nature human behaviour

ARTICLES

DOI: 10.1038/s41562-017-0190-6

Contagious disruptions and complexity traps in economic development

Charles D. Brummitt[1,2], Kenan Huremović[3,4], Paolo Pin[5], Matthew H. Bonds*[2,6] and Fernando Vega-Redondo[5]

Poor economies not only produce less; they typically produce things that involve fewer inputs and fewer intermediate steps. Yet the supply chains of poor countries face more frequent disruptions—delivery failures, faulty parts, delays, power outages, theft and government failures—that systematically thwart the production process. To understand how these disruptions affect economic development, we modelled an evolving input–output network in which disruptions spread contagiously among optimizing agents. The key finding was that a poverty trap can emerge: agents adapt to frequent disruptions by producing simpler, less valuable goods, yet disruptions persist. Growing out of poverty requires that agents invest in buffers to disruptions. These buffers rise and then fall as the economy produces more complex goods, a prediction consistent with global patterns of input inventories. Large jumps in economic complexity can backfire. This result suggests why 'big push' policies can fail and it underscores the importance of reliability and gradual increases in technological complexity.

Producing valuable goods and services is a complex, intricate process. One obtains inputs from a multitude of suppliers who must honour their contracts and deliver those inputs without them breaking, spoiling or being stolen. These inputs must be stored safely and manipulated in interdependent stages using labour from workers who may fall ill or shirk their duties, together with complex equipment and vast infrastructure that may malfunction. These complex interdependencies underlie specialization and trade that are the foundation of economic growth and material progress[1,2].

Yet this progress, and the disruptions that thwart it, are unevenly distributed around the world. In low-income countries, disruptions can be frequent, long lasting and severe. They include power outages[3,4], worker absenteeism[5], failed deliveries of products, water shortages, customs delays, damage from natural disasters and epidemic disease (Fig. 1). Poor countries also tend to produce simpler goods, especially primary resources such as timber, mining and subsistence agriculture[6–8].

In contrast, in middle- and high-income countries, inputs tend to be more reliable and the goods produced tend to be more complex. However, rich economies are not immune to disruptions: competition drives firms to build lean supply chains with buffers so small that disruptions can cascade around the globe, causing large aggregate losses[9,10].

Might the mechanisms causing globalized supply chains to become fragile also be preventing poor economies from becoming more complex and global? This question stretches the limits of our understanding of economic growth and complexity. Input–output linkages among firms—wherein one firm's output is another firm's input—are known to have large, nonlinear effects on economies. In theoretical models, these linkages propagate changes in productivity[11–14], disruptions[15] and bankruptcies[16–21]. Empirical research on industrialized economies finds that supply-chain disruptions often lead to lower stock prices and sales growth[22–25]. These disruptions, and the uncertainty that they entail, affect development: they cause firms to use less capital[15], misallocate inputs[12,13] or form shorter supply chains[20], generally hindering industrialization of the economy[11] and limiting the effectiveness of policy[26]. However, in these models, disruptions are treated as exogenous, and firms interact once in a static network. These assumptions preclude the dynamic feedback that can generate complex outcomes such as poverty traps and periodic cycles.

Modelling dynamic production networks is a challenging problem involving heterogeneous input–output patterns and input elasticities[27]. Recent models have considered firms that endogenously form input–output linkages[28–30]; others have considered firms deciding how to source their inputs in a risky supply chain with one[31,32] or more[33–35] tiers. What is missing is an understanding of how fast dynamics in economic networks, such as disruptions in supply chains, affect their long-run evolution and their growth in complexity.

We aimed to fill this theoretical gap by introducing a simple model that captures the complex dynamics of disruptions spreading in an evolving input–output network. The main result was that poverty can emerge and reinforce itself: facing an unreliable environment of potential inputs, agents choose simple production processes that require few inputs, but disruptions remain frequent. Escaping this trap requires investing in buffers against disruption, such as arranging for extra suppliers or storing inventories of inputs. We found empirical support for the prediction that these buffers grow and then shrink as economies develop. When they shrink too much, disruptions can spike in number, as occurs in lean supply chains today. This mechanism also imperils developing economies: jumping abruptly to a more complex technology can backfire by causing greater dysfunction, suggesting that 'big push' policies[36] may benefit from technological gradualism. We suggest that this alternative perspective—focused on contagion in evolving supply

[1]Center for the Management of Systemic Risk, Columbia University, New York, NY 10027, USA. [2]Department of Global Health and Social Medicine, Harvard Medical School, Boston, MA 02115, USA. [3]IMT School for Advanced Studies, Piazza San Francesco, 19, 55100 Lucca, Italy. [4]Aix-Marseille School of Economics, Aix-Marseille University, 5 Boulevard Maurice Bourdet, 13001 Marseille, France. [5]Department of Decision Sciences, Innocenzo Gasparini Institute for Economic Research, and Bocconi Institute for Data Science and Analytics, Università Bocconi, Via Roentgen 1, Milano 20136, Italy. [6]School of Medicine, Stanford University, Stanford, CA 94305, USA. *e-mail: matthew_bonds@hms.harvard.edu

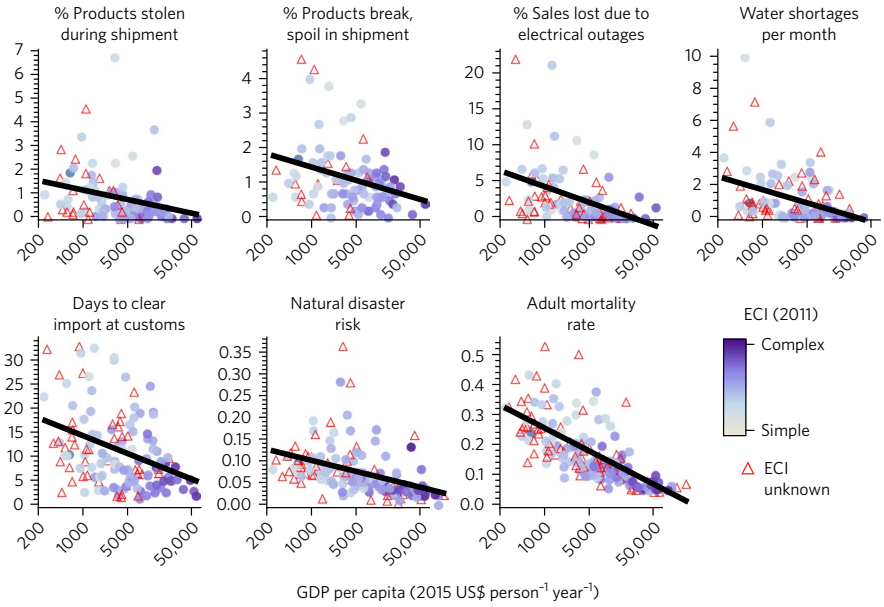

Fig. 1 | Disruptions to the production process tend to be more frequent in poorer, less complex economies. The colour of each dot indicates the country's economic complexity index (ECI)[63,64]; a red triangle represents a missing ECI value. The black lines are least-squares fits, with per-capita incomes[74] on a logarithmic scale. The natural disaster risk combines exposure and ability to cope[75]. The adult mortality rate is the chance that a 15 year old dies before the age of 60[76]. The data in the plots in the top row and in the bottomleft corner are from ref. [4].

chains—may shed light on why poor economies are not catching up and why some interventions fail.

