

# Food Spoilage, Storage, and Transport: Implications for a Sustainable Future

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*Human societies have always faced temporal and spatial fluctuations in food availability. The length of time that food remains edible and nutritious depends on temperature, moisture, and other factors that affect the growth rates of organisms that cause spoilage. Some storage techniques, such as drying, salting, and smoking, date back to ancient hunter-gatherer and early agricultural societies and use relatively low energy inputs. Newer technologies developed since the industrial revolution, such as canning and compressed-gas refrigeration, require much greater energy inputs. Coincident with the development of storage technologies, the transportation of food helped to overcome spatial and temporal fluctuations in productivity, culminating in today's global transport system, which delivers fresh and preserved foods worldwide. Because most contemporary humans rely on energy-intensive technologies for storing and transporting food, there are formidable challenges for feeding a growing and increasingly urbanized global population as finite supplies of fossil fuels rapidly deplete.*

*Keywords: food security, human macroecology, Malthusian–Darwinian dynamic, technological innovation, sustainability*

**A**lthough often taken for granted by consumers in modern, developed societies, maintaining a reliable food supply has always played a major role in the history of our species. In addressing issues of food security and sustainability, agricultural production has garnered considerable attention from researchers and policymakers (Godfray et al. 2010, Tilman et al. 2011), but food spoilage, storage, and transport have received much less attention. The inescapable realities that food production is inherently patchy in both time and space and that all food inevitably spoils have led to numerous technological innovations in preservation, storage, and transportation, but their roles in shaping human history have arguably received insufficient attention from sustainability scholars and human ecologists. Here we document the central roles that food preservation, storage, and transport played in the geographic expansion and socioeconomic development of human societies. We also show how these issues remain significant for the future of human civilization.

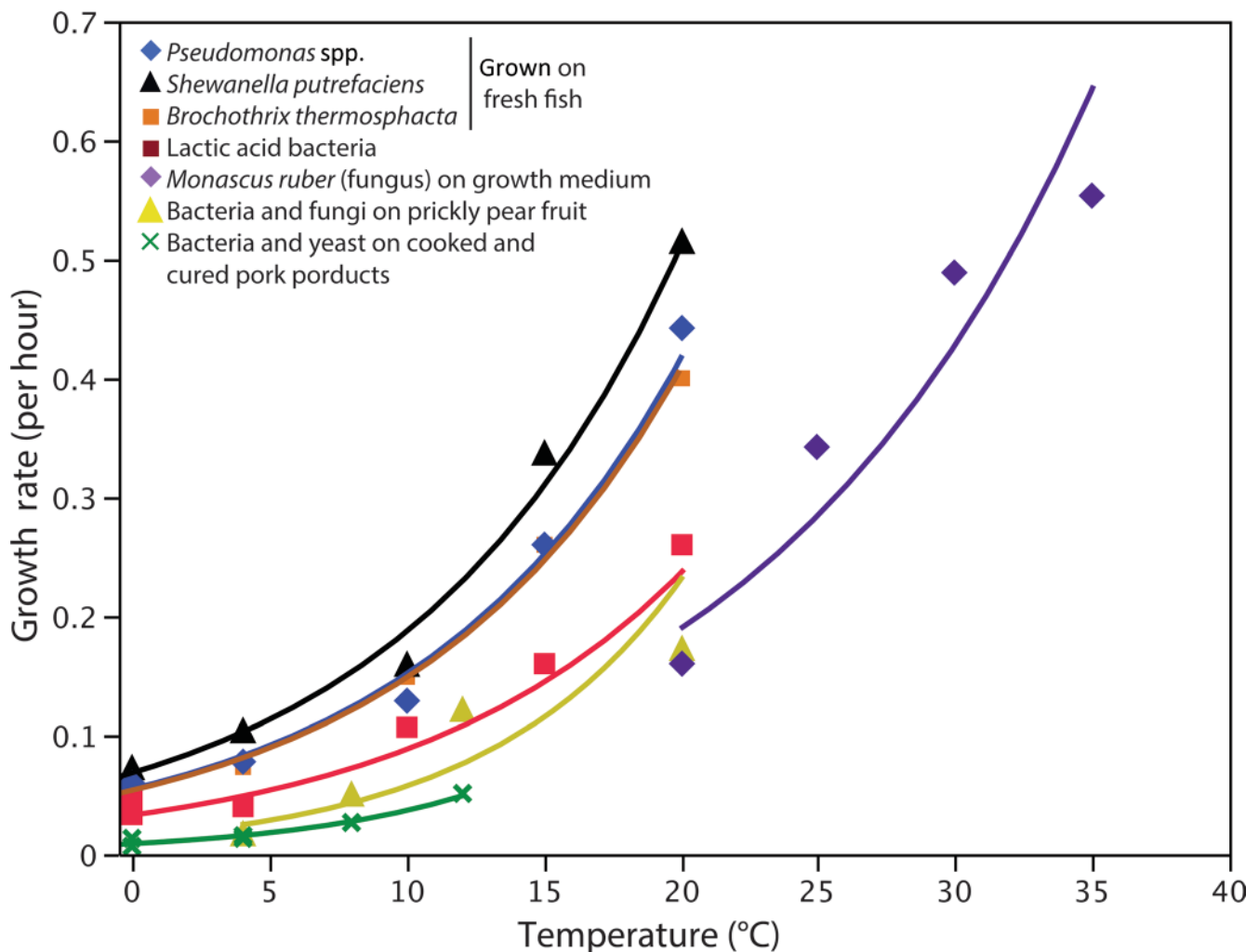
## Food

Humans need to eat. Like other animals, humans require a reliable food supply to meet metabolic requirements for maintenance, growth, and reproduction. An average human weighing 62 kilograms (kg) requires approximately 10,500

kilojoules (kj)—2500 kilocalories (kcal)—of energy in the form of food per day, as well as additional quantities of protein, lipids, vitamins, and minerals for a nutritionally balanced diet (Jones 2003, Hill et al. 2010, Walpole et al. 2012). Humans can withstand brief periods of fasting, but if deprived of all food, starvation usually occurs within 30 to 40 days (Peel 1997, Lieberson 2004). A minimal caloric diet does not ensure good health, however. Diets deficient in vitamins, minerals, and other essential nutrients cause diseases that become increasingly and permanently debilitating on time scales of months to years (Shils et al. 2006) and are a major cause of the physical, physiological, and psychological impairments that often accompany poverty (Kibirige 1997). Because humans are omnivores, their caloric and nutritional needs can be met by eating a wide variety of foods. This dietary generalization provides some buffering against spatial and temporal fluctuations in food supply and has contributed to dramatic increases in human range size.

## Spoilage, preservation, and storage

All food spoils. Some deterioration occurs through the spontaneous breakdown of complex organic molecules. Food can also be consumed by other animals, notably certain insects and rodents. However, most spoilage of food meant for human consumption is caused by microorganisms, which effectively



**Figure 1.** The temperature-dependent growth rates of various microbes involved in food spoilage. An exponential curve has been fitted to the data points for each culture using ordinary least squares. See supplemental table S1 for the data sources and statistical methods. Abbreviation: °C, degrees Celsius.

compete with humans for limited and valuable food resources. Given access to unprotected foodstuffs, bacteria and fungi rapidly colonize, increase in population, and produce toxic and distasteful chemicals (Janzen 1977, Blackburn 2006, Pitt and Hocking 2009). To help prevent microbe-caused food spoilage, humans use two main strategies: (1) obstructing colonization by reducing access to susceptible foodstuffs and (2) inhibiting population growth and limiting population size by creating an unfavorable environment.

