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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,

9 stock dependent partnership and trade dynamics, our trading model goes  
10 beyond current state of the art modelling approaches. By studying instan-  
11 taneous shocks to farm-level supply and demand we show that behavioural  
12 responses of farms lead to trading systems that are highly resistant to shocks  
13 with only temporary disturbances to trade observed. Individual adaptation  
14 in response to permanent alterations to trading propensities, such that ani-  
15 mal flows are maintained, illustrates the ability for farms to find new avenues  
16 of trade, minimising disruptions imposed by such alterations to trade that  
17 common modelling approaches cannot adequately capture. In the context of  
18 endemic disease control, we show that these adaptations hinder the potential  
19 beneficial reductions in prevalence such changes to trading propensities have  
20 previously been shown to confer. Assessing the impact of a common disease  
21 control measure, post-movement batch testing, highlights the ability for our  
22 model to measure the stress on multiple components of trade imposed by  
23 such control measures and also highlights the temporary and, in some cases,  
24 the permanent disturbances to trade that post-movement testing has on the  
25 trading system.

## 26 **1 Introduction**

27 Trade plays a critical role in the interactions of individuals, firms, and nations [1,  
28 2]. In recent years, the development of network theory has provided a novel frame-  
29 work with which to model and understand the actions of individuals that does not  
30 require the simplifying assumptions of more classical modelling approaches, for ex-  
31 ample making a well-mixed assumption [3, 4]. Representing individuals as nodes  
32 and interactions between these nodes as edges (either directed or undirected, as  
33 well as possibly weighted by the interaction) allows for highly complex interaction  
34 patterns, elegantly capturing scale-free (or approximately scale-free [5]) behaviour  
35 often observed in real-world trading systems [6, 7, 8, 9, 10, 11]. Despite these  
36 clear advantages, network approaches frequently assume the network is static, i.e.  
37 the connections of individuals are permanent and do not change, or that it is an  
38 aggregated time series of successive static snapshots of the network [12]. Exten-

39 sions, whereby network connections change over time but the overall connectivity of  
40 the network is maintained, e.g. neighbour exchange models [13, 14], have recently  
41 been proposed. However, all these approaches neglect the highly temporal nature  
42 of the real-world systems they represent, obscuring dynamical properties of individ-  
43 uals such as seasonal trading patterns or behavioural responses to changes in trade  
44 [15, 16, 17]. Temporal networks, and specifically generative models of temporal net-  
45 works, in which the dynamic network develops and changes based on individual-level  
46 properties is an area of network theory that is currently lacking [18] and is the focus  
47 of this article.

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

66 Trade has frequently been shown to be a risk-factor in disease spread [8, 11, 21, 25,  
67 26, 27, 28]. Indeed, the 2001 FMD outbreak initially spread due to the movement  
68 of animals to market, allowing for widespread dissemination of the disease [21, 24].

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

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

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

94 Here we extend our previous trading model outlined in [38], incorporating a stochas-  
95 tic dynamical trading model including the individual supply- and demand-based  
96 trading behaviour of [36, 37]. This represents, to our knowledge, the first attempt  
97 at creating a truly dynamic generative model of trade in which the actions of indi-  
98 viduals are adaptive to system-wide stock properties. Our model is not intended to

99 replicate any known trading system, however some assumptions outlined below are  
100 informed by past analyses and studies of the Scottish cattle trading system. In this  
101 model, farm trading patterns are determined by current demand, and the resulting  
102 trading system is an emergent property of the collective actions of farms' attempts  
103 to form trading partnerships and trade with appropriate sellers. We will show that  
104 this dynamic modelling approach leads to trading systems that are highly resilient  
105 to shocks in farm stock levels (Section 3.2.2), and the trading patterns of farms  
106 will adapt to long-term changes in trade, finding new avenues by which demand is  
107 satisfied and animal flows are maintained (Section 3.2.3). We will explore the poten-  
108 tial of such adaptive behaviour on endemic disease spread, finding that adaptation  
109 hinders the potential benefits of changes to trade, meaning that significant stress  
110 must be imposed on the system for meaningful reductions in between-farm preva-  
111 lence (Section 3.3.1). We will analyse the impact of post-movement batch testing on  
112 both between-farm prevalence and on the trading system (Section 3.3.2). It will be  
113 shown that testing can be an effective disease control measure when test sensitivi-  
114 ties are high, with short-term disturbances to trade observed while disease is cleared  
115 from the system. However, for low sensitivity tests, we will show that long-term  
116 disturbances to the trading system emerge, and disease cannot be fully eradicated.