Model of contagious disruption in an evolving input–output network

We considered a large population of agents who represent entrepreneurs or firms producing goods and services that require inputs from other agents. The model framework is meant to correspond to a variety of situations that broadly represent the process of coordinating inputs and outputs for economic production: launching a business requires intermediate goods from suppliers; coordinating stakeholder meetings requires a quorum of attendees; repairing equipment requires parts supplied by others; and so on.

Our focus on fragility has antecedents in Kremer's 'O-ring theory' of economic development, in which a single mistake—such as the malfunctioning O-ring that triggered the explosion of the Challenger Space Shuttle—can doom a sequence of interrelated tasks[15]. That study shows how fragility can lead to highly skilled workers matching with each other. Here, we focus on how people respond by using simpler technology or by investing in buffers against disruption so that some failures can be endured.

Balls-and-urn model of production and contagious dysfunction. At each time t, all agents exist in one of two states. A fraction F_t of agents are functional: they recently succeeded in producing and can provide inputs to others upon request. The remaining fraction $1-F_t$ are dysfunctional: they recently failed to produce and cannot provide inputs to others.

Agents become functional and dysfunctional as they succeed and fail, respectively, in producing goods or accomplishing tasks. Each agent attempts to produce a good requiring τ inputs. Attempts to produce a good occur randomly at a constant rate (as a Markov process). We do not track types of inputs nor economic sectors. This simplification allows us to abstract from which pairs of inputs are substitutes by using a simple threshold rule: an agent attempts to obtain inputs from m agents in the population, and they succeed in producing if and only if at least τ of those m inputs are successfully produced and delivered to them (see Fig. 2). We call m the number of attempted inputs, and we think of it as the in-degree when viewing these interactions as an input–output network.

This threshold rule captures the idea that some inputs are critical: without them, production halts or fails. For example, the earthquake near Japan on 11 March 2011 closed the Hitachi factory that produced most of the world's airflow sensors, a critical input for cars. As a result, automobile factories on the other side of the globe had to curb production or close[10]. In the developing world, drip irrigation has failed in Sub-Saharan Africa due to disruptions in water infrastructure and scarce knowledge about repairs[37]; adulterated fertilizer sold in Ugandan markets yields negative average returns[38]; and Internet-connected kiosks in India fell into disuse because of unreliable electricity and insufficient service from operators[39].

The simplifications above allow us to describe an evolving input–output network, together with disruptions spreading on it, using a single differential equation for the expected fraction of functional agents F_t:

$$\mathrm{d}F/\mathrm{d}t = \mathbb{P}(\mathrm{Binomial}(m, F_t) \geq \tau) - F_t \qquad (1)$$

for $t \geq 0$ and integers $m \geq 0$ and $\tau > 0$. Note that if $\tau = 0$, then there is little to model, so we let $\mathrm{d}F/\mathrm{d}t = 0$. This framework is a

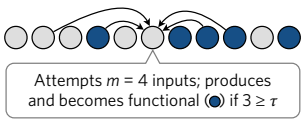

Fig. 2 | Illustration of the model. Agents (drawn as disks) are people or firms who are either functional or dysfunctional at any moment in time. Functional means that the agent has enough inputs to produce or to accomplish a task and that other agents can rely on this agent for inputs. Agents attempt to produce a good (or to have a meeting with other people, and so on) using m inputs drawn randomly from the population (indicated by the arrows) and they succeed when at least τ of those suppliers are functional.

balls-and-urn model[40,41] taken to an infinite-population, continuous-time limit, so that transition probabilities become deterministic rates of change in the mean-field master equation (1) (ref. [42]). Master equations are used to describe the dynamics of microeconomic actors in social science[43] and economics[44,45]. Our derivation of equation (1) is shown in note 1 of the Supplementary Information and explained below.

For simplicity, the input–output network is random and 'annealed': in each production attempt, inputs are chosen uniformly at random with replacement from the population. This annealed network captures the idea that people perform different tasks that require different inputs; for example, an engineer may fix a machine on Monday and lead a meeting on Wednesday, and an entrepreneur may try one business idea this year and another next year. Different inputs are required for each step. Later, we relax this assumption.

All agents use the same values of (m,τ); that is, they play 'symmetric strategies'. Therefore, the chance of successful production is the probability $\mathbb{P}$ that a binomial random variable with parameters m and F_t is $\geq \tau$, where τ is the number of critical inputs needed. This threshold rule resembles the essential inputs and critical subtasks in the 'O-ring theory' of Kremer[15], but here people can have buffers against failures: the number of attempted inputs (m) can exceed the number of inputs needed (τ). This threshold rule also appears in models of social contagion and collective behaviour[46–48], but here we have an annealed network, bidirectional changes in state and decision-making, which are described later.

Some disruptions may result from causes other than other agents' dysfunction, such as fires, insect outbreaks, weather and so on. To capture these exogenous disruptions, we assume that all agents independently become dysfunctional for exogenous reasons at a small rate ε (according to a Poisson process). This assumption introduces a $-\varepsilon F_t$ term to the master equation (1):

$$\mathrm{d}F/\mathrm{d}t = (1-F_t)P - F_t(1-P+\varepsilon) \tag{2}$$

$$= P - F_t(1+\varepsilon), \tag{3}$$

where P is the probability that an agent successfully produces, $\mathbb{P}(\mathrm{Binomial}(m,F_t)\geq\tau)$. The first term in equation (2) is the rate $1-F_t$ at which dysfunctional agents attempt to produce; each attempt succeeds with probability P; if the attempt succeeds, F_t rises; otherwise F_t stays the same, and vice versa for the second term. Equation (2) is derived in note 1 of the Supplementary Information and recovers equation (1) with $\varepsilon=0$.

The initial amount of dysfunction $1-F_0$ is exogenous; after that, disruptions are entirely endogenous, spreading from supplier to customer. Driving this contagion is the assumption that an agent delivers an input on request if (and only if) they successfully produced in their most recent attempt to produce. For example, a Ugandan farmer who discovers that their seeds were inauthentic[38], an Ethiopian farmer whose drip irrigation system fails because of upstream failures[37] or an automobile manufacturer who failed to produce due to missing parts[9,10] all may subsequently fail to deliver output promised to a customer.

