



Biotic stress and yield stability in English organic silvoarable agroforestry

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Abstract

In-field trees are thought to buffer arable crops from climate extremes through the creation of microclimates that may reduce the impacts of heat, wind, and cold. Much less is known about how trees and their biotic interactions (e.g. with natural enemies of pests and wild understory plants) impact crop yield stability to biotic stresses such as crop pests and disease. Modelling these interactions using conventional approaches is complex and time consuming, and we take a simplified approach, representing the agroecosystem as a Boolean regulatory network and parameterising Boolean functions using expert opinion. This allies our approach with decision analysis, which is increasingly finding applications in agriculture. Despite the naivety of our model, we demonstrate that it outputs complex and realistic agroecosystem dynamics. It predicts that, in English silvoarable, the biotic interactions of in-field trees boost arable crop yield overall, but they do not increase yield stability to biotic stress. Sensitivity analysis shows that arable crop yield is very sensitive to disease and weeds. We suggest that the focus of studies and debate on ecosystem service provision by English agroforestry needs to shift from natural enemies and pests to these ecosystem components. We discuss how our model can be improved through validation and parameterisation using real field data. Finally, we discuss how our approach can be used to rapidly model systems (agricultural or otherwise) than can be represented as dynamic interaction networks.

Keywords Agroforestry · Silvoarable · Crop yield · Agroecology · Boolean regulatory network

1 Introduction

The interaction of trees with arable crops (as seen in silvoarable agriculture) has largely been modelled as a process of biophysical competition. Trees compete with crops for light, nutrients, and water and are usually thought to reduce crop yield while potentially buffering it against the impacts of extreme climate (Nasielski et al. 2015; Reyes et al. 2021). This is reasonable, but of equal or more interest to farmers and society generally are the living things that trees attract and interact with (the biotic interactions) and how these impact the dynamics and stability of the agroecosystem. There have been empirical studies on this topic (Pumariño et al. 2015; Staton et al. 2019, 2021), but modelling investigations are lacking because of the complexity of the interactions between crop yield and the biological assemblages with which crops interact. Consider, for example, the system we model here (Fig. 1 and 2) consisting of trees, their major biotic interactions in the agroecosystem, and the impacts of these interactions on arable crop yield. Modelling such a system by conventional means would

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Fig. 1 Oats growing between willow coppice at Wakelyns Agroforestry in Suffolk, England. An example of organic silvoarable agroforestry (Smith et al. 2024). ©Organic Research Centre

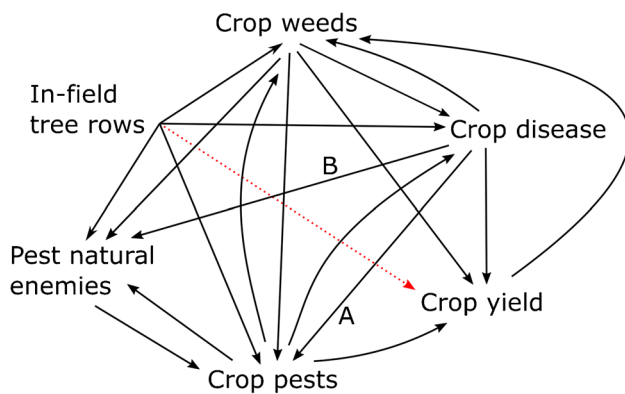


Fig. 2 A network diagram showing the agroecosystem modelled. Nodes contain the principal ecosystem components considered, and edges (arrows) show the influence of nodes on each other. Arrowheads show the direction of influence. The red arrow is the direct influence of trees on crop yield. This is the subject of major biophysical models of agroforestry and is systematically omitted from the current model. Lettered edges were included only after studying the literature (see main text for more details on literature)

require the development of numerous field-parameterised, time-dynamic equations with each a complex function of several other ecosystem components. This is not impossible (see Dahood et al. (2020)) but a formidable empirical and analytical task, especially given the inherent stochasticity of most ecological systems, that limits the number of systems such techniques can be applied to (Luedeling et al. 2016).

Here, we make two major compromises to make the analysis of dynamic interaction networks more accessible, hopefully allowing the modelling of more real-world systems and providing analytical capacity to more people like farmers that depend on such systems. We firstly assume that

each network component (or “node” to use graph theory terminology) can only exist on one of two states: high or low, good or bad etc. Time dynamic relationships between nodes therefore become much simplified, and Boolean formulas are embodied in what are called truth tables (Kauffman 1969, 1993). In their simplest non-probabilistic form, such networks are known as Boolean regulatory networks (Kauffman 1969, 1993). In their probabilistic form used here (see Methods Section 2.2 for more information), they are known as probabilistic Boolean regulatory networks (Shmulevich et al. 2002) and are amenable to Bayesian approaches, which we nevertheless do not use (see Methods Section 2.2 for explanation). The second major compromise we make is to allow experts to parameterise these much simplified Boolean formulas. The use of probabilistic, expert-driven approaches allies our technique with decision analysis which is beginning to find application in agriculture (Hardaker and Lien 2010; Luedeling and Shepherd 2016).

This paper is partly a showcase for the application of Boolean regulatory networks to agroforestry, agriculture, and wider real-life dynamical network systems. Thus, we keep network nodes generic (“crop disease” rather than “BYDV (barley yellow dwarf virus)” or *Septoria tritici*), and we show that ecological dynamics simulated by such simplified means can be complex and realistic. The paper also addresses a more specific issue of great relevance to agriculture under climate change: namely the issue of trees, their biotic interactions, and crop yield stability in the face of biotic disturbance. As introduced briefly above, trees, through their biophysical interactions with crops, are thought to increase crop yield stability, albeit at the expense of overall yield (Nasielski et al. 2015; Redhead et al. 2020; Reyes et al. 2021). This is assumed to be due to shade and favourable microclimatic effects in extreme heat or protection from frost in the cold (Lasco et al. 2014; Nasielski et al. 2015; Reyes et al. 2021). Predicting patterns of biotic disturbance (e.g. crop pests and disease) of agroecosystems under climate change is extremely challenging, and it is difficult to generalise on the frequency and extent of extreme events in a way that can be done for numerous climatic variables. Nevertheless, crop pests and disease dynamics are likely to be *different* from current patterns, with geographic range expansions expected (Sutherst et al. 2011), and agricultural systems that are robust to these uncertain patterns of biotic disturbance are likely to be advantageous. Furthermore, even without climate change, agroecosystem resilience (of which yield stability is one component) is an important property, especially in organic agriculture which has fewer means to intervene during pest and disease outbreaks.

We hypothesise that the introduction of trees into arable cropping increases the stability of arable crop yield due to the numerous organisms (natural enemies, wild understory plants etc.) that they bring with them and the assumed

relationship between biodiversity and ecosystem stability (McCann 2000; Dardonville et al. 2022). We wish to be explicit that we do not study “resilience” of the agroforestry system here. Resilience is a whole system property and we only study one component of it: arable crop yield stability or arable crop yield at harvest following biotic disturbance. A system with high yield despite biotic challenge indicates a system with high yield stability. To test the hypothesis that agroforestry promotes higher crop yield stability, we develop a model of English, organic silvoarable, examine whether the model reproduces intuitively realistic dynamic interactions between ecosystem components, and compare the impact of biotic stress on yield in systems with and without trees. We carry out a sensitivity analysis to identify the most important components driving crop yield. Finally, we propose ways in which our model can be validated and parameterised using field data and extended to other systems that can be represented as dynamic interaction networks.

