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A mechanistic model captures livestock trading, disease dynamics, and compensatory behaviour in response to control measures

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Abstract

Trade is a complex, multi-faceted process that can contribute to the spread and persistence of disease. We here develop novel mechanistic models of dynamic trade in which individual-level trading patterns are determined by time-varying state variables determining stock demanded and available supply. Our model is framed within a livestock trading system, where farms form and end trade partnerships with rates dependent on current demand, with these trade partnerships facilitating trade between partners. With these time-varying, stock dependent partnership and trade dynamics, our trading model goes beyond current state of the art modelling approaches. By studying instantaneous shocks to farm-level supply and demand we show that behavioural responses of farms lead to trading systems that are highly resistant to shocks with only temporary disturbances to trade observed. Individual adaptation in response to permanent alterations to trading propensities, such that animal flows are maintained, illustrates the ability for farms to find new avenues of trade, minimising disruptions imposed by such alterations to trade that common modelling approaches cannot adequately capture. In the context of endemic disease control, we show that these adaptations hinder the potential beneficial reductions in prevalence such changes to trading propensities have previously been shown to confer. Assessing the impact of a common disease control measure, post-movement batch testing, highlights the ability for our model to measure the stress on multiple components of trade imposed by such control measures and also highlights the temporary and, in some cases, the permanent disturbances to trade that post-movement testing has on the trading system.

1 Introduction

Trade plays a critical role in the interactions of individuals, firms, and nations [1, 2]. In recent years, the development of network theory has provided a novel framework with which to model and understand the actions of individuals that does not require the simplifying assumptions of more classical modelling approaches, for example making a well-mixed assumption [3, 4]. Representing individuals as nodes and interactions between these nodes as edges (either directed or undirected, as well as possibly weighted by the interaction) allows for highly complex interaction patterns, elegantly capturing scale-free (or approximately scale-free [5]) behaviour often observed in real-world trading systems [6, 7, 8, 9, 10, 11]. Despite these clear advantages, network approaches frequently assume the network is static, i.e. the connections of individuals are permanent and do not change, or that it is an aggregated time series of successive static snapshots of the network [12]. Extensions, whereby network connections change over time but the overall connectivity of the network is maintained, e.g. neighbour exchange models [13, 14], have recently been proposed. However, all these approaches neglect the highly temporal nature of the real-world systems they represent, obscuring dynamical properties of individuals such as seasonal trading patterns or behavioural responses to changes in trade [15, 16, 17]. Temporal networks, and specifically generative models of temporal networks, in which the dynamic network develops and changes based on individual-level properties is an area of network theory that is currently lacking [18] and is the focus of this article.

In this article, we develop a dynamical trading model in the context of a livestock trading system. Much work has been done to understand the dynamics of these systems, and they are often framed in a network context representing farms as nodes, and trades between farms as temporal edges in the network [10, 11, 19]. Moreover, the increasing availability of large-scale datasets in which animal movements are recorded at individual-animal level allows for detailed replications of past animal movements, offering insight into long-term trading patterns, disturbances to trade caused by external perturbations, and the impact of changes in policy [6, 8, 16, 17]. As such, these systems act as an exemplar of trade dynamics. Beyond the commercial benefits of trade itself, there is a further economic incentive to understand the complexities of livestock trade owing to the continual presence of endemic disease and risks of outbreaks, which impose ongoing and unexpected costs to farms and governments. Bovine tuberculosis, or bTB, for example, is estimated to cost the UK in excess of £100 million per year [20]. There can also be significant short-term disturbances to trade in response to an epidemic outbreak, as was the case with the 2001 UK Foot-and-Mouth disease epidemic [21, 22]. This outbreak cost the UK approximately £3.1 billion due to stock losses [23] and £3.2 billion due to other economic factors such as closure of countryside impacting tourism [24].

Trade has frequently been shown to be a risk-factor in disease spread [8, 11, 21, 25, 26, 27, 28]. Indeed, the 2001 FMD outbreak initially spread due to the movement of animals to market, allowing for widespread dissemination of the disease [21, 24].

Moreover, the disturbances to trade imposed by disease control measures and the resulting atypical trading patterns, such as increases in traded animal batch sizes, following the outbreak have been suggested as a contributing factor in the recent surge in bTB persistence in England and Wales [23, 29].

Disease outbreaks have resulted in policy changes, such as post-movement standstills and mandatory batch testing [30] which have previously been shown to alter trading patterns of farms [31]. In Scotland, for example, the introduction of mandatory bTB testing from high-risk areas of England and Wales resulted in Scottish farms avoiding trades from these areas, trading more frequently within Scotland [32]. This behaviour is known as risk aversion, and has been shown to be an important consideration when modelling disease spread within a population [33]. Adaptation in response to policy change, however, has also been reported to mitigate the potential benefits of these policies, leading to temporary reductions in prevalence followed by gradual increases, and long-term boom and bust dynamics as new policies are introduced [15].

While many approaches to modelling disease spread via livestock trade have involved replaying a historic set of animal movements overlayed with a simulated disease process [10, 11, 19, 21, 34, 35], it is challenging to infer future trading patterns using this approach, or indeed how farms may change their trading patterns in response to new policy. Despite these inadequacies, there have been few attempts to develop mechanistic and generative models of trade using data to inform general trading propensities and patterns of farms. Such attempts have focused on analysing the global properties of the system, ignoring individual heterogeneity and responses [36] or restrict trading dynamics by assuming a fixed list of farms from whom animals can be purchased [37].

Here we extend our previous trading model outlined in [38], incorporating a stochastic dynamical trading model including the individual supply- and demand-based trading behaviour of [36, 37]. This represents, to our knowledge, the first attempt at creating a truly dynamic generative model of trade in which the actions of individuals are adaptive to system-wide stock properties. Our model is not intended to replicate any known trading system, however some assumptions outlined below are informed by past analyses and studies of the Scottish cattle trading system. In this model, farm trading patterns are determined by current demand, and the resulting trading system is an emergent property of the collective actions of farms' attempts to form trading partnerships and trade with appropriate sellers. We will show that this dynamic modelling approach leads to trading systems that are highly resilient to shocks in farm stock levels (Section 3.2.2), and the trading patterns of farms will adapt to long-term changes in trade, finding new avenues by which demand is satisfied and animal flows are maintained (Section 3.2.3). We will explore the potential of such adaptive behaviour on endemic disease spread, finding that adaptation hinders the potential benefits of changes to trade, meaning that significant stress must be imposed on the system for meaningful reductions in between-farm prevalence (Section 3.3.1). We will analyse the impact of post-movement batch testing on both between-farm prevalence and on the trading system (Section 3.3.2). It will be shown that testing can be an effective disease control measure when test sensitivities are high, with short-term disturbances to trade observed while disease is cleared from the system. However, for low sensitivity tests, we will show that long-term disturbances to the trading system emerge, and disease cannot be fully eradicated.

2 Materials and methods

2.1 An individual-based systems models of trade dynamics

We assume a closed system of N competitive, interacting market agents (farms) that both form and end dynamic, directed trading partnerships, and trades occur in the direction of these partnerships with variable batch sizes. The dynamic elements of this trading system are determined by individual-level time-varying stock quantities, representing an individual's available supply and demand at a given time t. We define $S_i(t)$ and $D_i(t)$ as individual i's available supply and quantity of goods demanded at time t, respectively. Thus, in contrast to earlier studies [36, 37] this model represents both dynamic trade events and a dynamic partnership network between farms whose

