Tracing the role of human civilization in the globalization of plant pathogens

Alberto Santini[1*], Andrew Liebhold[2], Duccio Migliorini[1,4] and Steve Woodward[3]

[1] Institute for Sustainable Plant Protection – C.N.R., Via Madonna del Piano, 10 - 50019 Sesto fiorentino, Italy

[2] US Forest Service Northern Research Station, Morgantown, West Virginia 26505, USA.

[3] University of Aberdeen, Department of Plant and Soil Science, Institute of Biological and Environmental Sciences, Cruickshank Building, Aberdeen AB24 3UU, UK

[4] Present address: Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa.

Type of article: Perspective

Number of words in the Main text: 2999 words

Number of references: 25

3 colour figures.

There is no conflict of interest that authors should disclose.

Author for correspondence:

Alberto Santini

IPSP-CNR

Via Madonna del Piano, 10 - 50019 Sesto fiorentino, Firenze, Italy.

Tel: +39 055 5225586

Email: alberto.santini@cnr.it

Co-evolution between plants and parasites, including herbivores and pathogens, has arguably generated much of Earth's biological diversity. Within an ecosystem, co-evolution of plants and pathogens is a stepwise reciprocal evolutionary interaction: epidemics result in intense selection pressures on both host and pathogen populations, ultimately allowing long-term persistence and ecosystem stability. Historically, plants and pathogens evolved in unique regional assemblages, largely isolated from other assemblages by geographical barriers. When barriers are broken, non-indigenous pathogenic organisms are introduced into new environments, potentially finding suitable hosts lacking resistance genes and environments favouring pathogenic behaviour; this process may result in epidemics of newly emerging diseases. Biological invasions are tightly linked to human activities and have been a constant feature throughout human history. Several pathways enable pathogens to enter new environments, the great majority being human mediated.

The fossil record provides evidence that diseases commonly affected plants some 250 million years ago (Dark & Gent, 2001). The recurrence of wheat rust outbreaks is reported by Roman authors such as Cicero, Varro and Columella (2100-1950 BP). Rust outbreaks were so feared that there was a god/goddess of rust (Robigus/Robigine) to whom processions, sacrifices and feasts were dedicated in order to prevent crop destruction.

During the last 200 years the incidence of plant diseases has increased exponentially in terms of both numbers and severity (Santini et al, 2013). Alien pathogen introductions can lead to novel host-pathogen associations or novel pathogen-pathogen combinations, with no previous co-evolutionary history.

Why are so many invasive plant pathogens now appearing? The aim of this paper is to increase understanding of the means of introduction and spread of these pathogens, which, as with most invasive species, can be traced to human behaviour, societal development,

technological change, and geopolitical trends. We believe that reviewing historical developments enhances our ability to anticipate future developments.

Prehistory

Limited information exists about the impact and spread of plant diseases before the onset of major human migrations, although some evidence suggests that pathogens played an active role in shaping the composition of prehistoric forests and other vegetation (Davis, 1981). Pollen analysis from the mid Holocene suggests two catastrophic declines occurred in Northern Hemisphere forests: a hemlock (*Tsuga*) decline in eastern North America and an elm (*Ulmus*) decline in western, central and northern Europe. Decline of *Tsuga* spp. was recorded at 60 sites and dated around 5500 BP (Bennett & Fuller, 2002), while elm decline occurred 6347 – 5281 BP based on a comprehensive review of 139 dated sites (see Waller, 2013 and references therein). Both declines are characterised by the same specific features, such as strong synchrony of events over wide regions (Eastern North America and central, north-west Europe); rapidity of the decline; long periods in which these trees were largely absent. These features suggest an invasion by a non co-evolved pathogen that eliminated the majority of hosts. The eventual re-emergence of these tree species may have been associated with a gradual development of resistance. Mid-Holocene pollen records associated with these events resemble those arising during modern epidemics of forest pathogens, including chestnut blight and Dutch elm disease (see Waller, 2013 and references therein).