2 Methods

2.1 Boolean regulatory network modelling (BRNM)

BRNM was first introduced in the 1960s by computer scientist Stuart Kauffman with the purpose of modelling the regulatory control and temporal dynamics of gene expression (Kauffman 1969), and use of this model has largely been restricted to this area ever since. Strictly speaking, however, BRNs are just very stripped back models of dynamic networks and seem amenable to applications outside genetics so long as network nodes (to use graph theory terminology) can reasonably be described in only two states (on-off, good-bad, high-low, etc).

The networks represented in BRNM can be considered as consisting of a number of nodes (“genes” or “agroecosystem components” such as trees, weeds, and pests in the current application) and edges that represent the influence of nodes on each other. As just alluded to, a key feature of BRNMs is that nodes can only exist in one of two states at any given time. BRNMs operate algorithmically to model the temporal dynamics of network node expression state (Kauffman 1969, 1993). In each time iteration of the model, each node is assessed in relation to the current state of all other nodes that influence it, i.e. through network edges. Each node has a “truth table” associated with it. This is a table of all possible states of other influencer nodes and the state that the focal node should assume for each possible combination in the next time iteration. All nodes are updated to enter the next time iteration, and the whole process is repeated over the specified number of time iterations of the model.

2.2 Special components and a general description of the current BRNM

The type of applications we consider here where BRNMs are applied to model systems outside gene regulatory modelling, we term generalised Boolean regulatory network modelling or GBRNM. There are three main areas where the current application differs fundamentally from the classic BRNM described in Section 2.1. Firstly, we use probabilistic truth tables. Thus, rather than stating: “if influencer node 1 is in state 1 and influencer node 2 is in state 0, I should assume state 0 in the next time iteration” (as in the classic BRNM model), we state “if influencer node 1 is in state 1 and influencer node 2 is in state 0, I should assume state 0 in the next time iteration with a given probability”. This probabilistic Boolean regulatory network modelling approach is well characterised (see Shmulevich et al. 2002 for a mathematical description of probabilistic Boolean regulatory networks) and makes networks amenable to Bayesian approaches. Readers who are interested in knowing more about the similarities and differences between probabilistic Boolean regulatory networks and Bayesian networks should refer to Shmulevich et al. (2002) and Lähdesmäki et al. (2006). We do not undertake a classic static Bayesian network analysis here as we are interested in temporal network dynamics (not classically a concern of Bayesian modelling), and we analyse network behaviour after a relatively short number of time iterations (maximum 26, representing the 26 weeks of English Spring-Summer-Autumn crop growth) in a far-from-terminal state. It should be noted, however, that time dynamic Bayesian networks have been developed and certain subsets of these behave similarly to probabilistic Boolean regulatory networks (Lähdesmäki et al. 2006). Thus, whether the current model is described in the terminology of the dynamic probabilistic Boolean network or dynamic Bayesian network (e.g. “truth table” vs “conditional probability table”) may largely be down to the background and preferences of the author/s.

The probabilities alluded to above are determined by human experts in a process described further below in Section 2.3.2. This use of carefully considered human opinion to allocate truth table probabilities relates to the second fundamental difference of our current application to the classic BRNM. Whereas Kauffman (1969, 1993) was careful to randomise system structure (he was interested in how gross biological system structure *per se* can generate behavioural order in that system), here we are highly systematic in ordering network edges and truth table structure to represent a specific ecological system. Details of this process are given below in Section 2.3.1 and Section 2.3.2.

Lastly, classic BRNMs give no consideration to the current state of the focal node during the update process when determining that node’s next state. Here, however, we do

consider a focal node's state during updating, and transition probabilities are calculated for nodes in both states. This was necessary due to specifics of the system (an agroecosystem) we are modelling. In particular, processes such as plant disease seem particularly "asymmetric" in their dynamics: given the presence of a pathogen, plants can acquire that pathogen and it can spread relatively rapidly among the crop, but, once established, the likelihood of a pathogen diminishing in incidence without intervention to insignificance is relatively low. Future expression state of gene is not considered to be dependent on the gene's current state, but it is likely that in many ecological networks, this assumption of independence of node temporal state will be untrue.

2.3 Specifics of the GBRNM agroecosystem model

2.3.1 The agroecological network

A network diagram of the system modelled is shown in Fig. 2. It shows the influence of in-field trees on arable yield, mediated through the biotic (living) components of the agroecosystem. We appreciate that "yield" is a late season phenomenon for many crops while we model and ask expert reviewers (see Section 2.3.2) to envision crop growth across the whole of the English spring-summer-autumn growing season. We use the term "crop yield" for convenience in the main text of this paper, while using the more encompassing term "crop growth/yield" in the data collection exercise with experts. The direct influence of trees on arable crop yield is well studied using major biophysical models of temperate agroforestry such as Yield-SAFE (van der Werf et al. 2007) and Hi-sAFe (Dupraz et al. 2019) and has the potential to obscure biotic effects in the current model. The direct influence of trees on arable crop yield is therefore systematically omitted from the current model. The effects of trees on crop yield demonstrated in this current study, therefore, represent effects that might be expected from trees and their biotic interactions in the artificially constructed absence of all biophysical competitive processes between trees and the arable crop (such as competition for light, water, and nutrients). Edges were omitted from the Diagram (Fig. 2) if an influence between nodes seemed tenuous to the authors from their knowledge, and they were included if they seemed obvious. A few edges lay between these extremes and were included only after careful study of the literature. In particular, the influence of crop disease on crop pest behaviour was only included after reviewing the evidence of Donaldson and Gratton 2007; Moreno-Delafuente et al. 2013; Su et al. 2015, and the influence of crop disease on natural enemies of pests was included following Gross (2016) who demonstrated that natural enemies of pests can respond to changes in leaf volatile profiles due to plant pathogen infection. It should be noted that in-field trees are assumed to influence numerous

agroecosystem components but are not influenced by them in turn. This is a convenience to simplify the connective architecture of the network and so reduce expert effort in parameterizing the model (see below). However, it does also reflect the current tendency in agroforestry research to consider trees as ecosystem service providers rather than service receivers. Another way of describing this convenience is that "in-field trees" is the only static node in the network whose state does not change during the course of simulations unless through manipulation by the modeler. Lastly, we decided to omit pollinators from the interactions network. Again, this was done partly to simplify the network but also because we wanted the system modelled to reflect as broadly as possible English arable agriculture, which is dominated by cereals that do not require insect pollinators. It should be borne in mind, however, that benefits of trees for arable crop yield shown in this paper are likely to be conservative relative to the benefits of trees and their understory in association with pollinator-dependent crops (Castle et al. 2019; Staton et al. 2019).

2.3.2 Parameterizing truth tables using expert opinion

There are models and methods of fitting specific ecological systems to model interaction networks based on more conventional time-dynamic equation approaches (e.g. see Dahood et al. (2020)), but they are typically complex and require long-term datasets on the incidence of the organisms involved. The authors' experience of interacting with farmers and agricultural researchers and policymakers suggests to us that there are numerous agricultural systems where stakeholders could benefit from an easily and rapidly developed "brushstrokes" model of the dynamics of the system to assist in planning and decision-making. Here, we propose GBRNM with expert parameterisation of time-dynamic model elements as a potential framework to fill that gap. A key to this approach is the reduction of possible node states to two. All but the most accomplished mathematician would find it impossible to parameterise a multivariate differential equation linking future node state to current and influencer node state, but reducing possible node states to two makes this task of future node state prediction based on current states feasible. In the current network, the "crop weeds" node, for example, can exist in two states ("high or "low"), and it is influenced by four other nodes (Fig. 2) that can each also exist in two states. In the algorithmic implementation of our model, that means that 2^4 influencer node states in combinations with the two weed states (a total of 32 combinations) must be assessed by experts to predict the state of weeds in the next model time step for any given combination of influencer and focal node states. By similar reasoning, 16 combinations must be assessed for crop disease, 16 for yield, 32 for crop pests, and 32 for natural enemies of pests: A total

of 128 system states that must be assessed by experts and future state (1 week, 2 weeks, and 1 month in the future) of focal nodes predicted.