Deciding on complexity τ and buffers against disruption $m-\tau$. The threshold τ loosely captures the complexity of the good or service being produced: more complex goods require more inputs[49,50]. To capture the incentives to create high-value products, we present a simple, reduced-form model in which agents derive utility from successfully producing goods that require more inputs. We assume that when an agent successfully produces, their induced utility grows with the complexity of production; for simplicity, we express this utility as τ^β, where $\beta\in(0,1)$. The assumption that complexity underlies rising productivity is standard in economic models[2,49,50]. For a derivation of τ^β, see note 2 of the Supplementary Information. We also assume that each attempted input costs $\alpha>0$. This parameter α represents the marginal cost of finding suppliers, maintaining multiple suppliers for the same input[51], incentivizing suppliers to have multiple manufacturing sites[52] or maintaining an inventory of inputs[53] (for details, see note 3 of the Supplementary Information).

For simplicity, we assume that each agent knows the current likelihood F_t that a uniformly random supplier would successfully produce and deliver an input on request. Based on that reliability F_t, agents revise their strategy regarding how complex a product to produce ($\tau\in\{0,1,2,\ldots\}$) and how many inputs $m\in\{0,1,2,\ldots\}$ are required to attempt to procure in order to produce that good. For instance, if suppliers are unreliable (that is, F_t is small), agents arrange for redundant inputs (that is, $m-\tau>0$) provided that they can afford it. Agents must commit to a certain technology and production technique for a certain amount of time T, so we assume that every amount of time T all agents simultaneously update their strategy to the 'best response', the maximizer (m^*,τ^*) of the utility function:

$$\mathcal{U}(m,\tau,F_t;\alpha,\beta) = P(m,\tau,F_t)\tau^\beta - \alpha m \tag{4}$$

Thus, agents' strategies at time t are:

$$(m^*,\tau^*) = \underset{m,\tau\geq 0}{\arg\max}\ \mathcal{U}(m,\tau,F_{kT};\alpha,\beta) \tag{5}$$

for $t\in(kT,\ (k+1)T)$ where $k\in\{0,1,2,\ldots\}$. Together, equations (2)–(5) and the initial F_0 define the model.

We abstracted from considerations about market equilibrium and price formation, hence expressing all payoff magnitudes in terms of some fixed numeraire. Only τ goods are used in production, even if more than τ of m suppliers are functional, as unused inputs are assumed to be perfect substitutes for used ones. In note 2.2 of the Supplementary Information, we explain three alternative interpretations of the relationship between inputs and outputs in the production process.

Results

Figure 3 illustrates the three phases of an economy in this model: trapped, emerging and rich. To understand the figure, suppose that at time $t=0$ agents successfully produce and deliver an input only

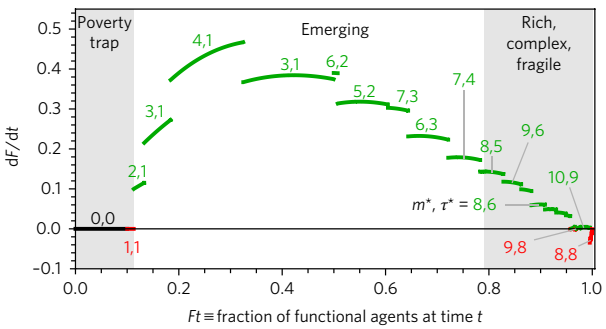

Fig. 3 | Representative phase portrait showing the three phases of a model economy. Here, $(\alpha,\beta,\varepsilon)=(0.1,0.4,0.001)$. The black, green and red curves are the right-hand side of ODE 2 as a function of F_t, with labels indicating the best response (m^*,τ^*) and colours denoting the sign of dF/dt *(green is dF/dt > 0; black is dF/dt = 0; red is dF/dt < 0)*. The best responses are computed numerically using the method explained in note 4 of the Supplementary Information.

50% of the time (that is, $F_0 = 50\%$). Then, from equation (4), agents choose the strategy $(m^*,\tau^*) = (3,1)$, meaning that agents produce a good requiring $\tau^* = 1$ input, but they arrange for $m^* - \tau^* = 2$ extra suppliers because disruptions are common ($1 - F_0 = 50\%$). Using this strategy in an economy with reliability $F_0 = 0.5$ causes disruptions to become less frequent ($dF/dt > 0$), as indicated by the green curve marked '3,1' in Fig. 3.

Figure 3 corresponds to an economy in which agents best respond arbitrarily quickly based on the reliability F_t of their fellow agents; that is, the best-response timescale T is arbitrarily close to 0. This $T \to 0$ limit is more analytically tractable because dF/dt changes discontinuously whenever the best response (m^*,τ^*) changes as a function of F_t. We relax this assumption later when we discuss fragility in rich economies.

Next, we explain the economy's three main phases and a pitfall in reaching the 'industrialized' phase.

Poverty trap with simple technology and frequent disruptions. In an economy with frequent disruptions (F_t near zero), agents choose to withdraw from the economy by not relying on any inputs from others ($m^* = \tau^* = 0$). This strategy resembles subsistence agriculture, hunting and pastoralism. Such an economy is in steady state: dF/dt is equal to 0 from equation (2) and no agent wants to deviate from the strategy (0,0).

This steady state also has a basin of attraction (marked 'poverty trap' in Fig. 3), provided that there are some exogenous sources of disruption ($\varepsilon > 0$). Specifically, for F just above α, the best response is $(m^*,\tau^*) = (1,1)$. That strategy means attempting a task that requires $\tau^* = 1$ input and requesting that one input from $m^* = 1$ other agent. This strategy has no redundant inputs. It succeeds in producing with probability $P(1,1,F) = F$; so, from equation (2), $dF/dt = F - F - \varepsilon < 0$.

Emerging economies' buffers to disruption rise and then fall. If an economy is sufficiently reliable, it begins to develop. For instance, in Fig. 3 if $F_t > 2^{-(\beta+1)}(1-\sqrt{1-\alpha 2^{\beta+2}}) \approx 11\%$, agents choose to produce goods that require some inputs ($\tau^* > 0$). Provided that F_t is not too close to 1 (a case described later), the agents also arrange for some extra inputs ($m^* > \tau^*$) in anticipation that some inputs will not be functional. This strategy results in the economy becoming more functional over time ($dF/dt > 0$) and producing ever more complex goods (τ^* rises with F_t).

As this economy develops, two features rise and then fall over time: the speed of development dF/dt and the buffer against disruptions $m^* - \tau^*$. Later, we examine this inverted-U pattern empirically. This inverted-U reflects the following ideas. Firms in a very unreliable economy need costly buffers against disruption to produce even simple, low-value goods (such as goods with complexity $\tau^* = 1$). The economy barely manages to produce such simple goods using the small amounts of redundancy afforded by the low earnings (for example, with redundancy $m^* - \tau^* = 2$). When the economy is more reliable (higher F_t), more complex tasks become feasible with large buffers against disruption, such as complexity $\tau^* = 3$ with buffer $m^* - \tau^* = 4$. Finally, as the economy becomes maximally reliable (F_t approaches 1), agents economize on their costly buffer against disruptions ($m^* - \tau^*$), which leads to new vulnerabilities.

