al.* (2022) designed a serious game to help users (farmers or students) explore and assess a bundle of ecosystem services (i.e. cereal and legume grain yield, cereal protein content, potential nitrogen supply to the next crop, maintenance of soil structure and pest regulation) provided by a wide range of binary cereal–grain legume intercrops (Figure 4). The serious game encapsulates a modelling chain that they constructed from three modelling approaches:

(i) STICS (Brisson *et al.* 2008) was used to simulate the potential and water-limited biomasses of the cereal and legume sole crops independently under a variety of soil-climate conditions and management practices.

(ii) A statistical model built using R software (R Core Team 2018), using a field-trial database of cereal-legume intercrops and their corresponding sole crops, was used to correct these potential and water-limited biomasses into attainable (i.e. water and nutrient-limited) biomasses (Van Ittersum *et al.* 2013).

(iii) A knowledge-based multi-attribute model built using DEXi software (Bohanec 2008) was used to turn attainable biomass into actual biomass considering pest damage and assessing pest-regulation services. Other multi-attribute models also enabled assessment of five more ecosystem services that result from the actual biomass of the cereal-legume intercrop at harvest and/or cropping-system features.

The serious game was designed to explore the ecosystem services provided by both common and less-common intercropping scenarios, and to promote debate and knowledge sharing among users.

4. Upscaling models from local interactions to ecosystem services: realities, opportunities and obstacles

4.1. Modelling solutions to benefit from model complementarities

From the examples listed above, different strategies can be identified to combine models at different scales and predict consequences of plant-plant interactions, from local responses up to ecosystem services at the cropping system and farm scales (Figure 5). Besides direct coupling of models, which is rarely feasible across all scales, we identified three particularly promising approaches to address this issue:

- **Inverse modelling**, which connects models by identifying input parameters from simulated data. This approach is common to many scientific disciplines (Evans *et al.* 2016) and uses simulated datasets to determine parameter values from other models to supplement the observed data available. Using simulated datasets to improve exchanges between models and modellers is particularly valuable to facilitate parametrization of existing models, as illustrated by the adaptive parametrization of density responses and dominance ratios in crop models (individual-based model to a crop model, Van Oijen *et al.* 2020) or the definition of input scenarios in serious games (crop model to a farm-management model; Meunier *et al.* 2022).
- **Metamodelling**, which connects models by developing a simpler model of outputs from a more complex model (Jin *et al.* 2001). Defining such new models is a particularly interesting way to simplify complex simulation models that have high computing costs into something tractable and reusable in a particular domain using a more integrated approach. For instance, this is illustrated by the integration of a root-morphogenesis metamodel in FlorSys to represent root competition (from root FSPM to a cropping-system model, Pointurier *et al.* 2021). The approach has also been effective at scaling up local plant interactions over large areas and representing vegetation dynamics by considering soil and landscape variability (e.g. Moorcroft *et al.* 2001). Metamodelling can reduce the computing costs of complex models by several orders of magnitude.
- **Hybrid modelling**, which connects models by combining the strengths of existing models in a new model (Louarn and Song 2020). The goal is to perform hierarchical modelling at multiple scales by including only the level of detail required to represent the critical processes involved in targeted outputs of the system (e.g. scaling-up a mechanistic model of dynamic protein turnover from leaf to canopy level, to provide a physiological explanation of the photosynthetic acclimation under various light availability and nitrogen supply environments; Pao *et al.* 2019). A direct example is the re-use of complementary modules from existing models in original modelling solutions (e.g. individual-based plant models with soil and management modules from crop models; Faverjon *et al*. 2019). Merging knowledge can also result in formalizing emergent properties of a complex model in simpler robust equations or in validating a simplified formalism used in cropping-system models (Barillot *et al.* 2011). Although not yet developed for agroecosystems, hybrid modelling could also consider Bayesian approaches that have been effective at aggregating different types of models and data, including those that concern consequences of plant-plant interactions in natural systems (Pagel and Schurr 2012).