## 117 **2 Materials and methods**

### 118 **2.1 An individual-based systems models of trade dynamics**

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

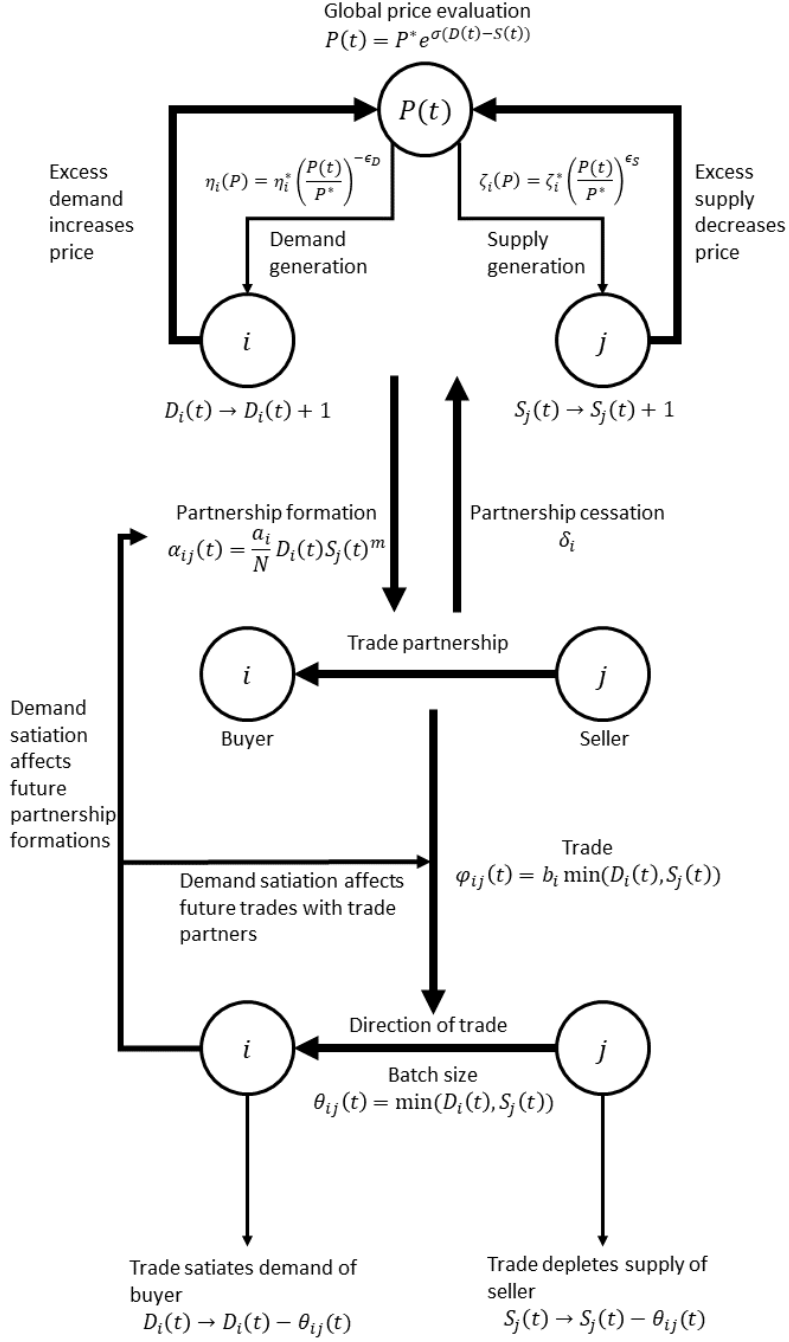


Figure 1: **Dynamic trading network** Model flow diagram highlighting system processes that generate the trading network

127 trading needs are not constant over time [38] but vary contingent on past trades as  
 128 well as continuous generation of new demand. A full outline of model quantities

129 and parameters are presented in Table 1, model processes are illustrated in Figure  
 130 1, and all results presented are generated using a Gillespie Stochastic Simulation  
 131 Algorithm (SSA) [39, 40]. All processes defined below are stochastically generated.  
 132 Our model is general so that distributions of these quantities are arbitrary, however  
 133 in Section 3.1 we specify how these quantities are distributed for this study.

## 134 **2.2 A global pricing strategy and mechanisms of stock gen-** 135 **eration**

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

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

141 where  $P_0$ ,  $D_0$ , and  $S_0$  are, respectively, the price, global demand, and global supply  
 142 at  $t = 0$ . The constant  $\sigma$  represents the sensitivity of price to excess demand, i.e.  
 143 the market response to imbalances in stock levels. For small values of  $\sigma$ , large stock  
 144 imbalances are required for large changes in price, and vice versa for large values of  
 145  $\sigma$ . Unlike the pricing model of [36],  $\sigma$  is not dimensionless, and there is an implicit  
 146 dependence on the system size  $N$ . We assume that the system begins in an initial  
 147 stock-free state, so that  $D_0 = S_0 = 0$ , meaning  $P_0 = P^*$  can be interpreted as the  
 148 equilibrium price when supply and demand are balanced (when the market is in  
 149 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
$\sigma$	Price sensitivity to global excess demand
$\eta_i(P) = \eta_i^* (P(t)/P^*)^{-\epsilon_D}$	Rate at which farm $i$ generates new demand given current price $P(t)$
$\eta_i^*$	Rate at which farm $i$ generates new demand at market equilibrium
$\epsilon_D$	Price elasticity of demand
$\zeta_i(P) = \zeta_i^* (P(t)/P^*)^{\epsilon_S}$	Rate at which farm $i$ generates new supply given current price $P(t)$
$\zeta_i^*$	Rate at which farm $i$ generates new supply at market equilibrium
$\epsilon_S$	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
$\delta_i$	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

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

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

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

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

163 however we exclude stock losses, external flows (flows of goods leaving the system  
164 or entering the system from external sources), and we do not characterise farms as  
165 strict buyers or sellers. The constants  $\eta_i^*$  and  $\zeta_i^*$  represent stock generation rates  
166 at market equilibrium, i.e. when global stock levels are balanced and  $P(t) = P^*$ .  
167 While individual farms are not explicitly defined as buyers or sellers, this can be  
168 included in the model by choosing appropriate values for  $\eta_i^*$  and  $\zeta_i^*$ , for example  
169 setting  $\eta_i^* = 0$  and  $\zeta_i^* > 0$  results in farm  $i$  generating no demand and generating  
170 supply at some non-zero rate; thus, farm  $i$  is a strict supplier. The constants  $\epsilon_D$   
171 and  $\epsilon_S$  are, respectively, the price elasticities of demand and supply. Their values  
172 determine the sensitivity of stock generation to perturbations of the price around  
173 the market equilibrium price and, for simplicity, we have assumed they are constant  
174 across farms, so that the market as a whole responds in a similar relative manner to  
175 alterations in price. We note that changes in price do not alter current farm-level

176 supply and demand, rather they alter the rates at which farms generate future supply  
 177 and demand. Increases in price beyond the market equilibrium price decrease the  
 178 rate at which new demand is generated and increases the rate at which new supply  
 179 is generated, and vice versa. This, combined with our pricing model described  
 180 above replicates the so-called Law of Supply and Demand. There is a feedback loop  
 181 between the price of goods and stock levels: surplus demand leads to increases in  
 182 price, which causes the demand generation rate,  $\eta_i(P)$ , to decrease and the supply  
 183 generation rate,  $\zeta_i(P)$ , to increase. Over time, this results in more supply generated  
 184 than demand, the surplus demand diminishing, and the price begins to return to the  
 185 market equilibrium price  $P^*$ . As the price returns to the equilibrium price, the stock  
 186 generation rates return to their equilibrium values  $\eta_i^*$  and  $\zeta_i^*$ . Thus, the inclusion of  
 187 a pricing model can act as a corrective mechanism to prevent stock divergences. We  
 188 will show in Section 3.2.1 that the exclusion of a pricing model will indeed lead to  
 189 long-term imbalances in supply and demand levels.

