Nature-inspired design principles promote supply network resilience

Matthew J. Hasenjager [a,b,*], Graham Derryberry [b], Xiaohui Guo [c,1], Noa Pinter-Wollman [c], Nina H. Fefferman [a,b,d]

[a] *Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA*
[b] *National Institute for Modeling Biological Systems, University of Tennessee, Knoxville, TN, USA*
[c] *Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA*
[d] *Department of Mathematics, University of Tennessee, Knoxville, TN, USA*

ABSTRACT

The dynamic, interconnected nature of modern supply chains makes it important to understand how firm-level decision-making will impact the robustness of supply chains to disruption. The behavior of naturally evolved distribution systems offers a useful starting point to identify potential design features that can promote robustness without compromising the viability of individual firms. Drawing inspiration from how ant food-sharing networks respond to supply shortages, we developed an agent-based model of a generalized supply network and evaluated how different local strategies influenced the ability of firms to acquire sufficient resources to meet their demand. Our simulations reveal that differences among firms in strategic behavior can reduce variation in outcomes across firms while maintaining mean performance, thereby buffering system-level robustness. In addition, the ability to expand one's supplier network bolstered performance when firms experienced difficulty in meeting their demand. Conversely, under the assumptions of our model, overly relying on distributors to gain access to additional suppliers or to gain competitive advantages was ineffective in helping firms to meet their consumptive demand. Our nature-inspired modeling framework provides a potentially useful approach for evaluating how different participant decision-making strategies may impact the robustness and resilience of global supply chains that are increasingly likely to face frequent and unpredictable disruptions.

1. Introduction

Resource distribution systems, whether artificial (e.g., supply networks: [4]) or naturally occurring (e.g., ant colonies: [31,43]; fungal hyphae networks: [3]), must balance competing priorities. For instance, robustness to route disruption must be weighed against the costs of maintaining potentially redundant routes. Current supply chain management (SCM) theory typically assumes relatively stable social, political, and economic conditions and therefore often prioritizes efficiency and predictability over competing concerns

[37,52,8]. For example, just-in-time delivery systems aim to reduce inventory levels and associated storage costs, and cost efficiencies drive elimination of redundant distribution pathways [1,27,33,7]. However, overly focusing on efficiency and optimality may also increase the vulnerability of supply networks when conditions change [10,14,52,9]. Such vulnerability has been apparent during the COVID-19 pandemic, as supply chains struggled to respond to systemic shifts in consumer demand, labor shortages, disrupted transport routes, and supply shortfalls [21,39]. To mitigate the impacts of disruption, it is important to understand how local, firm-level decision-making influences supply network resilience.

SCM theory has traditionally viewed resilience as the speed at which a company can return to normal performance following disruption (i.e., 'engineering' resilience: [22,45]. Conversely, 'ecological' resilience is the capacity of a system to absorb shocks while maintaining its structure and function [14,22]. Wieland [52] has recently argued that this latter view of resilience—focused on factors that enable systems to persist, adapt, or transform when faced with perturbations—should be more widely adopted by SCM theorists, as it offers a framework for understanding how supply networks can operate under the dynamic, unpredictable, and often disruptive conditions typical of contemporary social, economic, and environmental landscapes. A key component of ecological resilience is robustness: the ability of a system to reduce the magnitude of disruptive effects over its functioning. For instance, if disrupted conditions persist, greater robustness can provide crucial time and resources to mount more effective, long-term responses [14,47]. However, how firm-level decision-making shapes network-level robustness to disruption is poorly understood due to the complex, interdependent nature of modern supply networks.

Supply networks are composed of individual firms linked by supplier-customer relationships defined by the transfer and exchange of information, goods, and funds [36,38,48]. Supply chain management concerns decisions regarding local networks of partnerships (e.g., demand forecasting, inventory management), but the effects of these decisions cascade throughout the wider network [25,46,6]. In addition, networks of inter-firm relationships evolve in response to shifts in demand, supply, and transport capacity [39,4]. Consequently, SCM theorists have increasingly adopted a complex adaptive systems perspective that emphasizes features such as emergent behavior, self-organization, multi-scale structure, and interdependence among system entities [37,38,48,6]. Such a perspective shifts the aim of supply chain management from attempting to control and optimize an entire supply network and its processes to an approach that employs targeted control efforts while allowing for emergent patterns that can be leveraged to promote innovation and flexibility in the face of unforeseen challenges [6]. For example, a firm may seek to cultivate relationships with suppliers from whom it may not directly receive high-value products and services, but that nevertheless occupy central positions within the broader supply network, making them likely sources of information and innovation (i.e., strategic *vs.* nexus suppliers; [44,53]).

From a complex adaptive systems perspective, supply network robustness is thus conceptualized as an emergent property that arises from the decision-making of individual businesses and the overall network structure. Indeed, the relative contribution of a firm to supply network robustness may often have less to do with that firm's overall size and activity than how it is connected within its broader supply network [10]. For example, clusters of highly interdependent firms can increase supply network vulnerability by facilitating the propagation of shocks through the network [10,25,9]. In addition, efforts to enhance supply chain efficiency—e.g., supply base reduction, global sourcing, inventory reduction—often come at the cost of reductions in robustness at the firm- and network-level [7,9]. Reducing the size of a firm's supply base, for instance, can lower transaction costs, facilitate order volume discounts, and promote supplier responsiveness [7], yet greater reliance on one or a few suppliers increases the risk of severe disruptions should any of these critical suppliers fail [26,49,9]. Likewise, if multiple firms across the supply network are highly reliant on a few critical nodes, initial shocks are more likely to result in widespread and severe disruption [10]. This emergent nature of robustness highlights the challenges involved in predicting the impact of local decisions over supply network functioning and therefore to design and implement decision tools that can simultaneously promote system-level resiliency without compromising the viability of individual firms.

To address these design challenges, considering the behavior of naturally evolved distribution systems offers potentially useful and novel solutions. The underlying logic of bioinspired design is that, while natural selection does not necessarily favor optimal or efficient solutions, natural selection is expected to act against fragility [12,13,20]; in other words, easily disrupted biological systems and processes are unlikely to persist over evolutionary time. Thus, by studying how naturally evolved distribution systems operate, it may be possible to uncover fundamental functional components that can be employed usefully in novel circumstances [11,29], including in organizational and management contexts [20,50]. Whereas traditional bioinspired approaches seek to emulate specific natural solutions to analogous design challenges, we employ a novel approach that identifies the elements that enable a natural system to function and uses those elements to design a system that is analogous in its function, rather than its structure.

Here, we borrow our inspiration from ant colonies, representing a complementary example of a complex adaptive system. An ant colony is a highly integrated collective whose survival depends on the acquisition and distribution of food resources among workers and developing larvae [17]. The food collection and distribution process is self-organized yet tightly regulated according to the nutritional demands of the colony and the availability of food in the surrounding environment [17,18,43,5]. Foragers act as upstream suppliers of the system by acquiring food resources and transporting them into the colony [18]. Within the colony, food is distributed via mouth-to-mouth liquid food exchange (i.e., trophallaxis: [19,30]), with food exchange dynamics being responsive to both individual- and colony-level needs [18,23,43]. In essence, an ant colony represents a microcosmic supply chain that is highly amenable to observation and experimentation, thereby enabling the elements of ant behavior that promote robustness to be identified and their functions adapted for novel applications.

