

Living With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets

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Coupled human and natural systems (CHANS) are systems of feedback linking people and ecosystems. A feature of CHANS is that this ecological feedback connects people across time and space. Failing to account for these dynamic links results in intertemporal and spatial externalities, reaping benefits in the present but imposing costs on future and distant people, such as occurs with overgrazing. Recent findings about locust–nutrient dynamics create new opportunities to address spatiodynamic ecosystem externalities and develop new sustainable strategies to understand and manage locust outbreaks. These findings in northeast China demonstrate that excessive livestock grazing promotes locust outbreaks in an unexpected way: by lowering plant nitrogen content due to soil degradation. We use these human–locust–livestock–nutrient interactions in grasslands to illustrate CHANS concepts. Such empirical discoveries provide opportunities to address externalities such as locust outbreaks, but society’s ability to act may be limited by preexisting institutional arrangements.

Keywords: coupled human and natural systems, sustainable agriculture, telecoupling, institutions, ecosystem externality

Locust outbreaks have affected communities for millennia. Exodus describes the devastation of a locust plague (Exod. 10:15 RSV): “They covered the face of the whole land so that the land was darkened, and they ate all the plants in the land and all the fruit of the trees which the hail had left; not a green thing remained, neither tree nor plant of the field, through all the land of Egypt.” Large locust outbreaks, often called plagues, affect multicountry regions with devastating consequences on ecology and agriculture. For example, during plague years, the desert locust (*Schistocerca gregaria*) has adverse impacts on more than 60 countries and the livelihood of one out of every 10 people on the planet (Symmons and Cressman 2001). Desert locust plagues have been recorded since biblical times. More recently, other locusts have increasingly inflicted agricultural damage. For example, the Senegalese locust (*Oedaleus senegalensis*) was not reported to cause economic damage before the 1970s, but a plague in the mid-1980s required pesticide treatment of 5 million hectares, and this locust is now considered the main pest of the African Sahel (Maiga et al. 2008). There are at least 20 different agriculturally important locust species affecting the economies of large fractions of all continents except North America and Antarctica, and many locusts originate in grasslands (reviewed in Pener and Simpson 2009).

As with most ecosystems, grasslands are driven by feedback between human and ecological processes (Qi et al. 2012) and are a classic example of how resource degradation can come about from unmanaged and uncoordinated use (Hardin 1968). In particular, ecological interactions can extend human impacts through time and over space, producing both local and far-reaching environmental and social impacts, a process called *telecoupling* (Liu et al. 2013). Research on natural resource institutions (Ostrom 1990) and social–ecological systems (Berkes et al. 2003) has flourished recently but often underplays *ecosystem externalities* (Crocker and Tschirhart 1992)—the negative impacts of human actions on other aspects of ecosystem function that, in turn, affect people. Swarming locust outbreaks are a clear example of a kind of ecosystem externality in which the decisions in one location can dramatically affect the outcomes in other—often distant—localities.

Some locusts, such as the desert locust, originate in remote areas and only become an economic problem when they migrate to agricultural lands. In these scenarios, there may be minimal potential for mitigation because initial outbreaks are dependent on factors not heavily influenced by people. However, other locusts, such as the Senegalese locust, originate in human-dominated (usually agricultural) landscapes, where there is considerable potential for