Because microbes are so small, have such enormous populations, and often disperse as resistant air-, water-, or soil-borne spores, they rapidly colonize unprotected foodstuffs. Colonization can be retarded by covering or otherwise isolating foods, but it can be prevented only by sealing sterile food in an impermeable container. For example, many fruits, nuts, and bird eggs are encased in relatively impermeable skins, shells, or waxy layers that resist microbial invasion. This is also the principle behind canning.

The alternative, more commonly employed strategy is to retard spoilage by creating conditions that inhibit the growth or limit the size of microbial populations. Washing food, for example, removes some microbes from the surface, and techniques such as pasteurization and irradiation kill microbes.

Microbial population growth rates also depend on environmental conditions. Temperature is especially important because the metabolic rates and population growth of food-spoiling microbes are effectively zero when below freezing and increase approximately exponentially with temperatures over the range of 0–40 degrees Celsius (°C; figure 1). This can be quantified in terms of  $Q_{10}$ , the factor by which growth rate increases with every 10°C increase in temperature. The typical  $Q_{10}$  values for microbes that spoil food range between 2.3 and 4.1 (see supplemental table S1). To appreciate the implications, note that with  $Q_{10} = 3$ , a single microbe that doubles every two days at 4°C will double about every hour

at 34°C and will produce roughly 280 trillion ( $2.8 \times 10^{14}$ ) descendants over a 2-day time period.

Microbial growth also varies with other environmental and physiochemical conditions. Growth rates are generally highest on substrates that provide a well-hydrated, well-balanced mix of carbohydrates, proteins, and lipids and sufficient quantities of essential minerals (Sterner and Elser 2002). These conditions are most readily met on fresh meat, fish, seafood, fruits, and some vegetables. Microbial growth rates are lower, and may approach zero, when the composition of food deviates from such ideal mixtures (Blackburn 2006, Pitt and Hocking 2009).

Water content is especially important. Microbes growing on fresh animal and plant tissues are in approximate osmotic balance, because the water content of active bacterial and fungal cells and of these substrates are similar (Pennington and Douglass 2005). The dehydration of food causes osmotic physiological stress and reduced growth rates for the microbes (Blackburn 2006, Pitt and Hocking 2009). Some foods are naturally preserved by having low water content and high concentrations of osmotically active compounds. For example, dry seeds in approximate equilibrium with the surrounding air typically have water contents in the range of 5–15% (Ellis et al. 1990). In this condition, they can resist microbial growth and remain viable and nutritious for many years. Many nuts contain high concentrations of fats and oils but relatively little water and carbohydrate (Pennington and Douglass 2005). Honey contains superabundant sugar but relatively little water, protein, and lipid, and it resists bacterial colonization but is more susceptible to certain types of xerophilic fungi (Kunčič et al. 2013).

In addition, many of the herbs and spices that have been used for millennia to preserve food produce secondary compounds that are distasteful, toxic, or antibiotic (Mitscher 1975, Swain 1977). For example, the common herb thyme (*Thymus vulgaris*) contains thymol—a monoterpene—which is a powerful inhibitor of microbial growth (figure 2; Marino et al. 1999).

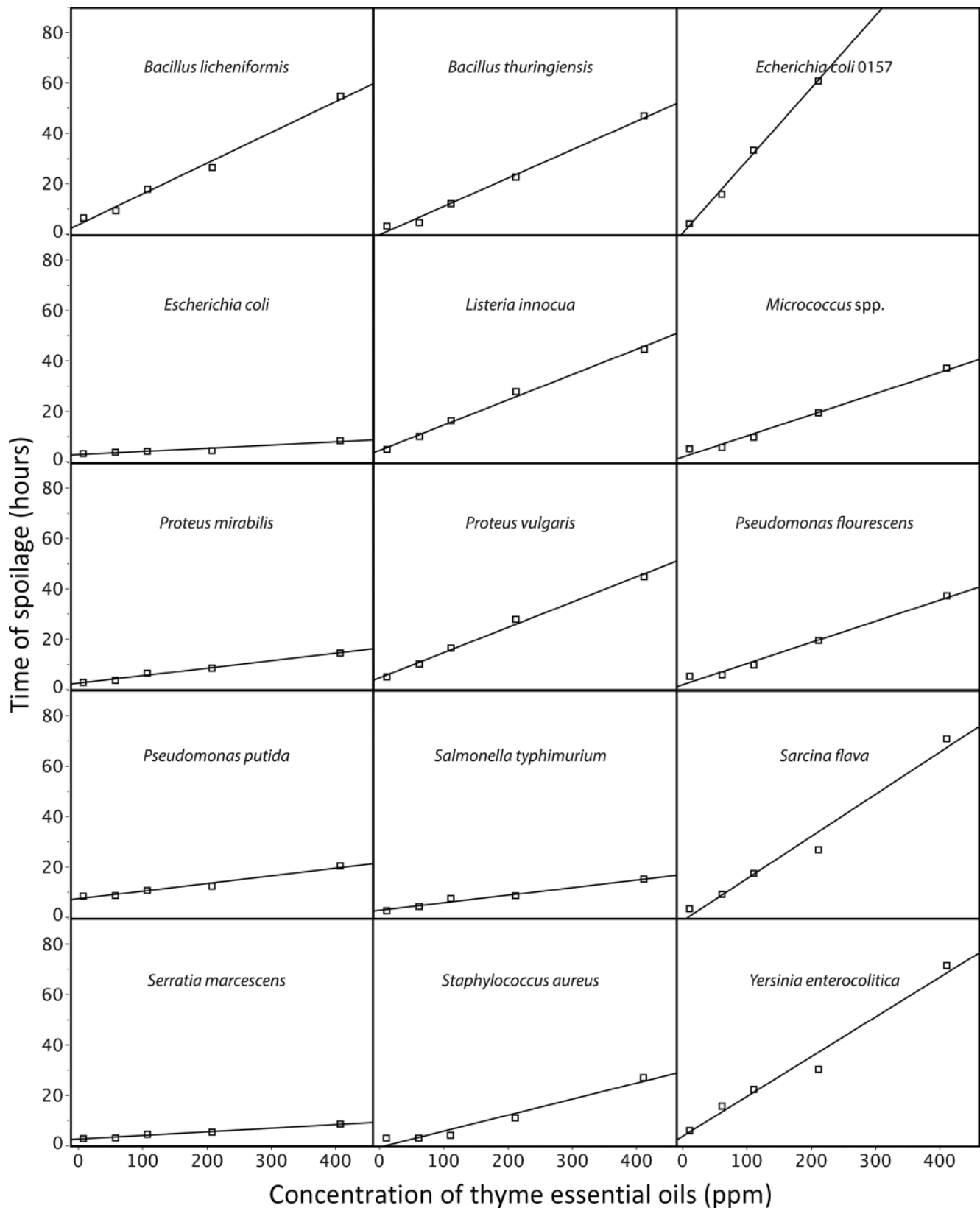
Depending on temperature, water content, nutrient composition, and the presence or absence of antibiotic compounds, foodstuffs remain nutritious and nontoxic to humans for periods from a few hours to many years. Food scientists use shelf life to quantify the length of time a food can be stored and remain suitable for human consumption or commercial sale, but the storage times can vary by orders of magnitude depending on the identity of the foodstuff, environmental conditions, and methods of preservation (figure 3). At one extreme, fresh fish, meat, shellfish, and many fruits and vegetables can be stored for only a few days, even under refrigeration (see supplemental table S2). Foods that naturally contain little water, an unbalanced nutritional composition, or possess antibiotic compounds or protective layers last longer. At the other extreme, dry seeds and frozen foods can be stored for years.