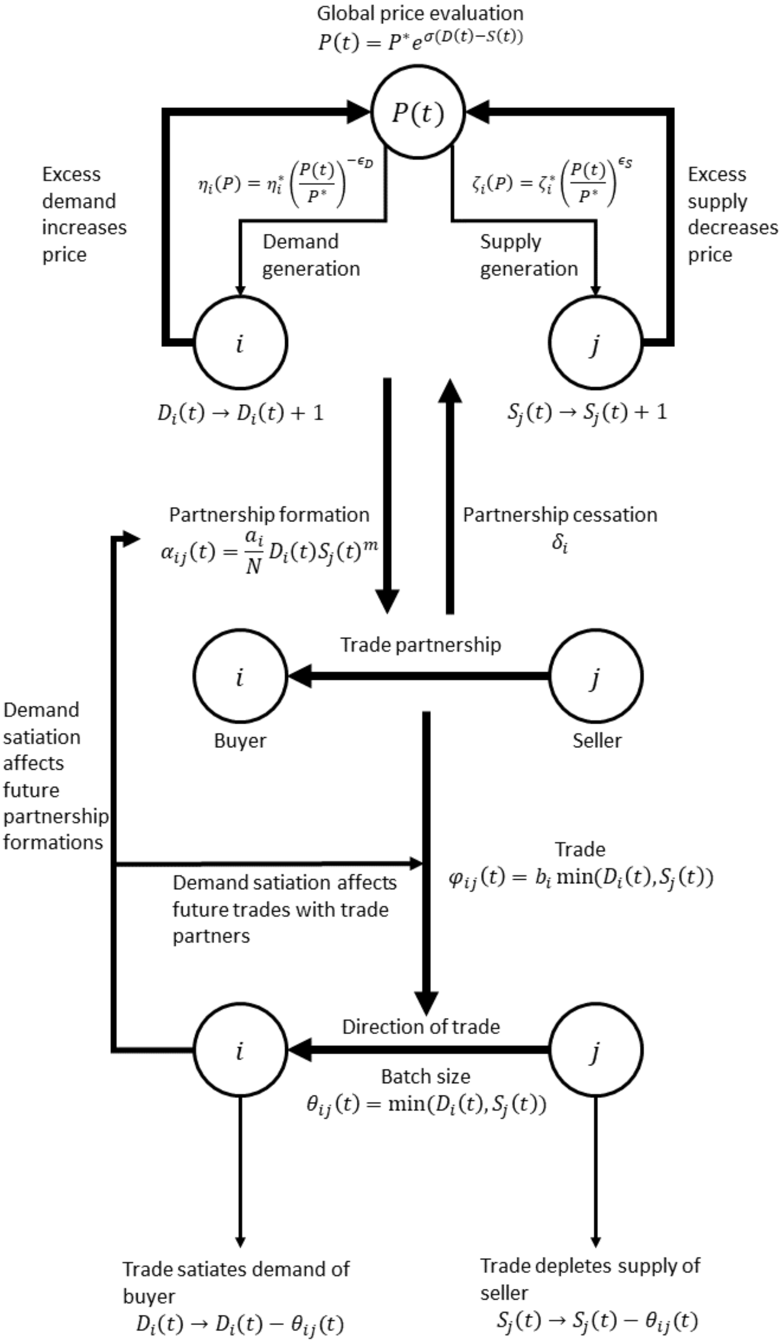

Figure 1: **Dynamic trading network** Model flow diagram highlighting system processes that generate the trading network

trading needs are not constant over time [38] but vary contingent on past trades as well as continuous generation of new demand. A full outline of model quantities and parameters are presented in Table 1, model processes are illustrated in Figure 1, and all results presented are generated using a Gillespie Stochastic Simulation Algorithm (SSA) [39, 40]. All processes defined below are stochastically generated. Our model is general so that distributions of these quantities are arbitrary, however in Section 3.1 we specify how these quantities are distributed for this study.

2.2 A global pricing strategy and mechanisms of stock generation

The global (system-wide) supply and demand, defined as $\mathcal{S}(t) = \sum_{i=1}^{N} S_i(t)$ and $\mathcal{D}(t) = \sum_{i=1}^{N} D_i(t)$, respectively, determine a global price of goods at a given time t, $P(t)$. We adopt the pricing model of [36] and assume that the rate of change of the logarithm of the price is proportional to the rate of change of the global excess demand, defined as $\mathcal{D}(t) - \mathcal{S}(t)$, i.e.

$$\begin{aligned} &\frac{d}{dt}P(t) = \sigma P(t)\frac{d}{dt}\left(\mathcal{D}(t) - \mathcal{S}(t)\right), \\ &\Rightarrow P(t) = P_0 \exp(\sigma(\mathcal{D}(t) - \mathcal{S}(t) - (D_0 - S_0))) \end{aligned}$$

where P_0, D_0, and S_0 are, respectively, the price, global demand, and global supply at $t = 0$. The constant σ represents the sensitivity of price to excess demand, i.e. the market response to imbalances in stock levels. For small values of σ, large stock imbalances are required for large changes in price, and vice versa for large values of σ. Unlike the pricing model of [36], σ is not dimensionless, and there is an implicit dependence on the system size N. We assume that the system begins in an initial stock-free state, so that $D_0 = S_0 = 0$, meaning $P_0 = P^*$ can be interpreted as the equilibrium price when supply and demand are balanced (when the market is in price equilibrium). Thus, we have

$$P(t) = P^* e^{\sigma(\mathcal{D}(t) - \mathcal{S}(t))}. \tag{1}$$

Quantity	**Definition**
N	Number of farms
$D_i(t)$	Demand of farm i at time t
$S_i(t)$	Supply of farm i at time t
$\mathcal{D}(t)$	Global demand at time t
$\mathcal{S}(t)$	Global supply at time t
$P(t) = P^* \exp(\sigma(\mathcal{D}(t) - \mathcal{S}(t)))$	Price of goods at time t
P^*	Market equilibrium price
σ	Price sensitivity to global excess demand
$\eta_i(P) = \eta_i^* \left(P(t)/P^*\right)^{-\epsilon_D}$	Rate at which farm i generates new demand given current price $P(t)$
η_i^*	Rate at which farm i generates new demand at market equilibrium
ϵ_D	Price elasticity of demand
$\zeta_i(P) = \zeta_i^* \left(P(t)/P^*\right)^{\epsilon_S}$	Rate at which farm i generates new supply given current price $P(t)$
ζ_i^*	Rate at which farm i generates new supply at market equilibrium
ϵ_S	Price elasticity of supply
$\alpha_{ij}(t) = \frac{a_i}{N} D_i(t) S_j(t)^m$	Rate at which farm i forms a trading partnership with farm j given no current partnership
δ_i	Rate at which farm i ends a current trading partnership
$\varphi_{ij}(t) = b_i \min(D_i(t), S_j(t))$	Rate at which farm i trades with its trade partner j at time t
$\theta_{ij}(t) = \min(D_i(t), S_j(t))$	Size of trade following a trade between farm i and its trade partner j

Table 1: Table of model quantities and their respective definitions

Note that the price is determined not by the absolute value of global supply and demand, rather by the relative imbalance between them. The functional form of $P(t)$ is desirable as it does not permit negative prices, and replicates simple macroeconomic properties, namely that positive excess demand (global demand larger than global supply) causes price increases, negative excess demand (global demand smaller than global supply) causes price drops, and balanced supply and demand causes the price to equilibriate.

Our global pricing model contains information on system-wide imbalances in supply and demand at a given time t. This information instantaneously propagates throughout the system via proportionate alterations to farm-level stock generation. We assume market agents (farms) generate single units of stock with per-farm, at time t price dependent rate $\eta_i(P)$ for farm i's demand and $\zeta_i(P)$ for i's supply. Following [36] we assume the functional forms of $\eta_i(P)$ and $\zeta_i(P)$ are

$$\eta_i(P) = \eta_i^* \left(\frac{P(t)}{P^*}\right)^{-\epsilon_D}, \tag{2}$$

$$\zeta_i(P) = \zeta_i^* \left(\frac{P(t)}{P^*}\right)^{\epsilon_S}, \tag{3}$$

however we exclude stock losses, external flows (flows of goods leaving the system or entering the system from external sources), and we do not characterise farms as strict buyers or sellers. The constants η_i^* and ζ_i^* represent stock generation rates at market equilibrium, i.e. when global stock levels are balanced and $P(t) = P^*$. While individual farms are not explicitly defined as buyers or sellers, this can be included in the model by choosing appropriate values for η_i^* and ζ_i^*, for example setting $\eta_i^* = 0$ and $\zeta_i^* > 0$ results in farm i generating no demand and generating supply at some non-zero rate; thus, farm i is a strict supplier. The constants ϵ_D and ϵ_S are, respectively, the price elasticities of demand and supply. Their values determine the sensitivity of stock generation to perturbations of the price around the market equilibrium price and, for simplicity, we have assumed they are constant across farms, so that the market as a whole responds in a similar relative manner to alterations in price. We note that changes in price do not alter current farm-level supply and demand, rather they alter the rates at which farms generate future supply and demand. Increases in price beyond the market equilibrium price decrease the rate at which new demand is generated and increases the rate at which new supply is generated, and vice versa. This, combined with our pricing model described above replicates the so-called Law of Supply and Demand. There is a feedback loop between the price of goods and stock levels: surplus demand leads to increases in price, which causes the demand generation rate, $\eta_i(P)$, to decrease and the supply generation rate, $\zeta_i(P)$, to increase. Over time, this results in more supply generated than demand, the surplus demand diminishing, and the price begins to return to the market equilibrium price P^*. As the price returns to the equilibrium price, the stock generation rates return to their equilibrium values η_i^* and ζ_i^*. Thus, the inclusion of a pricing model can act as a corrective mechanism to prevent stock divergences. We will show in Section 3.2.1 that the exclusion of a pricing model will indeed lead to long-term imbalances in supply and demand levels.

2.3 The dynamics of trade partnerships

In a previous model of dynamic trade, we introduced dynamical trading partnerships between farms that facilitated the movement of animals [38]. This innovation enabled representation of a dynamic network of trade partnerships on which trades occurred. Here we extend this concept to our supply- and demand-based model by supposing the rates at which farms seek out new trading partners is influenced by current farm-level demand, i.e. farms with large demand will seek out new trading partners with greater urgency than a similar farm with low demand. The rate at which a farm i forms a trading partnership with another farm j, assuming there is not a partnership currently present, is given by

$$\alpha_{ij}(t) = \frac{a_i}{N} D_i(t) S_j(t)^m, \tag{4}$$

where a_i is a constant representing the general propensity for farm i to seek out new trading partners, and m is a measure of the influence prospective trading partners' supply has on whether a given farm is chosen to be a trading partner. For small m, and especially the extreme case when $m = 0$, supply is less of a determinant in the choice of trade partners and trade partners are chosen more uniformly. Conversely for large m, farm-level supply is much more influential and large supply farms are more readily chosen as trade partners than small supply farms. The functional form of $\alpha_{ij}(t)$ is informed by past analysis of the Scottish cattle trade system [38], and has functional similarities with the gravity model of trade describing flows between individuals [41], though we neglect distance between farms as a consideration in farms' choice in trade partners. For simplicity, and again informed by past analysis of cattle trade dynamics [38], we assume that current trade partnerships end with a constant rate δ_i for farm i. The number of concurrent trading partnerships of farm i at time t, equivalent to i's degree in network terminology, is defined as $k_i(t)$.