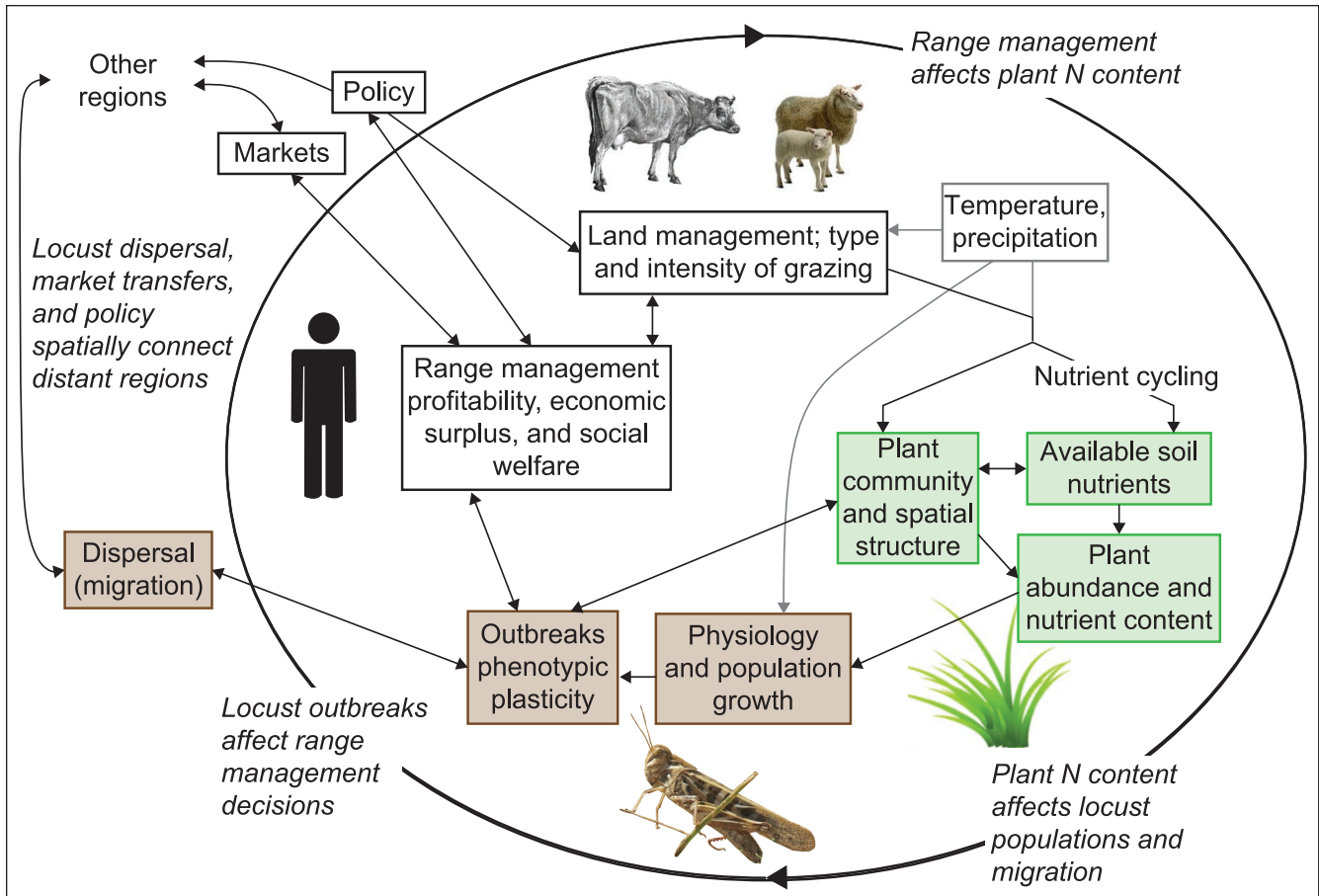


Figure 1. Human behavior, market forces, and ecological systems in situations in which overgrazing alters plant nutrient content, potentially producing outbreaks of agriculturally damaging locusts.

mitigative and adaptive responses. Recent research by Cease and colleagues (2012) uncovered mechanisms showing how degraded grasslands change the nutritional quality of vegetation in ways that promote outbreaks of the Mongolian locust (*Oedaleus asiaticus*). This signals the potential for grassland system management rules and property rights, which we broadly refer to as *institutions* (North 1990), to mitigate or exacerbate locust plagues. Here, we frame livestock grazing systems, with locusts embedded, as a telecoupled social–ecological system (figure 1) and examine the potential for managing grazing systems to reduce the probability and severity of locust outbreaks.