These three broad categories are not mutually exclusive and can be combined to build original models across scales. Each can help illustrate the potential of process-based models to assess certain key ecosystem services (related mainly to crop productivity, biogeochemical cycling and weed control). Moreover, the temporal scale at which processes and interactions occur and ecosystem services are built may require long-term simulations (Figure 5). Generally, when the spatial scale increases (from plant-plant to the landscape), the temporal scale increases. However, modelling could target more ambitious applications than those documented to date, such as more comprehensive representation of environmental drivers (e.g. pests and pathogens, soil phosphorus content, climate change) and greater detail in the relationships between plant diversity (crop, service and weed plants) and biodiversity at other trophic levels in agroecosystems (pests and diseases).

4.2. Challenges and difficulties linked to modelling solutions

Reusing and coupling existing models faces several methodological and technical challenges. To be effective, direct coupling and hybrid modelling often require developing specific adapters or new model code. Too many inconsistencies between models, such as differences in temporal and spatial resolutions, concepts and coupling variables, can make it more difficult to couple the models. The coupling time step must be defined and be consistent with the time step of the interactions between the simulated systems. This indicates that it may be necessary to increase (temporal upscaling) or decrease (temporal downscaling) the time step of one of the coupled models; the latter assumes knowing how to describe processes at a finer temporal resolution. Furthermore, the processes considered can occur at different spatial scales (e.g. from field to watershed) depending on the type of organisms and the factors involved, and can be influenced by multiple interactions. Modelling platforms do not always have sufficient technical development to combine these contrasting resolutions to describe systems and their functioning. Moreover, coupling models promotes dialogue between disciplines (e.g. agronomy and hydrology) and thus requires agreeing on a common lexicon or an ontology.

4.3. Modelling perspectives and opportunities

Many consequences of multispecies systems remain to be explored, both experimentally and through modelling and theoretical studies. We advocate practicing both during the transition towards more agroecological systems. Models cannot be developed without supporting data, and a lack of reliable models hinders data analysis. This is particularly true regarding consequences of plant-plant interactions, for which the magnitude and hierarchy of the major processes involved remain hotly debated despite over 80 years of manipulative and observational studies (Brooker 2006; Weisser *et al.* 2017). This lack of understanding prevents identification of a consensual, much less optimal, model structure. However, it also promotes the development of a variety of models to test and benchmark interactions between mechanisms that act simultaneously (e.g. competition and complementarity for resources, different forms of facilitation, physical and chemical signalling). In this context, combining specific model developments with effective strategies to aggregate them encourages parallel progress in key disciplinary issues (related to biophysical aspects and social sciences in managed ecosystems), while still enabling integration of outputs relevant for predicting ecosystem services at different scales.

Connecting data with models to develop diversified cropping systems provides an opportunity to address issues involved in quantifying biodiversity-based services. As a part of managed ecosystems, these services are scrutinized more closely than those in natural systems and benefit from observation in agricultural networks (e.g. Lechenet *et al.* 2017), as well as developments in digital agriculture that are increasingly used for diversified systems (Reboud 2019; Chen *et al.* 2019). They also depend greatly on crops that have a long history of biological characterization and modelling and are now benefiting from the early development of high-throughput information systems in plants (Tardieu *et al.* 2017). Rich benchmarking datasets that cover multiple ecosystem services rather than only productivity are increasingly available. These data remain rare, but they are required to understand potential trade-offs between services and to identify inconsistent predictions across scales (Schneider *et al.* 2014). Here, models are needed to go beyond the observational posture of naturalists and quantitatively represent and analyse effects of plant diversity in a high number of possible scenarios

To this end, the ability to predict consequences of within-field diversity at different spatial and temporal scales is required in order to assess the overall interest of various diversification scenarios. A general belief about natural ecosystems is that plant diversity alone provides the ecosystem services targeted, and that increasing species and genetic diversity in cropping systems should be a goal to provide multiple services. However, how and why a particular arrangement of practices, or a given range of diversity, should be chosen largely remain to be solved. By definition, managed agroecosystems have an economic purpose and often target particular marketable products. From a farmer's perspective, diversification thus has advantages (resilience) and disadvantages (not all species are equal from an economic viewpoint; more complex management). Our opinion is that combining models that can represent plant diversity and predict ecosystem services at multiple scales is critical to support the spatial and temporal prediction of the many systems that could be designed.