As farm-level supply and demand are dynamic and vary over time, so do the dynamics of trade partnership formation; periods of high demand will cause a surge in partnership formations, followed by the gradual removal of these trade partners as demand is satisfied.

2.4 The dynamics of trade

The movement of animals between farms via trade is mediated by the presence of trade partnerships; trades can only occur between a farm i and another farm j if j is a current trading partner of i. Previous mechanistic models of trade have assumed trade dynamics are dependent on long-term properties of farms, namely in- and out-flows of animals [36, 37, 38]. This results in trading patterns that are unaffected by changes in farms' business requirements, for example satiation of farm-level demand. As with the dynamics of trade partnerships, we incorporate a dynamic rate of trade between farms of the form

$$\varphi_{ij}(t) = b_i \min(D_i(t), S_j(t)) \tag{5}$$

for farm i and its trading partner j. The constant b_i is intended to represent any impediment to efficient trade (trade friction) [36]. As with the partnership formation rate $\alpha_{ij}(t)$, the rate at which farms purchase stock is driven entirely by current demand levels, rather than long-term trading trends. For a farm i, $\varphi_{ij}(t)$ allocates the highest trade rate to a trade partner j that can match or exceed i's demand. Therefore, trading partners that exceed i's demand are essentially equivalent and have the same probability of being chosen for trade. Our trade rate neglects harder to quantify variables that may be present in real-world trading systems, e.g. farmer reputation. In addition, current price of goods $P(t)$ does not directly influence the rate at which farms trade, though may impact it indirectly as, for example, periods of high prices correspond to periods of large demand generation via $\eta_i(P)$, increasing demand and thus $\varphi_{ij}(t)$.

Trades initiate a batch movement of animals, which lead to a depletion of the demand of the purchasing farm and the supply of the selling farm, the size of which is also determined by current stock levels:

$$\theta_{ij}(t) = \min(D_i(t), S_j(t)). \tag{6}$$

At most, farms will purchase enough animals to satisfy their demand at a given time, and sellers operate on a first-come, first-served basis, i.e. sellers will offload their entire supply in a single trade if demanded. Farms, therefore, buy and sell based on current market pressures, excluding any forecasting, allocation of stock, future agreements to sell, etc. Analysis in [37] for a subset of the French cattle trading system found that batch sizes that allocated stock in this manner resulted in simulation output most closely resembling real-world movement dynamics, suggesting that farms do indeed purchase and sell animals in the most fluid way possible.

Interpreting $\theta_{ij}(t)$ is straightforward: supply and demand are indivisible quantities in our model, representing animals available for sale and number of animals a farm wants to buy at a given time, respectively. As such, batches can take minimum size 1, i.e. a single animal moved. The maximum size, however, is determined by current stock quantities of the buying and selling farm, which can lead to residual supply or demand following a batch movement if, for example, a buying farm's demand is greater than the selling farm's supply. Therefore, transactions are *imperfect* [36] in the sense that batch movements may not fully satisfy the buyer's demand. Residual stock from a trade is carried over and influences future trades. In all cases, trades will always fully satisfy either the demand of the buying farm or the supply of the selling farm (or both) as batch sizes allocate the maximum amount of available goods between buyer and seller.

When running a simulation, the trading system of our mechanistic model develops from an initial disconnected state (farms do not possess any trade partners) in which farms have no supply or demand. As farms generate new supply and demand, they dynamically search for appropriate trading partners and begin trading. Thus, the trading system develops based on individuals' desire to meet current business requirements, and is adaptive to global stock imbalances via alterations to pricing and new stock generation. Moreover, at the individual level, farms modify their trading patterns based on changes to their demand and other farms' supply.

3 Results

3.1 System parameterisation

Throughout this article we assume a constant $N = 1000$ farms. To parameterise the system, we assume equilibrium (at price equilibrium P^*) farm stock generation rates, η_i^* and ζ_i^* for farm i, and the average duration of trade partnerships, $\tau_i = 1/\delta_i$, are drawn from Power-Law distributions of the form $p_x \sim x^{-y}$ with parameters given in Table 2. For stock generation rates, we impose maximum values for η_i^* and ζ_i^*, set to 1000 each, and any values that exceed this maximum are rejected and another sample from the distribution is drawn. We do not impose any such maximums for partnership durations, as very long partnership durations correspond to effectively permanent trading partnerships. We note here that our parameter values are not intended to replicate any known trading system, rather values are chosen that result in a highly active trading system in which large numbers of animals

Parameter	**Value**	**Definition**
$\eta_{\min}$	5	Minimum demand generation rate
$\zeta_{\min}$	5	Minimum supply generation rate
$\eta_{\max}$	1000	Maximum demand generation rate
$\zeta_{\max}$	1000	Maximum supply generation rate
$<\eta>$	20	System average demand generation rate
$<\zeta>$	20	System average supply generation rate
$\eta_{\exp}$	2.33	Exponent for distribution of η_i^*
$\zeta_{\exp}$	2.33	Exponent for distribution of ζ_i^*
$\tau_{\min}$	0.5	Minimum partnership duration
$<\tau>$	1.5	System average partnership duration
$\tau_{\exp}$	2.5	Exponent for distribution of τ
P^*	1	Market equilibrium price
σ	0.0001	Price sensitivity to global excess demand
ϵ_D	0.412	Price elasticity of demand
ϵ_S	0.821	Price elasticity of supply

Table 2: Table of model parameters, their values, and corresponding definitions. Values for the price elasticities of supply and demand are taken from *UK-FAPRI model 2011* [42]

are exchanged between farms. Power-Law distributions are chosen because scale-free (or approximately scale-free) trading behaviour has been observed in many trading systems [6, 8, 9], and such distributions produce large heterogeneity in individual trading patterns.

To match desired system averages for each quantity (as given in Table 2), we scale each value sampled from the Power-Law distribution by a necessary scaling factor, except for farms whose values are either the minimum value of the respective distribution or, in the case of in- and out-flows, whose η_i^* and/or ζ_i^* exceed the maximum of the distribution. This in turn ensures that total in- and out-flows are equal. For simplicity, we here neglect explicit correlations between farm flows, however previous analysis of the Scottish cattle trading system revealed only weak positive relationships between a farm's in- and out-flows [38].

From past analyses of the Scottish cattle trading system, a strong positive linear relationship between a farm's in-flow and number of concurrent trading partners $k_i(t)$, and number of trades and concurrent trading partners has been observed [38]. To exploit these relationships, we relate farm flows to stock generation rates by assuming that over sufficiently long time periods, the two quantities are equal [36, 37]. In other words, over time farms find patterns of trade such that animal in-flows match the demand generated, and similarly for animal out-flows and generated supply. This equivalency allows us to obtain expected numbers of trading partners, $<k_i>$, and number of trades, $<\Phi_i>$, for individual farms i solely from their equilibrium demand generation rate η_i^* by assuming linear relationships of the form

$$\begin{aligned} <k_i> &= m_k \eta_i^*, \\ <\Phi_i> &= m_\Phi <k_i>. \end{aligned}$$

We choose $m_k = 0.25$ and $m_\Phi = 1.5$ for each farm i, which, given $<\eta> = 20$, yields a system-average number of concurrent trading partners of 5 and system-average number of trades of 7.5.

Obtaining values of a_i and b_i so that per-farm average number of concurrent trading partners and number of trades are maintained is challenging. This is due to the dynamic nature of the partnership formation rate $\alpha_{ij}(t)$ and trade rate $\varphi_{ij}(t)$ through their dependence on farm-level at time t supply and demand. To obtain values of a_i and b_i, we use an iterative process outlined in Electronic Supplementary Material (ESM) Section 1 that takes initial values of a_i and b_i, simulates the system, and calculates the factor difference between the simulated output for number of trading partners and trades for each farm i and their expected value as described above. The values of a_i and b_i are scaled by these factor differences, the system is re-simulated and the process repeats. ESM Figure 2 shows that this process is able to obtain values of a_i and b_i such that desired global individual trading properties for each farm are met.