Rich yet fragile. When the economy becomes very reliable (large F_t), agents produce very complex goods requiring many inputs (large τ^*). Yet this high reliability also induces agents to economize on their buffers to disruptions. In fact, when F_t is close to 1, they eliminate their buffer ($m^* = \tau^*$). Then, disruptions spread like a virus to which no one is immune: F_t falls, as indicated by the red curves in the bottom-right corner of Fig. 3, where $dF/dt < 0$. Falling F_t means that more and more agents are unable to produce and the drop in output resembles a recession. Such downturns occur generically in rich, highly functional economies: theorem 1 in note 5 of the Supplementary Information shows that the state $F_t = 1$ (a completely functional economy) is unstable to perturbations. In our model, a rich, highly functional economy is 'fragile' in the sense that there are large values of F_t close to 1 for which $dF/dt < 0$. This 'rich yet fragile' phenomenon accords with recent events: firms face pressure to build leaner supply chains, to invest in smaller buffers against disruptions and to produce ever more complex goods, resulting in occasional cascading disruptions[9,10].

What happens after F_t begins to fall depends on how quickly agents best respond and whether the best response is discrete. If agents commit to a strategy for a positive amount of time $T > 0$, the economy's reliability F_t falls until either (1) the economy enters the poverty trap (which occurs only for very large T) or (2) agents best respond in a way that causes F_t to begin to rise. F_t can rise because agents produce simpler, lower-value goods (smaller τ) or because they increase the buffer against disruption (larger m). If m and τ are discrete (as considered here) and $T > 0$, the economy can cycle: after F_t rises for a while, agents best respond again, and because their economy is quite reliable they choose to produce very complex goods or to decrease their buffer against disruption, and the process can repeat. If the decision variables m and τ were made continuous, or if $T \to 0$, the economy may settle onto a value of F smaller than 1.

This fragility of rich economies complements theories of 'aggregate fluctuations'[14,27,54–57]. Those theories show how exogenous shocks to firms can result in large changes in the total production in the economy. One reason is heterogeneity: some firms and sectors are much larger[55] or more connected[14,56] than others, so a small shock to these important firms can have large consequences. The models in[14,55–57] are static and timeless, whereas our model is inherently dynamic, with most 'shocks' caused by the endogenous failure of other firms. Another reason for aggregate fluctuations is that firms' inventories self-organize to a critical point[54]. In the model in ref. [54], firms request inputs from suppliers and these requests spread through a fixed network. Here, firms also request inputs from suppliers, but disruptions (that is, failures to produce due to insufficient functional inputs) spread contagiously in a network that changes over time.

Overshooting complexity can backfire. The core mechanism that causes downturns in the rich economy also makes it difficult for emerging economies to become rich and complex themselves. Specifically, if an economy tries to 'prematurely jump' to a more complex technology, it can slide backwards and become more dysfunctional. To make this idea precise, suppose that agents do not use the best response (m^*,τ^*), but instead attempt a more complex strategy that requires s more inputs: $(m^* + s, \tau^* + s)$. The buffer against disruptions remains the same; it is still $m^* - \tau^*$. The difference is that agents try to produce goods that require more inputs or they try to produce the same good as before but using technology that depends on more inputs, such as drip irrigation instead of traditional irrigation[37].

Figure 4 shows that this strategy $(m^* + 2, \tau^* + 2)$ often results in dysfunction rising over time ($dF/dt < 0$), as indicated by the red curves. In these intervals with $dF/dt < 0$, agents are 'overshooting' in complexity: they are attempting a production process more complex than the surrounding system can support. This overshooting echoes failures to adopt complex technologies in developing countries because the technologies depend on myriad inputs prone to disruption, such as drip irrigation systems[37] and Internet kiosks[39].

Emerging economies are especially vulnerable to overshooting in complexity: notice in Fig. 4 that $dF/dt < 0$ for many intermediate values of F_t. As a result, the poverty trap in Fig. 4 is dramatically larger than when agents use the best response (compare with Fig. 3). For example, an economy with F_t near 50% can fall into the poverty trap if it overshoots in complexity for a sufficiently long amount

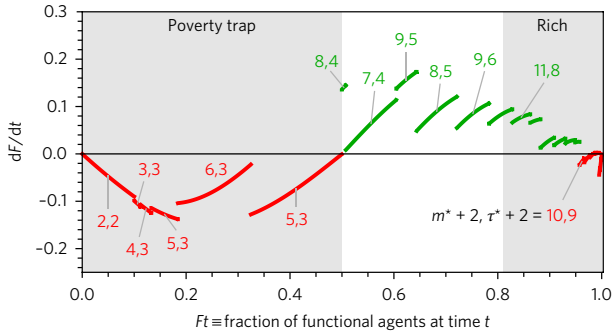

Fig. 4 | Jumping to a more complex technology can backfire by causing dysfunction to rise, especially for emerging economies. Here, agents use a strategy that requires two more inputs than they would have chosen given the reliability F_t of their potential inputs: they use the strategy (m^*+2,τ^*+2), where (m^*,τ^*) is the best response. The parameters are the same as in Fig. 3.

of time. In contrast, a rich economy can typically accommodate a jump in complexity without causing dysfunction to rise: in Fig. 4 there are many large values of F_t with $dF/dt>0$.

Comparing Figs. 3 and 4, we see the benefit of gradual growth in technological complexity. This prescription is at odds with the classic idea of a 'big push' of simultaneously industrializing many sectors of an economy[36]: a big push overcomes coordination problems, but it can add fragility by introducing complex technologies that depend on unreliable inputs. This prescription for slow, gradual reform mirrors the suggestions given by a model of trust and social capital[58].

Phase diagram. To demonstrate that the phenomena in Fig. 3 are rather generic, Fig. 5 shows the sign of dF/dt and the best response

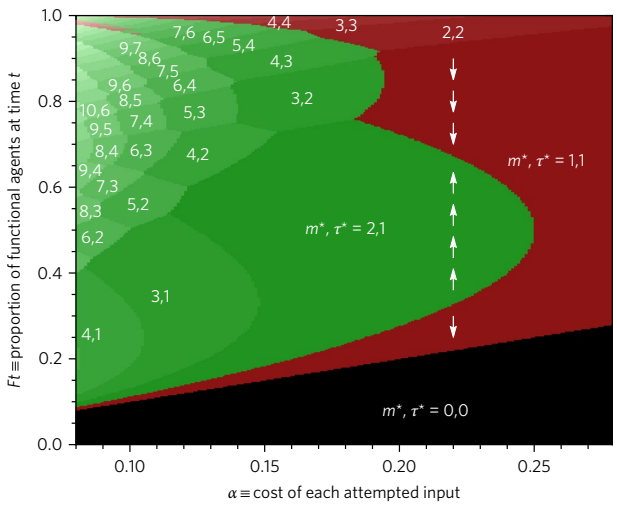

Fig. 5 | Phase diagram of the sign of dF/dt. The green area represents $dF/dt>0$, red is $dF/dt<0$ and black is $dF/dt=0$. The best response (m^*,τ^*) (white text) is shown as a function of α and F_t. The parameter α is assumed to change slowly, if at all. The vertical white arrows illustrate the dynamics dF/dt. Here, as in Fig. 3, $\beta=0.4$ and $\varepsilon=0.001$, so the strategy $(m^*,\tau^*)=(1,1)$ results in $dF/dt<0$. Poor economies get stuck in the region labelled '0,0'. Rich, complex economies settle on limit cycles near where green lies below red at the top of the diagram.