Empirical work studying famine relief in food-deprived ant colonies has revealed behavioral features that are likely to contribute to robust resource distribution (Table 1). One such feature is that a recipient ant commonly receives food from multiple donors, even when a single donor possesses sufficient food to fully satiate it [18,19]. Receiving food in this manner appears to act as a form of

bet-hedging: by investing time in seeking out multiple donors, individuals can better achieve nutritional targets and limit the likelihood of potentially catastrophic negative outcomes (e.g., ingesting toxin from a tainted food source: [43]). During famine relief, worker ants are also more likely to act as both food donor and receiver (in other words, a distributor) [19,43], enabling an especially rapid and widespread distribution of food through the colony under stressful conditions. Finally, famine relief alters patterns of interaction within the nest. Ant workers are often segregated spatially according to task (e.g., foraging, brood care) [35], but this segregation relaxes during famine relief, leading to greater mixing among subsets of individuals that usually do not interact [23,43]. Moreover, foragers and recipients in need of food will actively seek out one another—e.g., foragers attempt to initiate more food-sharing interactions and venture deeper into the nest while unfed ants cluster around the returning foragers [18,23,43]. These behavioral responses facilitate interactions between otherwise disconnected workers and help achieve an effective distribution of food.

To evaluate how these behavioral features—bet-hedging, reliance on distributors, and creating new supply routes—contribute to the robustness of distribution systems faced with disruption, we built an agent-based model capturing a generalized supply network of customer-supplier relationships [36]. Customers place demand-driven orders for goods with upstream suppliers, who in turn seek to procure goods and enact deliveries according to the orders they receive. Using this simulation testbed, we evaluated the impact of the following nature-inspired design principles: (i) bet-hedging strategies that limit the risk of supply shortages by utilizing multiple suppliers; (ii) strategies that aim to increase a customer's competitive advantage in placing orders with suppliers; (iii) strategies that seek to reach additional suppliers by preferentially relying on distributors; and (iv) behavioral responses that promote the establishment of new supplier-customer relationships. Our results demonstrate how efficacy differs across strategies, at both the level of the individual firm and the overall supply network and point toward actions that may help to reduce volatility in outcomes and limit negative impacts on firms' mean expected performance following system-wide disruption.

2. Model description

We constructed an agent-based model that captures core elements of a generalized supply network [36], in which local decisions generate indirect effects throughout the network as customers and suppliers respectively place and fulfill orders for a product. The model generates supply networks that contain three mutually exclusive node types (Fig. 1a). Source nodes represent upstream manufacturers that repeatedly produce units of an unspecified good. Sink nodes represent downstream retailers or consumers that place orders with upstream suppliers (either source or distributor nodes) to meet their consumptive demand for this good. Distributors neither purchase goods for their own consumption nor produce them, but instead receive orders from sink nodes and other distributor nodes and purchase goods from suppliers to meet their customers' demand. We use the terms 'customer' and 'supplier' with respect to the nature of an interaction because actions are not necessarily linked to particular node types—e.g., distributors may act as both customer and supplier, depending on the interaction (Fig. 1b). Note that it is possible for sink nodes to place orders directly with source nodes and for source nodes to supply directly to sink nodes if they share a direct connection. In the following sections, we briefly describe the features and operation of the model. The model was developed and implemented in R ver.4.1.0 [42] and code is available on GitHub (see 'Data availability').
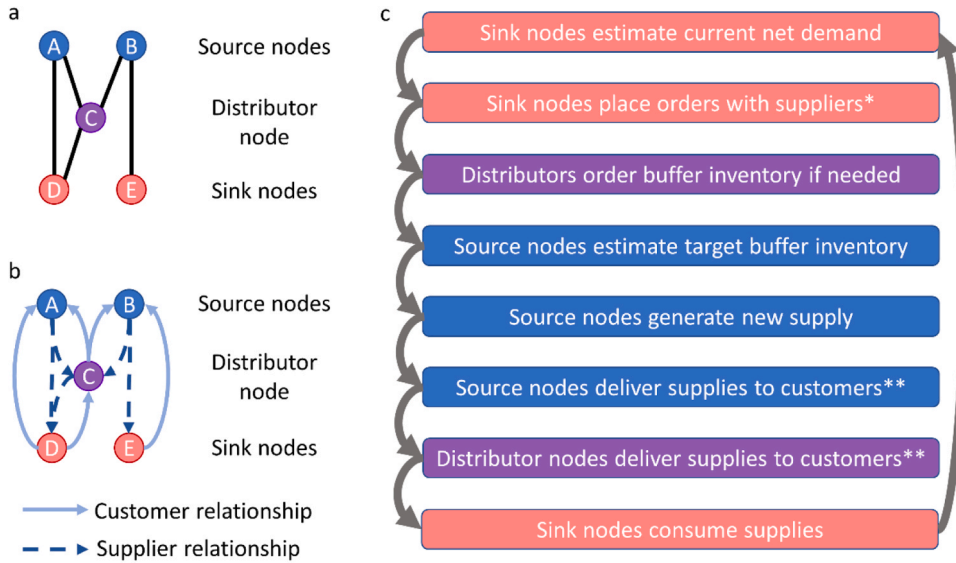
2.1. Generating the supply network

The simulation is initialized by stochastically generating a network of supplier-customer relationships amongst N_{Source}, $N_{Distributor}$, and N_{Sink} nodes (Table 2). Each source node forms 1-2 links with downstream distributor or sink nodes; likewise, each sink node generates 1-2 links with upstream suppliers (i.e., distributor or source nodes). Distributor nodes generate 1-2 links with source nodes, 1-2 links with sink nodes, and 0-1 links with another distributor node. The number of links formed by each node type were selected to yield a supply network density that resembles what would be expected in many real world supply networks [25,4], given the need to balance market access against the burden of securing multiple contracts for the trade of a specific good.

Each source and distributor node sets a price per unit $p_{Source,i}$ and $p_{Distributor,i}$ respectively. Here, we assume that distributor prices are higher than source prices, reflecting markups to maintain profit margins and/or value-added products or services [15,24]. However, customers can benefit from a distributor aggregating many small orders into a larger order volume, because suppliers (i.e., source and distributor nodes) prioritize deliveries based on order volume. Each source node is also assigned a mean replenishment rate, R_i, which indicates the mean number of units that a source node can generate each turn. Each sink node is assigned a mean gross demand, D_i, governing the mean amount of goods that it seeks to consume each turn and the total amount of liquid funds that it can use to purchase

Table 1
Overview of nature-inspired design principles implemented in the supply network model.

Famine relief responses in ant colonies	Potential function(s)	Proposed design principle	References
Ants receive food from multiple donors	• Enhanced ability to achieve consumptive targets. • Reduced risk of negative outcomes from overreliance on a single supplier.	Customer utilization of multiple suppliers where possible.	[19,18]
Ants frequently act as both donor and receiver of food	• Promote rapid and/or widespread resource distribution.	Customer reliance on distributors to increase access to resources.	[19,43]
Enhanced mixing among foragers and nest workers.	• Increased interaction and resource exchange among otherwise weakly connected individuals.	Customers should be willing and able to form new customer-supplier relationships.	[23,43]

Fig. 1. Model overview. (*a*) Example supply network indicating connections between source (A,B), distributor (C), and sink (D,E) nodes. (*b*) Indicates potential customer-supplier relationships for the supply network depicted in (*a*). For example, B can act as a supplier to C (a distributor) and to E (a sink node), yet E cannot purchase from C as they are not connected in the network depicted in (*a*). Conversely, sink node D can be a customer for both C and A. (*c*) Overview of model processes across a single time step. *: When a sink node places an order with a distributor, the distributor handles any orders that it needs to make to fulfill that order as part of the same process before the sink node proceeds with any further ordering. **: Payment is handled as part of the delivery process. Note that 'customer' can include both distributor and sink nodes.