Many of the food-processing techniques used to retard spoilage and extend shelf life date back over at least tens

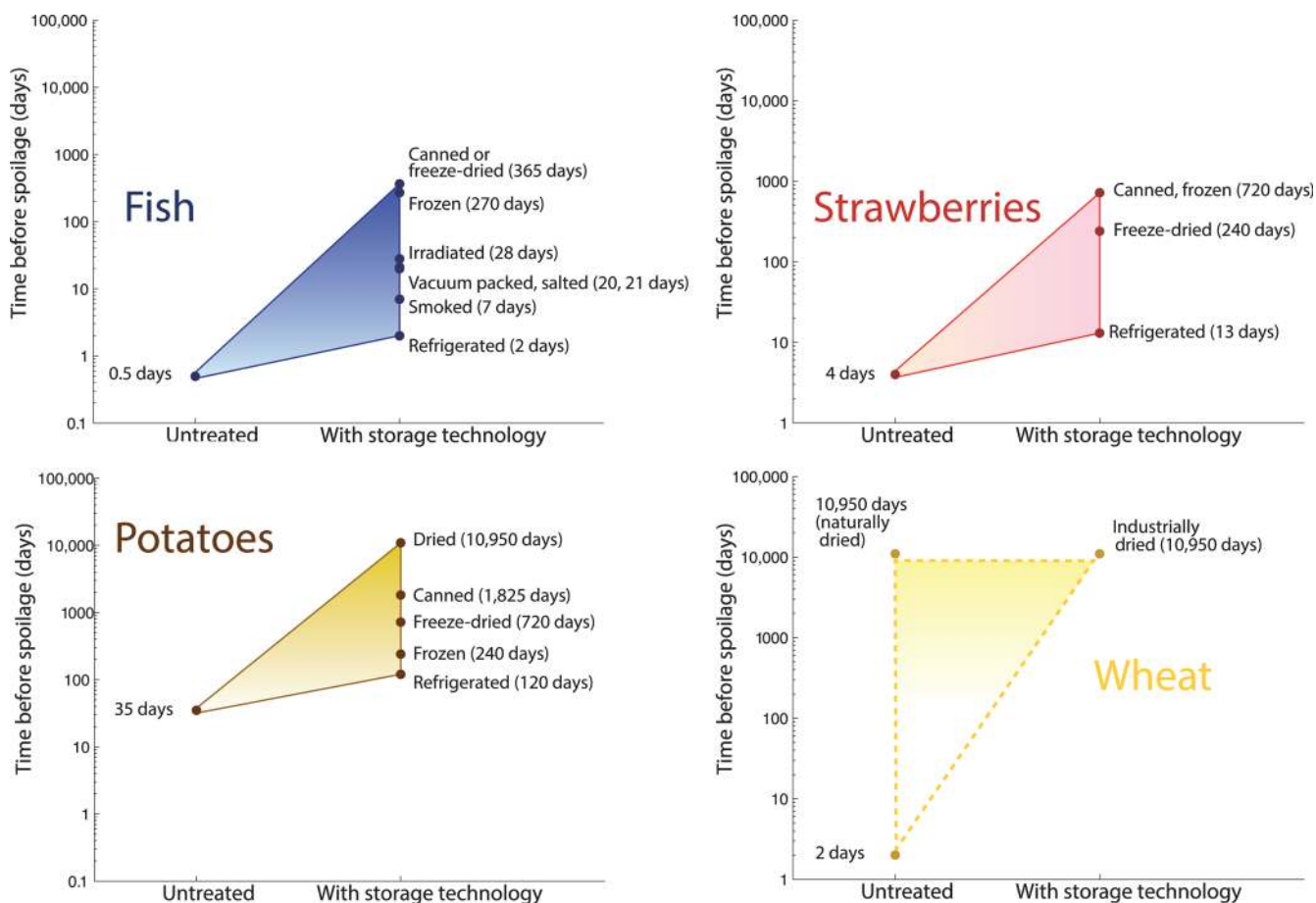
of thousands of years (figure 3). When they could, hunter-gatherers avoided spoilage by eating food soon after harvest and by keeping animals and plants alive until they were eaten (Bailey 1981). Nevertheless, most early cultures inhabited temporally and spatially fluctuating environments, so they collected food during times of abundance and stored it for times of scarcity. They understood enough about the causes of spoilage and the variation in susceptibilities among different foods to develop simple, robust techniques for processing and storing foods. Through millennia of observation and experimentation and depending on geographic location and cultural history, humans developed many methods to extend the shelf life of common foodstuffs. They learned how to manipulate osmotic conditions through the addition of sugars, salts, or lipids (e.g., sugar for jams, jellies, and syrups; salt for fish and meat; oil or fat from olives and butter) to inhibit deleterious microbial growth. They learned to use the secondary metabolites in various herbs and spices not only to mask the odor and taste of partially spoiled food but also to slow microbial growth and retard spoilage. Because microbial growth rates increase with higher temperatures and water availability, preventing spoilage has always been a major problem in tropical climates. It is no coincidence, therefore, that a wide variety of herbs and spices are used in the cuisines of tropical cultures throughout the world (Billing and Sherman 1998, Sherman and Billing 1999).

The development of agricultural societies and city-states resulted in high population densities, with only a proportion of the population directly involved in food procurement (Weiss et al. 1993, Willcox et al. 2012). By cultivating and domesticating wild plants, farmers were able to produce more food than they could themselves consume. This led to the diversification and specialization of labor, with some members of the population devoted to other tasks, such as toolmaking, animal husbandry, defense, and religion. Diets based on cereal grains or tubers were rich in carbohydrate but poor in protein, which were supplemented in various ways by different cultures: by fishing, hunting, keeping domestic animals, and consuming wild pulses (Cordain et al. 2000, Kerem et al. 2007). When milk from domesticated mammals became an important part of the diet of both sedentary and nomadic cultures, the shelf life of this highly perishable product was extended by separating the high-lipid cream and churning it to make butter, which is much more resistant to microbial spoilage. In some cases, specific microbial cultures were added to milk to make fermented products, such as yogurt and cheese, that extended storage time and allowed humans with adult hypolactasia to consume them (McCracken 1971).

Lengthening storage times using beneficial microbial cultures and controlled fermentation also became an important way to preserve fresh vegetables (e.g., sauerkraut, sauerbraten, and kimchi) and fruits (e.g., wine). For the most part, the storage technologies used by agriculturists were modest modifications of the methods developed by foraging societies. For example, farmers in temperate climates harvested



**Figure 2.** The effect of increasing concentrations of essential oils of the common herb thyme in retarding spoilage by different species of bacteria. Microbes were cultured in culture broth, and the time elapsed to grow to a threshold population density was recorded. The lines were fit using ordinary least-squares regression. Source: The data are from Marino and colleagues (1999) and Shils and colleagues (2006). Abbreviation: ppm, parts per million.



**Figure 3.** The shelf life of representative food items, with and without the use of storage technology. The time to spoilage varies widely over untreated food, from less than a day in fish to over a month in root vegetables such as potatoes to many years in grains such as wheat that have been naturally dried on the stalk. The increase in shelf life that results from the use of storage technology varies widely by the technology used but can be orders of magnitude different. See supplemental table S2 for additional information and data sources.