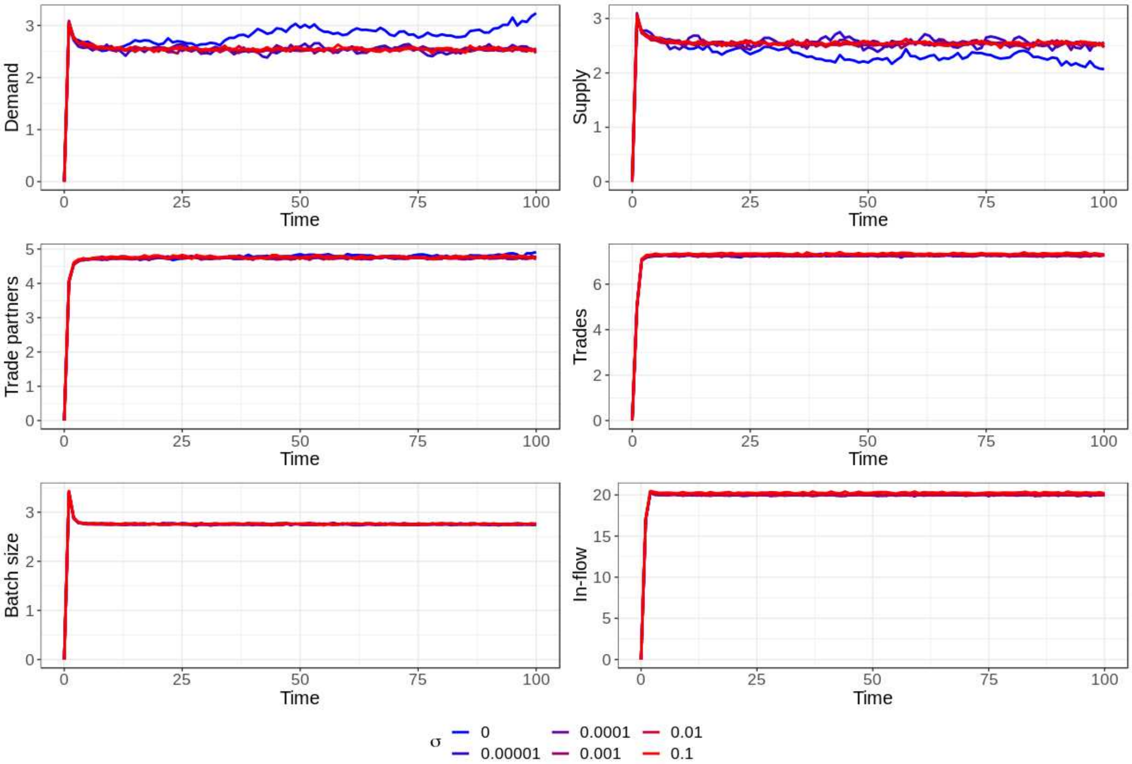

Figure 2: **Impact of price sensitivity on trade network** Trading system response to various values of σ. In all cases except when $\sigma = 0$ the trading system is largely unaffected by market sensitivity to stock imbalances, with the system reaching similar equilibria regardless of σ. The special cases when $\sigma = 0$, which corresponds to the absence of a price model, results in unstable system-level supply and demand, with long-term divergences observed. Each trajectory is obtained by averaging over 15 independent stochastic simulations

Our resulting parameterised trading system has stable equilibria, with independent stochastic simulations yielding very similar equilibrium values for all components of trade. Variation around these equilibria are the result of inherent stochasticity of stock generation, formation and cessation of trade partners, timing of trade, and batch sizes.

3.2 Model analysis

3.2.1 Exclusion of a pricing model can lead to divergent stock levels

We first explore the systems- and individual-level impact of various values of the price sensitivity parameter σ, which dictates the price response to imbalances in global supply and demand, and in turn informs alterations to farm-level supply and demand generation via $\zeta_i(P)$ and $\eta_i(P)$, respectively. Thus, large values of σ yield pricing models that are more sensitive to small imbalances in system-wide stock imbalances, e.g. small excess demand yields large increases in price. As these large increases in price yield large alterations to stock generation rates, large values of σ correspond to trading systems that can more readily correct stock imbalances and return to market equilibrium. Figure 2 shows that the long-run trading properties of the system are largely unaffected by the value of σ, with the system reaching similar equilibria even for very small σ, i.e. when the system is less responsive to stock imbalances. The exception is the special case when $\sigma = 0$, which is essentially equivalent to the absence of a pricing model. In this case, the price is always equal to its market equilibrium price ($P(t) = P^* \;\forall\; t$), such that farm stock generation rates do not deviate from their equilibrium values ($\eta_i(t) = \eta_i^*$ and $\zeta_i(t) = \zeta_i^* \;\forall\; i, t$). As such, imbalances in supply or demand are not corrected for by alterations to stock generation rates, leading to imbalances growing over time and stocks (supply and demand levels) diverging (see ESM Figure 3). ESM Figure 4 shows that these divergences can occur in both supply or demand and are not confined exclusively to either of these quantities. We note from ESM Figure 3 that larger values of σ result in individual- and systems-level responses as predicted above, namely that large σ results in price dynamics that are more responsive to global stock imbalances, which result in greater supply and demand generation rates. For small σ global supply and demand must become more imbalanced before price deviates from the market equilibrium price sufficiently such that stock generation rate values update and imbalances are corrected. We note that for real-world systems, σ will be partially determined by the product being sold. For example, for luxury or “rare” products, where the market may be more sensitive to the introduction of new supply or potential buyers (thus, increased demand), we would expect large values of σ. Thus, σ is a measure of price volatility [43].

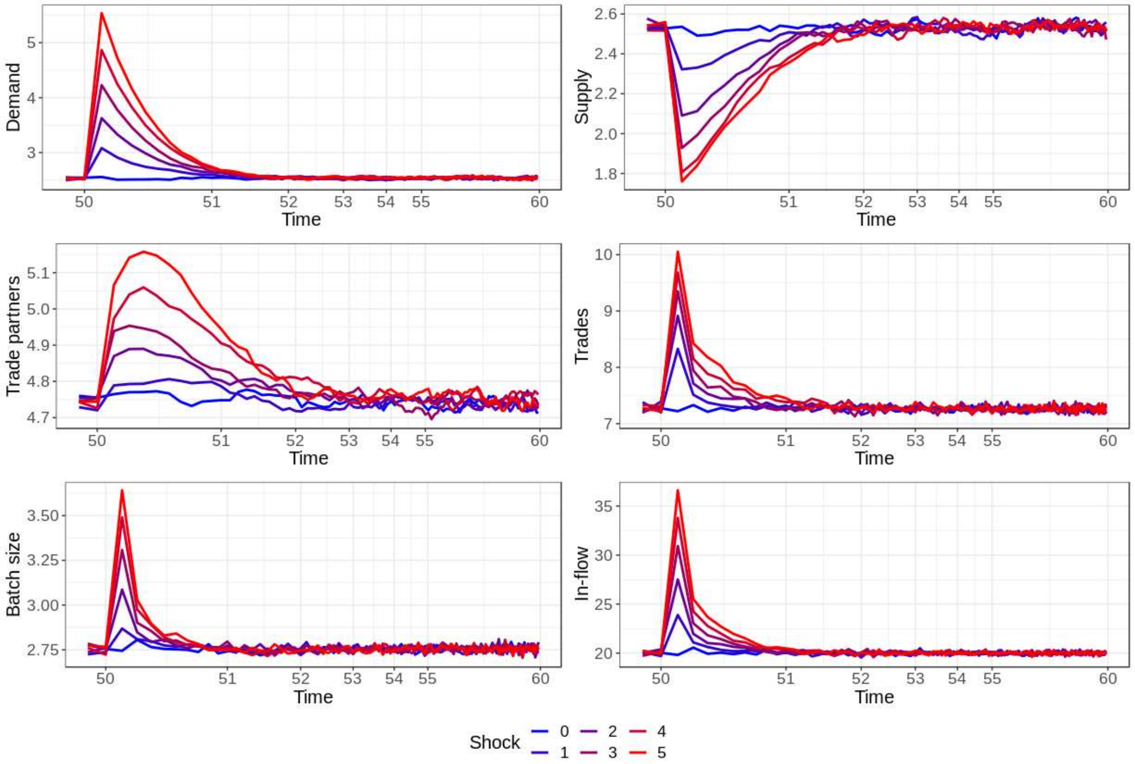

Figure 3: **Demand shocks on the trade network** System-level response to instantaneous shocks in farm-level demand. In all cases, shocks are applied at $t = 50$ and x-axes are $\log_{10}$ scaled. For a shock of size s, all farms i instantly update their demand to $D_i(t) \to D_i(t) + s$. Each trajectory is obtained by averaging over 15 independent stochastic simulations.