Livestock grazing systems, decisionmaking, and institutions

The pressure on grasslands is growing worldwide. Grassland–livestock systems cover 45% of the world’s land surface (Ramankutty and Foley 1999, Reid et al. 2008), they contribute over US\$1.4 trillion to the world economy (Thornton 2010), and the demand for grassland-based meat production is increasing as worldwide affluence grows (Foley et al. 2011). Therefore, grassland degradation is likely to increase

in the coming decades, most notably in developing regions (Tarawali et al. 2011), where livestock and grasslands support the livelihoods of over 600 million of the world’s poor (Thornton et al. 2002).

Mitigating degradation requires understanding how livestock managers make decisions. Livestock managers generally choose stocking rates on the basis of grassland and socioeconomic factors, including the prices for wool, milk, or meat products. Especially in developing regions, livestock can also function as “productive assets” because they contribute to farm activities and productivity (e.g., plowing, manure), diversify “savings” portfolios (Dercon 1998), and provide a buffer against risk (Jarvis 1974). While considering these factors, farm managers can potentially enhance the long-run productivity and value of livestock enterprises by including information on the long-term effects of stocking decisions on the quality of their land. In addition, the long-term productivity of a region or country may be enhanced by including information on the effects of ecosystem externalities, such as the negative effects of a migrating locust swarm on crop production of neighboring lands.

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Institutions and property-rights regimes influence the ability of communities or managers to use information about ecosystem externalities when developing grassland management strategies (McCarthy et al. 1999). Property rights are a foundational type of institution (North 1990) and are commonly classified into the following categories: individual private property, open access to a common resource, and socially optimal management (a theoretical best-case scenario in which resources are managed cooperatively and provide the greatest net benefits to society). Let us look at these three classic regimes in turn.

Private property managers generally have an incentive to consider the long-term effects of their decisions when managing their livestock and land holdings (Jensen and Meckling 1976). However, they have little incentive to account for spatial externalities (Smith et al. 2009) or similar ecosystem processes, such as locust outbreaks, that exceed the spatial scale of their property rights. Therefore, changing the spatial scale of management can drastically alter optimal private decisions (Hansen and Libecap 2004). Private property owners may also engage in strategic behavior, either complementing or free riding on neighbors' actions (Fenichel et al. 2014). For example, if one farmer sprays locust pesticides on his own land, this may increase (in the complementing case) or decrease (in the free-riding case) the incentives for neighboring farmers to spray pesticides on their lands. Livestock managers will likely only voluntarily incorporate new ecological knowledge into their management practices if they are able to internalize the benefits from a management change. If farm managers do not capture these benefits, then institutional change (such as a change in property rights or policy) may be able to provide incentives for them to do so.

Unregulated communal management seldom provides incentives for decisionmakers to proactively protect their resources (Stavins 2011). Anecdotal evidence from Inner Mongolia, China, suggests that some households with private (fenced) grazing plots choose to graze on communal grasslands and only use their own land after the common areas are severely degraded. The case of overgrazing was classically described by Hardin (1968) and has become the textbook example of the “tragedy of the commons.” However, communal property regimes can have a range of welfare outcomes—from a case in which no one earns any real profit from a grazing system to the case in which livestock managers benefit as much as a sole owner (Cheung 1970). How well a community fares depends on levels of trust and cooperation, the strength and appropriateness of rules, and, crucially for these cases, the scale at which rules are enacted and enforced (Robinson et al. 2013). Still, even communities with strong resource-management institutions do not have an incentive to incorporate effects beyond their boundaries.

Finally, a socially optimal strategy could guide society to act in a cooperative fashion and internalize the benefits from acting on knowledge of ecological links. However, the transaction costs from monitoring and enforcing such socially

optimal strategies can be prohibitively costly and must be taken into account for realistic policy solutions (McCarthy et al. 1999, Libecap 2014). In any case, it seems clear that when large-scale ecosystem externalities such as locust plagues occur, the coordination of activities at a higher spatial and temporal scale by public institutions is necessary to maximize social welfare.