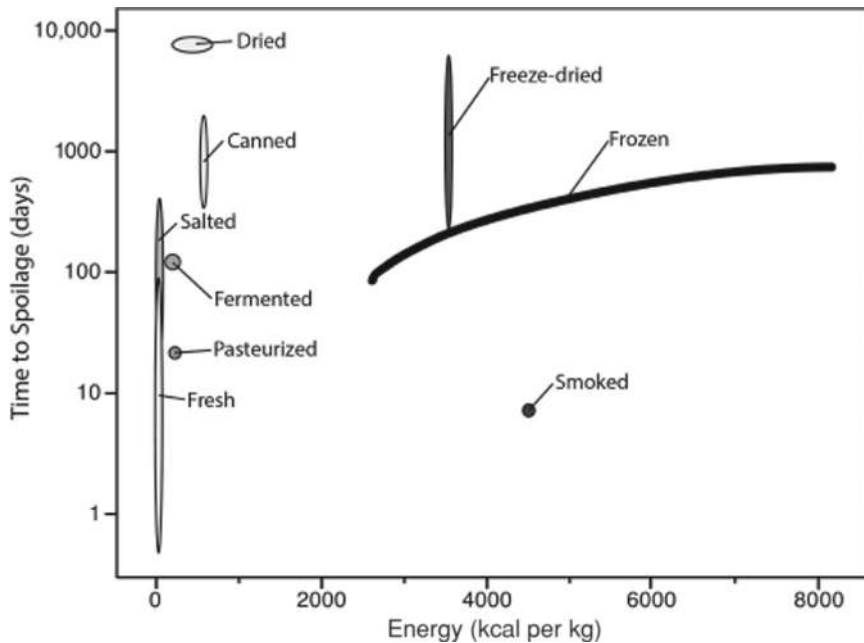
ice in the winter to keep stored food cold into the summer months, and agricultural societies in Mediterranean climates used ethanol, vinegar, brine, and olive oil to preserve a variety of foodstuffs.

Changes in food-storage technologies accelerated with the transition from agricultural to industrial-technological societies. The concentration of an ever-increasing proportion of the population in cities means that an ever-decreasing proportion of farmers and fishers must produce all the food and that larger harvest areas and longer supply lines are needed. The increasing distance between harvesters and consumers means that spoilage must be prevented for longer periods, typically days to weeks, because food is transported over distances of hundreds to thousands of kilometers.

The technological advances of the industrial age revolutionized the storage of many foodstuffs, allowing a greater variety of items to be preserved, but these new technologies often require large energy inputs to achieve increases in shelf life (figure 4). Canning—using a combination of heating to kill microbes and sealing the food in hermetic

containers to prevent recolonization—was pioneered by Appert in 1790 and developed commercially by Donkin in 1810 (Featherstone 2011). Refrigeration using compressed gas was pioneered in the early nineteenth century (Reif-Acherman 2012). Freezing—the natural extension of refrigeration—was commercialized by Birdseye in 1928 and rapidly applied to preserve a wide variety of foodstuffs (Archer 2004). Other currently used modern technologies include the following: (a) freeze-drying, which prevents microbial growth by combining extremely low temperature with dehydration; (b) vacuum packing, which reduces oxidative metabolism rates and prevents microbial colonization by evacuating the atmosphere surrounding foods within a tough, airtight seal; (c) storage in gasses, such as carbon dioxide and nitrogen, that inhibit oxidative metabolism; (d) the addition of chemicals (including sorbic acid, benzoic acid, calcium propionate, sodium nitrite, sulfites, disodium EDTA, BHA, BHT, TBHQ, propyl gallate, ethanol, organic acids, and methylchloroisothiazolinone) which inhibit microbial growth by interfering with metabolic pathways;





**Figure 4.** Energy use for food storage (in kilocalories per kilogram [kcal per kg]). Increased use of energy does not necessarily prolong shelf life. Much preservation still relies on ancient principles, which use little energy and can still preserve food for long periods. The most conspicuous exception is compressed gas refrigeration, especially freezing, which requires continual energy input. The bounding ellipses show the storage time and energy inputs for different food types for that storage type. See supplemental table S2 for additional information and data sources.

(e) irradiation using electrons, gamma rays, UV radiation, or x-rays, which can kill microbes (and insects), interrupt the chemical pathways leading to food ripening, and chemically alter food by breaking down complex organic molecules (Rahman 2007).

Despite the impressive innovations and technological advances that accompanied the industrial revolution, most preservation of foodstuffs still relies on the principles discovered by ancient cultures: retarding microbial population growth by using low temperature, dehydration, wood smoke, unbalanced nutritional composition, osmotic stress, or organic chemicals. Modern preservation techniques often combine multiple methods (e.g., added chemicals and freeze-drying) to increase the shelf life of industrially prepared foods. Even with the most modern techniques, the majority of the caloric requirements in contemporary industrial societies are typically met by cereal grains, which are still preserved primarily by simply keeping them dry.

### Transport

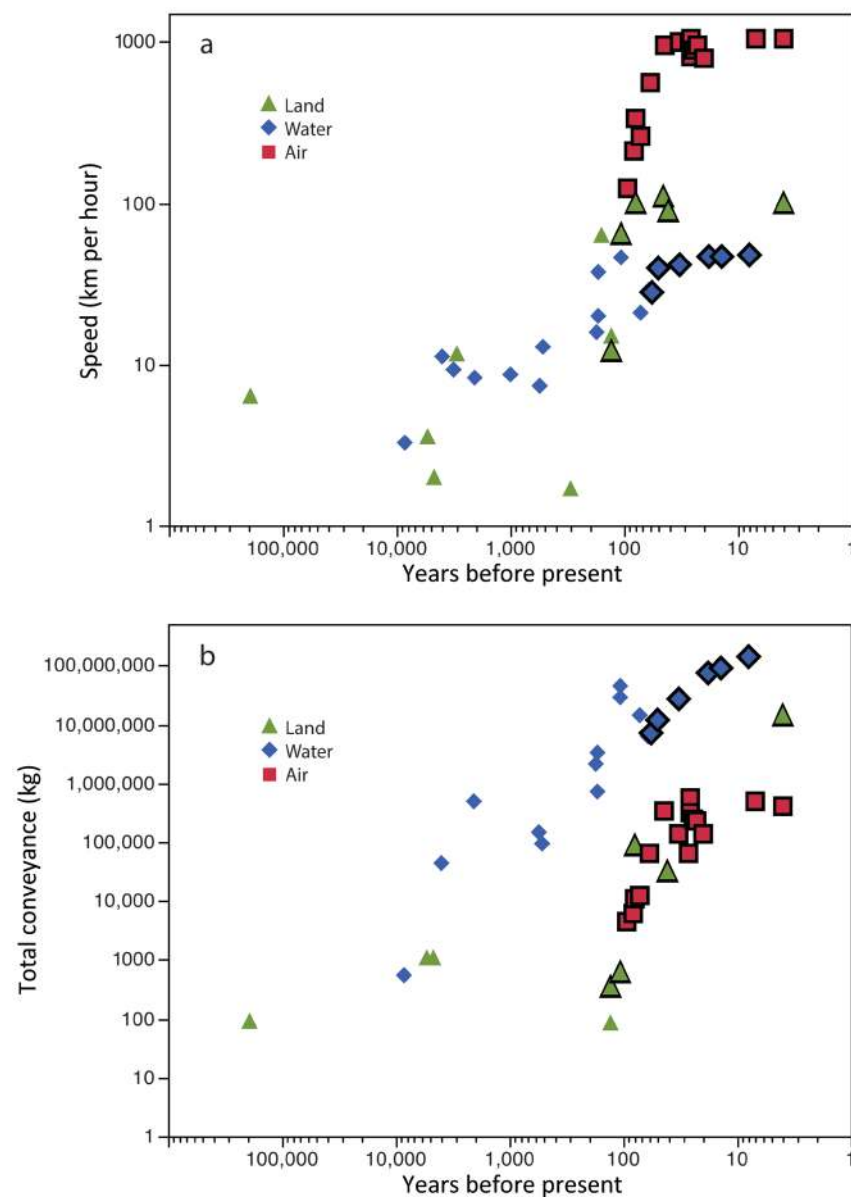
Food transport and storage are intimately interrelated, because transporting food over increasing distances requires preventing spoilage en route. Advances in transportation technologies have played a major role in feeding the growing and increasingly urbanized human population. As cities grow, so do their ecological footprints and their