3.2.2 System resilience to shocks in supply and demand

We now explore the resilience of our trading system to instantaneous individual-level shocks in supply and demand. This reveals the ability for individuals (and thus the system as a whole) to adapt trading patterns in response to perturbations from equilibrium in a way that leads to small disturbances in the long run. We first analyse shocks in demand, allowing the trading system to reach equilibrium before an instantaneous demand shock, at a given time t, to all farms, e.g. farm level demand instantaneously rises. This instantaneous generation of demand may occur following culling to control a disease outbreak. The response to similar shocks to supply, to both supply and demand, and also the removal of all supply and demand are shown in ESM Section 3. Figure 3 and ESM Figure 5 show the system is resilient to shocks in demand due to individual-level changes in trading patterns in response

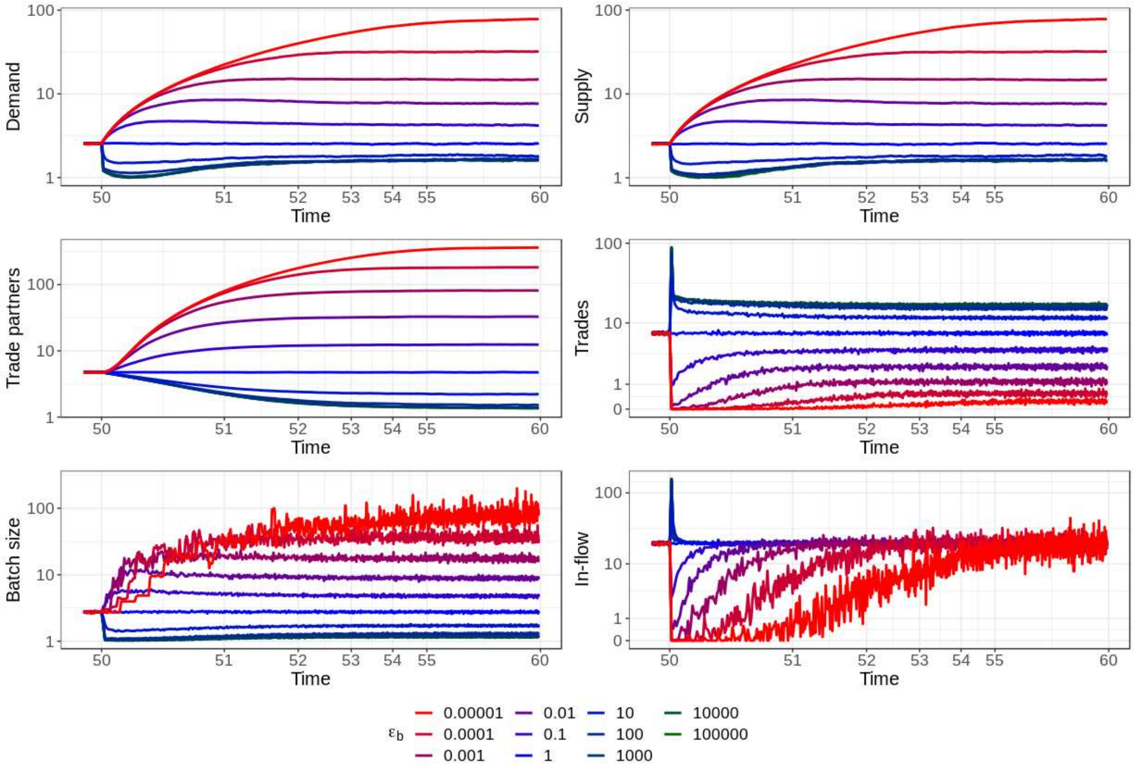

Figure 4: **Evolution of trade network in response to changes in trade frequency** System-level average trading quantities for various values of the trade frequency scaling parameter ε_b. For $\varepsilon_b < 1$, farms trade less frequently, and for $\varepsilon_b > 1$ farms trade more frequently. In all cases, the trading system reaches an equilibrium at $\varepsilon_b = 1$ before changes to ε_b are made at $t = 50$. Axes are $\log_{10}$ scaled. Each trajectory is obtained by averaging over 15 independent stochastic simulations.

to these shocks, as well as appropriate changes in stock generations rates caused by price increases in response to stock imbalances that demand shocks introduce. In particular, shocks (instantaneous increases in the presented case) in demand cause large imbalances in global supply and demand, which in turn increases price. This leads supply and demand generation rates $\zeta_i(P)$ and $\eta_i(P)$ to immediately adjust so that over time less demand, and more supply, is generated allowing excess demand to be cleared.

At the farm level, shocks alter trading patterns as farms seek to satisfy the additional demand these shocks introduce. Following the shock, farms immediately form new trading partnerships and trade more frequently, with trades occurring with larger batch sizes. Even for very large shocks in demand, average farm supply does not drop to zero because of the adjustment to stock generation rates resulting in very large supply generation to meet the increased demand of farms. For all shocks to demand, the system eventually returns to the pre-shock equilibrium, highlighting the system can respond appropriately to shocks such that long-term disturbances to the trading system are averted. Of note is the observation that the time for the system to return to pre-shock equilibrium is the same regardless of the size of shock to demand, indicating the systems-level response is proportionately similar regardless of the size of shock. We note that this may not be feasible for some real-world systems such as cattle trade, as there are biological constraints preventing unrestricted increases to the supply generation rate $\zeta_i(P)$. In addition, while the frequency and size of trade, and animal flows, quickly return to pre-shock equilibrium values, the dynamics of trading partnerships is slower to return (Figure 3). This is a consequence of the trade partnership cessation rate δ_i being a constant and unaffected by farm-level supply and demand. As such, the time for trade partnerships to return to pre-shock equilibrium values is determined by the per-farm expected partnership duration $1/\delta_i$.

3.2.3 Farm- and systems-level adaptation to long-term changes to trading patterns

Our analysis of shocks to demand in the previous section highlighted the ability for individuals to temporarily adapt their trading patterns and stock generation rates to instantaneous perturbations away from equilibrium. We now explore long-term individual and system adaptation to permanent alterations to trading propensities. To do so, we alter farm-level trading propensities in a manner similar to [38], by introducing scaling factors such that

$$
\begin{aligned}
b_i &\to \varepsilon_b b_i,\\
a_i &\to \varepsilon_a a_i,\\
\delta_i &\to \varepsilon_\delta \delta_i.
\end{aligned}
$$

Thus, ε_b, for example, alters the propensity for farms to trade with their trading partners, with $\varepsilon_b < 1$ decreasing the propensity trade, and vice versa. We introduce these scaling parameters once the trading system has reached equilibrium at baseline trading dynamics (in other words, for $\varepsilon_b = \varepsilon_a = \varepsilon_\delta = 1$), allowing us to investigate the initial disturbance to the trading system that permanent alterations to trade cause, as well as any long-term adaptation and persistent impacts on trading patterns. In contrast with previous work exploring such changes (in particular in the context of disease control) [36, 38], in which the system response to the above scaling parameters was linear, here we anticipate a nonlinear response for our dynamic trading system. This hypothesis is predicated on the fact that the rates determining trade and trade partnership dynamics are functions of at time t supply and demand of farms, which are likely to be affected by alterations to trading propensities.

We consider alterations to the propensity for farms to trade with their trade partners by exploring various values of ε_b (we perform similar analyses for ε_a and ε_δ in ESM Section 4). Figure 4 shows that in general, for $\varepsilon_b < 1$ farms trade less frequently and with larger batch size. Conversely, when $\varepsilon_b > 1$, farms trade more frequently and with smaller batch sizes. These results concur with previous findings [36, 38]. However, we observe that after an initial disturbance to trading patterns following the change in ε_b, farms adapt their trading patterns in response to increases or decreases in supply and demand to minimise disruptions caused by changes in trading propensities and maintain animal flows. For example, when $\varepsilon_b < 1$, initial reductions in animal in-flows are observed, farms trade with their current trade partners less frequently, and farm-level supply and demand begin to increase rapidly. These increases in supply and demand encourage farms to seek new trade partners, allowing farms to overcome the reductions in trading propensities imposed by ε_b and trades begin to occur more frequently (however they do not return to frequencies observed when $\varepsilon_b = 1$, i.e. at baseline trading patterns). As trades occur less frequently, farms accumulate greater levels of supply and demand before a trade occurs, resulting in increased batch sizes. This relationship between trade frequency and batch size allows farm flows to return to desired levels even for very small ε_b, however we note in these cases animal flows are more variable around the equilibrium than for large ε_b ($\varepsilon_b \geq 1$). The system reorganises itself so that animal flows return to the same equilibrium levels as before. However, the trading system itself returns to a new equilibrium with different numbers of trade partners, trading frequencies, and batch sizes compared with the system equilibrium before changes to trading propensities are introduced.

ESM Figure 11 shows that trade flows are maintained for a wide range of values of ε_b, but other aspects of the new equilibria the system reaches are exponentially related to ε_b for $\varepsilon_b < 1$. However this relationship is not observed for $\varepsilon_b > 1$. Larger values of ε_b leads to, in general, more frequent trade so that farm-level supply and demand, and batch sizes, decrease. However, batches can take minimum size 1, so there are threshold trading frequencies at which point increasing ε_b further result in negligible alterations to the equilibria the system reaches.

Thus, the dynamic trading behaviour of individual farms and the behavioural response as trading propensities are changed allow for farms to find new avenues of trade to maintain desired animal flows. These individual responses drive changes to the structure of the whole trading system, with the system rapidly adapting and adjusting its structure even for very large changes in trading propensities, before finding a new stable structure in which animal flows are maintained. Individual- and systems-level responses and adaptation to regulatory changes in trade such that individuals alter their trading patterns has previously been observed, for example within the UK cattle trade system [15, 31, 32].

3.3 Role of dynamic trade in endemic disease persistence

We have shown that our dynamic trading system can adapt at the individual level to shocks and long-term changes to trading patterns. Within the cattle trade industry, disease spread within and between farms is a major economic concern, due, for example, to production disruptions these diseases can incur [44]. We now explore the role of trade in disease spread and persistence, and the impacts of common biosecurity measures on both between-herd disease prevalence and the trading system itself.