Locusts and grasshoppers and their impacts on people

Some grasshoppers can become migratory locusts that link ecosystems, people, and land management decisions over long distances. Grasshoppers are key components of grassland ecosystems around the globe and play an important role in trophic dynamics and the cycling of nutrients. However, from the perspective of local livestock managers, some grasshopper species are serious pests, and outbreaks can have detrimental effects on livestock and agriculture, affecting the regional food supply. Under certain environmental conditions, including high grasshopper population density, some grasshopper species undergo a phenotypic shift termed *phase change*. In phase change, grasshoppers switch from shy and solitary individuals to gregarious and migratory individuals that can collectively form long-distance migratory swarms. Grasshoppers that have the ability to undergo this phase change are classified as *locusts* (Pener and Simpson 2009). The term *locust* is not a taxonomic classification; indeed, their trait of swarming and migrating likely has evolved independently multiple times within the grasshopper family (Acrididae) because locust species appear in several subfamilies (e.g., table 1; Song 2011). There are approximately 12,000 species of grasshoppers worldwide, but only about 20 have shown the potential to transform into locusts (Pener and Simpson 2009). Although many grasshopper species can threaten agriculture on a local scale, locusts are of special concern because they can threaten agricultural production and food security over large regions. Such migratory pests impose unique international challenges, requiring coordinated multinational strategies for pest control (Toleubayev et al. 2007).

Locust species are found on every continent outside of North America and Antarctica. North America was historically plagued by the Rocky Mountain locust (*Melanoplus spretus*), but it went extinct around 1900 (Lockwood 2004). The desert locust (*S. gregaria*) and the migratory locust (*Locusta migratoria*) are the most studied locusts because these species have broad distributions and dramatic population fluxes. The desert locust (*S. gregaria*) is found mostly in the Sahara Desert and other areas with low human population densities during nonoutbreak years. Although it originates in natural landscapes, it can cover 20% of Earth's land surfaces during severe plague years and cause widespread economic damage. The migratory locust (*L. migratoria*) is found in Africa, Europe, Asia, and Australia and has many subspecies that exhibit regional plagues (table 1). For example, the Madagascar locust plague involving *Locusta*

Table 1. Locust species discussed in this article.

Subfamily	Species	Common name	Distribution
Cyrtacanthacridinae	<i>Schistocerca gregaria</i>	Desert locust	Africa, Middle East, Asia
Oedipodinae	<i>Locusta migratoria</i>	Migratory locust	Broadly throughout Africa, Asia, Europe, Australia, and nearby islands
Oedipodinae	<i>Locusta migratoria capito</i> (subspecies)	Malagasy locust	Madagascar
Oedipodinae	<i>Oedaleus senegalensis</i>	Senegalese locust	African Sahel
Oedipodinae	<i>Oedaleus asiaticus</i>	Mongolian locust	China, Mongolia, Russia
Oedipodinae	<i>Chortoicetes terminifera</i>	Australian plague locust	Australia
Melanoplinae	<i>Melanoplus spretus</i> (extinct)	Rocky Mountain locust	North America

Note: All locusts are in the grasshopper family Acrididae.

migratoria capito began in June 2012 and continues (as of November 2014)—currently threatening the livelihoods and food security of 13 million people (see www.fao.org).

The desert locust (*S. gregaria*) and the migratory locust (*L. migratoria*) have affected people for thousands of years, but other locusts have only recently emerged as agricultural threats. Locusts in the *Oedaleus* genus, which are found throughout Africa, Europe, Asia, and Australia, are a good example and have been particularly well studied since they became a major agricultural problem. Prior to the early 1970s, the Senegalese locust (*Oedaleus senegalensis*) was not reported to occur in mass numbers or cause economic damage, but it is now considered the main pest of the African Sahel (Maiga et al. 2008). In 1986–1987, about 5 million hectares were treated for *O. senegalensis* infestations (Brader 1988), whereas in a period of 7 years (1986–1992), US\$177 million was spent on control (reviewed in Cheke 1990). In Asia, the Mongolian locust (*O. asiaticus*) was also rarely reported to cause agricultural damage before the 1970s, but it is now a similarly dominant pest of grasses and crops in northern China (Kang et al. 2007). Could the emergence of these new threatening locust pests be the result of land-use changes mediated by population growth and increasing human pressure on grasslands?