dependence on more distant environments (Wakernagel and Rees 1996, Burger et al. 2012). They are increasingly dependent on larger areas to produce enough food and on longer supply lines to import foodstuffs harvested on distant farms, grazing lands, oceans, lakes, and rivers. Because of spatial heterogeneity in soil types, climate, and aquatic productivity, these larger foodsheds allow for a more diverse and nutritious diet than was available to pre-industrial agricultural societies, although industrial agriculture has led to an overall homogeneity of commercially grown old- and new-world crops (Khoury et al. 2014).

Advances in food transport have been achieved by some technological innovations that shorten transport time by increasing speed and others that decrease spoilage en route. Travel speed has increased by orders of magnitude over human history, ranging from a few kilometers per hour for the human- and animal-powered conveyances of hunter-gatherer and early horticultural societies to more than 1000 km per hour for jet planes of modern urban-industrial societies (figure 5a). This increase in travel speed is primarily due to access to fossil

fuels and to the successive inventions of the steam engine, the internal combustion engine, the jet engine (figure 5a), and associated infrastructure. For each mode of transport, the maximum possible speed has increased continually but at a diminishing rate. More importantly, however, the commercially practical speed increased rapidly and then plateaued at approximately 40 km per hour for boats and 100 km per hour for railroad trains by the eighteenth century, 90 km per hour for automobiles (trucks) by the midtwentieth century, and 900 km per hour for airplanes by the late twentieth century (figure 5a). We suggest that this leveling off occurs at optimum economical speeds that reflect fundamental trade-offs due to physical and engineering constraints for each medium (water, land, or air) and source of power (animal, steam, internal combustion, or jet engine). Because energy use is a significant contributor to the economic cost of cargo transport, the economically optimal speed will be close to the speed that maximizes the energetic efficiency of cargo transport—the amount of energy required to transport a given mass of cargo across a given distance (Karman and Gabrielli 1950, Winebrake et al. 2008).

Although the commercially practical speed has remained relatively constant for at least the last 50 years, continual innovations—mostly in engine and conveyance design and cargo capacity (figure 5b)—have substantially increased energetic efficiency (figure 6). There is a general trade-off



**Figure 5.** The speed (a, in kilometers [km] per hour) and conveyance size (b, in kilograms [kg]) of human transport capacity, by medium, over time. The transport technologies powered by fossil fuels are outlined in black. See supplemental table S3 for sources and calculations.

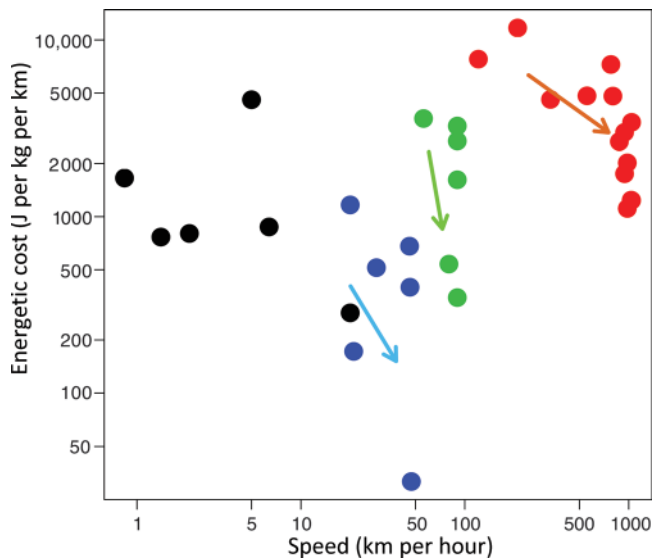
between speed and efficiency both within and across transportation technologies. Ships have always been more efficient than trucks, trains, or airplanes, and by far, the most energetically efficient means of long-distance transport is the cargo ship. Both the speed of a cargo jet and its per-capita energy cost of transport are approximately 20 times greater than those for a container ship (figure 6). To take advantage of the energetic efficiency of water transport, larger and more efficient sea vessels and the associated changes in infrastructure, such as ports and canals, are currently under construction (Panama Canal Authority 2006, Beaubien 2012).

by 2050 (e.g., Foley 2011, Barnosky et al. 2012, Burger et al. 2012, Gerland et al. 2014). To meet this demand, substantial increases in food production will be required. Severely limited arable land and depleted fisheries mean that more subsidies of energy, water, fertilizers, fishmeal, and infrastructure will be required to increase yields (Foley 2011). To further complicate the issue, the ongoing urban transition—with people migrating from rural, food-producing areas to rapidly growing, food-consuming cities—means that each farmer and fisher will need to feed even more people. For example, farmers, ranchers, and fishers together constitute less than 3% of today’s US population (USDA 2014).

Not surprisingly, the kind of vehicle used to transport foodstuffs depends primarily on economic optimization within physical and biological constraints. These depend mostly on the cost of fuel, shelf life, and distance moved (figure 7). Nearly all contemporary cargo ships, trains, trucks, and airplanes are powered by fossil fuel—mostly some form of petroleum—so the cost of oil figures large (Notteboom and Cariou 2009, Notteboom and Vernimmen 2009). Because of the trade-off between speed and efficiency, foodstuffs with short shelf lives have high transport costs. At one extreme are fresh seafood, meat, and some fruits and vegetables, which spoil so rapidly that airplanes are used to minimize travel time across long distances. Additional energy may be used to run compressor cooling for refrigeration or freezing during transport in order to retard spoilage. At the other extreme are cereal grains and other dried foods with long shelf lives. For these food types, travel time is not an issue, and transport by ship or rail is most economical over long distances. There are additional complications, however. For example, the journey of a food item from source to table almost always involves multiple modes of transport because of trade-offs among energy, speed, cargo size, distance traveled, and constraints to infrastructure.

**Implications for food security and sustainability**

As humans push up against the limits of the finite Earth, food security is a major concern, and several authors have addressed the formidable challenges of producing enough food to meet the needs of the growing global population, which is expected to reach 9–10 billion



**Figure 6.** The relationship between energetic costs (in joules [J] per kilometer [km] per kilogram [kg]) and speed (kilometers [km] per hour) for transportation fueled by animal metabolism (the black dots) and transportation fueled by extrametabolic processes (typically fossil fuels) in water (blue), land (green), and air (red) domains. In all cases, the mass used to calculate the energetic costs represents both the transportation vehicle plus its fully loaded cargo. The trajectory of the energy use  $\times$  speed relationship over time in extrametabolically fueled transportation is shown within each of the three groups by best-fit vectors, for which the angle represents the  $\arctan(\text{Spearman rank correlation coefficient [J per kg per km versus time]} / \text{Spearman rank correlation coefficient [km per hr versus time]})$ , whereas the length of the vector represents the Euclidean distance covered through the vector addition of these same two components. See supplemental table S3 for additional information and sources.