### 190 **2.3 The dynamics of trade partnerships**

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

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

200 where  $a_i$  is a constant representing the general propensity for farm  $i$  to seek out new  
 201 trading partners, and  $m$  is a measure of the influence prospective trading partners'

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

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

## 218 **2.4 The dynamics of trade**

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

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

227 for farm  $i$  and its trading partner  $j$ . The constant  $b_i$  is intended to represent any

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

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

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

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

250 Interpreting  $\theta_{ij}(t)$  is straightforward: supply and demand are indivisible quantities  
 251 in our model, representing animals available for sale and number of animals a farm  
 252 wants to buy at a given time, respectively. As such, batches can take minimum size  
 253 1, i.e. a single animal moved. The maximum size, however, is determined by current  
 254 stock quantities of the buying and selling farm, which can lead to residual supply

255 or demand following a batch movement if, for example, a buying farm's demand is  
256 greater than the selling farm's supply. Therefore, transactions are *imperfect* [36] in  
257 the sense that batch movements may not fully satisfy the buyer's demand. Residual  
258 stock from a trade is carried over and influences future trades. In all cases, trades  
259 will always fully satisfy either the demand of the buying farm or the supply of the  
260 selling farm (or both) as batch sizes allocate the maximum amount of available goods  
261 between buyer and seller.

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

## 270 **3 Results**

### 271 **3.1 System parameterisation**

272 Throughout this article we assume a constant  $N = 1000$  farms. To parameterise  
273 the system, we assume equilibrium (at price equilibrium  $P^*$ ) farm stock generation  
274 rates,  $\eta_i^*$  and  $\zeta_i^*$  for farm  $i$ , and the average duration of trade partnerships,  $\tau_i = 1/\delta_i$ ,  
275 are drawn from Power-Law distributions of the form  $p_x \sim x^{-y}$  with parameters  
276 given in Table 2. For stock generation rates, we impose maximum values for  $\eta_i^*$   
277 and  $\zeta_i^*$ , set to 1000 each, and any values that exceed this maximum are rejected  
278 and another sample from the distribution is drawn. We do not impose any such  
279 maximums for partnership durations, as very long partnership durations correspond  
280 to effectively permanent trading partnerships. We note here that our parameter  
281 values are not intended to replicate any known trading system, rather values are  
282 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
$\langle \eta \rangle$	20	System average demand generation rate
$\langle \zeta \rangle$	20	System average supply generation rate
$\eta_{\text{exp}}$	2.33	Exponent for distribution of $\eta_i^*$
$\zeta_{\text{exp}}$	2.33	Exponent for distribution of $\zeta_i^*$
$\tau_{\min}$	0.5	Minimum partnership duration
$\langle \tau \rangle$	1.5	System average partnership duration
$\tau_{\text{exp}}$	2.5	Exponent for distribution of $\tau$
$P^*$	1	Market equilibrium price
$\sigma$	0.0001	Price sensitivity to global excess demand
$\epsilon_D$	0.412	Price elasticity of demand
$\epsilon_S$	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]

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

287 To match desired system averages for each quantity (as given in Table 2), we scale  
288 each value sampled from the Power-Law distribution by a necessary scaling factor,  
289 except for farms whose values are either the minimum value of the respective distri-  
290 bution or, in the case of in- and out-flows, whose  $\eta_i^*$  and/or  $\zeta_i^*$  exceed the maximum  
291 of the distribution. This in turn ensures that total in- and out-flows are equal.  
292 For simplicity, we here neglect explicit correlations between farm flows, however  
293 previous analysis of the Scottish cattle trading system revealed only weak positive

294 relationships between a farm's in- and out-flows [38].

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

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

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

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



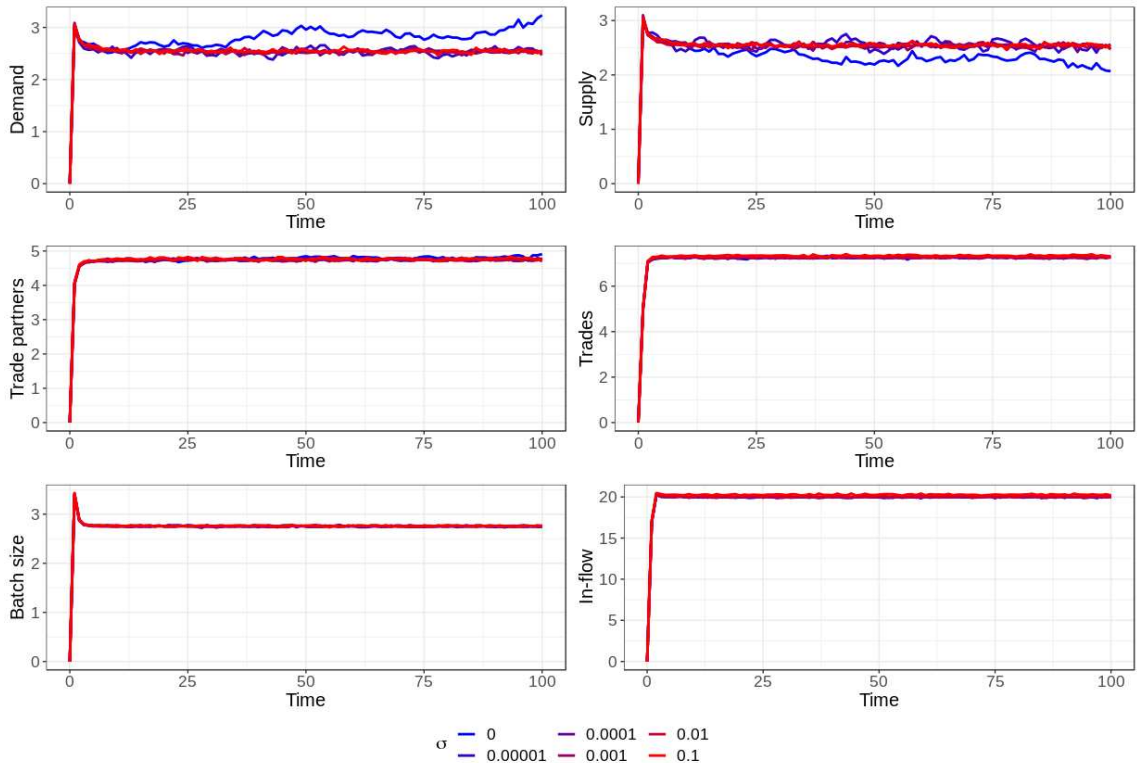


Figure 2: **Impact of price sensitivity on trade network** Trading system response to various values of  $\sigma$ . In all cases except when  $\sigma = 0$  the trading system is largely unaffected by market sensitivity to stock imbalances, with the system reaching similar equilibria regardless of  $\sigma$ . 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