Locust species are concentrated in arid grasslands (Uvarov 1957), where they compete with livestock and other grazers for plants. For example, Australian plague locust juveniles (*Chortoicetes terminifera*) form collective marching groups and pass through pastures, consuming nearly everything in their path (Hunter 2004). The Australian plague locust has been a frequent agricultural pest since at least the 1870s, when early swarms may have been promoted by the introduction of European livestock and agriculture to Australia (Deveson 2012). During the 1984 plague, crop loss was estimated at \$5 million AUD (see www.agriculture.gov.au); however, without locust control, an estimated \$100 million AUD in crops would have been lost. Such mechanisms of chemical control

include financial and poorly quantified costs to human health and the environment due to pesticide use. The primary locust control agency in Australia, the Department of Agriculture's Australian Plague Locust Commission, reduces the need for pesticide use through early detection and intervention, targeted spraying, and introducing biocontrol agents such as Green Guard (a fungus, genus *Metarhizium*, that targets grasshoppers; Hunter 2004).

In Africa and the Middle East, broadscale control of desert locust (*S. gregaria*) plagues is orchestrated by the United Nation's Food and Agriculture Organization Locust Watch. Since the 1960s, effective pesticides and concerted monitoring and control programs have

reduced the frequency and severity of desert locust plagues (van Huis et al. 2007). However, the monetary costs incurred by governments and international aid agencies to control locust plagues have been high. For example, US\$400 million was required to control the 2003–2005 desert locust plague in Africa (Brader et al. 2006). In addition, increasing pesticide use is accompanied by significant secondary effects on human health and ecosystem biodiversity and may not be conducive to long-term, sustainable intensification of agricultural production in Africa (Jepson et al. 2014).

Despite control measures, locust plagues still have significant socioeconomic impacts. Communities with persistent vulnerabilities, such as poorer regions that have strong dependencies on local agriculture, may be less resilient to locust plagues (and other shocks) because households have limited options and opportunities (Baro and Deubel 2006). Locust plagues often exacerbate other shocks such as drought or conflict, as was the case in the 2004–2006 Niger food crisis (Barrett 2010). In addition to immediate impacts on food supply, locust plagues can have far-reaching consequences. For example, De Vreyer and colleagues (2012) studied Mali's 1987–1989 desert locust plague's impact on educational outcomes. For both boys and girls born during 1987–1989 in rural locust-infested regions, there was a 25% reduction in the proportion of children to ever enroll in school relative to urban regions. These results suggest that the financial burden inflicted on families by the locust plague limited funds for school fees and increased the need for children to contribute to family incomes, further reducing school attendance. Therefore, whereas locusts may have major ecological impacts everywhere, their economic impacts are likely most severe on poorer, agriculturally based regions.

From grasshopper to locust

The ecological conditions that promote grasshopper population growth are diverse and vary by species. The underlying factors that promote explosions of swarming locust

populations are not well understood despite their social and ecological importance (Pener and Simpson 2009). For example, precipitation is a major abiotic factor influencing locust and grasshopper populations; however, the effects are complex and nonlinear and depend on life stage (Joern and Gaines 1990).

Locusts require specific soil conditions for ovipositing eggs in the ground: damp enough to prevent desiccation but not wet enough to promote fungal and bacterial infections. Rains that bring new vegetation can encourage the rapid growth of hatching nymphs. However, precipitation can create cooler microclimates, potentially slowing growth and extending intergenerational times. Locust plagues are often the result of multiple generations of population growth, culminating in one to several generations of sustained high populations followed by a crash in which populations return to low density levels (Joern and Gaines 1990).