(m^*,τ^*) for many values of the parameter α, the marginal cost of each attempted input. A poverty trap occurs for $F_t\in(0,\alpha)$; the boundary $F_t=\alpha$ is the indifference curve between $(m,\tau)=(1,1)$ and $(0,0)$. If the cost to arrange for an input is too high ($\alpha>1/4$ in Fig. 5), the only long-run outcome is poverty. Otherwise, there exists a good outcome in the long run in which the economy is complex and highly functional, and buffers against disruptions $m^*-\tau^*$ tend to rise and then fall as the economy approaches this rich state.

However, there are pitfalls in reaching this rich state. One pitfall is the 'overshooting' described above. Another is to decrease the cost α of each attempted input. The marginal cost α is exogenous, but it could change if, for example, communications technology were to make it easier to arrange alternative suppliers. Decreasing α can trigger an escape from the poverty trap if it puts the economy in the green region in Fig. 5. However, it can also make the economy more dysfunctional: if α is decreased into the red region, where agents choose $m^*=\tau^*=1$, dysfunction rises (provided that exogenous failures occur; that is, $\varepsilon>0$). The intuition is that decreasing α incentivizes people to attempt more complex production using more inputs (higher τ^*), which can lead to more failure than success, resulting in more frequent dysfunction in the new steady state (lower F_t). If policymakers sense this feedback, they may avoid actions that decrease α, keeping the economy stuck in the trap.

Countervailing effects of keeping functional suppliers and choosing popular suppliers. The model presented above is simplified by the assumption that agents choose new suppliers uniformly at random every time they try to produce. At the other extreme, many models of economic cascades assume a rigid input–output network[14,16,17,19–21]. To explore a more realistic middle ground between these extremes, in note 6 of the Supplementary Information we modify the choice of suppliers in two ways: (1) agents tend to keep functional suppliers and (2) they bias their search towards suppliers who already have many customers (that is, preferential attachment). These changes do not affect the qualitative results insights of the model, but they do have two interesting effects that we illustrate using numerical simulations in Supplementary Fig. 1. One effect is that the economy is less likely to fall into the trap. It is straightforward that a tendency to retain functional suppliers helps F_t grow. More interestingly, a tendency to choose popular suppliers also helps F_t grow: because functional agents tend to accumulate customers, having many customers is correlated with being functional. However, these two tendencies can generate fragility. Once the economy is complex and highly functional, it can rely on very few agents who supply almost everyone. When those 'supplier hubs' become dysfunctional (because they rely on dysfunctional suppliers or because they suffered a rate-ϵ exogenous failure), the brittle economy can undergo a severe downturn and cascading disruptions. In summary, what makes an economy more likely to emerge from the pull of poverty is precisely what makes the economy fragile upon becoming complex.

Empirical support. *Input inventories rise and then fall as economies become more complex.* There are scant data—especially in developing countries—on supply-chain disruptions and the responses to them. Relevant data from the World Bank's Enterprise Survey include the number of days of inventory that firms keep of their 'main input' (that is, their highest-value input)[4]. Stockpiling inputs is one costly way to mitigate the risk of disruptions in one's supply chain[31], so it loosely corresponds to our model's buffer against disruption $m^*-\tau^*$. Macroeconomic research has focused on inventories of finished goods, but inventories of inputs have drawn increasing attention[59,60] and some models of input inventories also consider intermediate goods and supply chains[61,62].

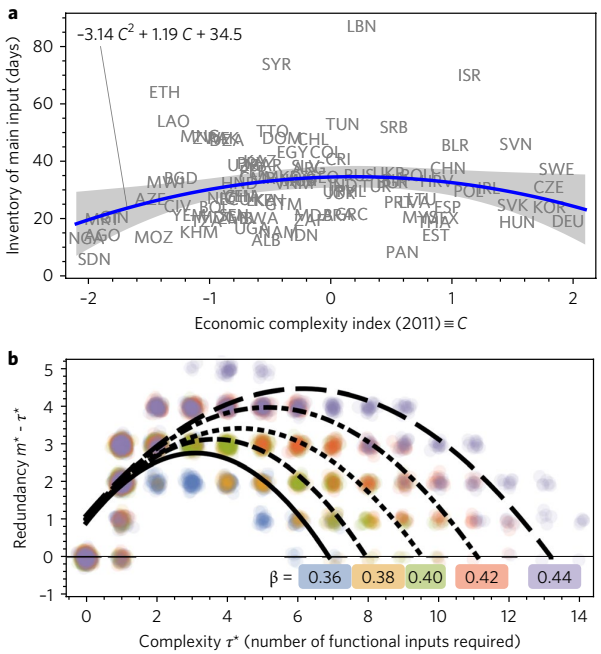

Fig. 6 | Qualitative match between empirical data on input inventories and the model's prediction that buffers to supply-chain disruptions rise and then fall as economies develop. a, Input inventories of firms, averaged at the country level[4], have an inverted-U relationship with the complexity of the economy[63,64]; $P=0.022$ for the C^2 coefficient; $R^2=0.063$; $n=95$ countries labelled by United Nations ISOalpha3 code (https://unstats.un.org/unsd/methodology/m49/); 95% mean prediction band shown in gray. **b**, Redundancy versus complexity for $\alpha=0.1$, $\varepsilon=0.001$ and five values of β, each a different colour. The curves show least-squares fits to $\delta_0+\delta_1\tau^*+\delta_2\tau^{*2}$. The data are dispersed by $\mathcal{N}(0, 0.008\times 1)$ to indicate density.

Recall from Fig. 3 that our model predicts that buffers against disruptions to inputs ($m^*-\tau^*$) tend to rise and then fall as economies develop. To test this qualitatively, we plotted in Fig. 6a the input inventory of firms averaged at the country level for 95 countries for which we have an estimate of the complexity of the economy[63,64]. This economic complexity index was calculated from the bipartite network of countries and the products they export[8]. We found that the input inventory had a statistically significant inverted-U relationship with the complexity C of an economy's production. A least-squares fit of inventory with $\gamma_0+\gamma_1 C+\gamma_2 C^2$ has $\hat{\gamma}_2=-3.14$, with $P=0.02$ (see Fig. 6a). This relationship qualitatively matches the inverted-U exhibited by the model (Fig. 6b).