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

## 325 3.2 Model analysis

### 326 3.2.1 Exclusion of a pricing model can lead to divergent stock levels

327 We first explore the systems- and individual-level impact of various values of the  
 328 price sensitivity parameter  $\sigma$ , which dictates the price response to imbalances in

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

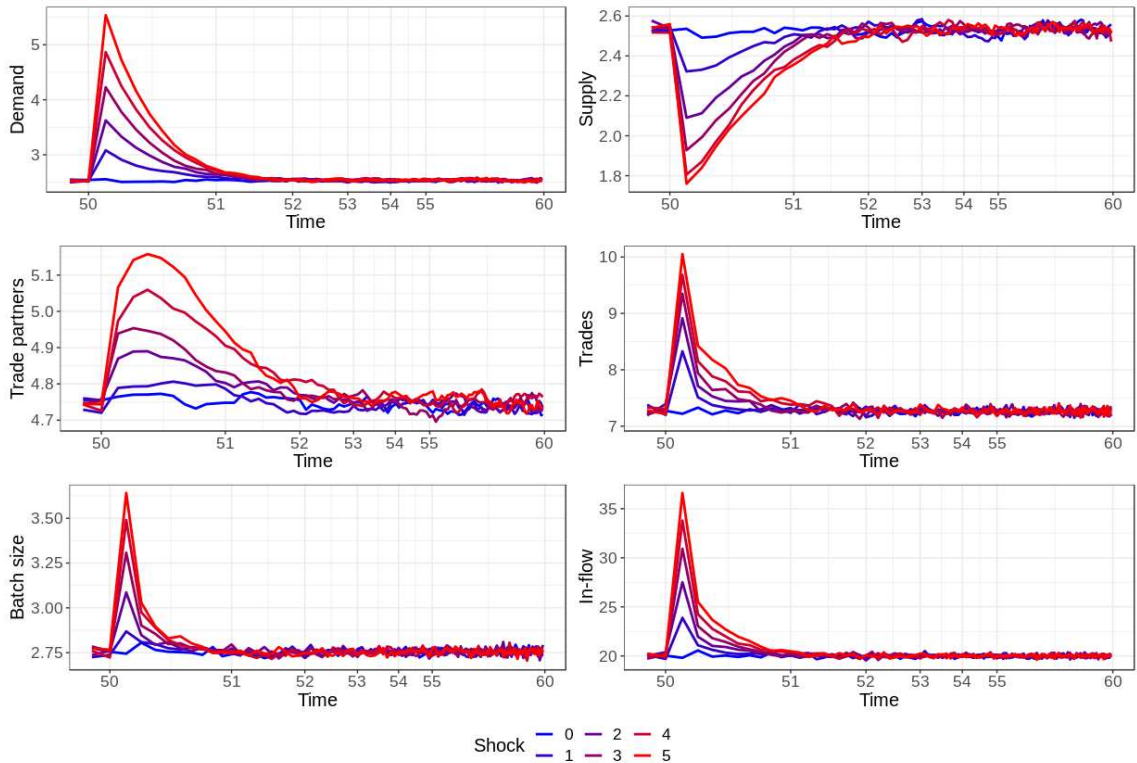


Figure 3: **Demand shocks on the trade network** System-level response to instantaneous shocks in farm-level demand. In all cases, shocks are applied at  $t = 50$  and x-axes are  $\log_{10}$  scaled. For a shock of size  $s$ , all farms  $i$  instantly update their demand to  $D_i(t) \rightarrow D_i(t)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

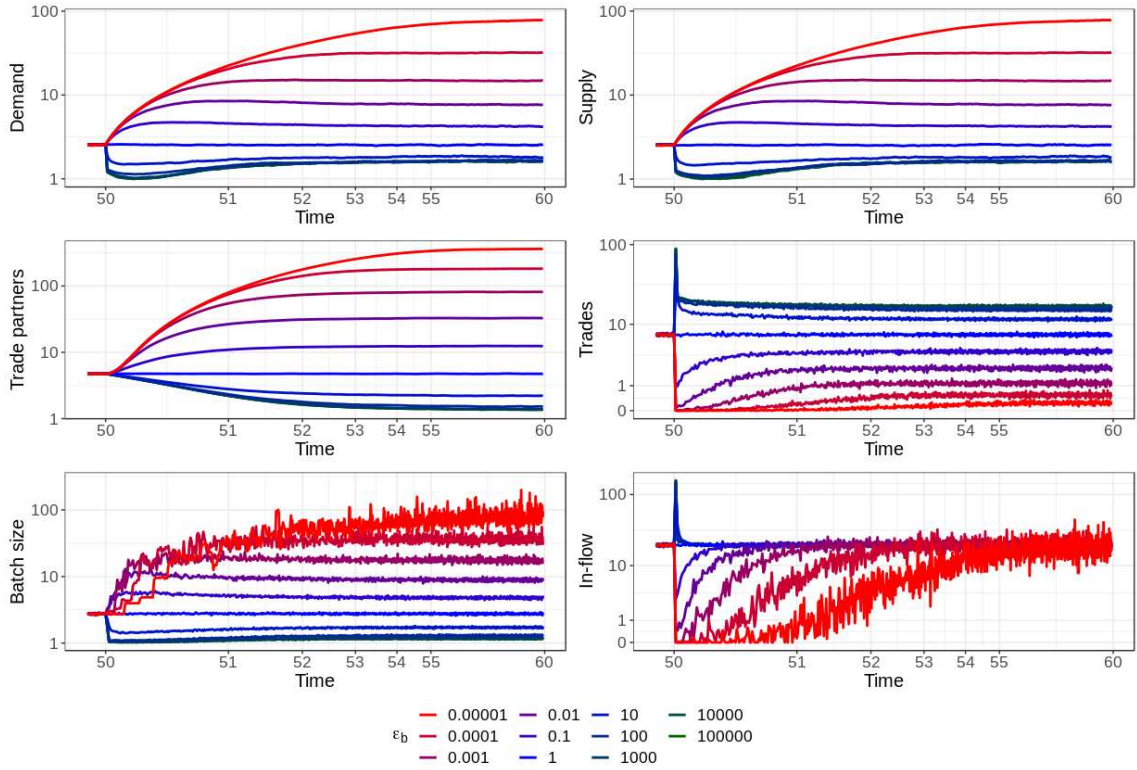


Figure 4: **Evolution of trade network in response to changes in trade frequency** System-level average trading quantities for various values of the trade frequency scaling parameter  $\varepsilon_b$ . For  $\varepsilon_b < 1$ , farms trade less frequently, and for  $\varepsilon_b > 1$  farms trade more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