However, precipitation is just one factor that is thought to influence the propensity for locust outbreaks; plant quality can also affect the growth rate, survival, and fecundity of individual insects, thereby affecting the rate of population increase. The specific aspects of plant quality that influence locust growth are also complex and vary across grasshopper species. For example, in the desert locust, *S. gregaria*, the fastest growth rates occur when the insects consume equal amounts (by mass) of protein and carbohydrate (Pener and Simpson 2009), whereas the Mongolian locust, *O. asiaticus*, favors diets with a 1:2 protein-to-carbohydrate ratio (Cease et al. 2012), a lower protein preference than that of any grasshopper previously studied (Behmer 2009). Plant quality—including the amounts and balance of protein, carbohydrate, and other nutrients that locusts can obtain from plants—depends greatly on soil quality and the nutrients that plants can extract from soils. In turn, soil quality is greatly influenced by land-use practices, particularly in rangelands and agricultural ecosystems.

Research in the arid grasslands of Inner Mongolia in northeast China illustrates the complex feedback that connects livestock management to Mongolian locust outbreaks in scenarios in which locusts originate from human-dominated landscapes (Cease et al. 2012). This literature demonstrated that excessive livestock grazing promotes Mongolian locust outbreaks in an unexpected way: by lowering plant nitrogen (N) content (Kang and Chen 1995, Cease et al. 2012). In this pathway, heavy grazing promotes loss of nutrients (e.g., nitrogen) by amplifying soil erosion through leaching and by export of manure (figure 1; Giese et al. 2013). This results in N-poor plant tissues (Chen et al. 2002). Because most N in plants is in the form of protein, low plant nitrogen content implies protein-poor forage. In contrast to the commonly held view that herbivores are ubiquitously protein limited (White 1993), Cease and colleagues (2012) showed that the Mongolian locust preferred and performed best on low-protein plants found in degraded or heavily grazed pastures. Anecdotal evidence suggests that related West African and Australian locusts have a

similar preference for low protein-to-carbohydrate ratios in their diets. Intriguingly, agricultural reports indicate that outbreaks of these species are common on degraded lands (Amatobi et al. 1988, Bailey 2007, Deveson 2012). However, the connections among land use, soil quality, plant nutrient content, and locust plagues have yet to be investigated in species other than the Mongolian locust.

The convergence of these patterns suggests that a common mechanism may promote locust outbreaks on degraded lands in several parts of the world. Excessive grazing depletes soil nitrogen, resulting in forage that is of lower quality for livestock (an intertemporal externality) but—because low-N plants are of higher quality for the locust—increasing the production of migratory locusts (an ecosystem externality). This feedback generates a spatial externality (Smith et al. 2009) that potentially induces feedback via market mechanisms and governmental responses. Therefore, to understand locust outbreaks, one needs to understand human systems, locust and grassland ecology, and the connections among them.

Telecoupling

Liu and colleagues (2013) suggested that the idea of telecoupling is a way of extending the concept of coupled human and natural systems (CHANS) analysis over space and capturing interactions across geographical locations. A notable difference between conceptualizing grassland–locust–livestock systems as telecoupled and previous telecoupling examples in the literature is the role of ecosystem externalities (Crocker and Tschirhart 1992). Although Liu and colleagues' (2013) framework is flexible enough to include ecosystem externalities, in their examples, humans either deliberately couple geographic regions (most notably through trade or material flows) or unintentionally couple systems, such as through the movement of invasive species. However, energy and materials naturally flow through ecosystem components, such as locusts, even in the absence of human intervention. Anthropogenic activities can create externalities that affect these natural energy and material flows through, say, the movement and behavior of animals, suggesting a potentially important role for mobile organisms as telecouplers themselves (Schmitz 2010). Such a role creates a pathway through which ecosystem externalities extend and transfer existing conventional externalities. In such a case, natural processes that are affected or perturbed by humans can result in undesirable outcomes, such as reduced ecological and economic productivity.