In addition to these massive declines, evidence exists of forest declines at more local or regional levels, ranging from temporary decreases in tree species richness, to full extinctions of specific tree taxa appearing in the Holocene pollen stratigraphy. Although many different, and sometimes contrasting, hypotheses have been advanced for the causes of these declines,

most recent accounts (Waller, 2013) adopt a multi-factor hypothesis in which disease pandemics likely played a role along with climate changes and impacts from human activities.

A starting date

Though early intercontinental raft voyages and migrations over land bridges could have transported certain organisms, for most purposes, we can consider the starting point for plant pathogen invasions to coincide with the "Columbian Exchange", ~1500 CE, which marked the beginning of large-scale human movement between Europe and the Americas (Crosby 2006). This time corresponded with initial European colonial activities which often involved trans-oceanic movement of plants and animals for cultivation in colonies, for consumption in Europe (Crosby, 2006) and for collection of botanical specimens aboard ships. Maize, *Zea mays,* for example, was probably initially domesticated via hybridization of native species in the Balsas River Valley of south-central Mexico by indigenous people (Piperno, 2011). As part of the Columbian Exchange it was brought to Europe in the 1500s and ultimately distributed further for cultivation in Asian and African colonies.

For these reasons invasion biologists use 1500 to divide alien plants in Europe into "archaeophytes", introduced before 1500, and "neophytes" introduced later. However, it is widely recognised that the spread of plants and their associated pathogens began much earlier.

Human migrations

Human migrations approximately 85000 years BP likely caused the earliest spread of invasive species following the migration of *Homo sapiens* out of central Africa (Cavalli-Sforza & Feldman, 2003) (Figure 1). Europe, for example was colonized between 9000 to 4500 BP by
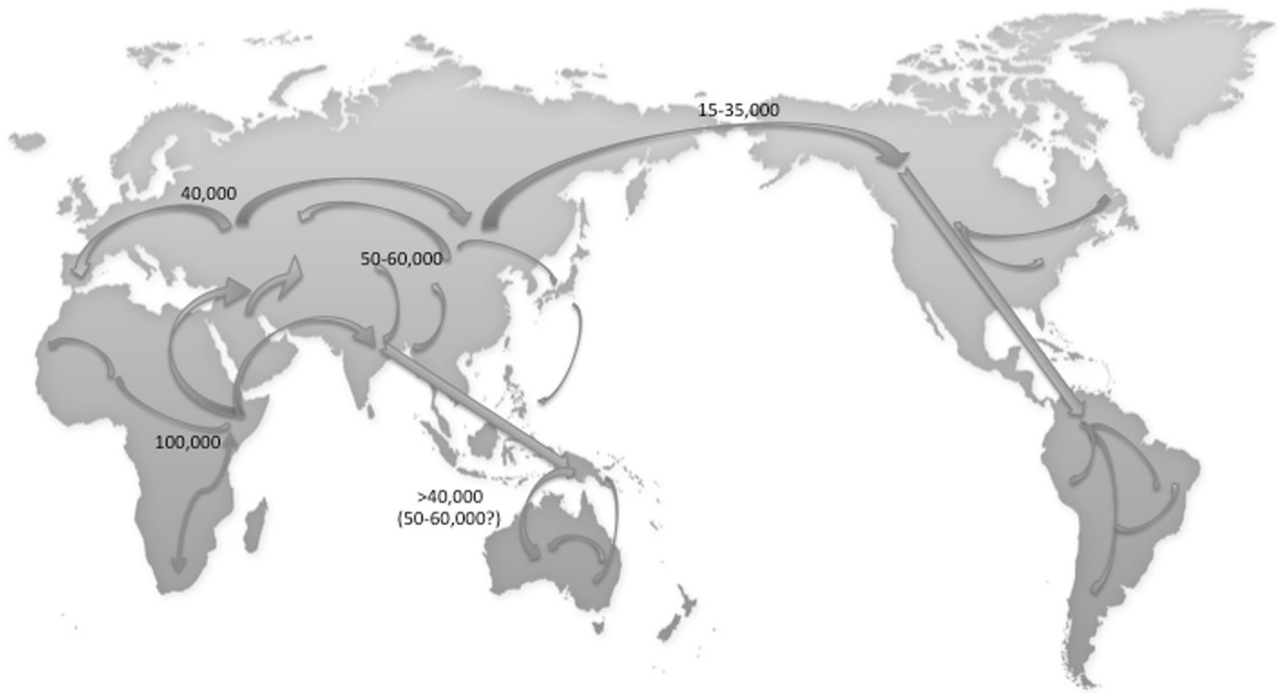
Figure 1. Migrations of modern Homo sapiens (Adapted by permission from Macmillan Publishers Ltd: [Nature Genetics] (L. Luca Cavalli-Sforza, Marcus W. Feldman, 2003. The application of molecular genetic approaches to the study of human evolution 33:266-275), copyright 2003.