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

376 At the farm level, shocks alter trading patterns as farms seek to satisfy the additional  
377 demand these shocks introduce. Following the shock, farms immediately form new  
378 trading partnerships and trade more frequently, with trades occurring with larger  
379 batch sizes. Even for very large shocks in demand, average farm supply does not  
380 drop to zero because of the adjustment to stock generation rates resulting in very

381 large supply generation to meet the increased demand of farms. For all shocks to  
 382 demand, the system eventually returns to the pre-shock equilibrium, highlighting the  
 383 system can respond appropriately to shocks such that long-term disturbances to the  
 384 trading system are averted. Of note is the observation that the time for the system to  
 385 return to pre-shock equilibrium is the same regardless of the size of shock to demand,  
 386 indicating the systems-level response is proportionately similar regardless of the size  
 387 of shock. We note that this may not be feasible for some real-world systems such as  
 388 cattle trade, as there are biological constraints preventing unrestricted increases to  
 389 the supply generation rate  $\zeta_i(P)$ . In addition, while the frequency and size of trade,  
 390 and animal flows, quickly return to pre-shock equilibrium values, the dynamics of  
 391 trading partnerships is slower to return (Figure 3). This is a consequence of the  
 392 trade partnership cessation rate  $\delta_i$  being a constant and unaffected by farm-level  
 393 supply and demand. As such, the time for trade partnerships to return to pre-shock  
 394 equilibrium values is determined by the per-farm expected partnership duration  $1/\delta_i$ .

### 395 **3.2.3 Farm- and systems-level adaptation to long-term changes to trad-** 396 **ing patterns**

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

$$b_i \rightarrow \varepsilon_b b_i,$$

$$a_i \rightarrow \varepsilon_a a_i,$$

$$\delta_i \rightarrow \varepsilon_\delta \delta_i.$$

403 Thus,  $\varepsilon_b$ , for example, alters the propensity for farms to trade with their trading  
 404 partners, with  $\varepsilon_b < 1$  decreasing the propensity trade, and vice versa. We introduce

405 these scaling parameters once the trading system has reached equilibrium at baseline  
406 trading dynamics (in other words, for  $\varepsilon_b = \varepsilon_a = \varepsilon_\delta = 1$ ), allowing us to investigate  
407 the initial disturbance to the trading system that permanent alterations to trade  
408 cause, as well as any long-term adaptation and persistent impacts on trading pat-  
409 terns. In contrast with previous work exploring such changes (in particular in the  
410 context of disease control) [36, 38], in which the system response to the above scal-  
411 ing parameters was linear, here we anticipate a nonlinear response for our dynamic  
412 trading system. This hypothesis is predicated on the fact that the rates determining  
413 trade and trade partnership dynamics are functions of at time  $t$  supply and demand  
414 of farms, which are likely to be affected by alterations to trading propensities.

415 We consider alterations to the propensity for farms to trade with their trade partners  
416 by exploring various values of  $\varepsilon_b$  (we perform similar analyses for  $\varepsilon_a$  and  $\varepsilon_\delta$  in ESM  
417 Section 4). Figure 4 shows that in general, for  $\varepsilon_b < 1$  farms trade less frequently  
418 and with larger batch size. Conversely, when  $\varepsilon_b > 1$ , farms trade more frequently  
419 and with smaller batch sizes. These results concur with previous findings [36, 38].  
420 However, we observe that after an initial disturbance to trading patterns following  
421 the change in  $\varepsilon_b$ , farms adapt their trading patterns in response to increases or de-  
422 creases in supply and demand to minimise disruptions caused by changes in trading  
423 propensities and maintain animal flows. For example, when  $\varepsilon_b < 1$ , initial reductions  
424 in animal in-flows are observed, farms trade with their current trade partners less  
425 frequently, and farm-level supply and demand begin to increase rapidly. These in-  
426 creases in supply and demand encourage farms to seek new trade partners, allowing  
427 farms to overcome the reductions in trading propensities imposed by  $\varepsilon_b$  and trades  
428 begin to occur more frequently (however they do not return to frequencies observed  
429 when  $\varepsilon_b = 1$ , i.e. at baseline trading patterns). As trades occur less frequently, farms  
430 accumulate greater levels of supply and demand before a trade occurs, resulting in  
431 increased batch sizes. This relationship between trade frequency and batch size al-  
432 lows farm flows to return to desired levels even for very small  $\varepsilon_b$ , however we note  
433 in these cases animal flows are more variable around the equilibrium than for large  
434  $\varepsilon_b$  ( $\varepsilon_b \geq 1$ ). The system reorganises itself so that animal flows return to the same

435 equilibrium levels as before. However, the trading system itself returns to a new  
436 equilibrium with different numbers of trade partners, trading frequencies, and batch  
437 sizes compared with the system equilibrium before changes to trading propensities  
438 are introduced.