Experts predicted different durations into the future (and subsequently ran models at these three different timesteps) because we felt that changes in different ecosystem components are likely to occur on different timescales. For example, many natural enemies of pest arthropods can smell the pests or the infested plants and will aggregate at the pest infestation rapidly. Such effects will operate at the relatively fine weekly timestep we use. Newly germinated weeds growing in a crop that is growing poorly, on the other hand, may still be relatively small and not considered serious issue in one week, but in a month, they are likely to be competing with the crop and considered serious. This type of dynamic would be more relevant to the monthly timestep used. Generally, we found that model network dynamics were qualitatively similar regardless of iteration period, with the long iteration model typically showing slightly larger effects when they existed (see Section 3). Most of our presentation in the main text focuses on the most conservative model run at weekly time iterations, but a full analysis of models is presented in the Supplementary Information.

The spreadsheets given to experts in this study in which these various combinations of agroecosystem components are represented are shown in Supplementary Dataset 1. Before this exercise could be completed by experts, however, there were numerous questions on the ecological system considered that needed to be clarified: What type of agricultural system is it (high-input vs organic)? What type of agroforestry system is it when in-field trees are present and how is it managed? Where in the world is the agroecosystem located? What do “high” and “low” mean when applied to agroecosystem component states? What are the precise definitions of each agroecosystem component? All these questions are addressed in a “setting the scene” passage of text that is presented to each expert in the spreadsheet before they begin to complete the predictive exercises. The passage is reproduced here:

“The tables below should be completed by imagining an English, organic, arable cropping system with and without agroforestry. Where agroforestry is present, it is in the form of a typical alley cropping system with in-field tree rows and crop strips in between. The crop within strips comprises only one crop species, and it is of the herbaceous, annual type typical of English agriculture. It can be assumed that this crop is not dependent on insect pollination. Tree rows can be assumed to have non-cropped understories that are maintained but not augmented in any way: Grasses and other wild plants grow as they establish. The system without agroforestry is of the same overall field dimensions, but trees and understories are no longer there and are replaced by crop, i.e. an organic monocropped field. Crop growth is assumed

to occur during the English spring-summer-autumn growing season. “High” and “Low” in the tables below should be interpreted in terms of what would be satisfactory to the grower: a high level of crop disease or pests would be considered unsatisfactory to the grower, but a low level would be considered satisfactory. A high level of crop growth/yield, on the other hand, is considered satisfactory to the grower but a low value unsatisfactory. Assume the grower makes no intervention to address any pest, disease, and weed issues. Note that “Crop pests” (insects and other animals that eat the crop) are distinguished from “Crop disease” (crop ailments caused by microorganisms). “Crop” refers to the arable crop in between tree rows, not any “crop” that may be produced by the trees (timber, fruit, nuts, etc.)”

Blocks of scenarios within spreadsheets were randomised for each expert as were rows within blocks. Column headings of influencer nodes within blocks were also randomised between experts. All such measures were taken to ensure that effects such as expert fatigue did not impact particular treatments disproportionately. To feed into model simulations, all transition probabilities produced by the four experts were averaged to produce a consensus dynamic network; however, specifics of expert predictions (including inter-expert variation in opinion) were subject to statistical analysis (see Section 2.3.3). Experts were asked to produce transition probabilities for each ecosystem component, 1 week, 2 weeks and 4 weeks in the future.

The four experts who complete the truth table exercises were the authors of the current paper. TS and AC were completely naïve as to the purpose of the spreadsheet exercise and wider study at the time of completing spreadsheets. WS was partially naïve (CRT described the model he was working on in conversation), and CRT was fully aware of the purpose of the spreadsheet and wider study. Short biographies of experts can be found in the Supplementary Information.

Future work will aim to include experts beyond the professional agricultural research community, such as farmers themselves, and could potentially analyse impact of professional background on attitudes displayed within truth tables. Here, potential differences in the opinion of experts were analysed statistically as a random effect, as described in the next section. Spreadsheets took each expert several hours to complete. It should be noted by readers interested in using the modelling framework described in this paper to model their own system that systems with more nodes than ours are likely to represent an unrealistic burden on expert time unless their network is of lower connective complexity (see Fig. 2).

2.3.3 Specifics of simulations and analysis

Simulations and their analysis The current application of the model investigated the indirect role of trees (realised through

biotic intermediates) on arable yield and arable yield stability to biotic stress such as sudden increases in plant disease or pest incidence. Presence or absence of trees was therefore systematically manipulated. Excluding this factor, there were 32 possible network starting states, and “crop yield performance” was assessed for each starting state and summarised across all 32 using means and 95% CIs, with treatment comparisons undertaken using independent sample *t*-tests. “Crop yield performance” was defined as the proportion of crop yields showing satisfactory/high (i.e. = 1) at 6 months or model time iteration 26 (1 week model time iteration), 13 (2 week), and 6 (1 month), assessed over 1000 stochastic simulation repeats.

A sensitivity analysis was undertaken to determine which ecological component of the agroecosystem the GBRNM model was most sensitive to. A value of 0.05 was added to each transition probability for each agroecosystem component in the model, and the impact on crop yield was analysed only for the 1-week time iteration model. (Note that the converse operation of subtracting 0.05 from each transition probability could not be undertaken due to the low absolute value of some probabilities.)

Expert opinion and its analysis Experts analysed a long list of combinations of agroecosystem components (“agroecosystem components” are the nodes of Fig. 2), with each described as being in either a high or low state (present/absent in the case of in-field trees). For each combination, they then looked at the current state of a different focal agroecosystem component and predicted its likelihood of changing state within one week, 2 weeks, and 4 weeks’ time, given the current state of the other components of the agroecosystem. As each focal agroecosystem component was assessed in both a high and low state, we produced two sets of data that were analysed separately: one for low to high transition probabilities of the focal agroecosystem component and one for high to low transition probabilities. These transition probabilities were analysed with a linear mixed model statistical framework with presence/absence of in-field trees and agroecosystem component (crop weeds, crop disease, crop pests, natural enemies of pests—crop yield was not included as the direct influence of trees on it was removed from the network model) as fixed effects and the identity of the expert as a random factor. The interaction between fixed effects was also included in the model.

Expert opinion on transition probabilities of each of the network nodes was analysed using linear mixed models in R (Version 1.4.1717). Impacts of trees and agroecosystem component/node were analysed as main effects and in interaction, with expert identity considered a random effect. The significance of the random effect was assessed using the likelihood ratio test in R using the aforescribed mixed effects model with random effect term, and the same model

without the random effect term. Effect sizes were calculated as Hedge’s *g* which is preferable to Cohen’s *d* in samples below 20 in size (Lakens 2013). The Supplementary_Data_2 package accompanying this article contains all code and data used to run statistical tests. R code used to run the main Boolean model is included as Supplementary_Code_File_1.

3 Results

3.1 Some examples of the dynamics produced by a GBRNM model of an agroecosystem

Before we can use the GBRNM to generate predictions on how trees impact stability of arable crop yield to biotic shock, it is firstly necessary to demonstrate that the model outputs meaningful, intuitively reasonable dynamics. GBRNM is a new method for modelling ecological networks and has no prior record in this area. This issue may be particularly relevant for Boolean networks as the deterministic, rule-randomised form of these networks (not used here) displays strong attractors that could conceivably impact network dynamics. Here, we analyse network dynamics over a number of relevant scenarios, but it should be noted that wider adoption of GBRNM will require comparison with other forms of systemic modelling, more extensive appropriate sensitivity analysis, and field validation.