Neolithic farmers, moving from the Fertile Crescent of Mesopotamia. Indigenous populations settled in North America after crossing the Bering Strait to Alaska during milder periods in the midst of the last ice age (15000-14000 BP). Expanding Neolithic farming cultures probably carried plant material over considerable distances (Diamond and Bellwood 2003). In addition, transport by sea began as far back as the Pleistocene (2588000 to 11700 BP). The earliest archaeological evidence of maritime trade between Mesopotamia and the Persian Gulf was dated to the seventh and eighth millennia BP (Carter, 2006). Though not impossible, extraction of fungal DNA from archaeological artifacts is challenging and, to our knowledge, there are few reports of such analyses. However, it can be speculated that seed-borne fungi survived long periods of transport and storage, at least as long as the useful life of the seed (Maude, 1996). Dark and Gent (2001) suggest that the increased incidence of plant diseases during the late Iron Age and Roman periods could have been due to increasing trade in seeds, especially within the Roman Empire.

Humans have a long history of migrations and conquests during which select plants and animals were deliberately introduced to new global regions for domestication. For example, so-called English elm (*Ulmus procera* Salisb.) was introduced to Britain by the Romans for use in vineyards (Gil et al, 2004). The largest Euro-Asian chestnut (*Castanea sativa* Mill.) glacial refuge is in the Caucasian-Armenian area. By the 11-9th Century BP humans were cultivating chestnuts between the Caspian and Black Sea. Chestnut cultivation quickly spread from Asia Minor to Greece and the Balkans. The Romans quickly discovered the practical potential of chestnut cultivation and since the 1st Century, Italy has been the European centre of chestnut culture (Adua, 1999). A number of crop species including cereals, legumes and trees such as tamarind and baobab were moved from Africa to the Indian subcontinent during prehistory (Bell et al, 2015 and references therein). Humans have long moved plants both to satisfy food needs, and also for ornamental purposes (Supplementary material S1).

Nearly every individual of any wild plant species can be expected to host hundreds of species of endophytic and plant pathogenic fungi, so it is certain that many fungal species have accompanied human movements of plants. For centuries, the time taken to travel long distances probably limited survival of potentially harmful propagules of many invasive pathogen species, but increasing speed of transport has improved the probability of propagule survival, sometimes with disastrous consequences for invaded ecosystems. For example, wheat has been cultivated in Europe and China since 6000–7000 BP; when European farmers moved into the Americas, Australia, and South Africa during the past 500 years, they introduced wheat as well as its pathogens *Phaeosphaeria nodorum* and *Mycosphaerella graminicola* (Stukenbrock et al, 2006).

Invasive pathogen species may not be simply a consequence of human migrations: they have also forced humans to move. Plant disease outbreaks that trigged famines and, as a consequence, mass human migrations have been reported since the beginning of history and are still a major cause of this phenomenon (Supplementary material S1).