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

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

### 455 **3.3 Role of dynamic trade in endemic disease persistence**

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

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

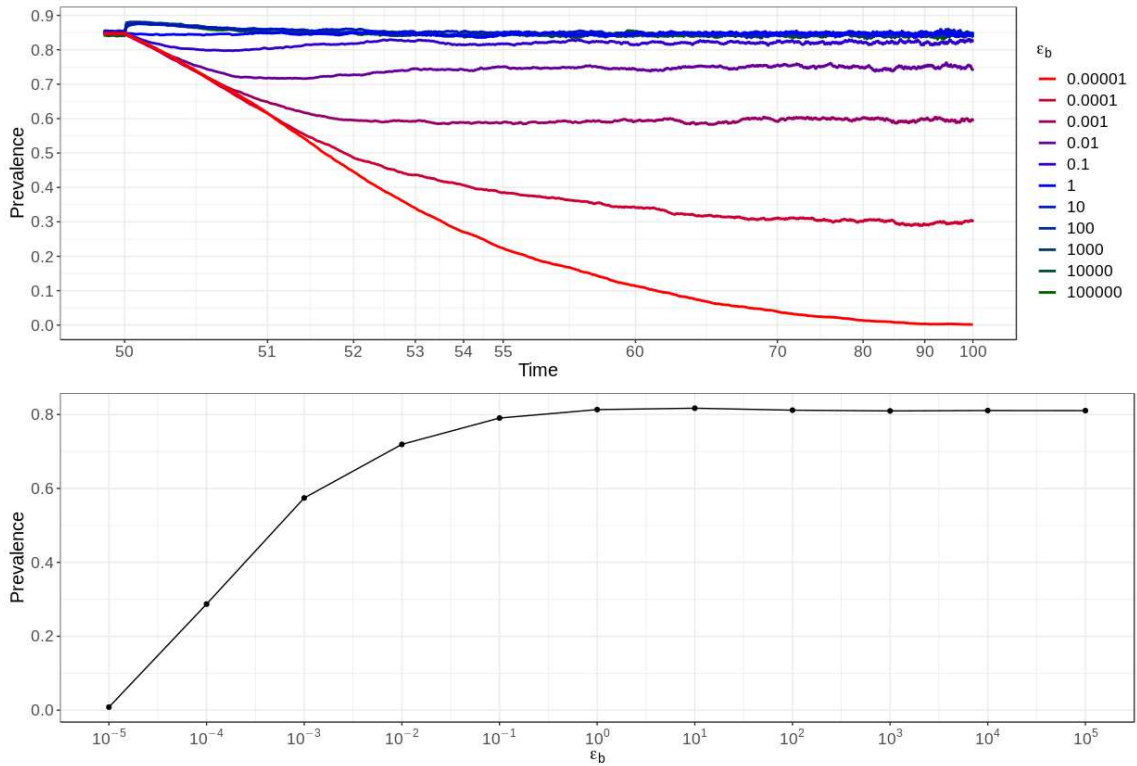


Figure 5: **Impact of changes in trade frequency on disease** Disease prevalence over time (top panel) and equilibrium prevalence (bottom panel) for various values of the trade frequency scaling parameter  $\varepsilon_b$ . In all cases, the trading system reaches an equilibrium at  $\varepsilon_b = 1$  before changes to  $\varepsilon_b$  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.

464 and disease status can be applied to the whole farm, that is to say we ignore within-  
 465 herd disease dynamics. As such, farms are classified as either susceptible ( $S$ ) and  
 466 can be infected by others, or infectious ( $I$ ) allowing them to infect other premises.  
 467 For simplicity, disease spread is modulated entirely through trade, ignoring other  
 468 sources of infection such as external wildlife reservoirs and non-trade related con-  
 469 tacts between farms. An infected farm has constant within-herd prevalence  $\lambda$  while  
 470 infected. This prevalence is unaffected by herd demographics (for example births  
 471 and deaths) or farm flows (introduction of new animals into the herd or animals  
 472 leaving the herd via trade). Thus, we neglect the potential for trade to remove  
 473 infection from a farm by selling infected animals (rapid trade as a counter intuitive  
 474 measure to reduce disease persistence has previously been shown in a trading model  
 475 with mandatory post-movement animal testing [45]). As such, estimated reductions



476 in prevalence are likely to be conservative. Infectious farms remain infectious for  
 477 an exponentially distributed period of time with expectation  $1/\gamma$  at which point  
 478 they return to the susceptible category and can be infected once again. We assume  
 479 recovery from disease does not incur any financial burden on farms, nor does it alter  
 480 supply and demand levels. In addition, infected farms are naïve to their disease sta-  
 481 tus, incurring no financial burdens and do not alter their trading patterns. Trades  
 482 modulate the spread of disease through both the frequency of infectious contacts  
 483 and the probability of infection by assuming that larger batch sizes increase the  
 484 probability of transmission. The probability that a susceptible farm  $i$  is infected by  
 485 its infectious trade partner  $j$  is given by

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

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

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

### 497 **3.3.1 Individual adaptation to changes in trading propensities hinders** 498 **disease control**

499 Altering individual trading propensities has previously been shown to be beneficial in  
 500 controlling disease, with infrequent large trades reducing endemic disease prevalence  
 501 [36, 38]. However, in Section 3.2.3 we showed that individuals adapt their trading

502 patterns in response to alterations in trading propensities, finding new avenues of  
503 trade that maintain animal flows. We now explore the potentially hindering conse-  
504 quences on disease prevalence reduction incurred by such adaptation by introducing  
505 similar long-term changes to trade via the scaling parameters outlined in Section  
506 3.2.3. To highlight the role of adaptation in our dynamic trading model, in ESM  
507 Section 6 we simulate our system under our previous trading model introduced in  
508 [38]. We here focus on changes to trade frequency via the scaling parameter  $\varepsilon_b$  (see  
509 ESM Section 5 for similar exploration of changes to trade partnership dynamics via  
510  $\varepsilon_a$  and  $\varepsilon_\delta$ ).

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

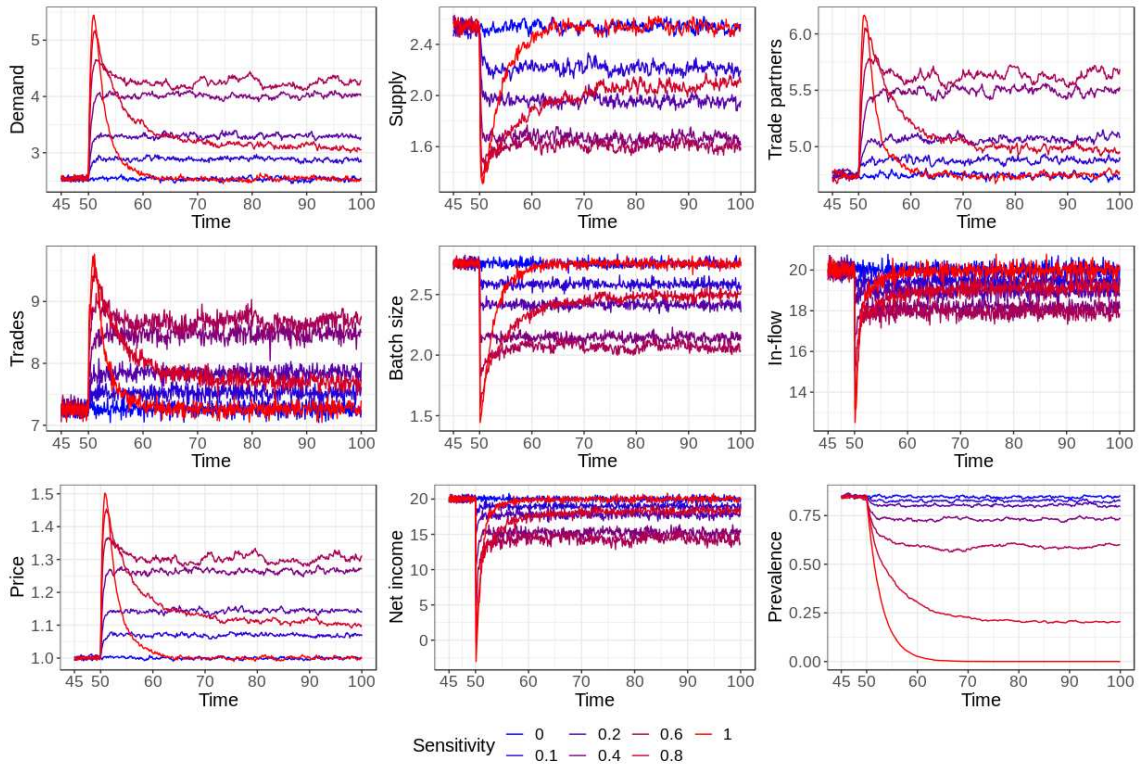


Figure 6: **Impact of movement testing on the trade network and disease prevalence**

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.