We chose one of a possible 32 starting scenarios for these simulations: a likely common starting scenario where all ecosystem components except crop yield/growth are at low levels. To make interdependencies easier to visualise, we additionally perturbed the system between weeks 8 and 12 with a period of high crop pest and disease incidence (simulated by assuming all simulations displayed high (=1) levels of these ecosystem components during that period). This “open” type of system where dynamics are subject to external perturbations is examined further in subsequent sections. In-field trees were also assumed present.

Crop disease, crop weeds, and crop pests (and the natural enemies that prey on them) all increased from very low initial levels as would be expected in an English organic arable system at the start of the spring-summer-autumn growing season, and there was a concurrent drop in crop yield (Fig. 3A and B, weeks 1–7). With the introduction of a 4-week pest perturbation (landmark 1 in red in Fig. 3A), there was a rapid increase in natural enemy numbers (landmark 2, Fig. 3A) that prey on the pests and a small increase in plant disease (landmark 3), presumably due to a perception among the experts who parameterised the model of pests as vectors of plant disease. Due to landmarks 1 and 3, crop yield fell at an increasing rate when a pest perturbation was introduced (landmark 4) but tailed off at a low terminal

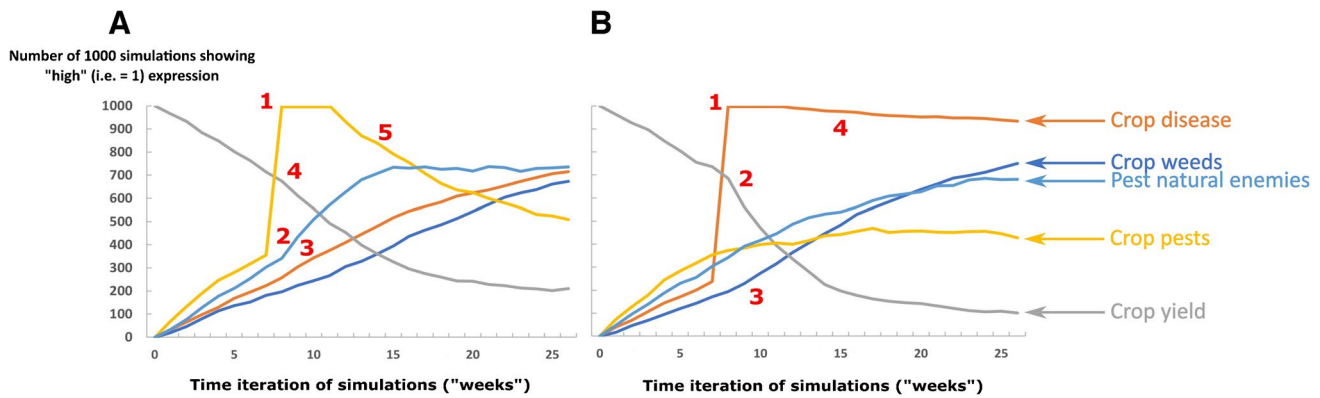


Fig. 3 Dynamics of two example simulations run at weekly time iterations in which external crop pest (A) and crop disease (B) perturbations are introduced between weeks 8 and 12. Both simulations assume trees are present. Lines in the graph describe the state of each network node in Fig. 2, quantified as the number of 1000 simulations showing the 1 or “high” node state at each time interval. Only one of a possible 32 starting states for simulations are shown here, in which

value as weeds and diseases asymptoted at their high terminal value. It should be noted that, due to the build-up of natural enemies during the pest perturbation event, when the pest perturbation ended, natural enemies remained at high levels and pest numbers fell rapidly (landmark 5), presumably elevating terminal crop yield above that expected in the absence of natural enemy proliferation.

When the system was perturbed with high levels of crop disease for four time iterations (Fig. 3B, landmark 1), there was a rapid and extensive drop in crop yield (landmark 2), suggesting the primacy of disease in the dynamics of this system (confirmed in later simulations, Section 3.5). This drop in crop vigour was such that it allowed weeds to proliferate (landmark 3). Weeds and a continued high rate of plant disease after the end of perturbation (as might be expected if plant disease is left untreated, landmark 4) ensured that the crop arrived at a state of very low yield at the end of the growing season.

Therefore, while we have not used field data to construct the model and have not compared its dynamics to real data, many aspects of the model’s dynamics are intuitively sensible and, at the very least, the model represents an effective exploratory model for preliminary system manipulation and analysis.

3.2 The impact of the biotic interactions of in-field trees on arable crop yield

Simulations with and without trees were run across all 32 possible system starting states, and yield ($n = 32$ for means and 95% CIs) after 6 months or iteration 26 (1 week model time iteration), 13 (2-week time iteration), and 6 (1 month time iteration) was analysed (Fig. 4). Trees and their biotic

all ecosystem components except crop yield/growth start at low levels. Numbers shown next to lines within plots describe landmarks in the dynamics of ecosystem components and are referred to in the main text (paragraphs 3 and 4 of Section 3.1). In both plots, “1” is the start of the 4-week artificially induced biotic stressor, and the other numbers are phenomena consequent of this action.

interactions increased crop yield. In simulations run at weekly time iterations (Fig. 4A), this was not significant at $\alpha = 0.05$ ($P = 0.08$), but it is clear that the size of this effect was depressed by the half of simulations where plant disease was high at the beginning of simulations and where crop vigour is expected to be depressed regardless of the state of other agroecosystem components. In the half of simulations that did not start with high levels of plant disease (within the curly brackets of Fig. 4A), trees conferred a clear yield advantage. The statistical probability of tree vs no tree effects on crop yield across all starting states was below 0.05 in simulations run at 2-week and 1-month time iterations (Fig. 4 B and C).

3.3 In-field trees and arable crop yield stability to biotic shock

The model was subject to a pest perturbation between time iterations 8–12 (one week time iterations), and its ability to maintain crop yield in the face of this challenge was analysed as a measure of yield stability. This same scenario was investigated above (Section 3.1) for 1 of 32 model starting states in the presence of trees (Fig. 3A and B). Here, we expand this analysis across all possible 32 starting states of the model and all time iteration variants of the model and investigate dynamics with and without in-field trees.

Trees made no significant difference to the amount that crop yield performance fell when subject to a pest perturbation (Fig. 5A3), and trees had little impact on the final value (iteration/week 26) of crop yield performance in the presence of pest perturbation (Fig. 5A4). In other words, trees did not increase crop yield stability to a biotic shock in the form of a crop pest.