Technological progress

Over the last 500 years, transport technology has progressively improved, decreasing trans-oceanic shipping times and facilitating the rapid movement of living plants, some of which transport plant pathogens. The S.S. Savannah, the first steamboat to cross the Atlantic Ocean (1819), represented an important milestone in transport technology and consequently in rapid plant movement. Previously, crossing the Atlantic by sailing ship required 8-12 weeks, so transport of living plants was impossible without the use of elaborate portable greenhouses, where plants needed to be potted and often re-potted during transit, using foreign soil and consequently spreading soil-borne pathogens. Continuous progress in naval and aeronautical engineering has enabled incremental improvement in the ease of trans-
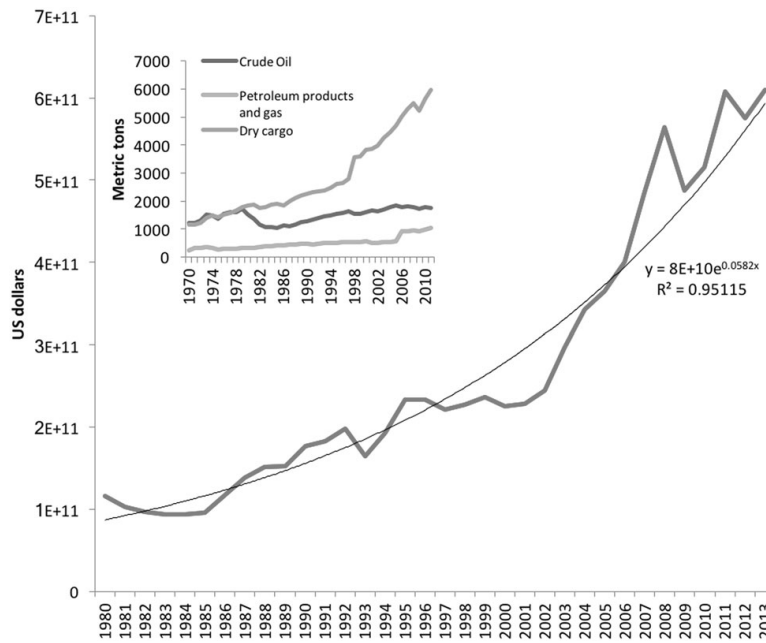
Figure 2. Trend of European agricultural imports per year (1980-2014) expressed in USD (UNCTAD, 2014). In the box: World seaborne trade by type of cargo per year (1970-2011) Plants fall into the dry cargo category (UNCTAD, 2014).
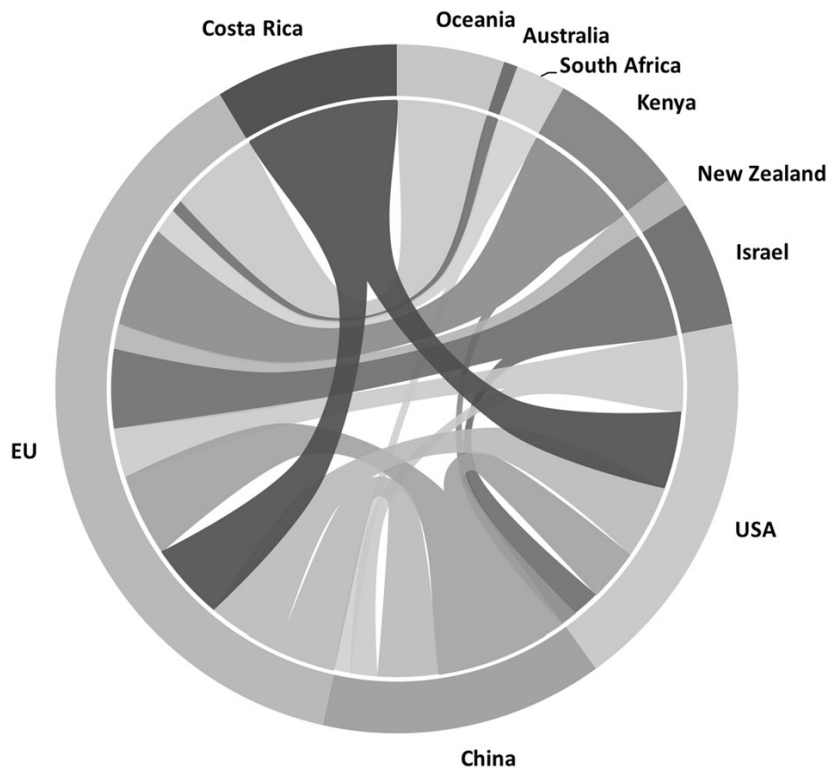