532 prevalence observed in Figure 5 when  $\varepsilon_b$  is increased is not a unique case, but is  
 533 rather a characteristic of the farm adaptation described above.

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

### 538 **3.3.2 Assessing the effect of post-movement testing on prevalence and** 539 **the trading system**

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

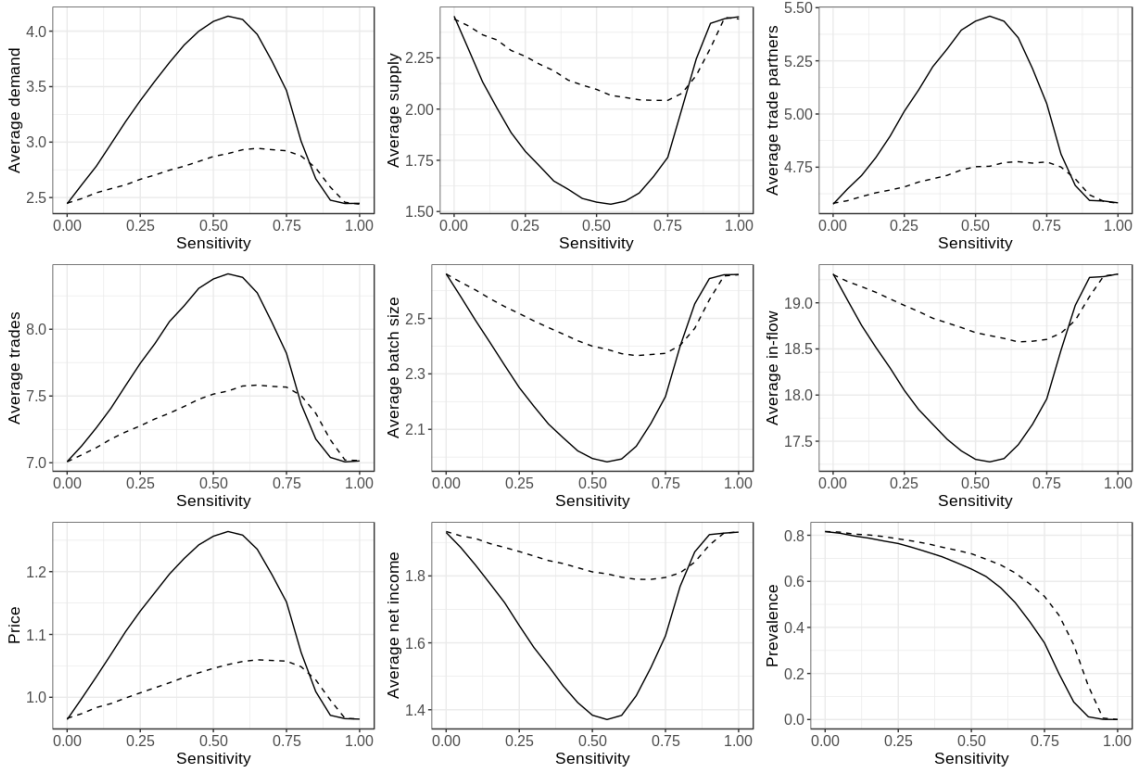


Figure 7: **Impact of test sensitivity on long-run trade dynamics and prevalence under movement testing** Equilibrium values of various trading quantities after testing is introduced for the whole batch rejection (solid lines) and individual animal rejection (dashed lines) regimes. For all test sensitivities  $\xi$ , 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  $\xi < 0.85$ .

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

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

553 demand of  $i$  and supply of  $j$  following a trade is

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

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

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

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

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

573 Figures 6 shows the impact of whole batch rejection on the trading system and  
574 between-herd disease prevalence (equivalent figure for individual animal rejection is

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

## 593 **4 Discussion**

594 In this article we have introduced a dynamic trading model in which individuals'  
595 trading patterns vary based on individual stock quantities representing supply and  
596 demand, framed in the context of a closed system of cattle trade between farms. This  
597 model is inspired by previous work but goes beyond current mechanistic models of  
598 trade by incorporating dynamic trade partnerships, as well as incorporating supply  
599 and demand levels into partnership formation rates and trade rates [36, 37, 38].  
600 Individuals in our trading system are competitive, seeking to minimise their unmet  
601 demand by forming trade partnerships with large supply sellers and make trades  
602 with these trade partners. The resulting temporal trade network is an emergent  
603 property of our system. The development of generative models of network dynamics

604 is a current pressing issue [18] and specifically within livestock trade, mechanistic  
605 models of trade are needed to understand the interplay between economic and epi-  
606 demiological interactions in order to design effective proposed measures for disease  
607 control [47]. Epidemic and endemic diseases within livestock herds are of major  
608 concern to farmers and governments due to the significant financial burden they im-  
609 pose [44]. It is well documented that trade contributes to the persistence of endemic  
610 diseases [8, 11, 21, 25, 26, 27, 28], and was a contributing factor to the long-range  
611 dispersal of Foot-and-Mouth disease during the 2001 outbreak in the United King-  
612 dom [21, 22, 24]. Thus, an understanding of the complexities of trade in an effort to  
613 control disease is of vital importance. The model presented here is one of the few  
614 attempts to gain a mechanistic understanding of these intricate processes and goes  
615 beyond earlier studies in its analysis of the dynamic nature of livestock trade and  
616 its impact on disease spread and persistence [36, 37, 38].