Concluding remarks

Diversified agriculture points a clear route toward more sustainable systems able to provide a range of services to the society beyond agricultural production. Exploring and evaluating the diversity of possible solutions is by no means simple, and will require the combination of different approaches relying on field experiments, farmers networking and new technological tools taking advantage of heterogeneous sources of data. We support that plant, crop and cropping system models will be among the key tools to help achieving this goal. We illustrated it here through the example of one major option regarding crop diversification, the increase of within-field variability by mixing different crops, and highlighted potential connection and complementarities in the range of models already at hand. A proximate use of multi-scale modelling solutions could be to help explore numerically the benefits and constraints of different diversification scenarios and address the “diversification dilemma” of an almost infinite number of combinations to test. At the very least, it could help focusing the experimental development efforts on the most promising solutions and limit the test in field trials of non-beneficial systems (e.g. non-compatible diversity that does not provide the expected services or whose costs decrease system resilience or farmers’ incomes). When mature and more robust, an ultimate use of these models could also be to help quantify non-productive ecosystem services. It is clear that intercropping and other diversification practices will not become widespread without sufficient economic justification. Such models could be very useful to help determine the added value of diversified systems. We are witnessing a renewal of interest for these systems and anticipate that further developments of models in this area will be critical in the coming years.

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Contribution of authors

- M.L., N.G. and G.L. conceived and wrote the manuscript
- R.B., C.M. and R.V. contributed ideas, supported the writing, read and commented on the entire manuscript

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Figure 1. Different features are required to upscale from plant-plant interactions (e.g. competition, complementary, facilitation) to agroecosystems that provide ecosystem services. This combines the individual (plant) model level with biophysical (abiotic and biotic environments) and technical levels. However, the corollary of this upscaling is downscaling, in the sense that modellers and users may need to apply parsimony to simulate these systems at large scales (at which only a few factors explain variability in performance) (Pearson and Dawson 2003; Evans et al. 2016), or to identify an optimal system that responds to a set of constraints and objectives at a given location. Adapted from Louarn and Song (2020).

Figure 2. Illustration of facilitation against pests resulting from mixing two wheat cultivars that vary in height and resistance to pests. An aerial functional-structural plant model (FSPM) and a rain-splash model were coupled to simulate facilitation (Vidal et al. 2018). Source of photographs: Sébastien Saint-Jean (INRAE, UMR EcoSys).

Figure 3. Overview of the main processes that connect the FlorSys individual-based model (IBM, Colbach et al. 2014), which simulates the aboveground crop-weed canopy, to the RSCone metamodel (Pagès et al. 2020), which simulates root growth, and the STICS crop model (Brisson et al. 2008), which provides soil structure and climate and their effects on root growth. Adapted from Pointurier et al. (2021).

Figure 4. Introduction to the serious game “Interplay”, used to assess a bundle of ecosystem services provided by including crop mixtures in a crop rotation. The game and overall structure of the modelling chain are illustrated. Green boxes are examples of options selected in a designed intercropping scenario. The main steps of the game and the variables of the modelling chain are in white, the dry matter (DM) of cereal biomass in the scenario is in light orange, the DM of legume biomass is in green and additional variables that influence soil structure are in dark orange.