Table 2
Overview of model parameters and values used in our simulations.

Name	Description	Initial value(s)
N	Number of nodes in the network	$N_{Source} = 18$
		$N_{Distributor} = 27$
		$N_{Sink} = 45$
p_i	Price per unit set by node i	$p_{Source,i} \sim N(15, 1.5)$
		$p_{Distributor,i} \sim 15 * (1 + m_i)$
m_i	Price markup set by distributor i	$m_i \sim N(0.3, 0.3)$
R_i	Mean replenishment for source node i	$R_i \sim N(150, 30)$
D_i	Mean consumptive demand for sink node i	$D_i \sim N(50, 10)$
B_i	Total budget for sink node i	$B_i = a * 15 * (D_i * t_{Max})$
a	Adjustment to sink node budgets to account for distributor markups	1.08
$r_i(t)$	Anticipated replenishment for source node i during time step t	$r_i(t) \sim N(R_i, 0.1 * R_i)$
$L_i(t)$	Maximum replenishment possible for source node i during time step t	$L_i(t) \sim N(r_i(t), 0.05 * r_i(t))$
$d_i(t)$	Current gross demand for sink node i during time step t	$d_i(t) \sim N(D_i, 0.1 * D_i)$
$e_i(t)$	Estimated gross demand for sink node i during time step t	$e_i(t) \sim N(D_i, 0.1 * D_i)$
$I_i(t)$	Current inventory of node i at the beginning of time step t	n/a
μ	Sets a supplier's target buffer inventory (i.e., safety stock) as a function of its received order volume	0.15
t_{Max}	Number of time steps in simulation	100

goods across the simulation, B_i. The amount of funds that a sink node can spend each time step, b_i, is determined by its current liquid funds, B_i, divided by the time steps remaining in the simulation, reflecting decision-making based on estimation of a firm's annual budget. Prior to beginning the simulation, source nodes estimate their anticipated replenishment (representing current manufacturing capacity or access to raw materials) for the initial time step, $r_i(t = 1)$. Sink nodes likewise generate their gross demand for the initial time step, $d_i(t = 1)$, and their estimate of this value, $e_i(t = 1)$. Consequently, sink nodes do not have perfect knowledge of the demand that they will experience. Finally, source and distributor nodes generate an initial inventory, $I_i \sim U(1, 100)$. Parameter values were selected to yield stable supply networks that under baseline, pre-disruption conditions allow sink nodes to meet their gross demand with a high probability on each time step.

2.2. Model processes

The simulation occurs over 100 discrete time steps. During each time step, nodes complete a round of ordering, distribution, and consumption (Fig. 1c). On each time step, sink nodes act in a randomly assigned sequence to place orders with distributors and/or

source nodes to meet their estimated gross demand. A sink node, i, first determines its current net demand as its estimated gross demand minus current inventory, $e_i(t)$ - $I_i(t)$, before assembling a list of suppliers composed of all source and distributor nodes with which it is connected. The sink node ranks its suppliers according to its purchasing strategy (see below) and proceeds to place orders, starting with its highest ranked supplier. A supplier's inventory differs depending on whether it is a source or distributor node. A source node's available inventory equals its current inventory level plus anticipated replenishment, $I_i(t) + r_i(t)$, minus units reserved from orders received earlier during the current time step (as sink nodes act sequentially). Conversely, a distributor's advertised inventory equals its current inventory level, $I_i(t)$, plus available inventory held by any source nodes to which it is connected. This means that a distributor node will accept orders from sink nodes that it can fulfill by placing its own orders with source nodes; these latter orders are handled at the same time as the former (i.e., there is no distinct phase in which distributors place their own orders based on received orders). Note that it is possible that the active sink node's suppliers possess insufficient inventory to fully satisfy its current net demand, in which case it simply orders as much inventory as it can, following its purchasing strategy (see below). When each order is placed, both sink node and supplier record the order volume and the supplier reserves that amount of its anticipated inventory for delivery. If a sink node has not yet ordered sufficient inventory to meet its estimated demand, has not exhausted its funds for the time step, and has other suppliers available, it proceeds to the next supplier on its list (ranked according to its purchasing strategy (see below)).

Once sink nodes have placed their orders, distributor nodes determine their target buffer inventory by multiplying their received order volume by μ and order additional inventory accordingly. Following this second round μ ordering, source nodes follow the same procedure to determine their target buffer inventory. Each source node i then determines both the maximum amount of inventory that it can produce that turn, $L_i(t)$, and its target replenishment amount

$$\text{round}\big(\mu * O_{received,t}(t)\big) + O_{received,i}(t) - \quad I_i(t)$$

where $O_{received,i}(t)$ is the total order volume received by node i on the current time step, $I_i(t)$ is node i's current inventory, and μ sets a node's target buffer inventory as a proportion of its current received order volume. Source nodes then replenish stock equal to the lesser of either their target or maximum replenishment value.

Next, order delivery proceeds with source nodes acting first, followed by distributors. A supplier, i, (whether source or distributor) first aggregates all orders received from the same customer (whether distributor or sink node) and prioritizes deliveries based on total order volume. Where insufficient inventory is available to fulfill an order completely, all remaining inventory is delivered to that customer. Payment is based on the delivery volume and the supplier's price per unit. Following delivery, the supplier and customer update their inventory and payment. Following distribution, each sink node i proceeds to consume inventory equal to min (I_i, $d_i(t)$). Stability metrics are then recorded for the current time step. If time step, t_{Max}, has not been reached, source nodes determine their anticipated replenishment, $r_i(t + 1)$, and sink nodes determine their current gross demand, $d_i(t + 1)$, and estimated gross demand, $e_i(t + 1)$, for the following time step.

2.3. Resilience measures and disruption

On each time step, we record several measures that capture different aspects of supply network resilience. These measures reflect: (i) mean order fill rate (i.e., the mean final status of orders placed by sink nodes)

$$\frac{1}{N_{Sink}} \left(\sum_{i=1}^{N_{Sink}} \frac{O_{Delivered,i}(t)}{O_{Placed,i}(t)} \right)$$

where O refers to order volume delivered to or placed by node i at time t; (ii) the mean proportion of sink nodes' current gross demand that remains unsatisfied

$$\frac{1}{N_{Sink}} \left(\sum_{i=1}^{N_{Sink}} \frac{d_i(t) - \min(d_i(t), I_i(t) + O_{Delivered,i}(t))}{d_i(t)} \right)$$

where $d_i(t)$ is node i's current gross demand at time t and $I_i(t)$ is the units of inventory node i has at time t prior to order delivery; and (iii) the mean price paid per unit by sink nodes:

$$\frac{1}{N_{Sink}} \left(\sum_{i=1}^{N_{Sink}} \frac{f_i(t)}{O_{Delivered,i}(t)} \right)$$

where $f_i(t)$ is the total payment amount made by node i at time t. In addition to mean outcomes, we also examined the coefficient of variation (i.e., ratio of the standard deviation to the mean) of these measures to evaluate the relative disparity in outcomes across sink nodes.