Not only must sufficient grains, vegetables, fruits, meats, fish, and shellfish be produced, but also these foodstuffs must be kept from spoiling between harvest and consumption. The modern system of food supply transports an enormous variety of foodstuffs, extends over thousands of kilometers, and uses a combination of ship, rail, truck, and air transport. It relies on specialized energy-intensive industrial-technological processes to preserve and store food and to transport it from producer to consumer. Even with the vast array of preservation, storage, and transport options available, in the United States, as much of 40% of food is lost or wasted “from farm to fork to landfill” (Gunders 2012). The percentage is much lower—on the order of 10%—in the developing countries of southeastern Asia, such as India, Pakistan, and Bangladesh, largely because of different diets that reflect cultural norms (Parfitt et al. 2010). Some of the losses are due to inefficient harvesting, and some are due to the disposal of perfectly edible food, but a substantial proportion is due to spoilage because of inadequate preservation, storage, and

transport. Many writers have left the impression that waste can be reduced to near zero (Kantor et al. 1997), but this is impractical and potentially risky: A resilient food system with sufficient buffers to cope with inevitable temporal fluctuations in supply requires extra food stores, and there is always a risk that some of this extra food will spoil or be wasted (Parfitt et al. 2010).

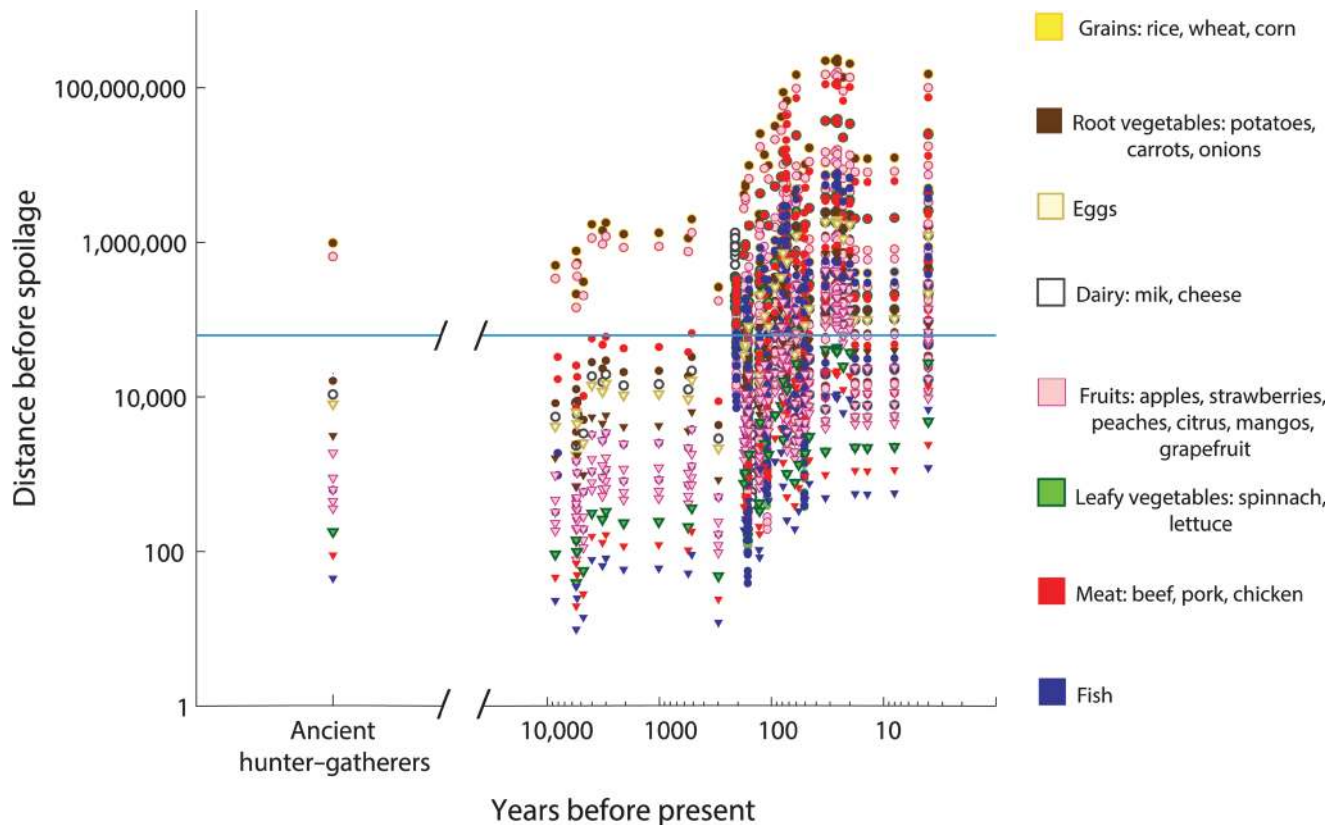
There will always be substantial spoilage and wastage, in large part because we will never completely win the battle with our competitors. Substantial quantities of food are lost because of consumption and spoilage by rodents and insects, but we have focused here on bacteria and fungi, which cause most of the spoilage (Ruxton et al. 2014). Both humans and microbes are subject to the Malthusian–Darwinian dynamic: the universal tendency of all organisms to push against the limits and grow exponentially in population (Nekola et al. 2013). The result is an evolutionary arms race, with each party continually seeking any advantage (Janzen 1977, Ruxton et al. 2014). In this case, it is mostly a race between the capacity of microbe populations to grow on human foodstuffs and evolve adaptations to changing conditions and the capacity of humans to come up with new technologies for preserving, storing, and transporting food. Although less heralded than the evolution of antibiotic resistance in microbial pathogens, food-spoiling microbes rapidly evolve adaptations to resist new preservation technologies so as to colonize and grow on foodstuffs (Bower and Daeschel 1999). Although we briefly mentioned preservation technologies that fundamentally alter the thermodynamic, kinetic, or stoichiometric properties of food, given the enormous natural variety, adaptability, and rapid generation time of many microbes, it will be impossible to completely defeat the ones that cause food spoilage, just as it will be impossible to eliminate all disease.

The ecology of the food-supply system outlined above has major implications for food security and sustainability. As the demographic transition continues and cities grow, their ecological footprint increases. An increasing food shadow means that food must be preserved for greater transport distances and longer travel times, leading to even greater preservation challenges. The trade-off between speed and energetic efficiency of transport means that reducing travel time by increasing speed—by airplane rather than rail, truck, or ship—is possible, but only by expending increasingly costly energy. Keeping food cold by refrigeration or freezing during transport retards spoilage but requires continual energy expenditure to run the compressors in refrigerated transport vehicles.

The fastest growing cities are in economically challenged, developing countries, mostly in the tropics (UNDESA 2011). These densely populated tropical cities in developing countries have food security issues not experienced by similar-sized cities in the middle and high latitudes: Higher ambient temperatures and higher humidity in the tropics mean that foods spoil more rapidly without preservation and that more energy must be expended to maintain a set refrigeration temperature.