Figure 5. Conceptual illustration of modelling solutions (i.e. inverse modelling, metamodelling, coupling and hybrid modelling) used to simulate crop mixtures at different spatial scales (plant, field, farm and landscape), which are characterized by contrasting processes and ecosystem services. Asterisks indicate that the multiple spatial scales involve both short- and long-term simulations.

Figure 1

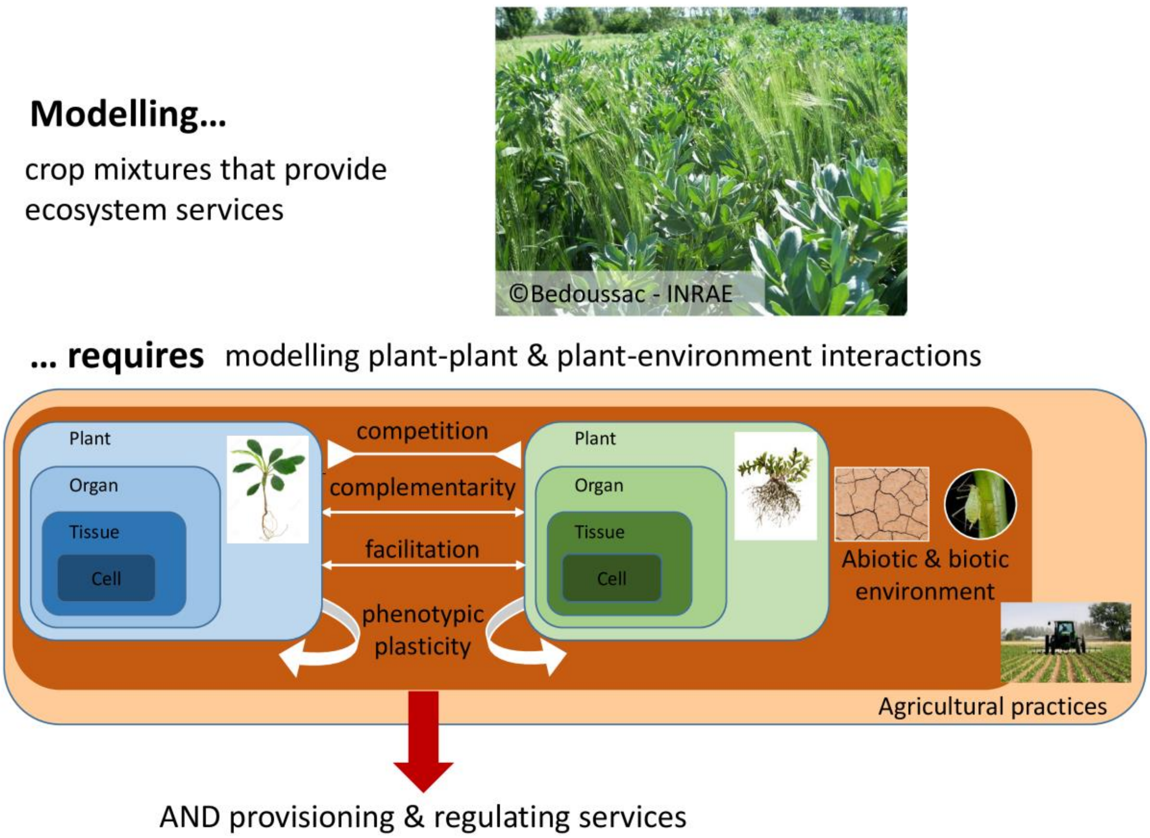

Modelling…
crop mixtures that provide ecosystem services
©Bedoussac - INRAE
… requires modelling plant-plant & plant-environment interactions
Plant
Organ
Tissue
Cell
competition
complementarity
facilitation
phenotypic plasticity
Plant
Organ
Tissue
Cell
Abiotic & biotic environment
Agricultural practices
AND provisioning & regulating services