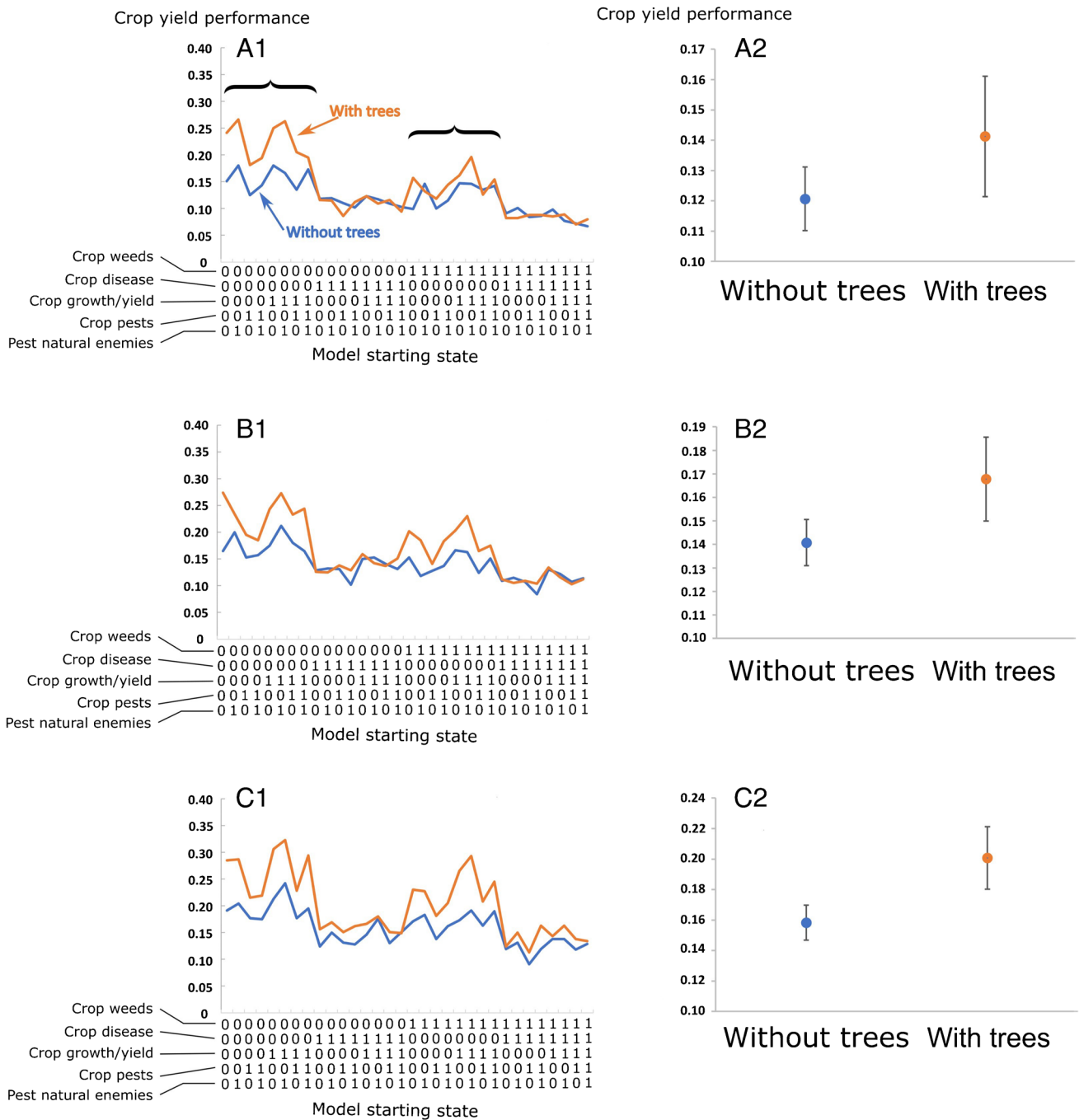


Fig. 4 Crop yield performance after 26 (1 week model time iteration) (A1–A2), 13 (2-week time iteration) (B1–B2), and 6 (1 month time iteration) time iterations (C1–C2) of the model with (orange) and without (blue) in-field trees. Yield means are quantified in A–C part 2 across all 32 starting states of simulations as means and 95% CIs and analysed using t-tests. Simulation starting states are shown by the binary grid with 1 representing “high” and 0 “low.” Agroecosystem components represented by each row in the grid are shown in the first

plot of (A). The y-axis “Crop yield performance” is the proportion of 1000 simulations that showed yield in a “high” state at the end of the simulation period. Curly brackets contain simulations that were not begun with high levels of plant disease. Note that the use of lines joining points in plots A1–C1 does not indicate a series. Data in plots A2–C2 are means ± 95% CIs, $N = 32$. A2 – $t = -1.77$, $df = 47.1$, $P = 0.0835$. B2 – $t = -2.56$, $df = 48.2$, $P = 0.0138$. C2 – $t = -3.49$, $df = 48.6$, $P = 0.00102$.

Crop yield performance fell less in the absence of trees when the system was subject to a crop disease perturbation over the same period as above (Fig. 5B3); however,

this simply reflects the fact that crop yield performance is higher in the presence of trees (see previous section). Trees made no difference to the final level of crop yield with crop

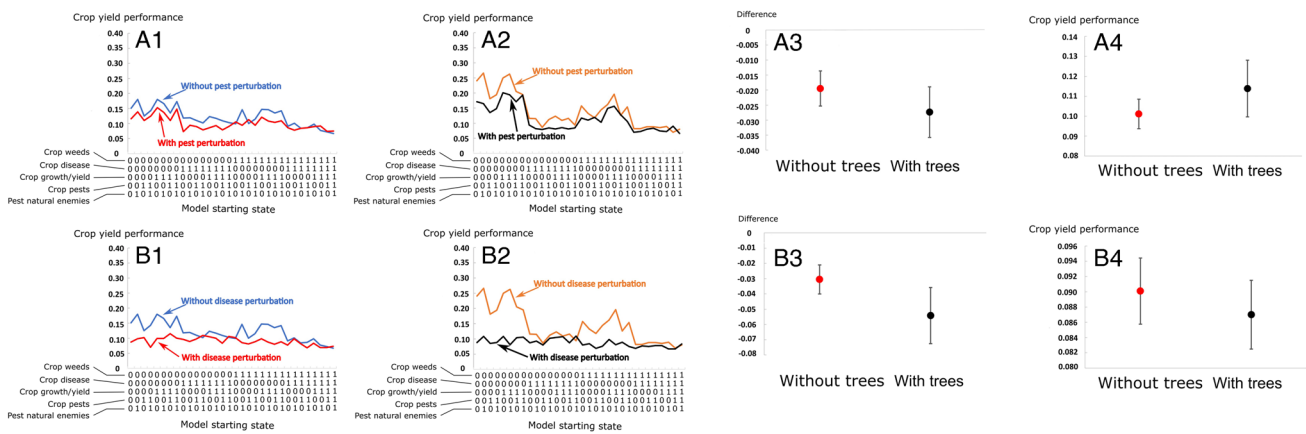


Fig. 5 Crop yield performance after 26 (1 week model time iteration) time iterations of the model with and without in-field trees, where the system is additionally subjected to a crop pest and crop disease perturbation between iterations 8 and 12. Plot A1 shows the difference in yield performance with and without pest perturbation in the absence of in-field trees. A2 is equivalent but with in-field trees. Plot A3 shows the average difference between with and without pest perturbation (plots A1 and A2) in the absence and presence of in field trees.

Shown are means \pm 95% CI, $N = 32$. Plot A4 is the average yield performance with pest perturbation, without trees and with trees. Shown are means \pm 95% CI, $N = 32$. Plots B1–B4 are equivalent to A1–A4 but show response to crop disease perturbation. Additional figure details are as Fig. 4. Note that the use of lines joining points in plots A, B, E, and F does not indicate a series. $A3 - t = 1.48$, $df = 55.2$, $P = 0.144$. $A4 - t = -1.53$, $df = 46.6$, $P = 0.133$, $B3 - t = 2.21$, $df = 46.4$, $P = 0.0323$.

disease perturbation (Fig. 5B4). Again, trees do not appear to increase crop yield stability to biotic shock.

These analyses were repeated for simulations run over 13 (2-week time iteration) and 6 (1 month time iteration) time iterations. Results are shown in the Supplementary Information (Fig. S1 and Fig. S2). The findings were similar to those above but with larger effects as the number of iterations decreased. In the case of simulations with 1-month time iterations, trees did result in a higher final yield performance with pest perturbation (Fig. S2). This represents the only evidence that trees may improve crop yield stability to pest shock. There is no evidence that trees improve crop yield performance to crop disease perturbation. Overall, evidence that trees increase stability of the arable crop yield to biotic shock is scant.