Figure 3. Trade of plants and plant parts among principle trading countries. For each country flow widths are proportional to 2015 import and export values. Colours correspond to exports from a single country, coded by the colour of the outer band. Imports are represented by different colours flowing into each country (Commodity code 0602: Live trees, including roots, cuttings, slips and mushroom spawn). Source UN Comtrade Database http://comtrade.un.org/.

8

oceanic transport of live plants. This technology has allowed increases in numbers of plants transported in a single trip, resulting in an equivalent increment in viable pathogen inoculum arriving at final destinations, and increasing chances of infections occurring on new hosts.

The use of maritime containers, including refrigerated containers, has greatly facilitated large-scale movement of plants and other potential vectors of plant pathogens. The first commercial container ship, the Clifford J. Rogers, was launched in Seattle in 1955 and carried 58 metal containers. Modern container ships can carry up to 18,000 twenty-foot equivalent units (TEUs). World container port throughput was estimated at 651.1 million TEUs in 2013 (Clarkson Research Services 2014; Fig. 2). International commerce in agricultural products, has increased four-fold from US$ 414.723 million in 1990, to US$ 1.765.405 million in 2014 (www.wto.org/statistics).

Among agricultural products, imports of live plants probably represent the most important pathway for transport of plant pathogens (Liebhold et al, 2012, Santini et al, 2013). Given advances in transport technologies, a complex network of global commerce in live plants has developed (Fig. 2). Favourable climates and labour costs provide incentives for production of many types of plants in tropical regions. Billions of plants consumed in North America are produced in Central America, and Europe receives large numbers of plants from Africa and Asia (Fig. 3).

Geopolitics and regulation of trade

Legislation limiting plant diseases was born more than 300 years ago in France where laws were enacted requiring destruction of barberry (*Berberis* spp.) to control the spread of stem rust in wheat. Prior to the mid-1800s, however, there was little recognition of the potential dangers associated with accidental movement of plant pathogens on live plants and other objects. The first attempt at regulating international movement of plants took place in Europe

in 1878, as a reaction to massive damage to the viticulture industry caused by the grape Phylloxera; seven European countries agreed to implement the "International Convention on Measures to be taken against *Phylloxera vastatrix*" (now *Daktulosphaira vitifolia*). The convention specified procedures for exporting countries to certify disease- and insect-free plant material for export along with plant import inspection procedures. During this era, several European countries (MacLeod et al, 2010), initiated their own measures to stem the flow of dangerous plant pests. In the USA, importation of live plants was not regulated until the passage of the Plant Quarantine Act in 1912 (Liebhold & Griffin, 2016). Previously, large numbers of live plants were imported without limits and many damaging insects and plant pathogens were accidentally introduced with such shipments.

World War II represented a turning point in the global movement of plant pathogens. Allied army supplies provided a pathway for movement of at least three important forest pathogens: *Seiridium cardinale*; *Ceratocystis platani* and *Heterobasidion irregulare* (Santini et al, 2013). But it was the aftermath of the war that brought massive geopolitical changes, laying the foundation for our modern globalized economy. Economists argued for the elimination of barriers to free trade ultimately leading to the General Agreement on Tariffs and Trade (GATT) in 1948.