We assume from an epidemiological perspective that farms can be treated as a unit

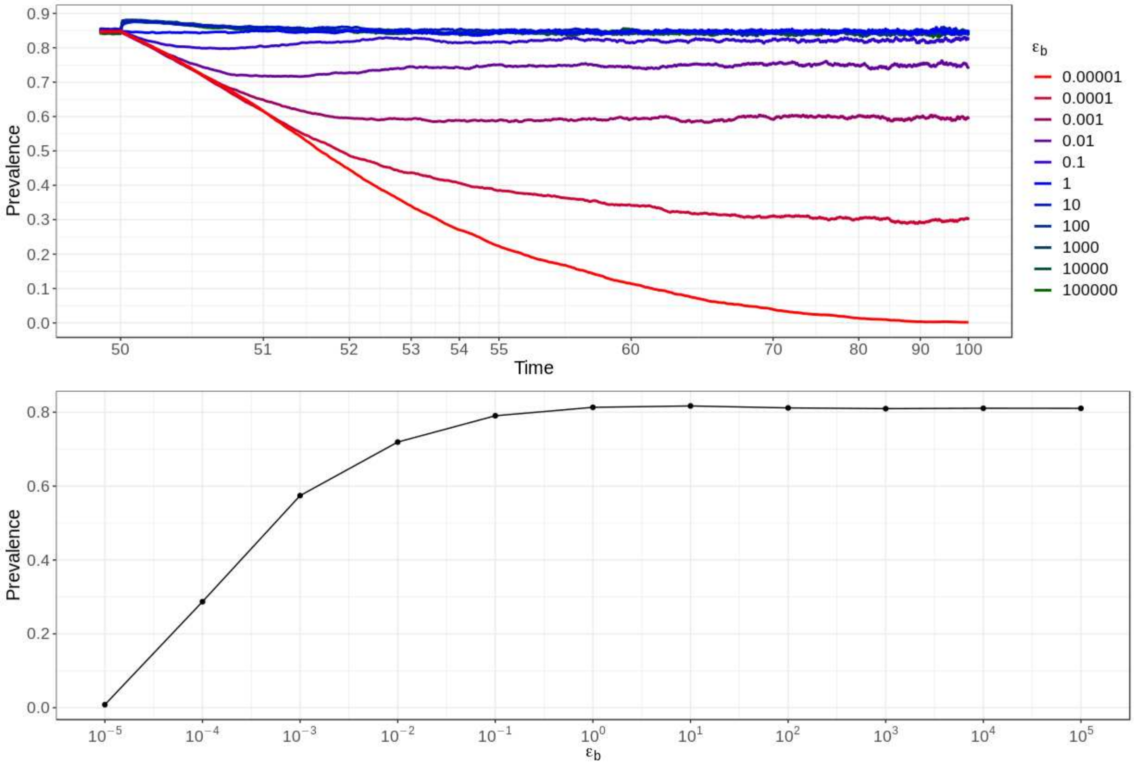

Figure 5: **Impact of changes in trade frequency on disease** Disease prevalence over time (top panel) and equilibrium prevalence (bottom panel) for various values of the trade frequency scaling parameter ε_b. In all cases, the trading system reaches an equilibrium at $\varepsilon_b = 1$ before changes to ε_b are made at $t = 50$. For top panel, the x-axis is $\log_{10}$ scaled. Each trajectory is obtained by averaging over 15 independent stochastic simulations.

and disease status can be applied to the whole farm, that is to say we ignore within-herd disease dynamics. As such, farms are classified as either susceptible (S) and can be infected by others, or infectious (I) allowing them to infect other premises. For simplicity, disease spread is modulated entirely through trade, ignoring other sources of infection such as external wildlife reservoirs and non-trade related contacts between farms. An infected farm has constant within-herd prevalence λ while infected. This prevalence is unaffected by herd demographics (for example births and deaths) or farm flows (introduction of new animals into the herd or animals leaving the herd via trade). Thus, we neglect the potential for trade to remove infection from a farm by selling infected animals (rapid trade as a counter intuitive measure to reduce disease persistence has previously been shown in a trading model with mandatory post-movement animal testing [45]). As such, estimated reductions in prevalence are likely to be conservative. Infectious farms remain infectious for an exponentially distributed period of time with expectation $1/\gamma$ at which point they return to the susceptible category and can be infected once again. We assume recovery from disease does not incur any financial burden on farms, nor does it alter supply and demand levels. In addition, infected farms are naïve to their disease status, incurring no financial burdens and do not alter their trading patterns. Trades modulate the spread of disease through both the frequency of infectious contacts and the probability of infection by assuming that larger batch sizes increase the probability of transmission. The probability that a susceptible farm i is infected by its infectious trade partner j is given by

$$B\left(\theta_{ij}(t)\right) = 1 - (1 - \lambda)^{\theta_{ij}(t)}, \tag{7}$$

so that trades of larger batch size are more likely to spread disease. The transmission rate between i and j (while the trade partnership exists) is thus $\beta_{ij}(t) = \varphi_{ij}(t)B(\theta_{ij}(t))$, i.e. the rate at which i initiates a trade with j multiplied by the probability the resulting trade results in disease transmission.

In all cases below, we assume $\lambda = 0.25$ and $1/\gamma = 3$, intended to represent a highly prevalent and persistent disease. Under the parameterisation outlined in Table 2, this disease results in an equilibrium between-herd prevalence of 0.85, i.e. at any given time only 15% of farms are disease free. In all simulations presented, we allow the disease to reach equilibrium before we impose any changes to trade. Thus our analysis restricts itself to the impact of changes to trade on endemic diseases at equilibrium within the trading system.

3.3.1 Individual adaptation to changes in trading propensities hinders disease control

Altering individual trading propensities has previously been shown to be beneficial in controlling disease, with infrequent large trades reducing endemic disease prevalence [36, 38]. However, in Section 3.2.3 we showed that individuals adapt their trading patterns in response to alterations in trading propensities, finding new avenues of trade that maintain animal flows. We now explore the potentially hindering consequences on disease prevalence reduction incurred by such adaptation by introducing similar long-term changes to trade via the scaling parameters outlined in Section 3.2.3. To highlight the role of adaptation in our dynamic trading model, in ESM Section 6 we simulate our system under our previous trading model introduced in [38]. We here focus on changes to trade frequency via the scaling parameter ε_b (see ESM Section 5 for similar exploration of changes to trade partnership dynamics via ε_a and ε_δ).

Figure 5 shows the impact of changes to ε_b on disease prevalence. In general, decreasing ε_b decreases prevalence, i.e. trading infrequently decrease prevalence. However, complete eradication is only possible in the extreme case when trades occur very infrequently and with batches of very large size. This is a consequence of the adaptation of farms, with increased supply and demand causing farms to seek out a larger number of trade partners increasing the connectivity of the system, and thus susceptible farms are more exposed to infected farms. Comparing with ESM Figure 19, we see that this adaptation prevents disease eradication for a large range of values of ε_b. While decreasing ε_b can reduce prevalence if the system is stressed sufficiently, significantly increasing ε_b (so that the farms trade more frequently with smaller batch sizes) does not increase disease prevalence. Large ε_b increases the frequency of trade which reduces farm-level unmet supply and demand and the batch size of trades. As such, farms decrease their number of trade partners reducing their exposure to infected farms, preventing increased disease spread as may be expected. ESM Figure 19 shows that without this dynamic feedback, increased values of ε_b do lead to increased disease prevalence, though we note that this increase is small and saturates as ε_b increases. To investigate whether this is due to the high baseline prevalence observed when $\varepsilon_b = 1$, we investigated increasing ε_b for a disease characterised by herd prevalence $\lambda = 0.1$ and recovery rate $\gamma = 2/3$, resulting in a long-run disease prevalence of approximately 40%. ESM Figure 16 shows that increasing ε_b does not significantly alter disease prevalence, suggesting the negligible changes in