3.4 Analysis of expert predictions used to parameterise the model

Statistical findings are shown in pages 3-8 of the SI with a graphical presentation of the data in Figs. S3-S5.

The impact of trees on transition probabilities was not significant at the $\alpha = 0.05$ level, and there was no interaction of trees with agroecosystem component. Thus, the impact of trees was not generally more pronounced when applied to different agroecosystem components. The only term that was consistently significant at $\alpha = 0.05$ was, unsurprisingly, agroecosystem component itself. So, for example, experts considered that natural enemies in a currently high state had a relatively high probability of being in a low state in a week. A diseased crop, on the other

hand, is very unlikely to become un-diseased 1 week later in the absence of intervention (Fig. S3). There was generally little difference in opinion between experts. Four of six statistical tests of this random effect were insignificant at $\alpha = 0.05$. However, expert identity was a significant factor for low to high transition probabilities predicted 2 and 4 weeks in the future.

These findings mean that the statistically significant impacts of trees on crop yield and yield stability shown by the GBRNM are due to effects of small size amplified over numerous ecological components and time iterations. We considered it of value to analyse these small effects of trees in more detail using an effects size approach. In data where predictions were made one week into the future only, we firstly removed expert identity from the visual presentation by averaging across all experts, thus better reflecting the data inputted into the model. Figure 6 and its effects size inset shows that experts consider that trees in English silvoarable have their largest (but still statistically insignificant) effect on disease, followed by natural enemies, then weeds, and then pests. Effect sizes are bi-directional and somewhat predictable in all cases except disease. Here, the opinion of experts on the effects of in-field trees is unidirectional and negative in effect. In other words, experts feel that the transition from high to low crop disease state is less likely in the presence of trees, presumably reflecting a perception that trees and their understory may harbour disease. Experts also feel that disease is less likely to go from low to high in the presence of in-field trees, probably reflecting a perception of in-fields tree rows as a barrier to the spores and insects that carry disease from one part of the field to another.

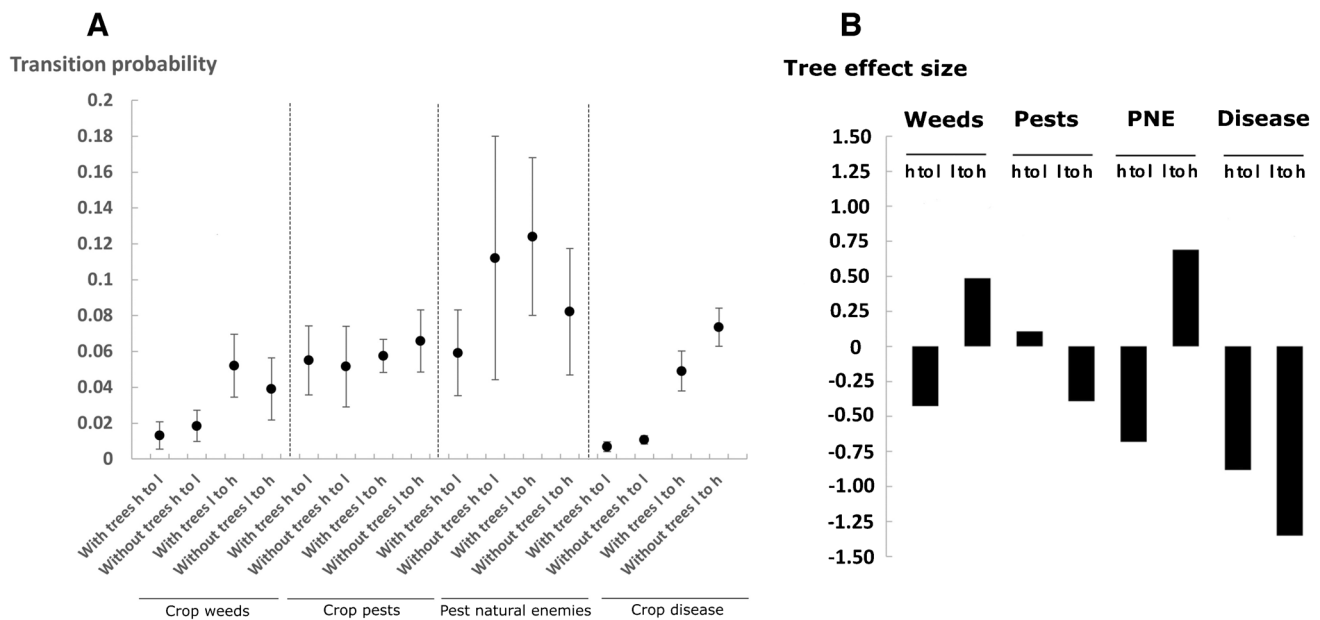


Fig. 6 Impacts of in-field trees on the probability of agroecosystem components transitioning from low to high and high to low states one week later. Results in (A) are shown for the consensus of expert

predictions where probabilities have been averaged across the four experts. Shown are means \pm 95% CI, $N = 8$ or 4 (crop disease). (B) Effect sizes (Hedges G) associated with tree-induced effects in (A).

3.5 GBRNM sensitivity analysis

The findings of the sensitivity analysis are shown in Fig. 7. Modelled crop yield was overwhelmingly most sensitive to plant disease, followed by weeds then pests. The model was notably insensitive to the presence of natural enemies. The presence or absence of trees had little overall impact on the sensitivity of the model.

4 Discussion

4.1 Silvoarable and arable crop yield stability

While there are many studies showing that silvoarable can dampen negative environment extremes (Smith et al. 2013; Lasco et al. 2014), there are few studies that show significant effects of this dampening on arable crop yield, and fewer still that have characterised the relationship between mean yield and its variation through time (stability). It is therefore a priority to characterise the relationship between mean yield and yield stability for both biophysical and biotic components of the agroforestry system because it potentially allows better predictive modelling of the response of arable yield to future environmental conditions. To our knowledge, only two studies have systematically described the relationship between mean arable yield and yield stability through biophysical mechanisms in silvoarable, and they both reach the same conclusion: Agroforestry decreases arable yield but

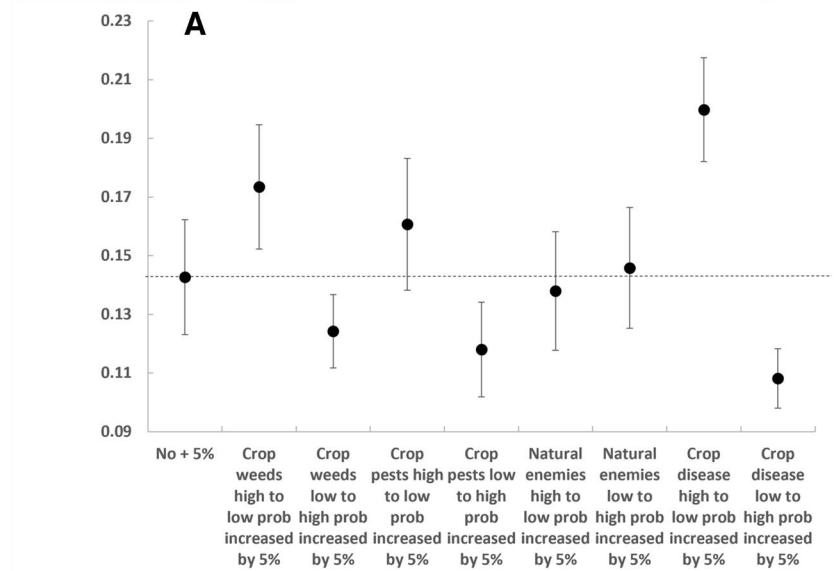
increases yield stability to environmental extremes (Nasielski et al. 2015; Reyes et al. 2021).