Case study: drip irrigation. The reported uneven success of drip irrigation in different countries[37] illustrates the assumptions and messages of this model. Drip irrigation applies water directly to roots at a small, consistent rate, which increases efficiency and transforms land from arid to arable. The technology is delicate and complex because it depends on a broad system of inputs: it requires high-quality water to be delivered at the right pressure in pipes and tubes that match the local soil, crop and weather. Its equipment needs expert advice and repair. There is little buffer against malfunction because crops fail quickly in dry soil if the water flow is interrupted. In our model, drip irrigation resembles a high threshold (high τ) technology (compared with rainwater), for which there is little buffer against disruptions ($m-\tau$). As described by Garb and Friedlander[37], drip irrigation has been "spectacularly successful" in Israel, but "the very same hardware often turned out to be completely useless in the sub-Saharan African context". Farmers in Israel enjoy an "extensive infrastructural network so pervasive and successful as to be nigh invisible". Their counterparts in Ethiopia and Zambia had equipment from the same company, but they faced problems in the surrounding socio-technical system (of expertise, supply of water, and so on). Many farmers in sub-Saharan Africa are "gradually convert(ing) (their farms) back to furrow irrigation as each block of the buried drip irrigation fails". Expressed in the language of our model, dysfunctional inputs (low F) can result in crops failing and farmers choosing simpler, less productive technology (lower τ). Drip irrigation has succeeded in poor regions (such as India) not because the technology was simplified but because of sufficient support from the surrounding socio-technical system[37].

Discussion

Poverty traps have long been used to explain disparities in incomes across countries and to justify a 'big push'—a coordinated investment in many sectors to unleash growth[36,65–67]. Yet many big pushes have failed[68] and understanding why is paramount.

Our model views industrialization as mutually reinforcing supply chains, broadly defined, that become more complex over time. Disruptions in these supply chains can spread contagiously. This systemic fragility can cause complex technologies to fail. Even if all firms coordinate their industrialization (as suggested by big push theories[36,66]), if the firms jump too far in technological complexity without sufficient buffers against disruptions, the economy can slide backwards, becoming poorer and less reliable. As in other complex systems[69], going slower may result in collectively going faster.

This work sits at the intersection of competing theories of economic development. According to research on poverty traps[36,65–67], positive feedback loops keep populations stuck in poverty and escaping these traps requires substantial investments. According to research on institutions, differences in the rules of the game (such as property rights and rule of law) explain why economies have diverged[70,71]. Our model provides a bridge between these views. Because some inputs for production are from government actors, our model is consistent with the institutional view of development: better institutions may imply fewer disruptions, less uncertainty and, hence, a greater appetite for complexity. Consistent with the poverty trap literature, our model has multiple equilibria. However, whereas poverty traps typically suggest making a large investment, we find reason for caution: without a focus on the reliability of the surrounding system, big changes fail. Interventions to many parts of a system may be needed. Unreliability affects economic performance in a multifaceted way, involving risk[72], network contagion, technology adoption[37] and psychology[73]. Understanding their interplay can elucidate the causes of persistent poverty.

Methods

In note 4 of the Supplementary Information, we show computations of the finite set of strategies that could be a best response for a given α, β and F_L. This derivation enabled the computations used to make Figs. 3–5 and 6b.

Code availability. The code used to produce the results of this study is available from the GitHub repository at https://doi.org/10.5281/zenodo.823260. Figures 1–6 were created in Wolfram Language version 11 (https://www.wolfram.com/language/new-in-11/) and can be read free of charge using the Wolfram Computable Document Format Player (https://www.wolfram.com/cdf-player/) or run free of charge using the Wolfram Cloud (https://www.wolfram.com/cloud/). Supplementary Fig. 1 was created using Python (3.5.2) (https://www.python.org/downloads/release/python-352/) and NumPy (1.11.3) (https://pypi.python.org/pypi/numpy/1.11.3).

Data availability. The data that support the findings of this study (that is, the empirical data used in Figs. 1 and 6a) are available from the original sources[4,63,64,74–76] (specifically, from ref. [75]: data in the columns 'Country' and 'WorldRiskIndex'; and from ref. [76]: data on adult mortality of both sexes in 2013) and the GitHub repository associated with this paper at https://doi.org/10.5281/zenodo.823260.

Received: 12 September 2016; Accepted: 26 July 2017;
Published online: 4 September 2017