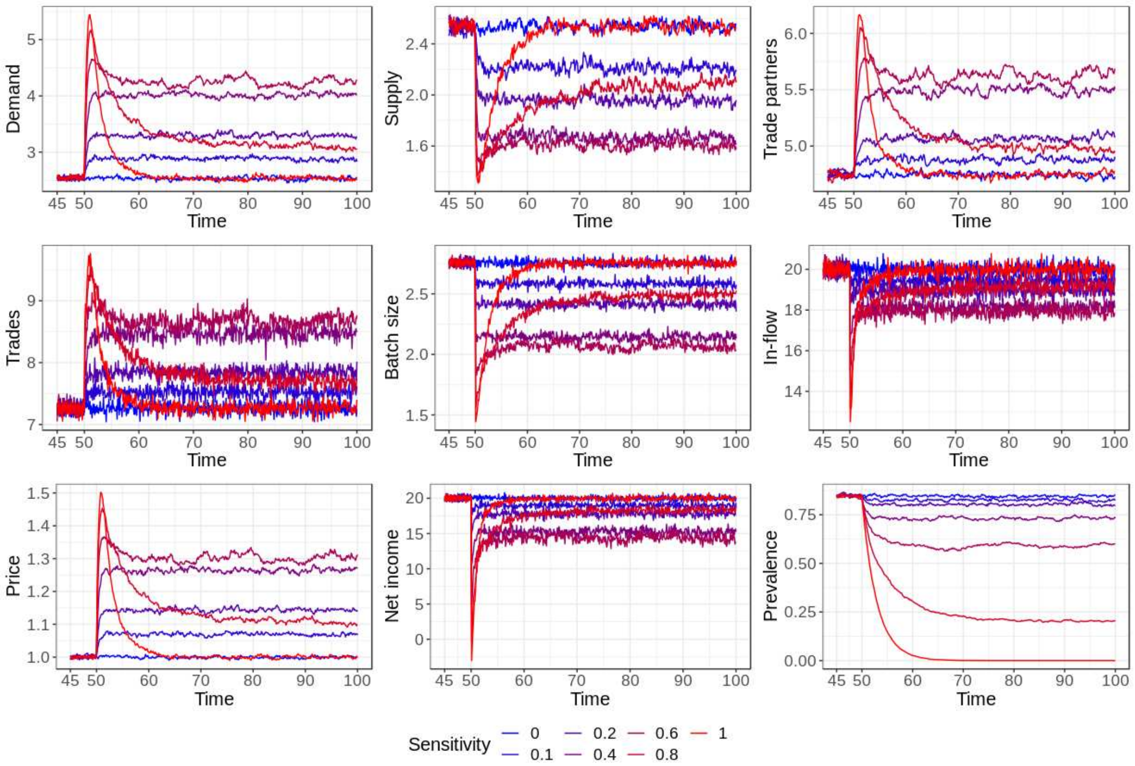

Figure 6: **Impact of movement testing on the trade network and disease prevalence** Impact of testing and whole batch removal on the trading system and disease prevalence for various test sensitivities. In all cases the trading system reaches an equilibrium in the absence of testing before testing is introduced at $t = 50$. Long-term disturbances to trade are observed for low test sensitivities, however for high sensitivities the system returns to pre-test equilibria. Each trajectory is obtained by averaging over 15 independent stochastic simulations.

prevalence observed in Figure 5 when ε_b is increased is not a unique case, but is rather a characteristic of the farm adaptation described above.

Thus, individual adaptation to changes in trade, while beneficial in maintaining animal flows, can be detrimental to disease control, highlighting the complexities of dynamic trade and the need to incorporate behavioural responses in assessments of disease control strategies.

3.3.2 Assessing the effect of post-movement testing on prevalence and the trading system

The testing of traded animals before introduction into herds is a commonly practiced control strategy for many livestock diseases, whether mandatory in the case of

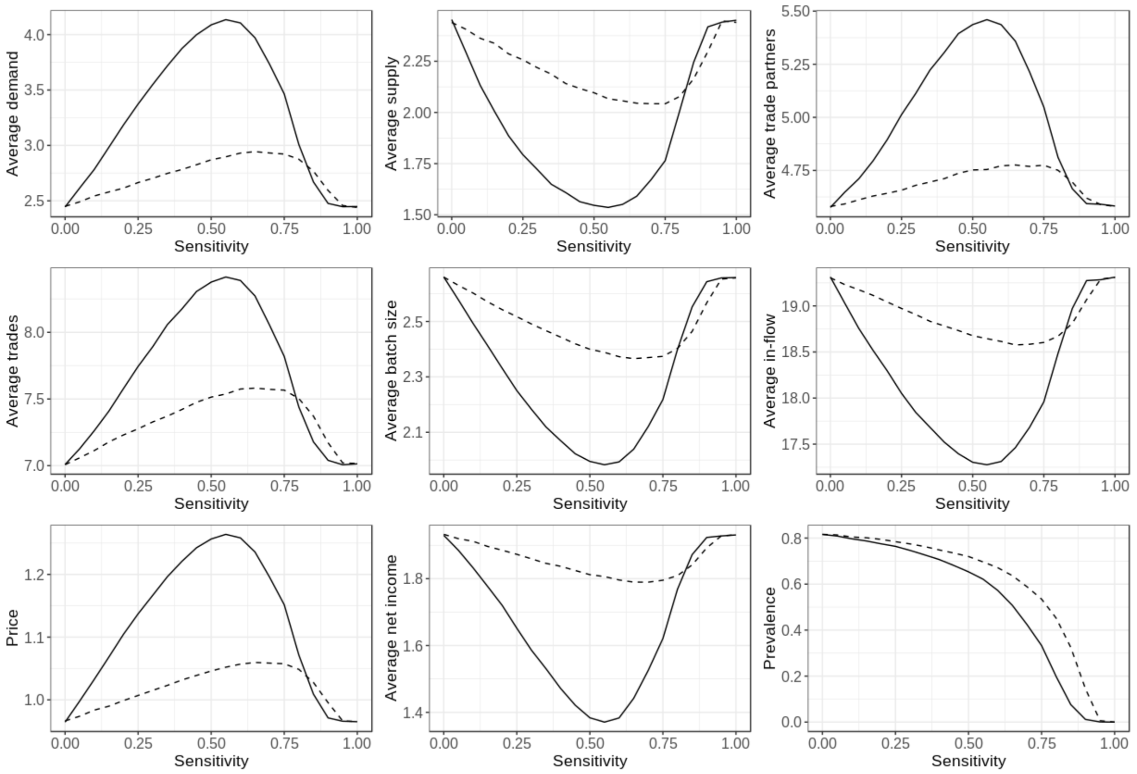

Figure 7: **Impact of test sensitivity on long-run trade dynamics and prevalence under movement testing** Equilibrium values of various trading quantities after testing is introduced for the whole batch rejection (solid lines) and individual animal rejection (dashed lines) regimes. For all test sensitivities ξ, whole batch rejection yields greater reductions in prevalence than individual animal rejection except for $\xi \geq 0.95$, where both regimes fully remove disease. Whole batch rejection, however, leads to greater disturbances to the trading system for $\xi < 0.85$.

Bovine Tuberculosis [30] or non-mandatory for paratuberculosis [46], for example. We here explore the potential benefits of mandatory post-movement testing on reducing between-herd disease prevalence, and the disturbances to the trading system that such testing incurs.

Consider a test-and-reject strategy in which buyers test batches of traded animals and reject the batch if at least one animal tests positive for infection (we implicitly assume 100% test specificity). Rejected animals are immediately removed from the system. Batches with infected animals that avoid detection can thereafter infect the buying farm. For a test with sensitivity ξ, the probability that a batch of size θ from an infected farm avoids detection is $(1 - \lambda\xi)^{\theta}$. For a farm pair i and j where j is a trading partner of i, and i is susceptible and j infected, the expected update to the demand of i and supply of j following a trade is

$$
\begin{aligned}
D_i(t) &\to D_i(t) - \theta_{ij}(t)\,(1 - \lambda\xi)^{\theta_{ij}(t)}\,,\\
S_j(t) &\to S_j(t) - \theta_{ij}(t).
\end{aligned}
$$

We note that the above update to stock is an *expectation*, permitting real-valued updates to demand. Supply, demand, and batch size are integer values so in simulation the number of animals rejected will also be integer-valued. In simulation, therefore, either the whole batch is accepted with probability $(1 - \lambda\xi)^{\theta_{ij}(t)}$, or the whole batch is rejected with probability $1 - (1 - \lambda\xi)^{\theta_{ij}(t)}$. Thus, our test-and-reject strategies will necessarily lead to stock imbalances, with the greatest imbalances for tests with higher sensitivity.

We also consider a test-and-reject individual animal regime. This is similar to the whole batch rejection regime, however individual animals are removed from the system if they test positive for infection rather than the entire batch. In this case the probability that an infected animal in a batch avoids detection is $1 - \xi$, and the expected update to stocks for the i, j pair above is

$$
\begin{aligned}
D_i(t) &\to D_i(t) - \theta_{ij}(t)(1 - \lambda\xi),\\
S_j(t) &\to S_j(t) - \theta_{ij}(t).
\end{aligned}
$$

As with the whole batch rejection regime, the above updates to demand represent an expectation so can be real-valued. In simulation, an integer number of test positive animals are removed from the batch so the batch size remains integer-valued. We see that for $0 < \xi \leq 1$, whole batch rejection will lead to greater imbalances in stocks when batches take size larger than 1. When $\xi = 1$, the two testing regimes will fully eradicate disease, however individual animal rejection is preferable as this testing regime will incur smaller temporary disturbances to the trading system.

Figures 6 shows the impact of whole batch rejection on the trading system and between-herd disease prevalence (equivalent figure for individual animal rejection is provided in ESM Section 7). We here introduce an additional measure of stress on farms, net income. We define a selling farm's net income as the number of animals in a batch that are not rejected multiplied by the current price, $P(t)$. In general, low test sensitivities are unable to fully remove disease resulting in persistent and long-term disturbances to the trading system, with increased prices resulting in farms permanently altering their stock generation dynamics. On the other hand, for high test sensitivities, disease can be fully removed and disturbances to the trading system are temporary and rapidly return to pre-testing equilibrium values. Considering Figure 7, which shows the equilibrium values of the trading system post-introduction of testing (for both whole batch and individual animal rejection), we see that there is a maximum long-term disturbance to the trading system when $\xi = 0.55$ for whole batch rejection, a test sensitivity for which detection occurs frequently enough to significantly disturb the trading system but is insufficient in fully removing disease. Moreover, whole batch rejection leads to larger long-term disturbances than individual animal rejection when $\xi < 0.85$. For higher test sensitivities, the disturbances of whole batch rejection are similar to individual animal rejection, and we observe that in this regime disease can be fully removed at lower test sensitivities than with individual animal rejection.