We compared these response variables across purchasing and response strategies (see below) both prior to and following a systemic disruption to available supply across the network. Each simulation underwent 50 time steps of baseline conditions in which, on average, sufficient supply is generated in the network each turn to meet customer demand. Following the baseline period, the network was disrupted and the simulation proceeded for an additional 50 time steps. The disruption simulated shortage in supply relative to demand by implementing a 30 % reduction in mean replenishment across source nodes. Under both baseline and disrupted conditions,

50 time steps were generally sufficient to reveal persistent differences in resilience measures across strategies. In addition, although not explored here, our model allows for other types of disruption, such as node removals and changes in demand, that could be used to investigate the outcomes of other shocks to the system.

2.4. Purchasing strategies

We evaluated the impact on supply network robustness of four different strategies governing how sink nodes place their orders:

- **Bet-hedging**: a sink node ranks its suppliers according to price. Beginning with the lowest priced supplier, a sink node places an order equal to half its remaining demand (rounded up to the nearest whole number) or however many units a supplier has remaining (whichever is less). The sink node proceeds to the next supplier and repeats this process. After dealing with the final supplier, the sink node cycles back to the first supplier and repeats the entire process so long as the sink node has not yet met its demand nor exhausted its budget for the current time step and suppliers have remaining units to sell. For example, a sink node with two suppliers would cycle between the two of them until these conditions are met. We emphasize that repeatedly cycling through available suppliers is not meant to reflect a real-world process, but rather to achieve a particular distribution of orders across suppliers. Put simply, higher-ranked suppliers receive larger order volumes, but sink nodes purposely utilize multiple suppliers when possible, even when it is not strictly necessary to do so.

- **Price prioritization**: a sink node ranks its suppliers (both source nodes and distributors) according to their price per unit and places orders based on the lowest price available, moving on to more expensive suppliers only after exhausting less expensive options.
- **Mixed**: when initializing the simulation, a sink node is randomly assigned to follow either the price prioritization or bet-hedging strategy. At the network level, 50 % of sink nodes on average initially follow each strategy. A sink node following one strategy will switch to the other strategy if its unfulfilled demand exceeds 20 % of its current gross demand and it has been at least 5 time steps since it last switched its purchasing strategy. Under baseline conditions, such a shortfall in inventory roughly indicates that a node is performing below average with respect to other sink nodes in the network. However, we prohibit nodes from switching strategy too frequently to limit volatility in firms' purchasing strategy.
- **Random**: a sink node orders its suppliers randomly each turn. A sink node only moves on to the next supplier once its currently selected supplier's inventory is exhausted.

2.5. Response strategies to unmet demand

Nodes utilizing the above strategies, apart from the 'mixed' purchasing strategy, do not alter their purchasing rules in response to their environment. In reality, both firms and ants adjust their behavior to meet changing circumstances. We therefore performed an additional set of simulations to explore the consequences of different responses that a sink node could make after a failure to meet its consumptive demand. In this set of simulations, all sink nodes within a simulation follow the same response strategy and all simulations were run using the 'mixed' purchasing strategy. A sink node that failed to acquire sufficient goods to meet at least 80 % of its gross demand on time step *t* altered its behavior on the following time step in one of the following ways:

- **No response**: sink nodes did not respond to unmet demand beyond potentially switching their purchasing strategy (same as 'mixed' strategy above).
- Larger order volumes are prioritized by suppliers for delivery. To increase the likelihood of successful delivery, sink nodes could:
  - o **Inflate orders**: after estimating how many units of inventory to purchase, a sink node increases this amount by 20 %.
  - o **Prioritize distributors**: when placing orders, a sink node ranks suppliers by both price and supplier type, prioritizing distributors over source nodes.
- **Add supplier**: with a 5 % probability, a sink node creates a new link with a randomly selected source or distributor node to which it was previously unconnected. The list of potential suppliers a sink node can connect to is composed of all suppliers that are 2 edges distant from the sink node at the start of the simulation. Therefore, the list of potential suppliers that a node can add does not grow as a sink node adds new suppliers to its network.

2.6. Statistical analysis

We examined the change in variance of mean network resilience measures across simulation runs as additional runs were completed and found that 30 runs per purchasing/response strategy were sufficient for mean values to converge. We fitted linear mixed effects regression models (LMMs) to evaluate differences in network stability across purchasing and response strategies. Separate models were fitted for pre- and post-disruption periods. In both cases, strategy (factor, 4 levels), time step (continuous), and their interaction were included as fixed effects and simulation ID was included as a random intercept term. Time step was included in the global model to account for potential changes in stability measures across time within a period (i.e., pre- or post-disruption). LMMs took the form of

$$Y_{ij} = \beta_0 + \sum_{k=1}^{3} \beta_k * strategy_{k,ij} + \beta_T * time\ step_{ij} + \sum_{k=1}^{3} \beta_{kT} * strategy_{k,ij} * time\ step_{ij} + b_j + \varepsilon_{ij}$$

where Y_{ij} is the response variable (e.g., mean fill rate, mean price per unit) for observation i from simulation j, β_0 is the mean response associated with either the 'random' or 'no response' strategies for the analyses of purchasing and response strategies respectively when all other predictors (i.e., $strategy_{k,ij}$, $time\ step_{ij}$) are set to 0, β_k is the estimated change in mean response associated with strategy k relative to that of the baseline strategy represented by β_0, $strategy_{k,ij}$ is an indicator variable that takes a value of 1 for the strategy used for observation i in simulation j and 0 otherwise, β_T is the estimated change in the response variable for an increase of 1 time step, $time\ step_{ij}$ represents the time step for observation i in simulation j, β_{kT} is the coefficient for an increase in 1 time step for under strategy k, b_j is the random intercept term associated with simulation j, and ε_{ij} is the residual error associated with observation i from simulation j. The random intercept term, b_j, is assumed to be normally distributed with mean 0 and variance σ_b^2. Following Zuur et al., [55], where necessary (as assessed by visual inspection of model residuals combined with support based on Akaike's Information Criterion corrected for sample size (AICc)), a variance structure was incorporated into the model to allow for heterogeneity in residual spread across k purchasing/response strategies

$$\varepsilon_{ij} \sim N(0, \sigma_k^2) \quad k = 1, \ldots, 4$$

Otherwise, residuals were assumed to be normally distributed with mean 0 and variance σ^2.