References

1. Schumpeter, J. A. *The Theory of Economic Development: An Inquiry Into Profits, Capital, Credit, Interest, and the Business Cycle* (Transaction Books, New Brunswick, NJ, 1983).
2. Romer, P. M. Growth based on increasing returns due to specialization. *Am. Econ. Rev.* **77**, 56–62 (1987).
3. Allcott, H., Collard-Wexler, A. & O'Connell, S. D. How do electricity shortages affect industry? Evidence from India. *Am. Econ. Rev.* **106**, 587–624 (2016).
4. World Bank Group *Enterprise Surveys Data* (accessed 15 October 2015); http://www.enterprisesurveys.org/data/
5. Chaudhury, N., Hammer, J., Kremer, M., Muralidharan, K. & Rogers, F. H. Missing in action: teacher and health worker absence in developing countries. *J. Econ. Perspect.* **20**, 91–116 (2006).
6. Caselli, F. in *Handbook of Economic Growth* vol. 1 (eds Aghion, P. & Durlauf, S. N.) 679–741 (Elsevier, 2005).
7. Hidalgo, C. A., Klinger, B., Barabási, A. L. & Hausmann, R. The product space conditions the development of nations. *Science* **317**, 482–487 (2007).
8. Hidalgo, C. A. & Hausmann, R. The building blocks of economic complexity. *Proc. Natl Acad. Sci. USA* **106**, 10570–10575 (2009).
9. Powell, B. The global supply chain: so very fragile. *Fortune* (12 December 2011)
10. Punter, A. *Supply Chain Failures. A Study of the Nature, Causes and Complexity of Supply Chain Disruptions*. (Airmic, London, 2013); https://www.riskmethods.net/resources/research/supply_chain_failures_2013_final_web.pdf
11. Ciccone, A. Input chains and industrialization. *Rev. Econ. Stud.* **69**, 565–587 (2002).
12. Jones, C. I. Intermediate goods and weak links in the theory of economic development. *Am. Econ. J. Macroecon.* **3**, 1–28 (2011).
13. Jones, C. I. *Misallocation, Economic Growth, and Input–Output Economics in 10th World Congress of the Econometric Society* (National Bureau of Economic Research, Cambridge, MA, 2011).
14. Acemoglu, D., Carvalho, V. M., Ozdaglar, A. & Tahbaz-Salehi, A. The network origins of aggregate fluctuations. *Econometrica* **80**, 1977–2016 (2012).
15. Kremer, M. The O-ring theory of economic development. *Q. J. Econ.* **108**, 551–575 (1993).
16. Battiston, S., Delli Gatti, D., Gallegati, M., Greenwald, B. & Stiglitz, J. E. Credit chains and bankruptcy propagation in production networks. *J. Econ. Dyn. Control* **31**, 2061–2084 (2007).
17. Weisbuch, G. & Battiston, S. From production networks to geographical economics. *J. Econ. Behav. Organ.* **64**, 448–469 (2007).
18. Mizgier, K. J., Wagner, S. M. & Holyst, J. A. Modeling defaults of companies in multi-stage supply chain networks. *Int. J. Prod. Econ.* **135**, 14–23 (2012).
19. Henriet, F., Hallegatte, S. & Tabourier, L. Firm-network characteristics and economic robustness to natural disasters. *J. Econ. Dyn. Control* **36**, 150–167 (2012).
20. Levine, D. K. Production chains. *Rev. Econ. Dyn.* **15**, 271–282 (2012).
21. Contreras, M. G. A. & Fagiolo, G. Propagation of economic shocks in input-output networks: a cross-country analysis. *Phys. Rev. E* **90**, 062812 (2014).
22. Hendricks, K. B. & Singhal, V. R. The effect of supply chain glitches on shareholder wealth. *J. Oper. Manag.* **21**, 501–522 (2003).
23. Hendricks, K. B. & Singhal, V. R. An empirical analysis of the effect of supply chain disruptions on long-run stock price performance and equity risk of the firm. *Prod. Oper. Manag.* **14**, 35–52 (2005).
24. Barrot, J.-N. & Sauvagnat, J. Input specificity and the propagation of idiosyncratic shocks in production networks. *Quart. J. Econ.* **131**, 1543–1592 (2016).
25. Wang, Y. I., Li, J. & Anupindi, R. Risky suppliers or risky supply chains? An empirical analysis of sub-tier supply network structure on firm performance in the high-tech sector. *Ross School of Business Paper No. 1297* Preprint at http://www.ssrn.com/abstract=2705654 (2015).
26. Aoki, M. & Yoshikawa, H. *Reconstructing Macroeconomics: A Perspective from Statistical Physics and Combinatorial Stochastic Processes* Ch. 4 (Cambridge Univ. Press, New York, NY, 2006).
27. Carvalho, V. M. From micro to macro via production networks. *J. Econ. Perspect.* **28**, 23–48 (2014).
28. Duan, W.-Q. Modelling the evolution of national economies based on input–output networks. *Comput. Econ.* **39**, 145–155 (2011).
29. Oberfield, E. Business networks, production chains, and productivity: a theory of input–output architecture. *FRB of Chicago Working Paper No. 2011-12* Preprint at http://ssrn.com/abstract=1967148 (2012).
30. Carvalho, V. M. & Voigtländer, N. Input diffusion and the evolution of production networks. *NBER Working Paper No. 20025* Preprint at http://www.nber.org/papers/w20025 (2014).
31. Tomlin, B. On the value of mitigation and contingency strategies for managing supply chain disruption risks. *Manag. Sci.* **52**, 639–657 (2006).
32. Aydin, G., Babich, V., Beil, D. & Yang, Z. in *The Handbook of Integrated Risk Management in Global Supply Chains* 387–424 (John Wiley & Sons, Hoboken, NJ, 2011).
33. Bimpikis, K., Fearing, D. & Tahbaz Salehi, A. Multi-sourcing and miscoordination in supply chain networks. *Stanford Business School Working Paper No. 3100* Preprint at https://www.gsb.stanford.edu/faculty-research/working-papers/multi-sourcing-miscoordination-supply-chain-networks (2014).
34. Ang, E., Iancu, D. A. & Swinney, R. Disruption risk and optimal sourcing in multi-tier supply networks. *Manag. Sci.* **63**, 2397–2419 (2016).
35. Bakshi, N. & Mohan, S. Mitigating disruption cascades in supply networks. Preprint at http://faculty.london.edu/nbakshi/Nw.pdf (2015).
36. Murphy, K. M., Shleifer, A. & Vishny, R. W. Industrialization and the big push. *J. Polit. Econ.* **97**, 1003 (1989).
37. Garb, Y. & Friedlander, L. From transfer to translation: using systemic understandings of technology to understand drip irrigation uptake. *Agric. Sys.* **128**, 13–24 (2014).
38. Bold, T., Kaizzi, K., Svensson, J. & Yanagizawa-Drott, D. Low quality, low returns, low adoption: evidence from the market for fertilizer and hybrid seed in uganda. *CEPR Discussion Papers 10743* Preprint at http://EconPapers.repec.org/RePEc:cpr:ceprdp:10743 (2015).
39. Sanjay, A. K. & Gupta, V. Gyandoot: trying to improve government services for rural citizens in India. *Tech. Rep. 11, eGovernment for Development* Preprint at http://www.egov4dev.org/transparency/case/gyandoot.shtml (2003).
40. Johnson, N. & Kotz, S. *Urn Models and Their Application: An Approach to Modern Discrete Probability Theory* (Wiley, 1977).
41. Woodbury, M. A. On a probability distribution. *Ann. Math. Stat.* **20**, 311–313 (1949).
42. Toral, R. & Colet, P. in *Stochastic Numerical Methods* 235–260 (Wiley-VCH, Weinheim, Germany, 2014).
43. Helbing, D. *Quantitative Sociodynamics: Stochastic Methods and Models of Social Interaction Processes* 2nd edn (Springer-Verlag, Berlin, Germany, 2010).
44. Aoki, M. *New Approaches to Macroeconomic Modeling: Evolutionary Stochastic Dynamics, Multiple Equilibria, and Externalities as Field Effects*. (Cambridge Univ. Press, 1998).
45. Aoki, M. *Modeling Aggregate Behavior and Fluctuations in Economics*. (Cambridge Univ. Press, New York, NY, 2004).
46. Granovetter, M. Threshold models of collective behavior. *Am. J. Sociol.* **83**, 1420–1443 (1978).
47. Watts, D. J. A simple model of global cascades on random networks. *Proc. Natl Acad. Sci. USA* **99**, 5766–5771 (2002).
48. Jackson, M. O. & Yariv, L. Diffusion of behavior and equilibrium properties in network games. *Am. Econ. Rev.* **97**, 92–98 (2007).
49. Ethier, W. J. National and international returns to scale in the modern theory of international trade. *Am. Econ. Rev.* **72**, 389–405 (1982).
50. Romer, P. M. Endogenous technological change. *J. Polit. Econ.* **98**, S71–S102 (1990).
51. Proviti. *Managing Supply Chain Disruption Risk* (2011); https://www.protiviti.com/US-en/insights/managing-supply-chain-disruption-risk
52. Simchi-Levi, D., Schmidt, W. & Wei, Y. *From Superstorms to Factory Fires: Managing Unpredictable Supply-Chain Disruptions* (Harvard Business Review, 2014); https://hbr.org/2014/01/from-superstorms-to-factory-fires-managing-unpredictable-supply-chain-disruptions
53. Tang, C. S. Robust strategies for mitigating supply chain disruptions. *Int. J. Logist. Res. Appl.* **9**, 33–45 (2006).
54. Bak, P., Chen, K., Scheinkman, J. & Woodford, M. Aggregate fluctuations from independent sectoral shocks: self-organized criticality in a model of production and inventory dynamics. *Res. Econom.* **47**, 3–30 (1993).
55. Gabaix, X. The granular origins of aggregate fluctuations. *Econometrica* **79**, 733–772 (2011).
56. Burlon, L. How do aggregate fluctuations depend on the network structure of the economy? *SSRN Electronic Journal* Preprint at http://www.ssrn.com/abstract=2028093 (2012).
57. Baqaee, D. R. Cascading failures in production networks. *SSRN Electronic Journal* Preprint at https://papers.ssrn.com/sol3/papers.cfm?abstract_id=2909868 (2015).
58. Francois, P. & Zabojnik, J. Trust, social captial, and economic development. *J. Eur. Econ. Assoc.* **3**, 51–94 (2005).
59. Humphreys, B. R., Maccini, L. J. & Schuh, S. Input and output inventories. *J. Monetary Econ.* **47**, 347–375 (2001).
60. Iacoviello, M., Schiantarelli, F. & Schuh, S. Input and output inventories in general equilibrium. *Int. Econ. Rev.* **52**, 1179–1213 (2011).