The greater poverty of the developing world increases the challenges of paying higher food prices, in large part





**Figure 7.** The increase in humans' ability to transport food before spoilage over historical time. Each data point represents a particular food item, treated with a specific storage technology, and transported using a specific transportation technology. The relative location on the x-axis indicates the earliest date that a storage–transportation technology became possible. Foods are grouped by general food group, with untreated (raw) food depicted using triangles and foods using storage technologies as circles. Even for ancient hunter–gatherers, it would be theoretically possible to carry naturally dried grains half the circumference of the Earth (the blue line) before they spoiled. The greatest gains in food transportation have come in the past 150 years and are primarily due to advances in transportation technology. Except for a handful of raw meats and fish, humans now have the potential to move most food items across the globe before spoilage.

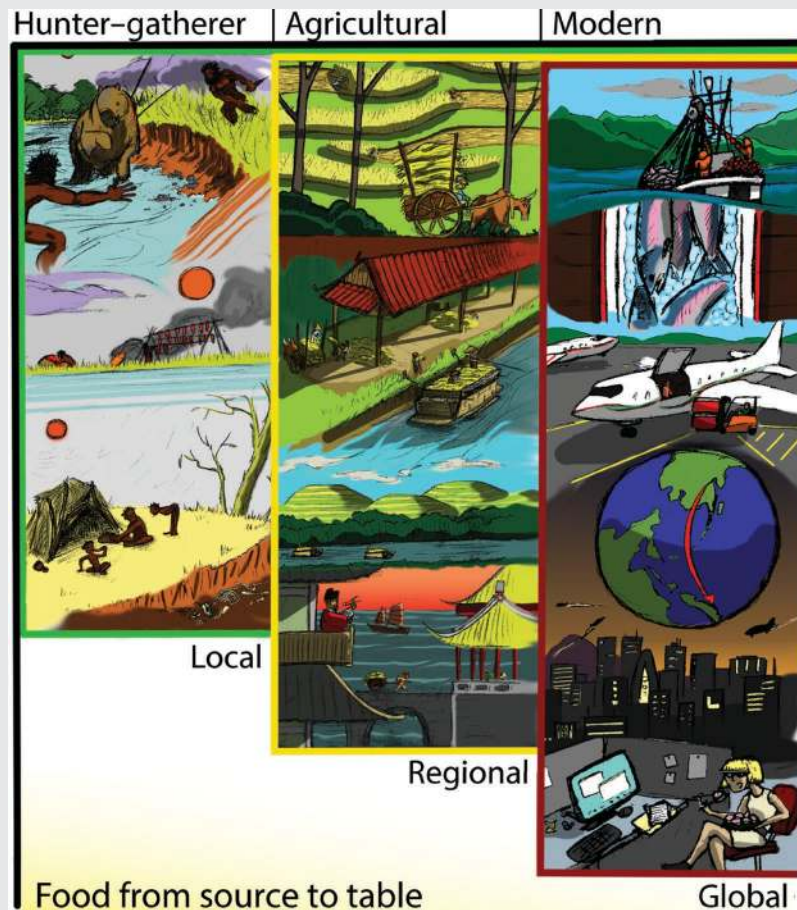
because of increasing energy costs for storage and transport. Although tropical cities in developing countries may be especially vulnerable, even the most developed countries, such as the United States, also face serious issues of food security (Godfray et al. 2010, Hinrichs 2013). After dropping during the last century because of cheap fossil fuels and advances in mechanization, global food prices have increased rapidly since 2000 (FAO 2013), correlated with increasing oil prices (USEI 2014). These trends are likely to continue as energy-dense fossil fuels are depleted and renewables are unable to compensate. Because food costs account for a much greater proportion of family budgets in developing countries (25–50% compared with less than 15% in the United States, the United Kingdom, Canada, the European Union, and Japan; ERS 2013), it is likely that these additional costs will most seriously affect those least able to afford them.

Spatial and temporal fluctuations in food supply will continue to threaten food security. With the inevitable depletion of fossil-fuel reserves and increasing energy costs, major changes in food-supply systems will be required to sustain

current populations, levels of economic prosperity, and quality of life. In areas of favorable climate and fertile soils, farms and small villages should be able to feed themselves cheaply and efficiently from local food production, making the local-food movement a trend of necessity rather than choice. The greatest gains in food preservation and transportation have allowed us to move food items across the globe before spoilage but have focused on increasing the geographic extent of food networks, ignoring the energetic cost. To diminish the impacts of future spatial and temporal fluctuations of food supply, more research is needed to increase the fuel efficiency of our current storage and transportation technologies and to motivate novel innovations that move storage and food-transportation technologies away from fossil fuels and toward more sustainable regional and global food networks.

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Over historical time, humans have used advances in storage and transportation technologies to increase the geographic extent of food networks. In hunter-gatherer cultures, these technologies have largely been used to buffer against the temporal variation in food supply. With the advent of agriculture, storage and transportation allowed for growing cities to be supported by regional food producers. In our modern industrial-technological society, continued technological advances and increasing fossil fuel energy inputs allow for a truly global food network: Even fresh seafood can be transported between continents.

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#### Supplemental material

The supplemental material is available online at <http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biv081/-/DC1>.

#### References cited

Archer DL. 2004. Freezing: An underutilized food safety technology? *International Journal of Food Microbiology* 90: 127–138.

- Bailey GN. 1981. Concepts of resource exploitation: Continuity and discontinuity in palaeoeconomy. *World Archaeology* 13: 1–15.
- Barnosky AD, et al. 2012. Approaching a state shift in Earth's biosphere. *Nature* 486: 52–58.
- Beaubien J. 2012. An Upgrade, and Bigger Ships, for the Panama Canal. National Public Radio. (22 May 2015; [www.npr.org/2012/04/04/149923363/an-upgrade-and-bigger-ships-for-the-panama-canal](http://www.npr.org/2012/04/04/149923363/an-upgrade-and-bigger-ships-for-the-panama-canal))
- Billing J, Sherman PW. 1998. Antimicrobial functions of spices: Why some like it hot. *Quarterly Review of Biology* 73: 3–49.
- Blackburn C de W. 2006. Food Spoilage Microorganisms. Woodhead.
- Bower CK, Daeschel MA. 1999. Resistance responses of microorganisms in food environments. *International Journal of Food Microbiology* 50: 33–44.
- Burger JR, et al. 2012. The macroecology of sustainability. *PLoS Biology* 10.6: e1001345.
- Cordain L, Miller JB, Eaton SB, Mann N, Holt SH, Speth JD. 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *American Journal of Clinical Nutrition* 71: 682–692.
- Ellis RH, Hong TD, Roberts EH, Tao K-L. 1990. Low moisture content limits to relations between seed longevity and moisture. *Annals of Botany* 65: 493–504.