Figure 2

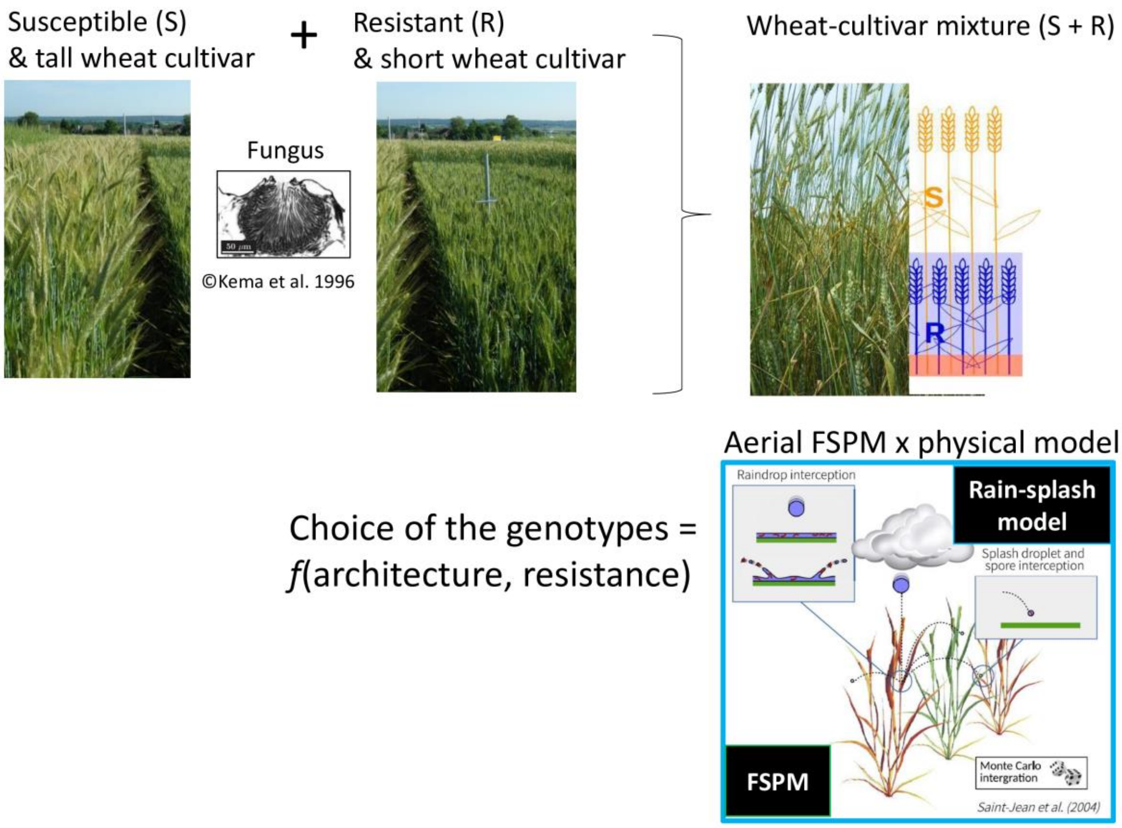