61. Khan, A. & Thomas, J. K. Inventories and the business cycle: an equilibrium analysis of (S, s) policies. *Am. Econ. Rev.* **97**, 1165–1188 (2007).
62. Wen, Y. Input and output inventory dynamics. *Am. Econ. J. Macroeconom.* **3**, 181–212 (2011).
63. Atlas of Economic Complexity. *Economic Complexity Index* (accessed 8 November 2015); http://atlas.cid.harvard.edu/rankings/country/download/
64. Hausmann, R., Hidalgo, C. A., Bustos, S., Coscia, M. & Simoes, A. *The Atlas of Economic Complexity: Mapping Paths to Prosperity* (MIT Press, Cambridge, MA, 2014).
65. McArthur, J. et al. Ending Africa's poverty trap. *Brookings Pap. Econ. Act.* **1**, 117–240 (2004).
66. Azariadis, C. & Stachurski, J. in *Handbook of Economic Growth* (eds Aghion, P. & Durlauf, S.) 295–384 (Elsevier, 2005).
67. Barrett, C. B., Garg, T. & McBride, L. Well-being dynamics and poverty traps. *Annu. Rev. Res. Econ.* **8**, 303–327 (2016).
68. Easterly, W. Reliving the 1950s: the big push, poverty traps, and takeoffs in economic development. *J. Econ. Growth* **11**, 289–318 (2006).
69. Gershenson, C. & Helbing, D. When slower is faster. *Complexity* **21**, 9–15 (2015).
70. North, D. C. *Institutions, Institutional Change and Economic Performance*. (Cambridge Univ. Press, Cambridge, UK, 1990).
71. Acemoglu, D., Johnson, S. & Robinson, J. A. in *Handbook of Economic Growth* (eds Aghion, P. & Durlauf, S. N.) 386–414 (Elsevier, 2005).
72. Morduch, J. Poverty and vulnerability. *Am. Econ. Rev.* **84**, 221–225 (1994).
73. Haushofer, J. & Fehr, E. On the psychology of poverty. *Science* **344**, 862–867 (2014).
74. The World Bank. *GDP Per Capita (in Current US$)* (accessed 15 February 2016); http://data.worldbank.org/indicator/NY.GDP.PCAP.CD
75. Hilft, B. E. in *Worldriskreport 2014*. 64–66 (United Nations University Institute for Environment and Human Security, accessed 11 February 2016); http://i.unu.edu/media/ehs.unu.edu/news/4070/11895.pdf.
76. World Health Organization. *Adult Mortality Data by Country* (accessed 15 February 2016); http://apps.who.int/gho/data/node.main.11?lang=en

Acknowledgements

C.D.B. and M.H.B. acknowledge funding from the James S. McDonnell Foundation for the Postdoctoral Award and the Scholar Award (respectively) in Complex Systems. P.P. and F.V.-R. acknowledge funding from the Italian Ministry of Education Progetti di Rilevante Interesse Nazionale grant 2015592CTH. No funders had any role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

Author contributions

All authors designed and performed the research and wrote the paper. C.D.B. and K.H. analysed the data.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at doi:10.1038/s41562-017-0190-6.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to C.D.B.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

nature research

Corresponding author(s): Charles Brummitt <brummitt@gmail.com>

☐ Initial submission ☒ Revised version ☐ Final submission

Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see Reporting Life Sciences Research. For further information on Nature Research policies, including our data availability policy, see Authors & Referees and the Editorial Policy Checklist.

Experimental design

1. Sample size

Describe how sample size was determined.

Supplementary Figure 1 shows the results of Monte-Carlo simulations, so we chose the sample sizes based on computational and time constraints (which were not a significant challenge). Panel (a) of Supplementary Figure 1 has 1000 simulations for each initial condition in the sample, and we report in the caption the results of a two-sided Mann-Whitney U test; the difference between the distributions is significant at the level of 10^(-5) in all the relevant cases. For panel (b), we report in the caption of Supplementary Figure 1 a two-sided t-test that compares the standard deviation of the time-series in 200 simulations of the two parameter specifications of the simulation model. The resulting p-value is extremely small: 10^(-251). These simulations and the Mann-Whitney and t-tests are included in the GitHub repository containing all the simulations, data, and code used to produce the results of this paper.

The number of countries used in Figure 6 is determined by the intersection of the countries for which we have the Economic Complexity Index (from Ref. [9, 10]) and the World Bank Enterprise Survey (from Ref. [4]). This intersection consists of 95 countries. That number of countries is reported in the caption of Figure 6. The definition of the sample of countries is written on page 8 in the left-hand column in lines 48–49 and right column lines 1–2.

2. Data exclusions

Describe any data exclusions.

No data was excluded from our analysis.

3. Replication

Describe whether the experimental findings were reliably reproduced.

Not applicable. This study does not involve an experiment. We use publicly available data, and we share that data in the Github repository in which the data and software code are shared.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Not applicable. This study does not involve randomizing into experiment groups. The set of countries used in our empirical test (the results of which are in Figure 6 and its caption) is explained in our response to question 1 above.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Not applicable. This study does not involve an experiment.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☒	☐	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☒	☐	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	Details on code availability are in the statement "Code availability" on page 9. In that statement, we explain the software used (Mathematica version 11, Python 3.5.2, and NumPy 1.11.3). Python and NumPy are open source software. We explain in the "Code availability" statement how others can read and reproduce the results obtained in the Wolfram Language, and we explain how they can do so for free without a Wolfram Language license.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	There are no restrictions on the availability of the code and data used in this paper. All the code and data used in the paper are included in the Github repository associated with the paper.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	Not applicable.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	Not applicable.
b. Describe the method of cell line authentication used.	Not applicable.
c. Report whether the cell lines were tested for mycoplasma contamination.	Not applicable.
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	Not applicable.

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	Not applicable.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	Not applicable.