In addition, GATT also led to important agreements that shaped international plant quarantine policy. Unjustified quarantines placed by countries on the importation of agricultural and other goods were identified as barriers to free trade. In 1994, GATT promoted the Agreement on the Application of Sanitary and Phytosanitary Measures (the SPS Agreement), which designated standards for regulatory measures implemented by member countries for the protection of plant, animal, and human life and health. The organization recognized in the agreement as the standard-setting body for plants was the International

Plant Protection Convention (IPPC), a multilateral treaty overseen by the Food and Agriculture Organization (FAO) of the United Nations.

The SPS agreement states that each country can set a desired level of risk for damaging pests associated with imports and outlines a science-based procedure for managing risk. Some countries, notably New Zealand and Australia, maintain very stringent regulations on plant imports in order to minimize risk (Eschen et al, 2015). In contrast, the European Union enforces much less strict import regulations; many plants may be imported without a permit and soil associated with plants is often allowed. The presence of soil represents a particularly significant opportunity for transport of invasive pathogens (Migliorini et al, 2015). The creation of the European Union and fall of the "Iron Curtain" resulted in much more open trade among European countries. These open borders increased movement among countries, potentially increasing movement of plant pests (Roques et al, 2016).

Following the passage of the Plant Quarantine Act in 1912, the US Department of Agriculture implemented "Quarantine 37" in 1919, which greatly curtailed plant imports and established a system of inspection and other quarantine practices (Liebhold & Griffin, 2016). These regulations resulted in a downward trend in numbers of plant pathogen introductions during the mid 20th Century (Liebhold & Griffin, 2016). The trend was the opposite in Europe – i.e. increasing rates of establishment (Santini et al, 2013) – suggesting that the 1912 Quarantine Act has been reasonably effective in reducing numbers of new introductions to the USA.

The IPPC aims to harmonize phytosanitary measures among countries. Nevertheless, some countries lack adequate financial recourses necessary for implementing strict plant quarantine regulations, which poses a risk even to countries that maintain high quarantine standards. Countries with more "porous" borders serve as bridgeheads where pathogens may establish, become abundant and then invade other world regions (Early et al, 2016).

Another significant problem facing effective plant quarantine programs is the high percentage of invasive pathogens of unknown origin (Santini et al, 2013; Xu et al, 2006). A major problem in managing invasion pathways utilized by fungi and Oomycetes is the difficulty in recognizing organisms at the species level. Many 'new' species are cryptic, resembling already known species, but with minor genetic differences which may create considerably higher virulence when exposed to host plants. The extent of this problem increases when the pathogens are endophytic or have an extended latent period before causing symptoms (Sakalidis et al, 2013).

Certain pathogen invasion pathways can be directly identified. For example, good evidence exists that Karnal bunt of wheat entered the United States across the land border with Mexico, inadvertently transported in private automobiles, trucks, and railway cars rather than with commercial cargo (Marshall et al, 2003). However because of the difficulty in identifying pathogens and the characteristically long delay between pathogen arrival and discovery, invasion pathways for many species can only be inferred rather than observed.

In the USA, Europe and China, the main pathway for plant pest and pathogen introductions is by far imports of living plants, (Liebhold et al, 2012; Santini et al, 2013; Xu et al, 2006). In Australia and New Zealand, where international trade in plants is more strictly regulated, the arrival of pathogens is mainly linked to contamination of traded goods other than live plants.