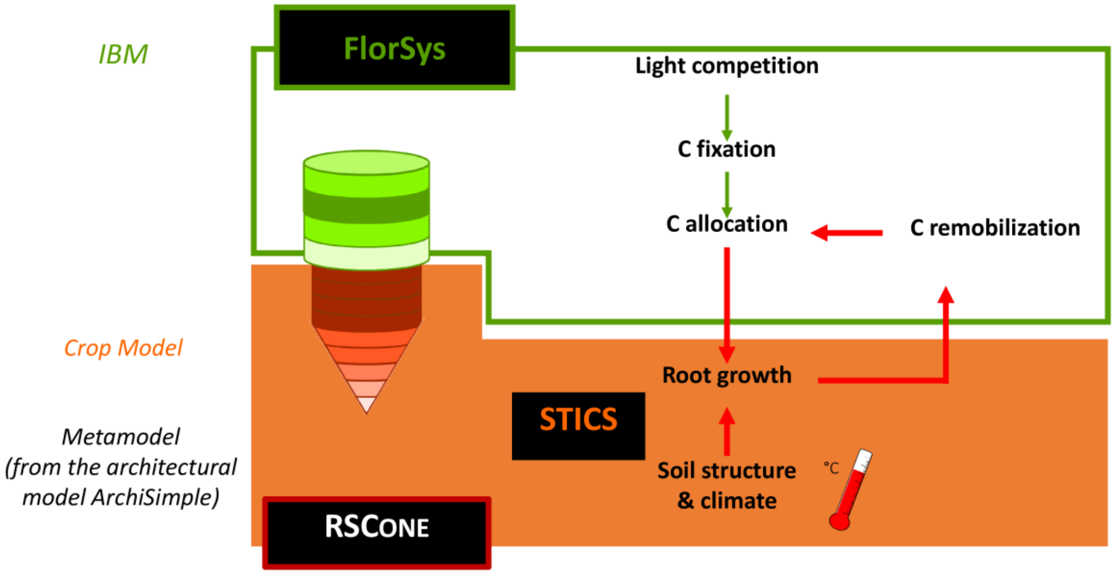
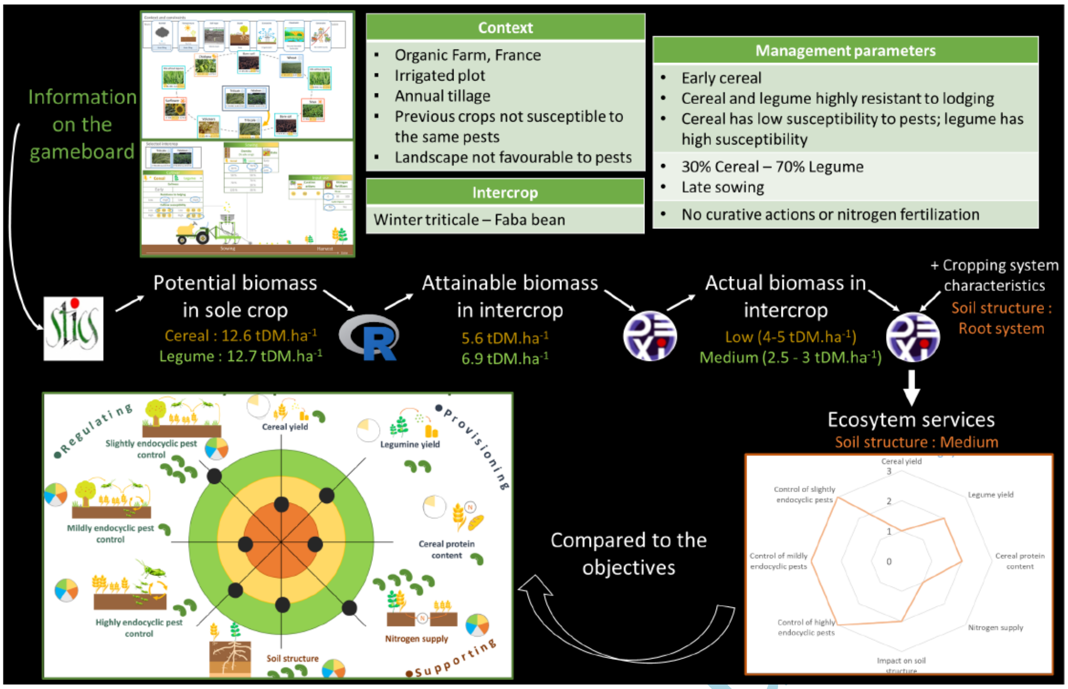