Support for a global model and all its subsets was evaluated based on AICc. Model-averaging was used to obtain parameter estimates and 95 % confidence intervals (CIs) in cases in which a single model did not receive overwhelming support (i.e., $w_i \geq 0.95$). Statistical analysis was carried out in R ver.4.1.0 [42] and code is available on GitHub (see 'Data availability'). LMMs were fitted using the 'nlme' package [41]. Multi-model inference was performed using the 'MuMIn' package [2]. Estimated marginal means were obtained using the 'emmeans' package [32]. Plots were produced using the 'ggplot2' package [51].
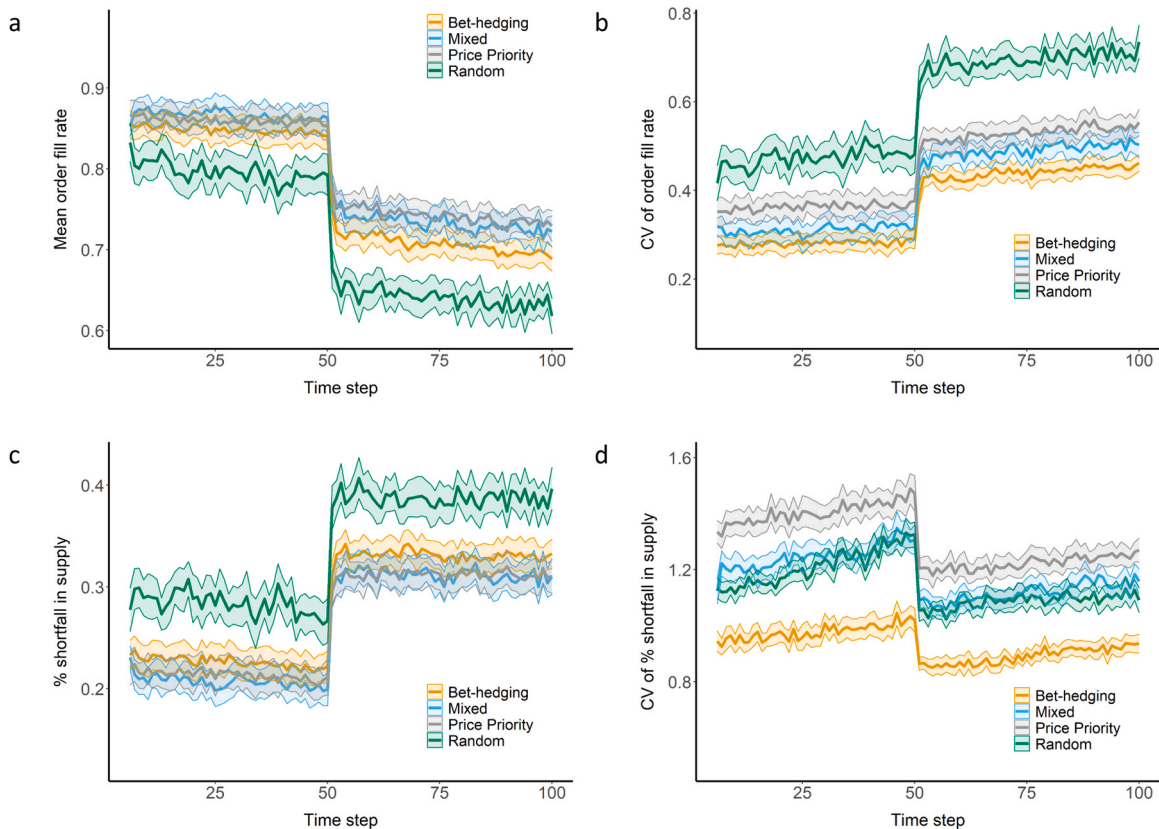
Fig. 2. Differences in stability measures among purchasing strategies. (*a*) Mean order fill rate, (*b*) coefficient of variation of mean order fill rate, (*c*) mean supply shortfall (%), and (*d*) coefficient of variation of mean supply shortfall across sink nodes over time, for the four different purchasing strategies. Supply disruption occurred at time step 50. Lines denote means across 30 simulation runs. Shaded regions correspond to 95 % CIs.

3. Results

Where the interaction between time step and strategy was supported, estimated marginal means for each strategy are reported with time step set to 25 or 75 for pre- and post-disruption periods respectively. Full results of all statistical models and post-hoc tests that support these findings are provided in the appendices.

3.1. Purchasing strategies

Sink nodes' ability to acquire sufficient goods to meet their consumptive demand was strongly influenced by purchasing strategy. Mean order fill rates (i.e., delivery volume received per order volume placed) decreased for all purchasing strategies following supply disruption (Fig. 2a). Prior to disruption, sink nodes experienced the lowest order fill rates when following a 'random' purchasing strategy (that is, one that did not prioritize ordering based on price) (Fig. 2a; Tables A1 & A2). Mean order fill rates were similar across the 'mixed', 'bet-hedging', and 'price prioritization' strategies (mean order fill rate: estimated marginal means (EMMs) (95 % CIs), time step (t) = 25: 'random': 0.80 (0.78–0.81); 'price priority': 0.86 (0.85–0.88); 'bet-hedging': 0.85 (0.83–0.87); 'mixed': 0.87 (0.85–0.88; Fig. 2a; Tables A1 & A2). Following supply disruption, all strategies experienced a reduction in mean order fill rates. The 'bet-hedging' strategy led to reduced mean order fill rates relative to the 'price prioritization' strategy, while the 'mixed' strategy produced outcomes intermediate between 'bet-hedging' and 'price prioritization' (Fig. 2a; Tables A3 & A4). Under disrupted conditions, all three strategies that prioritized ordering based on price experienced substantially higher mean order fill rates than the 'random' strategy (mean order fill rate: EMMs (95 % CIs): 'random': 0.64 (0.63–0.66); 'price priority': 0.74 (0.73–0.76); 'bet-hedging': 0.71 (0.69–0.72); 'mixed': 0.73 (0.72–0.75); Table A4). Prior to disruption, the 'mixed' and 'bet-hedging' strategies produced lower variation in mean order fill rates across sink nodes, relative to the 'random' and 'price prioritization' strategies (coefficient of variation (CV) of mean order fill rate: EMMs (95 % CIs), t = 25: 'random': 0.47 (0.45–0.49); 'price priority': 0.36 (0.34–0.39); 'bet-hedging': 0.28 (0.26–0.30); 'mixed': 0.31 (0.29–0.33); Fig. 2b; Tables A5 & A6). Following disruption, 'bet-hedging' produced the lowest variation in outcomes, whereas the 'random' strategy produced the greatest variation (Fig. 2b; Tables A7 & A8). The 'mixed' strategy produced less variable order fill rates compared to the 'price prioritization' strategy (CV of mean order fill rate: EMMs (95 % CIs): 'random': 0.69 (0.68–0.71); 'price priority': 0.53 (0.51–0.55); 'bet-hedging': 0.44 (0.42–0.46); 'mixed': 0.49 (0.47–0.51); Table A8).

Supply shortfall—measured per time step as units of unmet demand divided by a sink node's current gross demand—was also impacted by purchasing strategy and supply disruption. Mean supply shortfall increased for all strategies after disruption (Fig. 2c). In the 'random' strategy, sink nodes experienced substantially higher supply shortfalls relative to all other strategies, both prior to and following supply disruption (Fig. 2c; Tables A9-A13). Mean supply shortfall was similar across the 'mixed', 'price prioritization', and 'bet-hedging' strategies under baseline and disrupted conditions (mean supply shortfall: EMMs (95 % CIs): baseline: 'random': 0.28 (0.27–0.30); 'price priority': 0.21 (0.20–0.23); 'bet-hedging': 0.23 (0.21–0.24); 'mixed': 0.21 (0.19–0.22); disrupted: 'random': 0.39 (0.38–0.40); 'price priority': 0.31 (0.30–0.33); 'bet-hedging': 0.33 (0.32–0.35); 'mixed': 0.31 (0.30–0.33); Fig. 2c; Tables A1 & A13). However, 'bet-hedging' substantially reduced variability in supply shortfall across sink nodes compared to other strategies, both prior to and following disruption, whereas 'price prioritization' led to greater disparity in supply shortfall across nodes (CV of mean supply shortfall: EMMs (95 % CIs): baseline, t = 25: 'random': 1.20 (1.17–1.22); 'price priority': 1.40 (1.37–1.42); 'bet-hedging': 0.97 (0.95–1); 'mixed': 1.24 (1.21–1.27); disrupted, t = 75: 'random': 1.09 (1.06–1.11); 'price priority': 1.22 (1.20–1.25); 'bet-hedging': 0.89 (0.87–0.92); 'mixed': 1.12 (1.09–1.43); Fig. 2d; Tables A14-A17).