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

627 The model presented here is adaptive to instantaneous shocks to farm-level supply  
628 and demand, with farms rapidly altering their trading patterns over a short period  
629 of time so that excess stock is cleared, and the equilibrium of the trading system  
630 is maintained. In reality, responses such as increased supply generation may be  
631 constrained by biological processes introducing lags that our model does not incor-  
632 porate. As such, dynamics in response to shocks may be more complex, involving  
633 alterations to the supply chain from farm to consumer until farms can increase their

634 supply generation. We note that these lags due to the production cycle may also  
635 affect farm response to changes in price, a complexity we have not considered in  
636 this article instead assuming that stock generation alters instantaneously following  
637 a change in price.

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

652 We analysed the potential for post-movement animal batch testing and rejecting,  
653 a typical disease control strategy employed in cattle trading systems [30, 46], to  
654 reduce disease prevalence for a highly prevalent and persistent endemic disease while  
655 simultaneously measuring the temporary and long-term implications this control  
656 strategy has on the trading system. Considering two rejection strategies, one where  
657 the entire batch is rejected if a single animal tests positive for infection, the other  
658 where individual animals are rejected if they test positive, we showed that whole  
659 batch rejection had the greater potential to reduce disease prevalence. However,  
660 when disease could not be completely removed there were long-term disturbances  
661 (illustrating the potential for our model to measure stresses on individual farms  
662 at many levels) to the trading system, with farms altering their trading patterns  
663 permanently. These disturbances were greater for the whole batch rejection strategy



664 but were also observed for the individual animal rejection strategy. For the whole  
665 batch rejection, these disturbances were maximised for middling test sensitivities,  
666 whereas for the individual animal rejection they were maximised for much higher test  
667 sensitivities (approximate sensitivities of 75%). For high test sensitivities, despite  
668 small long-term disturbances, short-term shocks to the system were observed for  
669 both the whole batch and individual animal rejection strategies. Endemic diseases  
670 such as Bovine Tuberculosis generally have high sensitivity tests (87-90%) [49, 50]  
671 suggesting disruption to the trading system may be small long-term, however for  
672 paratuberculosis test sensitivities are generally lower and estimates vary significantly  
673 [51, 52] so the disruption to the trading system as predicted by our model would  
674 be much greater (especially for the whole batch rejection strategy). We assumed a  
675 test specificity of 100%, a not unreasonable assumption given test specificities are  
676 generally very high (for example, >99% for the bTB skin test and ELISA test for  
677 paraTB [49, 51]. However, for specificities <100% false positives will lead to greater  
678 disturbances to the trading system, but may not alter the long-run impact of testing  
679 high test sensitivities. Therefore, our results showing the disturbance to the trading  
680 system may be a slight underestimate, but a more thorough analysis of the impact  
681 of test specificity is required to fully understand the impact of low test specificity  
682 under our model. We note that the alterations to trading patterns observed here  
683 are a consequence of the impact on the trading system imposed by post-movement  
684 testing and subsequent removal of detected animals. However, it has previously been  
685 reported that behavioural responses altering trading patterns due to similar control  
686 measures were, at least partially, a result of risk aversion whereby farms avoid high-  
687 risk farms [32]. The inclusion and analysis of risk-averse trading is possible within  
688 our modelling framework and will be the basis of future work.

689 Our modelling framework is flexible and may be expanded to incorporate many el-  
690 ements of real-world trading. For example, we assume that trading behaviour and  
691 decisions are driven entirely by current farm-level supply and demand. As such,  
692 we neglect harder to quantify components of trade such as reputation, as well as  
693 future forecasting and decision making based on current price. Moreover, distance-

694 based considerations such as preferentially trading with closer individuals can be  
695 incorporated into our model and may have important consequences for the spatial  
696 distribution of disease. There is a trend towards fewer, larger farms in cattle trad-  
697 ing systems which may have important implications especially over the timescales  
698 considered in this study [7]. Such farm consolidation is likely to change network  
699 density, potentially increasing the susceptibility of the system to disease outbreaks.  
700 Incorporating such consolidation is a potential avenue for future work. Trade part-  
701 nerships and trades with farms based on animal/farm types, for example beef and  
702 dairy, is a complexity of many real-world systems not considered here. However,  
703 our model could be extended to include this increased complexity by, for example,  
704 defining farm-level supply and demand by animal type. We assumed that recovery  
705 from disease does not alter farm-level supply or demand, and imposes no financial  
706 burden on farms. For diseases that require farm intervention to remove, for exam-  
707 ple slaughter, it may be necessary to consider the resulting changes to farm-level  
708 supply. Reduced supply due to animal slaughter may lead to increased prices and  
709 changes to trading dynamics, thus impacting the efficacy of proposed changes to  
710 trade intended to control disease. Exploring these effects is an avenue for future  
711 work. Importantly, we have analysed a hypothetical trading system, however with  
712 the ever-growing availability of large-scale livestock trading datasets, in future work  
713 we aim to parameterise such a system to our dynamic trading model. We aim to  
714 assess the ability for our model to predict and replicate real-world trading dynam-  
715 ics and to explore potential disease control strategies and the resulting stress these  
716 impose on individuals and the trading system as a whole.

717 In this article we have framed our trading model within a livestock trading system.  
718 However, the model is intended to be general and we anticipate that it can be ex-  
719 tended to a number of real-world systems in which goods are moved between distinct  
720 individuals. For example, the trade of plants and trees between nurseries is a ma-  
721 jor route of disease transmission and persistence [53]. We expect our supply- and  
722 demand-based trading model to extend and compliment current joint economic-  
723 epidemiological models of disease spread between plant nurseries [54]. The cur-

724 rent COVID-19 pandemic and resulting control measures have impacted national  
725 economies and the day-to-day living of individuals. Modelling these impacts and  
726 subsequent behavioural changes in individuals is an application of our model we will  
727 explore in future work. Information- and risk-based behavioural changes have been  
728 shown to compound mandatory restrictions in reducing disease spread [55], how-  
729 ever to our knowledge, there has been little work in understanding, from a mech-  
730 anistic modelling perspective, how individual-based financial stresses may dictate  
731 decision-making and behaviour, nor how these may affect compliance with restric-  
732 tions. Extending the model presented here to account for human behaviour and  
733 interactions driven by individual-level demand that may lead to emergent routes of  
734 disease transmission is the basis of future work.

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

## 743 **Data accessibility**

744 All code and input files required to run the model are freely available at [https:](https://github.com/MKnight-bioass/mechanistic_livestock_trade)  
745 [//github.com/MKnight-bioass/mechanistic\\_livestock\\_trade](https://github.com/MKnight-bioass/mechanistic_livestock_trade).

## 746 **Author contributions**

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

## 750 **Competing interests**

751 We declare we have no competing interests.

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