Susceptible (S)
& tall wheat cultivar
+
Resistant (R)
& short wheat cultivar
Fungus
©Kema et al. 1996
Wheat-cultivar mixture (S + R)
S
R
Choice of the genotypes =
f(architecture, resistance)
Aerial FSPM x physical model
Raindrop interception
Rain-splash model
Splash droplet and spore interception
FSPM
Monte Carlo intergration
Saint-Jean et al. (2004)

Figure 3


IBM
FlorSys
Light competition
C fixation
C allocation
C remobilization
Root growth
Crop Model
STICS
Soil structure
& climate
°C
Metamodel
(from the architectural
model ArchiSimple)
RSCONE

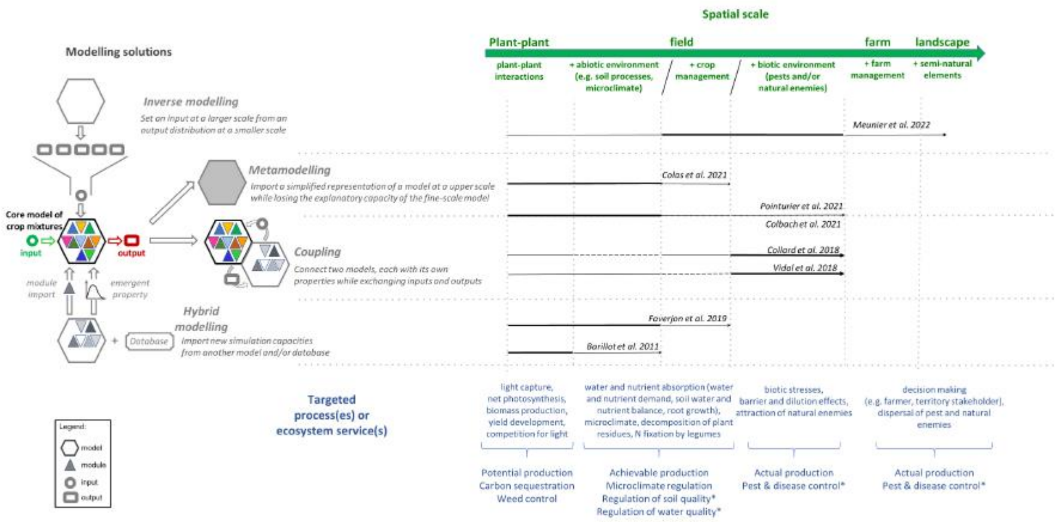
357 Figure 4



358

359

Figure 5



Modelling solutions
Inverse modelling
Set an input at a larger scale from an output distribution at a smaller scale
Metamodelling
Import a simplified representation of a model at a upper scale while losing the explanatory capacity of the fine-scale model
Core model of crop mixtures
input
output
Coupling
Connect two models, each with its own properties while exchanging inputs and outputs
module import
emergent property
Hybrid modelling
Database
Import new simulation capacities from another model and/or database
Legend:
model
module
input
output
Targeted process(es) or ecosystem service(s)
Spatial scale
Plant-plant
field
farm
landscape
plant-plant interactions
+ abiotic environment (e.g. soil processes, microclimate)
+ crop management
+ biotic environment (pests and/or natural enemies)
+ farm management
+ semi-natural elements
Meunier et al. 2022
Colas et al. 2021
Pointurier et al. 2021
Colbach et al. 2021
Collard et al. 2018
Vidal et al. 2018
Faverjon et al. 2019
Barillot et al. 2011
light capture, net photosynthesis, biomass production, yield development, competition for light
water and nutrient absorption (water and nutrient demand, soil water and nutrient balance, root growth), microclimate, decomposition of plant residues, N fixation by legumes
biotic stresses, barrier and dilution effects, attraction of natural enemies
decision making (e.g. farmer, territory stakeholder), dispersal of pest and natural enemies
Potential production
Carbon sequestration
Weed control
Achievable production
Microclimate regulation
Regulation of soil quality*
Regulation of water quality*
Actual production
Pest & disease control*
Actual production
Pest & disease control*