As expected, 'price prioritization' resulted in lower mean prices paid per unit, followed by the 'mixed', 'bet-hedging', and 'random'
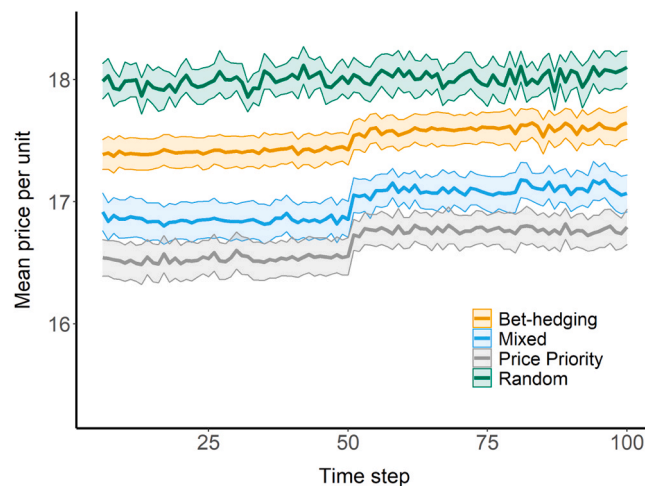
Fig. 3. Differences among purchasing stratagies in price per unit. Mean price paid per unit over time across purchasing strategies. Supply disruption occurred at time step 50. Lines indicate the mean value across 30 simulation runs. Shaded regions correspond to 95 % CIs.

strategies (Fig. 3). In the 'mixed' strategy, once sink nodes could modify their purchasing strategy (t > 5), there was a rapid increase in the proportion of sink nodes following the 'price prioritization' strategy, stabilizing at ~60 % (Fig. 4). Supply disruption had little impact on mean price per unit, with slight increases to price per unit in the 'mixed', 'price prioritization', and 'bet-hedging' strategies and no detectable effect in the 'random' strategy.

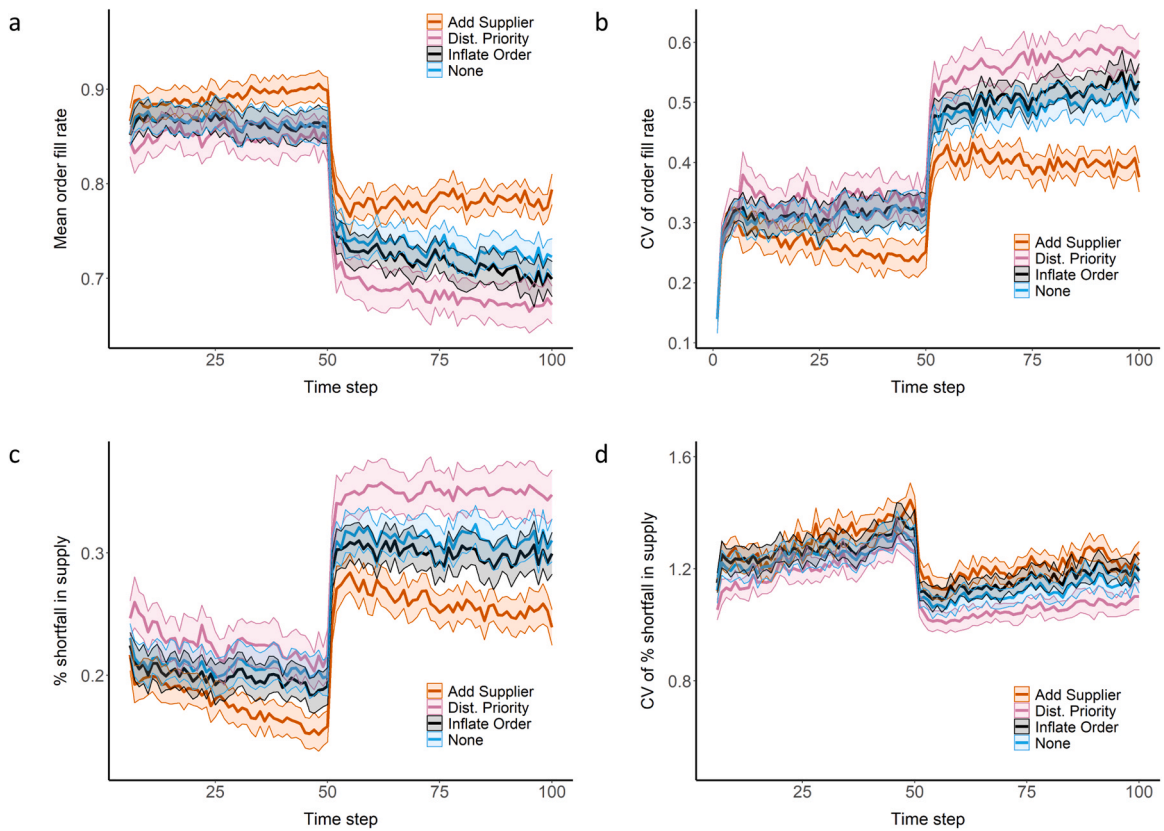### 3.2. Response strategies to unmet demand

The strategies that nodes could employ in response to failing to meet their consumptive demand strongly varied in effectiveness. Mean order fill rates decreased for all response strategies following supply disruption (Fig. 5a). Prior to disruption, the ability to form new supplier-customer relationships (the 'add supplier' strategy) resulted in higher mean order fill rates relative to the 'distributor priority' strategy (mean order fill rate: EMMs (95 % CIs), $t = 25$: 'no response': 0.87 (0.85–0.88); 'inflate order': 0.87 (0.85–0.88); 'distributor priority': 0.85 (0.84–0.86); 'add supplier': 0.89 (0.88–0.91); Fig. 5a; Tables A18 & A19). Following disruption, the 'add supplier' strategy resulted in higher mean order fill rates relative to all other strategies, whereas the 'distributor priority' strategy led to relatively low mean order fill rates (mean order fill rate: EMMs (95 % CIs), $t = 75$: 'no response': 0.73 (0.72–0.75); 'inflate order': 0.72 (0.70–0.73); 'distributor priority': 0.69 (0.67–0.70); 'add supplier': 0.78 (0.77–0.80); Fig. 5a; Tables A20 & A21). The 'add supplier' strategy also reduced variation among nodes in mean order fill rates, both pre- and post-disruption (Fig. 5b; Tables A22-A25). Prior to disruption, the 'distributor priority', 'inflate order', and 'no response' strategies produced similar levels of variation in mean order fill rate across nodes (CV of mean order fill rate: EMMs (95 % CIs), $t = 25$: 'no response': 0.31 (0.29–0.33); 'inflate order': 0.31 (0.29–0.34); 'distributor priority': 0.34 (0.32–0.36); 'add supplier': 0.26 (0.24–0.29); Tables A22 & A23). However, following disruption, 'distributor priority' produced greater variation in fill rate relative to all other strategies (CV of mean order fill rate: EMMs (95 % CIs), $t = 75$: 'no response': 0.49 (0.47–0.51); 'inflate order': 0.51 (0.49–0.53); 'distributor priority': 0.57 (0.55–0.59); 'add supplier': 0.40 (0.38–0.42); Fig. 5b, Tables A24 & A25).