- [ERS] Economic Research Service. 2013. Percent of Consumer Expenditures Spent on Food, Alcoholic Beverages, and Tobacco That Were Consumed at Home, by Selected Countries, 2012. US Department of Agriculture. (22 May 2015; [www.ers.usda.gov/datafiles/Food\\_Expenditures/Expenditures\\_on\\_food\\_and\\_alcoholic\\_beverages\\_that\\_were\\_consumed\\_at\\_home\\_by\\_selected\\_countries/table97\\_2012.xlsx](http://www.ers.usda.gov/datafiles/Food_Expenditures/Expenditures_on_food_and_alcoholic_beverages_that_were_consumed_at_home_by_selected_countries/table97_2012.xlsx))
- [FAO] Food and Agriculture Organization of the United Nations. 2013. FAO's Food Price Index Revisited. FAO.
- Featherstone S. 2011. A review of development in and challenges of thermal processing over the past 200 years: A tribute to Nicolas Appert. *Food Research International* 47: 156–160.
- Foley JA. 2011. Can we feed the world and sustain the planet? *Scientific American* 305: 60–65.
- Gerland P, et al. 2014. World population stabilization unlikely this century. *Science* 346: 234–237.
- Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. 2010. Food security: The challenge of feeding 9 billion people. *Science* 327: 812–818.
- Gunders D. 2012. Wasted: How America Is Losing up to 40 Percent of Its Food from Farm to Fork to Landfill. Natural Resources Defense Council.
- Hill N, Fallowfield J, Price S, Wilson D. 2010. Military nutrition: Maintaining health and rebuilding injured tissue. *Philosophical Transactions of the Royal Society B* 366: 231–240.
- Hinrichs CC. 2013. Regionalizing food security? Imperatives, intersections, and contestations in a post-9/11 world. *Journal of Rural Studies* 29: 7–18.
- Janzen DH. 1977. Why fruits rot, seeds mold, and meat spoils. *American Naturalist* 111: 691–713.
- Jones H. 2003. Design Rules for Space Life Support Systems. SAE Technical Paper no. 2003-01-2356.
- Kantor LS, Lipton K, Manchester A, Oliveira V. 1997. Estimating and addressing America's food losses. *Food Review* 20: 2–12.
- Karman Von T, Gabrielli G. 1950. What price speed? Specific power required for propulsion of vehicles. *Mechanical Engineering* 72: 775–781.
- Kerem Z, Lev-Yadun S, Gopher A, Weinberg P, Abbo S. 2007. Chickpea domestication in the Neolithic Levant through the nutritional perspective. *Journal of Archaeological Science* 34: 1289–1293.
- Khoury CK, Bjorkman AD, Dempewolf H, Ramirez-Villegas J, Guarino L, Jarvis A, Rieseberg LH, Struik PC. 2014. Increasing homogeneity in global food supplies and the implications for food security. *Proceedings of the National Academy of Sciences* 111: 4001–4006.
- Kibirige JS. 1997. Population growth, poverty, and health. *Social Science and Medicine* 45: 247–259.
- Kunčić MK, Zajc J, Drobne D, Tkalac ŽP, Gunde-Cimerman N. 2013. Morphological responses to high sugar concentrations differ from adaptation to high salt concentrations in the xerophilic fungi *Wallemia* spp. *Fungal Biology* 117: 466–478.
- Liebersohn AD. 2004. How long can a person survive without food? *Scientific American*. (22 May 2015; [www.scientificamerican.com/article/how-long-can-a-person-sur](http://www.scientificamerican.com/article/how-long-can-a-person-sur))
- Marino M, Bersani C, Comi G. 1999. Antimicrobial activity of the essential oils of thymus *vulgaris* L. measured using a bioimpedometric method. *Journal of Food Protection* 62: 1017–1023.
- McCracken RD. 1971. Lactase deficiency: An example of dietary evolution. *Current Anthropology* 12: 479–517.
- Mitscher LA. 1975. Antimicrobial Agents From Higher Plants. Pages 243–282 in *Runeckles VC, ed. Recent Advances in Phytochemistry*. Springer.
- Nekola JC, et al. 2013. The Malthusian–Darwinian dynamic and the trajectory of civilization. *Trends in Ecology and Evolution* 28: 127–130.
- Notteboom T, Carriou P. 2009. Fuel surcharge practices of container shipping lines: Is it about cost recovery or revenue making? Pages 1–25 in *Proceedings of the 2009 International Association of Maritime Economists (IAME) Conference*, June, Copenhagen, Denmark. IAME.
- Notteboom TE, Vernimmen B. 2009. The effect of high fuel costs on liner service configuration in container shipping. *Journal of Transport Geography* 17: 325–337.
- Panama Canal Authority. 2006. Proposal for the Expansion of the Panama Canal: Third Set of Locks Project. Panama Canal Authority.
- Parfitt J, Barthel M, Macnaughton S. 2010. Food waste within food supply chains: Quantification and potential for change to 2050. *Philosophical Transactions of the Royal Society B* 365: 3065–3081.
- Peel M. 1997. Hunger strikes: Understanding the underlying physiology will help doctors provide proper advice. *British Medical Journal* 315: 829–830.
- Pennington JAT, Douglass JS. 2005. *Bowes and Church's Food Values of Portions Commonly Used*, 18th ed. Lippincott Williams and Wilkins.
- Pitt JI, Hocking AD. 2009. *Fungi and Food Spoilage*, 3rd ed. Springer.
- Rahman MS, ed. 2007. *Handbook of Food Preservation*, 2nd ed. CRC Press.
- Reif-Acherman S. 2012. The early ice making systems in the nineteenth century. *International Journal of Refrigeration* 35: 1224–1252.
- Ruxton GD, Wilkinson DM, Schaefer HM, Sherratt TN. 2014. Why fruit rots: Theoretical support for Janzen's theory of microbe–macrobe competition. *Proceedings of the Royal Society B* 281 (art. 20133320).
- Sherman PW, Billing J. 1999. Darwinian gastronomy: Why we use spices. *BioScience* 49: 453–463.
- Shils ME, Shike M, Ross AC, Caballero B, Cousins RJ, eds. 2005. *Modern Nutrition in Health and Disease*, 10th ed. Lippincott Williams and Wilkins.
- Sterner RW, Elser JJ. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press.
- Swain T. 1977. Secondary compounds as protective agents. *Annual Review of Plant Physiology* 28: 479–501.
- Tilman D, Balzer C, Hill J, Befort BL. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences* 108: 20260–20264.
- [UNDESA] United Nations Department of Economic and Social Affairs Population Division. 2011. *Population Distribution, Urbanization, Internal Migration, and Development: An International Perspective*. United Nations. (22 May 2015; [www.un.org/esa/population/publications/PopDistribUrbanization/PopulationDistributionUrbanization.pdf](http://www.un.org/esa/population/publications/PopDistribUrbanization/PopulationDistributionUrbanization.pdf))
- [USDA] US Department of Agriculture. 2014. 2012 Census of Agriculture. Geographic Area Series, vol. 1. USDA.
- [USEI] US Energy Information Administration. Short-Term Energy Outlook Real and Nominal Prices, May 2015. (22 May 2015; [www.eia.gov/forecasts/steo/realprices/real\\_prices.xlsx](http://www.eia.gov/forecasts/steo/realprices/real_prices.xlsx))
- Wackernagel M, Rees W. 1996. Footprints and sustainability. Pages 31–60 in *Our Ecological Footprint: Reducing Human Impact on the Earth*. New Society.
- Walpole SC, Prieto-Merino D, Edwards P, Cleland J, Stevens G, Roberts I. 2012. The weight of nations: An estimation of adult human biomass. *BMC Public Health* 12: 1–6.
- Weiss H, Courty MA, Wetterstrom W, Guichard F, Senior L, Meadow R, Curnow A. 1993. The genesis and collapse of third millennium north Mesopotamian civilization. *Science* 261: 995–1004.
- Willcox G, Nesbitt M, Bittmann F. 2012. From collecting to cultivation: Transitions to a production economy in the Near East. *Vegetation History and Archaeobotany* 21: 81–83.
- Winebrake JJ, Corbett JJ, Falzarano A, Hawker JS, Korfmacher K, Ketha S, Zilora S. 2008. Assessing energy, environmental, and economic tradeoffs in intermodal freight transportation. *Journal of the Air and Waste Management Association* 58: 1004–1013.

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