The 'plants-for-planting' pathway is difficult to control for various reasons. Horticulture is a major global industry: in 2013, for example, 84,500 tonnes of live plants were imported into Europe, compared with exports of 400,000 tonnes (Eurostat Comext http://epp.eurostat.ec.europa.eu/newxtweb). Faced with such huge volumes, only a small percentage of plants can realistically be inspected at ports of entry (Liebhold et al, 2012). Moreover, markets in live plants, especially ornamentals, are constantly changing. Imported

species and geographical sources for obtaining a given species can change rapidly. This problem exacerbates the risk of introducing new pests from different exotic locations.

Conclusions

Since pre-history, humans have dramatically changed their living environment, for example by exploiting natural resources until depletion, or via movement and cultivation of plant species outside their natural range. Agricultural and forestry practices frequently rely on non-indigenous plant species. This human-mediated globalization of plant ranges has steadily increased throughout the history of human civilization. The trend for globalization has consequences that reach beyond impacts on individual humans and their societies, also including impacts on ecosystems. In many parts of the world, invasions of plant pests and pathogens have transformed managed and natural areas, often with cascading effects on ecosystem services (Lovett et al, 2016) as, for example, *Phytophthora ramorum* in UK, Ireland and US.

This paper describes how historical developments in human civilization and geopolitics have driven trends of increasing movement and impacts of plant pathogens. Even before the modern era of globalization, technological developments and societal changes facilitated new plant disease epidemics that adversely affected society and shaped social development. It is also evident that during the modern era of globalization we are poised to continue that trend, with potentially catastrophic effects on society and global ecosystems.

We argue here for closer integration of invasion biology with history and sociology, to significantly advance understanding of the causes of biological invasions and to limit future damage. Learning from this history it can be deduced that the solution to these increasing impacts lies not in halting the trend of globalization, which is neither realistic nor necessarily desirable, but to better capitalize on scientific knowledge. Implementation of scientifically-

based policies will allow globalization to proceed while simultaneously minimizing movement of plant pathogens, thus preventing further economic and ecological disasters. History is not merely a list of dates and names of famous people, but, as Cicero claimed in *De Oratore* "*Historia vero testis temporum, lux veritatis, vita memoriae, magistra vitae, nuntia vetustatis…*". In short '*history is life's teacher'.*

Literature

1. Adua M. (1999). The sweet chestnut throughout history from the Miocene to the Third Millennium. Acta Horticul 494: 29-36.

2. Bennett KD, Fuller JL. (2002). Determining the age of the mid-Holocene Tsuga canadensis (hemlock) decline, eastern North America. Holocene 12: 421–429.

3. Carter R. (2006). Boat remains and maritime trade in the Persian Gulf during the sixth and fifth millennia se. Antiquity 80:52-63.

4. Cavalli-Sforza LL, Feldman MW (2003). The application of molecular genetic approaches to the study of human evolution. Nat Genet 33, 266 – 275.

5. Clarkson Research Services (2014). Container Intelligence Monthly. June.

6. Crosby AW. (2006). Ecological Imperialism: The Biological Expansion of Europe, 900–1900, 2rd Edition. Cambridge University Press, Cambridge, UK.

7. Dark P, Gent H. (2001). Pests and Diseases of Prehistoric Crops: A Yield 'Honeymoon' for Early Grain Crops in Europe? Oxford J Archaeol 20: 59–78.

8. Davis MB. (1981). Outbreaks of forest pathogens in Quaternary history. In IV International Palynological Conference (1976–77), Vol. 3, Birks HJB (ed.). Palaeobotanical Society: Lucknow; pp. 216–227.

9. Diamond J, Bellwood P. (2003). Farmers and their languages: the first expansions. Science 300:597-603.

10. Eschen R, Britton K, Brockerhoff E, Burgess T, Dalley V, Epanchin-Niell RS, et al. (2015). International variation in phytosanitary legislation and regulations governing importation of plants for planting. Environ Sci Policy 51: 228-237.

11. Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, et al. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Com 7:12485.

12. Gil L, Fuentes-Utrilla P, Soto A, Teresa Cervera M, Collada C. (2004). English elm is a 2,000-year-old Roman clone. Nature 431: 1053.