Nodes' responses after failing to meet their current gross demand also varied in how effectively they buffered sink nodes from experiencing such supply shortfalls in the future. Mean supply shortfall increased for all response strategies after disruption (Fig. 5c). The 'add supplier' strategy resulted in the lowest mean supply shortfall relative to other strategies (particularly post-disruption), whereas 'distributor priority' often produced greater supply shortfalls (mean supply shortfall: EMMs (95 % CIs): baseline, $t = 25$: 'no response': 0.21 (0.20–0.22); 'inflate order': 0.20 (0.19–0.21); 'distributor priority': 0.23 (0.22–0.24); 'add supplier': 0.18 (0.17–0.19); disrupted, $t = 75$: 'no response': 0.31 (0.30–0.33); 'inflate order': 0.30 (0.29–0.31); 'distributor priority': 0.35 (0.34–0.36); 'add supplier': 0.26 (0.25–0.27); Fig. 5c; Tables A26-A29). However, 'distributor priority' was associated with a modest reduction in variation in mean supply shortfalls across sink nodes, especially following disruption (Tables A32 & A33), whereas the 'add supplier' and 'inflate order' strategies tended to generate greater disparities (CV of mean supply shortfall: EMMs (95 % CIs): baseline, $t = 25$: 'no response': 1.24 (1.22–1.26); 'inflate order': 1.27 (1.24–1.29); 'distributor priority': 1.19 (1.17–1.22); 'add supplier': 1.29 (1.26–1.31); disrupted, $t = 75$: 'no response': 1.12 (1.09–1.15); 'inflate order': 1.16 (1.13–1.18); 'distributor priority': 1.05 (1.03–1.08); 'add supplier': 1.20 (1.18–1.23); Fig. 5d; Tables A30-A33).

Mean price paid per unit slightly increased following disruption. As expected, 'distributor priority' and 'add supplier' strategies were respectively associated with higher and lower mean prices per unit (Fig. 6). For all response strategies, once sink nodes were able to switch their purchasing strategy, the proportion of sink nodes across the population following 'price prioritization' increased to ~60 % (Fig. 7).
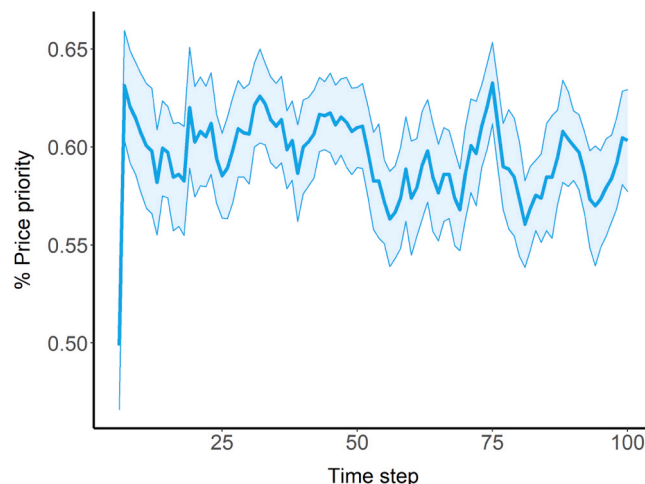
Fig. 4. Adoption of 'price prioritization' within 'mixed' strategy simulations. Mean proportion of sink nodes following the 'price prioritization' strategy over time within 'mixed' strategy simulations. Nodes were prohibited from switching strategies prior to time step 6. Supply disruption occurred at time step 50. The line indicates the mean value across 30 simulation runs. Shaded regions correspond to 95 % CIs.

Fig. 5. Differences among response strategies to unmet demand. (*a*) Mean order fill rate, (*b*) coefficient of variation of mean order fill rate, (*c*) mean supply shortfall (%), and (*d*) coefficient of variation of mean supply shortfall over time for response strategies. Supply disruption occurred at time step 50. Lines denote means across 30 simulation runs. Shaded regions correspond to 95 % CIs.
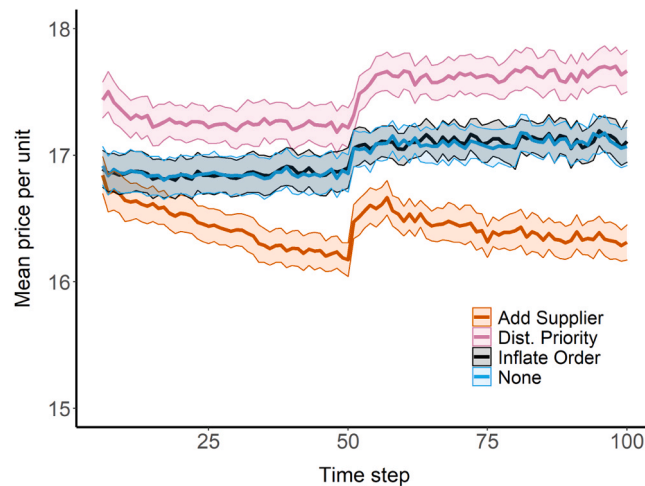
Fig. 6. Differences among response strategies in price per unit. Mean price paid per unit over time across response strategies. Supply disruption occurred at time step 50. Lines indicate the mean value across 30 simulation runs. Shaded regions correspond to 95 % CIs.

4. Discussion

Understanding how local decision-making impacts supply network robustness is important to ensure that supply networks can function adequately under unpredictable and disruptive conditions. We developed a simulation model to evaluate how different
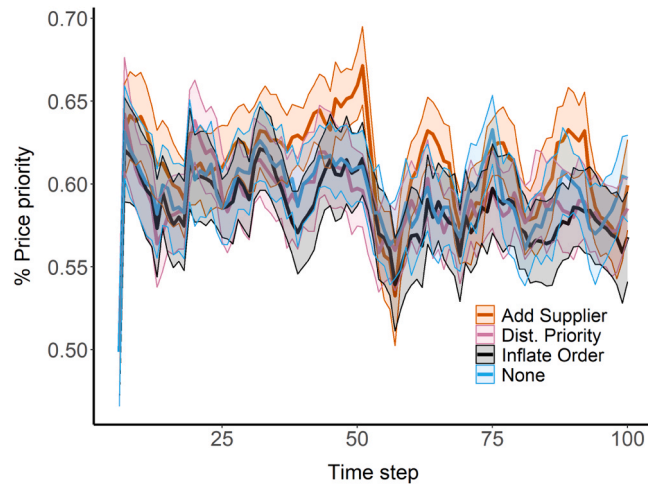
Fig. 7. Adoption of 'price prioritization' within 'mixed' strategy simulations. Mean proportion of sink nodes following the 'price prioritization' strategy over time across response strategies. Nodes were prohibited from switching strategies prior to time step 6. Supply disruption occurred at time step 50. Lines indicate the mean value across 30 simulation runs. Shaded regions correspond to 95 % CIs.

decision-making heuristics contribute to robustness prior to and following systemic disruption to production capacity. We found that supply network robustness strongly depended on the specific strategies employed by sink nodes (representing downstream retailers or consumers in our model) to meet their demand under uncertain conditions. Supply network robustness was bolstered by sink nodes employing a diversity of order allocation strategies (the 'mixed' purchasing strategy), as this reduced disparity in outcomes across sink nodes without impacting mean performance. In addition, when confronted with supply shortages, the capacity to forge new customer-supplier relationships (the 'add supplier' strategy) mitigated negative impacts on firms' performance. Conversely, under the assumptions of our model, relying on distributors to increase access to goods (the 'distributor priority' strategy) proved detrimental to sink nodes' performance. Taken together, we present a potentially useful approach that can inform participant decisions, with the aim of enhancing the robustness of system functioning in the face of diverse, frequent, and unpredictable disruptions that are inherent to real-world supply chain systems.