The current study suggests that biotic interactions of in-field trees impact the arable yield - yield stability relationship in a different way to Nasielski et al. (2015) and Reyes et al. (2021). They increase arable yield but have no impact on stability. The current model and its findings need to be validated with field studies, but if these predictions are true, it would then seem reasonable to determine if and how they vary year-on-year with climatic conditions in the field, recalling that climatic effects are not incorporated into the current model. Both positive and negative scenarios can be imagined with an increase or decrease in biophysically induced temporal stability and no, positive or negative change to overall yield. Determining the nature of these interactions seems a priority if we are to produce a more comprehensive predictive framework for the impact of agroforestry on the productivity of agricultural systems.

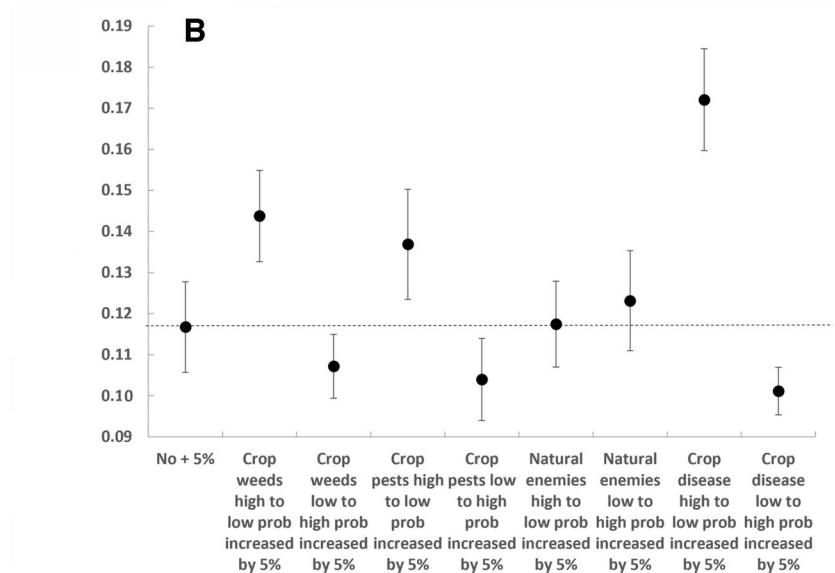
Whilst we found no relationship between biodiversity, in the form of in-field trees and their biotic interactions, and crop yield stability, a positive biodiversity-productivity relationship was demonstrated. This is contrary to some other studies in which biodiversity (of select taxonomic groups such as plants and microbes) is commonly associated with loss of crop productivity in agriculture, a finding that has been central to academic debates of the global value of organic agriculture, which typically promotes biodiversity at the expense of yield (Gabriel et al. 2013; Gong et al. 2022). The positive biodiversity-productivity relationship

Fig. 7 Sensitivity of crop yield modelled using the GBRNM model to an 0.05 change in high to low and low to high consensus transition probabilities associated with each of the agroecological components of the model. Simulations are run with (A) and without (B) trees. The first bar represents the unmanipulated model for comparison. Shown are means \pm 95% CIs, $N = 32$. Differences between means and bars for each component of the agroecosystem show their importance to the dynamics of the GBRNM model.

Crop yield performance



Crop yield performance



in our model presumably relates to the generally reductive impacts of trees on crop pests and disease predicted by experts (Fig. 6; however, note that experts also consider that agroforestry may harbour crop disease), with the model being reasonably sensitive to both ecosystem components (Fig. 7). Field testing of the validity of these predictions would, therefore, seem a priority.

A positive relationship between biodiversity and crop yield stability is commonly observed in arable agriculture (Snapp et al. 2010; Dardonville et al. 2022), contrary to the findings of the current study. It may be that situation of the current study in organic agriculture, which is usually more biodiverse than high-input farming (Hole et al. 2005), may

have persuaded experts that organic monoculture already had sufficient functional biodiversity to maintain a reasonable level of stability and that the addition of in-field trees would make little difference. Alternatively, it should be borne in mind that older syntheses of biodiversity-ecosystem functionality relationships in grasslands, from which current applications in agriculture derived, were conspicuous in emphasising that the positive biodiversity-stability relationship is an on-average response and that ecological networks whose members lack the necessary functional traits may not demonstrate this relationship (McCann 2000; Loreau et al. 2001). There is no reason why this conclusion should not apply in some arable systems.

Our findings also need to be considered in the context of the whole agricultural system or farm. Tree biotic interactions may add little to English arable crop stability but if the farmer makes those trees a significant additional source of income, for example, through fruit or nut harvesting, the losses to arable crops in extreme environmental conditions may be compensated by the relative stability of tree yield. For example, additional income from a high-value fruit crop can more than compensate for a minor reduction in cereal crop yield in agroforestry systems (Staton et al. 2022). Extending this line of thinking, if in-field trees become an integral part of the whole farm economy, as seen in many small-scale and subsistence farms, supplying food and fuel and building materials, then the relative stability and reliability of trees become integral to maintaining whole farm resilience. It is by such mechanisms that small-scale agroforestry farmers in Cameroon strongly feel trees contribute to the ability of the household to withstand the challenges of changing climate (Nyong et al. 2020).

4.2 Importance of natural enemies in temperate arable agriculture and their augmentation through silvoarable agroforestry

One of the most interesting and provocative insights from Section 3 is the difference between expert predictions on the impact of natural enemies and their real impact in the model agroecosystem. Experts parameterising the GBRNM model feel that in-field trees have a relatively (not absolutely) large impact on natural enemies of crop pests and presumably feel that this could be a significant driver of the system modelled. Sensitivity analysis, on the other hand, indicates that natural enemies have very little impact on the dynamics of the GBRNM model, with the model overwhelmingly most sensitive to crop disease.

Why was the initial expert estimation of the impact of natural enemies on crop pest so high, while the sensitivity analysis showed a negligible impact on crop yield? Part of the reason lies in the fact that the debate around ecosystem service provision in England and Europe has become focused on the role of crop pollination, natural enemy augmentation, and crop pest management (Fagerholm et al. 2016; Staton et al. 2019, 2021) at the expense of other agroecosystem components.

The data to address this issue on the relative importance of different biotic components of agroecosystems in English arable does not exist, but we can comment on studies across wider geographic areas and agricultural systems. Oerke (2006) quantified the relative importance of weeds, animal pests (arthropods, nematodes, rodents, birds, slugs, and snails), pathogens (bacteria and fungi), and viruses on wheat yield across 19 world regions. Without intervention, weeds were the most important determinant of

yield (23.0% loss, range 18–29), followed by pathogens (15.6% loss, range 12–20), then animal pests (8.7% loss, range 7–10), and then viruses (2.5% loss, range 2–3). Unfortunately, the author did not quantify the impact of natural enemies, but as they impact animal pests, which are already a relatively minor determinant of crop yield, it is likely that they in turn will be an even less significant determinant of yield. Incidentally, the lower importance of pathogens relative to weeds in Oerke (2006), which contradicts our findings using the GBRNM, can presumably be attributed to the specific temperate silvoarable focus of our GBRNM in which pathogens (especially fungi) assume a greater importance in crop yield dynamics due to the wetter, colder conditions (Fones and Gurr 2015).