Externalities that arise via spatial ecosystem telecoupling may be a common, important, and often overlooked aspect of CHANS. The introduction of exotic, invasive species is a good example in which the human-assisted dispersal of organisms acts as a telecoupler but the nonhuman organisms migrate, creating an ecosystem externality. The Mongolian locust system shows that such ecosystem externalities can also originate locally, in which human actions indirectly enhance the migration and dispersal behaviors of *Oedaleus*

locusts. Humans do not intentionally create the conditions that increase the likelihood of locusts forming migratory swarms, but when grassland users intensively compete for resources, they have little incentive to conserve grassland quality. As we discussed above, intensive grazing affects nitrogen cycling and nutrient availability, which, in turn, influences the propensity of locusts to migrate. In this case, migration is influenced by local human decisions, but the migration itself is what couples multiple regions. When this happens, humans in other areas must then respond to the locusts.

Two interconnected telecoupling paths play important roles in the coupled human–livestock–locust–grassland system: (1) markets, a traditional telecoupling pathway, and (2) locust migration, a novel telecoupling pathway. The elements of the traditional pathway can be mapped into Lui and colleagues' (2013) five telecoupling components: system, flows, agents, causes, and effects. The *system* has been well defined above as the grassland–locust–livestock system. Markets, especially livestock and agricultural markets, are telecoupling pathways that enable the *flows* of information (through prices) and materials (through global and regional trade in goods). The chief *agents* in the system are the individuals (herders, agricultural vendors), firms, and government entities that set the rules for market interactions, such as grazing policies and agricultural subsidies. Material *flows* through trade move resources from where they are plentiful to where they are needed (Varian 1992), and the root *cause* for this trade stems from local scarcities and individuals trying to improve their own condition. The trade of livestock and agricultural products is an obvious—but perhaps not the most important—way that markets couple regions. Markets also naturally send price signals, which provide information about the value and scarcity of a good in an economy, and help regulate production (supply) and consumption (demand) of that good. Herders and farmers adjust livestock and agricultural production—and consumers adjust their relative consumption of meat, grain, and vegetables—on the basis of these market signals. However, one consequence or *effect* of this system is that these markets often fail to adequately account for all the benefits and costs of these activities, especially because ecosystem interactions seem to play an important role.

Therefore, a novel telecoupling pathway exists in the grassland–locust–livestock CHANS, in which human activity affects the local ecosystem and components of the ecosystem (locusts) act as the telecouplers. Telecoupling through ecosystem externalities is likely not unique to our case, but we think it could apply to a range of CHANS contexts. In the grassland–locust–livestock case, a resulting key empirical question is how migrating locust swarms affect local and regional livestock and feed prices and subsequent range management. Does locust-induced crop or range damage increase the effective price of feed (because of decreased supply), thereby increasing livestock prices? If so, we might

expect such a price signal to encourage the intensification of grazing in neighboring locations (potentially causing longer-term range degradation). Alternatively, the grassland damage that results from a locust outbreak might lead herders to worry about having an adequate supply of grass for their current herd size, resulting in a dump of livestock onto the market. Livestock prices would then decrease, potentially reducing vulnerability to migrating locusts. Whether such price changes benefit livestock producers will depend on the producer's local situation, including the region's level of market integration. However, because locust risk generally goes unpriced in the market, the ecosystem externality must reduce overall social well-being. Recognizing the pathways through which this feedback occurs is important for creating institutions that decrease vulnerability and help promote welfare.

Conclusions

Ecosystem externalities and market-based information (generally via prices) link distant regions in seldom-considered ways. The locust–grassland example we present is interesting in itself: Locust management matters for food security for a substantial number of people globally. However, this type of system is not unique. The concern about the interconnections between market signaling and ecosystem externalities telecoupling geographically distinct human and natural systems touches many of Earth's most pressing problems. For example, markets may send signals in a similar fashion that influence conservation behavior with implications for biodiversity conservation (Horan and Shortle 1999). Ecosystem externalities coupling geographically distinct human populations via natural ecological processes may be crucially important for some of the most pressing emerging infectious diseases, such as West Nile virus (Kilpatrick 2011) and avian influenza (Vandegrift et al. 2010). Therefore, although understanding the grassland–locust–livestock system can inform solutions to pressing food security and livelihood issues, it also provides a heuristic framework for dissecting the pathways that connect human and ecological systems over large spatial distances.

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