Within many complex adaptive systems, heterogeneity in agent behavior can promote greater system-level robustness via reduction in competitive intensity [28,48,50]. We observed similar effects in our simulations, where variation in purchasing strategies across sink nodes (the 'mixed' purchasing strategy) reduced variation in node-level performance without substantially impacting mean outcomes (Fig. 2). Conversely, when all sink nodes followed either 'price prioritization' or 'bet-hedging' strategies, trade-offs were apparent between mean performance and disparity in performance across sink nodes. For example, when all sink nodes employed 'price prioritization', mean order fill rates were higher and mean supply shortfalls were lower, but at the cost of increased variation in these measures across sink nodes. The reduced disparity in sink node outcomes associated with 'mixed' and 'bet-hedging' strategies results in part from reduced competitive intensity among sink nodes due to a broader range of potential suppliers being utilized. This suggests that when competing firms differ in their behavior—as is typically expected, given differences in information, priorities, market access, etc.—this can potentially bolster the overall robustness of a supply network [38,48]. Our findings further suggest that system-level heterogeneity in firms' previous behavior could be used to estimate the vulnerability of a supply network to unexpected shocks.

A key feature of complex adaptive systems is the capacity for the lower-level entities that make up a system to respond to their changing environment, thereby altering system dynamics and functioning [48]. In our simulations, we examined potential responses that sink nodes could undertake after failing to meet their consumptive demand. For example, given that distributors function as intermediaries between upstream suppliers and downstream customers, we evaluated whether sink nodes that experienced difficulty in meeting their demand could gain increased access to goods by preferentially relying on distributors (the 'distributor priority' strategy). In our model, it is more expensive to purchase from distributors compared to suppliers yet sink nodes can benefit from ordering from distributors in two ways: (i) distributors often have access to more potential suppliers than a typical sink node; and (ii) distributors combine orders received before ordering from their own suppliers. Because order deliveries are prioritized based on order volume, aggregated orders from distributors have a greater likelihood to be filled than orders placed by lone sink nodes. Nevertheless, despite these potential benefits, the 'distributor priority' strategy led to poorer mean outcomes for sink nodes. This result was likely due, in large part, to the assumed higher costs for orders placed to distributors relative to source producers, which impacted a distributors' customers directly as well as indirectly (i.e., reduced utilization of distributors by other sink nodes, leading to smaller, less competitive combined orders). Exploring model outcomes in which distributors do not experience competitive disadvantages relative to source nodes would be interesting and readily accomplished in our model.

Rather than relying on existing relationships with distributors to access additional suppliers, firms can alternatively initiate new customer-supplier relationships. In our model, we therefore implemented the 'add supplier' strategy, by which sink nodes that fail to

meet their demand may form a new connection within their local neighborhood with a new supplier to which they were previously unconnected. Relative to other response strategies in our model, the 'add supplier' strategy was associated with substantial increases in mean node-level performance and in some cases, reduced disparity in outcomes across sink nodes (Fig. 5). An important caveat of our model is that these network expansions did not involve any additional costs to sink nodes, whereas under real-world conditions, significant overhead can be involved in developing new customer-supplier relationships [8]. Nevertheless, the substantial improvement in performance observed in our simulations suggests that a key target for government interventions or policies is facilitating the formation of new relationships between firms experiencing heightened demand and suppliers that can meet that demand [10,16,39].

The relatively simple networks generated by our model lack many features often observed in real-world supply networks, such as the presence of strongly connected hub-like nodes [15,25,4,40], non-linear pathways linking nodes within and across tiers [25,4], strongly linked clusters of mutually dependent nodes [10,15,4], and core-periphery structures [10]. Such features can strongly impact the severity, reach, and duration of shocks propagating through the network. For instance, supply networks exhibiting hub-like structures are robust to random disruptions (e.g., accidental fires, natural disasters), yet are highly vulnerable to targeted disruptions impacting those highly connected nodes [25,54]. Likewise, clusters of mutually dependent firms can increase the severity of shocks, as disruption of critical supplier relationships can lead to cascading failures [10,15]. In addition, relative to the primarily downstream flows typified by hierarchically structured networks, the presence of upstream and within-tier connections (e.g., among distributors) can lead to cycles in the network that can prolong the propagation of disruptions [25]. In contrast, we generate supply networks with a limited number of tiers (e.g., supplier, distributor, consumer), connections that primarily flow downstream, and relatively little variation in connectivity across nodes. The networks generated by our model may therefore be relatively more robust to disruption under certain scenarios than would be expected of many real-world supply networks [25]. Exploring how our findings might be impacted by incorporating more realistic network structures is an important future direction of this work.

By exploring how different local strategies can impact the global performance of a supply network, our simulations may inform supply chain management strategies aimed at enhancing supply chain robustness and could be usefully combined with other approaches to supply chain modeling (e.g., digital twins: [34]). Whereas it can be difficult to justify costs of implementing protective strategies for disruptions that may never occur, it is encouraging to note that many of the strategies we examine here yielded benefits to firms under both baseline and disturbed conditions, which can aid strategy uptake [45]. Our selection of features to explore in our model was guided by features that have been demonstrated to promote robust food distribution within ant colonies. During famine relief in ant colonies, for example, nest workers alter their behavior to increase the likelihood of encountering incoming foragers from which they are otherwise usually spatially segregated [18,23,43], analogous to our 'add supplier' strategy. Likewise, the 'distributor priority' strategy was inspired by observations that under challenging conditions, an increased proportion of ants both give and receive food, thereby accelerating dissemination of food to unfed ants through a network of intermediaries [19,43].

Our nature-inspired approach differs from many previous biomimicry efforts in that we did not seek to emulate any specific solution employed by ants to enact robust resource distribution but sought instead to develop features in our model that were analogous in their function to those observed in ant colonies (Table 1). Such an approach to nature-inspired design can broaden the applicability of insights drawn from naturally evolved systems, as it avoids requiring one-to-one correspondences between a naturally evolved solution and an analogous challenge in supply chain design or operation [13,20]. As this work demonstrates, this strategy allowed us to propose simple, easily enacted minor changes in the behavior of individual supply network participants that can increase both individual node- and whole-network stability. We look forward to future investigations into how lessons derived from nature can inform efforts to enhance the resiliency, robustness, and sustainability of supply networks and other complex systems that support the well-being of human populations.

CRediT authorship contribution statement

Xiaohui Guo: Writing – review & editing. **Graham Derryberry:** Software, Methodology. **Nina H Fefferman:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Noa Pinter-Wollman:** Writing – review & editing, Funding acquisition, Conceptualization. **Matthew Hasenjager:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article. Code to run the simulations is available at https://github.com/MJHasenjager/Nature-Inspired-Supply-Networks.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.physa.2024.130133.

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