4 Discussion

In this article we have introduced a dynamic trading model in which individuals' trading patterns vary based on individual stock quantities representing supply and demand, framed in the context of a closed system of cattle trade between farms. This model is inspired by previous work but goes beyond current mechanistic models of trade by incorporating dynamic trade partnerships, as well as incorporating supply and demand levels into partnership formation rates and trade rates [36, 37, 38]. Individuals in our trading system are competitive, seeking to minimise their unmet demand by forming trade partnerships with large supply sellers and make trades with these trade partners. The resulting temporal trade network is an emergent property of our system. The development of generative models of network dynamics is a current pressing issue [18] and specifically within livestock trade, mechanistic models of trade are needed to understand the interplay between economic and epidemiological interactions in order to design effective proposed measures for disease control [47]. Epidemic and endemic diseases within livestock herds are of major concern to farmers and governments due to the significant financial burden they impose [44]. It is well documented that trade contributes to the persistence of endemic diseases [8, 11, 21, 25, 26, 27, 28], and was a contributing factor to the long-range dispersal of Foot-and-Mouth disease during the 2001 outbreak in the United Kingdom [21, 22, 24]. Thus, an understanding of the complexities of trade in an effort to control disease is of vital importance. The model presented here is one of the few attempts to gain a mechanistic understanding of these intricate processes and goes beyond earlier studies in its analysis of the dynamic nature of livestock trade and its impact on disease spread and persistence [36, 37, 38].

As real-time trade requirements (represented by supply and demand levels) of individuals dictate trading patterns within our model, any individual- or systems-level change that impact these quantities result in adaptation and alterations to trading patterns. This adaptation to disturbances from equilibrium is a critical emergent property of our system, modulated by information on global supply and demand through changes in a system-wide pricing model. This pricing model informs necessary alterations to farm-level stock generation rates and elegantly captures simple macroeconomic concepts such as the Law of Supply and Demand [48]. Adaptation of trading patterns in response to regulatory changes in trade has previously been observed, for example within the UK cattle trading system [15, 32].

The model presented here is adaptive to instantaneous shocks to farm-level supply and demand, with farms rapidly altering their trading patterns over a short period of time so that excess stock is cleared, and the equilibrium of the trading system is maintained. In reality, responses such as increased supply generation may be constrained by biological processes introducing lags that our model does not incorporate. As such, dynamics in response to shocks may be more complex, involving alterations to the supply chain from farm to consumer until farms can increase their supply generation. We note that these lags due to the production cycle may also affect farm response to changes in price, a complexity we have not considered in this article instead assuming that stock generation alters instantaneously following a change in price.

We also showed that individuals will adapt their long-term trading patterns in response to permanent alterations to trading propensities, finding new avenues of trade that minimise unmet demand and allow for the maintenance of animal flows. Long-term adaptation was shown to have important consequences for the persistence of endemic disease. Indeed, despite previous results suggesting simple alterations to trading frequency could significantly reduce disease burden [36, 37, 38], we have shown that the pressure imposed on farms by unmet demand and their desire to maintain animal flows will counteract the potential benefit on disease prevalence of such changes to trade, with a high level of resistance to change shown except for when trade is significantly stressed. These results are a clear example of the Law of Unintended Consequences, where in this case system dynamics act to dampen the benefits of a well-intentioned intervention. In particular, they highlight the interactions in trading systems that must be accounted for if successful disease intervention strategies are to be developed.

We analysed the potential for post-movement animal batch testing and rejecting, a typical disease control strategy employed in cattle trading systems [30, 46], to reduce disease prevalence for a highly prevalent and persistent endemic disease while simultaneously measuring the temporary and long-term implications this control strategy has on the trading system. Considering two rejection strategies, one where the entire batch is rejected if a single animal tests positive for infection, the other where individual animals are rejected if they test positive, we showed that whole batch rejection had the greater potential to reduce disease prevalence. However, when disease could not be completely removed there were long-term disturbances (illustrating the potential for our model to measure stresses on individual farms at many levels) to the trading system, with farms altering their trading patterns permanently. These disturbances were greater for the whole batch rejection strategy but were also observed for the individual animal rejection strategy. For the whole batch rejection, these disturbances were maximised for middling test sensitivities, whereas for the individual animal rejection they were maximised for much higher test sensitivities (approximate sensitivities of 75%). For high test sensitivities, despite small long-term disturbances, short-term shocks to the system were observed for both the whole batch and individual animal rejection strategies. Endemic diseases such as Bovine Tuberculosis generally have high sensitivity tests (87-90%) [49, 50] suggesting disruption to the trading system may be small long-term, however for paratuberculosis test sensitivities are generally lower and estimates vary significantly [51, 52] so the disruption to the trading system as predicted by our model would be much greater (especially for the whole batch rejection strategy). We assumed a test specificity of 100%, a not unreasonable assumption given test specificities are generally very high (for example, >99% for the bTB skin test and ELISA test for paraTB [49, 51]. However, for specificities <100% false positives will lead to greater disturbances to the trading system, but may not alter the long-run impact of testing high test sensitivities. Therefore, our results showing the disturbance to the trading system may be a slight underestimate, but a more thorough analysis of the impact of test specificity is required to fully understand the impact of low test specificity under our model. We note that the alterations to trading patterns observed here are a consequence of the impact on the trading system imposed by post-movement testing and subsequent removal of detected animals. However, it has previously been reported that behavioural responses altering trading patterns due to similar control measures were, at least partially, a result of risk aversion whereby farms avoid high-risk farms [32]. The inclusion and analysis of risk-averse trading is possible within our modelling framework and will be the basis of future work.

Our modelling framework is flexible and may be expanded to incorporate many elements of real-world trading. For example, we assume that trading behaviour and decisions are driven entirely by current farm-level supply and demand. As such, we neglect harder to quantify components of trade such as reputation, as well as future forecasting and decision making based on current price. Moreover, distance-based considerations such as preferentially trading with closer individuals can be incorporated into our model and may have important consequences for the spatial distribution of disease. There is a trend towards fewer, larger farms in cattle trading systems which may have important implications especially over the timescales considered in this study [7]. Such farm consolidation is likely to change network density, potentially increasing the susceptibility of the system to disease outbreaks. Incorporating such consolidation is a potential avenue for future work. Trade partnerships and trades with farms based on animal/farm types, for example beef and dairy, is a complexity of many real-world systems not considered here. However, our model could be extended to include this increased complexity by, for example, defining farm-level supply and demand by animal type. We assumed that recovery from disease does not alter farm-level supply or demand, and imposes no financial burden on farms. For diseases that require farm intervention to remove, for example slaughter, it may be necessary to consider the resulting changes to farm-level supply. Reduced supply due to animal slaughter may lead to increased prices and changes to trading dynamics, thus impacting the efficacy of proposed changes to trade intended to control disease. Exploring these effects is an avenue for future work. Importantly, we have analysed a hypothetical trading system, however with the ever-growing availability of large-scale livestock trading datasets, in future work we aim to parameterise such a system to our dynamic trading model. We aim to assess the ability for our model to predict and replicate real-world trading dynamics and to explore potential disease control strategies and the resulting stress these impose on individuals and the trading system as a whole.

In this article we have framed our trading model within a livestock trading system. However, the model is intended to be general and we anticipate that it can be extended to a number of real-world systems in which goods are moved between distinct individuals. For example, the trade of plants and trees between nurseries is a major route of disease transmission and persistence [53]. We expect our supply- and demand-based trading model to extend and compliment current joint economic-epidemiological models of disease spread between plant nurseries [54]. The current COVID-19 pandemic and resulting control measures have impacted national economies and the day-to-day living of individuals. Modelling these impacts and subsequent behavioural changes in individuals is an application of our model we will explore in future work. Information- and risk-based behavioural changes have been shown to compound mandatory restrictions in reducing disease spread [55], however to our knowledge, there has been little work in understanding, from a mechanistic modelling perspective, how individual-based financial stresses may dictate decision-making and behaviour, nor how these may affect compliance with restrictions. Extending the model presented here to account for human behaviour and interactions driven by individual-level demand that may lead to emergent routes of disease transmission is the basis of future work.

In conclusion, we have introduced a dynamic trading model incorporating individual-level desire to minimise demand and maintain flows, with resulting trading networks an emergent property of the collective actions of these competing individuals. Individual-level adaptation results in a system that is highly resilient to shocks and can find new avenues of trade in response to long-term changes to trade. Adaptation is an important consequence of potential regulatory changes to trade that can impact the success of disease control strategies and therefore must be accounted for when designing and assessing effective interventions.

Data accessibility

All code and input files required to run the model are freely available at `https://github.com/MKnight-bioss/mechanistic_livestock_trade`.

Author contributions

The work was planned and the manuscript was prepared by M.A.K., M.R.H., P.C.L.W., R.S.D., and G.M. All code was written by and simulations and analysis were performed by M.A.K. All authors gave final approval for publication.

Competing interests

We declare we have no competing interests.

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