Studies of natural enemy augmentation in agroecosystems where impact on crop yield have been quantified can also help deduce the importance of natural enemies as a determinant of crop yield. However, few such studies focus on English arable systems, and research on conservation biological control has primarily focussed on measuring the abundance of pests and/or their natural enemies, while impacts on crop yield are more rarely quantified (Johnson et al. 2021). In Argentinian soybean fields, an approximately 70% increase in arthropod predator abundance due to adjacent woodland lead to an increase in crop yield of around 30% (González et al. 2020). In Dutch winter wheat, flower-rich flower strips caused a 14% increase in natural enemies of pests, but this had a negligible impact on crop yield (Mei et al. 2021). In New York State cabbage fields, augmentative release of natural enemies leading to a 47% increase in larval predation resulted in a 26% increase in crop biomass (Perez-Alvarez et al. 2019). Clearly, the impact of natural enemies on crop yield varies with the system under consideration, but these published findings suggest at least that if augmentative effect of trees or other features are high enough, this can have an impact on yield that is likely to be economically meaningful to the farmer.

To return specifically to English arable system and agroforestry, Staton et al. (2021) observed a doubling of natural enemy counts on apple trees due to the flower-rich understories of tree rows in English cereal agroforestry. Species richness of ground dwelling natural enemies in crop alleys was enhanced early in the growing season, and thrips were less abundant in crop alleys but there was no impact on five other crop pests, indicating that “bottom-up” factors such as plant community diversity and structure can be more important determinants of pest populations than “top-down” natural enemy control (Gurr et al. 2003). Staton et al. (2019), reviewing 12 studies of temperate silvoarable, found that natural enemies are enhanced by around 24% and crop pests decreased by roughly the same amount, but no impacts on crop yield were reported.

Therefore, to answer our initial questions, we believe that the recent focus on the benefits of agroforestry for natural enemy augmentation and pest control has not been misguided. Given a sufficient augmentative effect of trees and their understory on natural enemies, significant impacts on crop yield can be expected. Mechanisms of natural enemy augmentation through floral nectar provision and the provisions of natural enemy egg-laying substrate on and around trees are transparent and easy for farmers to appreciate, and there is a substantial literature on agroforestry and natural enemy augmentation and pest control (see references above and (Pumariño et al. 2015)). Nevertheless, the current GBRNM and the review of Oerke (2006) discussed above indicate that natural enemies are but one biotic determinant of crop yield and not necessarily the most fundamental one. It would seem that a shift in the silvoarable ecosystem service narrative away from natural enemies and pests and towards more fundamental determinants of yield in arable agroecosystems such as weeds and crop disease is due.

4.3 Impact of trees on arable crop disease: what is known?

This modelling study indicates that crop disease is the most important determinant of crop yield in English arable systems and so is likely to be a particularly effective biotic factor to manipulate through in-field tree rows. Unfortunately, almost nothing is known about how trees impact arable crop disease. One intuitively senses that some conventional farmers view agroforestry and the agroforestry understory with suspicion as potential overwintering habitat for crop disease, which may spread the following year. However, there does not appear to be any evidence supporting this point of view. Beule et al. (2019) studied mycotoxin accumulation in German oilseed rape and cereal monoculture with in-field tree rows and found that there was no difference between systems in rates of infection of cereal with five *Fusarium* species and oilseed rape with the fungal pathogens *Leptosphaeria biglobosa*, *Leptosphaeria maculans*, and *Sclerotinia sclerotiorum*. In fact, they found that colonisation of oilseed rape with *Verticillium longisporum* and wheat with the head blight pathogen *Fusarium tricinctum* was lower in agroforestry than in monoculture. Beule et al. (2019) discuss the relatively evident mechanisms of tree lines as “breaks” and “barriers” in reducing pathogen incidence through reduced dispersal but also raise the interesting possibility that tree lines could boost populations of soil-borne bacterial agonists of *V. longisporum* (see also (Ratnadass et al. 2012) for a discussion of the same mechanism and the role of intercrops in limiting dispersal of insect disease vectors). Trees may also impact microclimatic conditions that can impact the performance of

pathogenic microorganisms (Ratnadass et al. 2012; Beule et al. 2019).

We propose, based on the findings of the current GBRNM model, that research on the role of in-field tree lines on temperate arable crop disease be expanded and mechanisms of action of potentially beneficial effects identified.

4.4 A critique of the current GBRN model

The preliminary and experimental nature of the model presented here demands caution in the interpretation of its outputs. The GBRNM approach is most similar to decision analysis modelling that has been used extensively in economics and social science and which has recently found applications in agricultural decision-making (Hardaker and Lien 2010; Luedeling and Shepherd 2016; Do et al. 2020). Both approaches seek ways to predict reliable system dynamics in data-poor systems using expert opinion, and both emphasise retrospective analysis of the sensitivity of the system to standardised variation of component parts, thus targeting areas of further study to improve model reliability. In this way, we have recommended in the current study that researchers should focus on the role of trees in crop disease and weed dynamics as the network model is particularly sensitive to these components. Improvement of the current model could also proceed in a more holistic way with little extra effort. If growers are involved in agreeing thresholds for high/low values, researchers or growers themselves could undertake regular field checks (“Are crop disease levels acceptable?”, “Is the crop developing at an acceptable rate?”, etc.), and in this way, the most common transition probabilities could doubtless be quantified across a few silvoarable systems in a single season. The model would then be implemented using field-derived transitional probabilities for the most commonly encountered transitions in agroecosystem components, and less commonly encountered transitions could be parameterised, as before, by experts.

GBRNM is a versatile approach that can be applied to model any time-dynamic interaction network. We are currently applying the technique to analyse how trees, primarily used as farm input (e.g., through selling tree fruit in a farm shop or burning wood to heat the farmhouse), can impact farm economic viability in the face of farm input and commodity price volatility. Applications outside agriculture are equally valid; agriculture is simply the interest of this paper’s authors.

The technique is also simple, easy, and rapid to implement, contrary to complex predictive models, which are admirable and powerful but require time-consuming field or lab calibration of continuous equations. We envisage that a skilled and knowledgeable modeller could characterise, analyse, and feedback on a system of comparable complexity to the current application within a week given sufficient motivation on

the part of themselves and the set of participating experts. Thus, GBRNM models could help realise the dream of analytical provision for many systems and enterprises.

5 Conclusion

In this article, we describe a novel and easily implemented modelling framework called GBRNM that is used to describe the interactions of trees and arable crop yield mediated only through the biotic (living) components of the agroecosystem. Despite the model's simplicity and the fact it is parameterized only using expert opinion, it produces persuasive ecosystem dynamics. The model predicts that trees and their biotic interactions boost arable crop yield overall, but they do not increase stability of crop yield to biotic stress. We discuss how this new model can be parameterised using field data and explain how it can be extended to model other agricultural networks.

Authors' contributions CRT: study concept; model construction, coding and parameterisation; running simulations; writing of manuscript; revision of manuscript.

TS: assisted with model parameterisation; feedback on manuscript first draft.

AC: assisted with model parameterisation.

WS: assisted with model parameterisation; feedback on manuscript first draft.

Three anonymous reviewers provided detailed reviews that improved the manuscript.

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Supplementary_Data_2.zip has been saved to Zenodo <https://doi.org/10.5281/zenodo.12761168>.

Supplementary_Information.docx has been saved to Zenodo <https://doi.org/10.5281/zenodo.12761281>.

Code availability Supplementry_Code_File_1.R has been saved to Zenodo <https://doi.org/10.5281/zenodo.12761109>.

Declarations

Ethics approval The research was conducted according to the Organic Research Centre's PLY016 Research Ethics Policy.

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent for publication The authors affirm that human research participants provided informed consent for publication of their opinions on numerous ecological scenario projections, used to parametrise the main model in the study. Participant data are anonymised for publication.

Competing interests The authors declare no competing interests.

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