13. Liebhold AM, Griffin RL. (2016). The Legacy of Charles Marlatt and Efforts to Limit Plant Pest Invasions. Am Entomol 62:218-227.

14. Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO. (2012). Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front Ecol Environ 10:135–143

15. Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert, K,F, et al. (2016). Nonnative forest insects and pathogens in the United States: Impacts and policy options. Ecol App 26:1437-1455.

16. Marshall D, Work TT, Cavey J.F. (2003). Invasion pathways of Karnal bunt of wheat into the United States. Plant Dis. 87:999-1003.

17. Migliorini D, Ghelardini L, Tondini E, Luchi N, Santini A. (2015). The potential of symptomless potted plants for carrying invasive soil-borne plant pathogens. Divers Distrib 21:1218-1229.

18. Piperno DP. (2011). The Origins of Plant Cultivation and Domestication in the New World Tropics: Patterns, Process, and New Developments. Curr Anthropol 2011 52(S4), S453-S470

19. Roques A, Auger-Rozenberg MA, Blackburn TM, Garnas J, Pysek P, Rabitsch W, et al. (2016). Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. Biol Invasions 18:907-920

20. Sakalidis ML, Slippers B, Wingfield BD, Hardy GEStJ, Burgess TI. (2013). The challenge of understanding the origin, pathways and extent of fungal invasions: global populations of the *Neofusicoccum parvum–N. ribis* species complex. Divers Distrib, 19: 873–883.

21. Santini A, Ghelardini L, De Pace C, Desprez-Loustau ML, Capretti P, Chandelier A, et al. (2013). Biogeographical patterns and determinants of invasion by forest pathogens in Europe. New Phytol 197: 238–250

22. Stevens CJ, Murphy C, Roberts R, Lucas L, Silva F, Fuller DQ. (2016). Between China and South Asia: A Middle Asian corridor of crop dispersal and agricultural innovation in the Bronze Age, Holocene 26: 1541 – 1555

23. Stukenbrock EH, Banke S, McDonald BA. (2006). Global migration patterns in the fungal wheat pathogen *Phaeosphaeria nodorum*, Mol Ecol 15:2895–2904.

24. Waller MP. 2013. Drought, disease, defoliation and death: forest pathogens as agents of past vegetation change. J Quaternary Sci 28: 336–342.

25. Xu H, Ding H, Li M, Qiang S, Guo J, Han Z, et al. (2006). The distribution and economic losses of alien species invasion to China, Biol. Invasions 8:1495–1500.

Supplementary material
Plant hunters

The idea of importing exotic plants to "improve nature", embellish gardens, or for increased agricultural productivity is a concept that persisted for several centuries. The Egyptian Queen Hatshepsut of the Eighteen Dynasty, who reigned from 1478 to 1458 BCE, imported 31 live myrrh trees, from the Land of Punt (ancient Somalia) for planting in the courtyards of her mortuary temple complex (Tyler-Whittle, 1970).

It was during the 1800s CE that movement of plants among continents reached unprecedented levels. European colonies extended over vast areas in virtually every corner of the world. Also, the blossoming of European intellectualism motivated wealthy travellers to set out to collect and document exotic and previously unknown plant specimens (Fry, 2013). A turning point in the global spread of plants was the advent of "acclimatisation" societies, a trend initially starting in France and Britain but then spreading to the Americas and Oceania (Osborne, 2000). The central tenant of these groups was that natural environments could be vastly improved by establishment of non-native plant and animal species and that accomplishing this aim could be achieved via the gradual adaptation of species to new environments. It was noted that many imported species thrived in their new environment though the concept of invasive species and their associated damage had not yet been recognized.

In North America, a major player in the introduction of non-native plant species was the US Department of Agriculture (USDA). During the late 1800s, the USDA employed "plant explorers" to comb the world searching for plant species of potential use in agriculture, test-planting them in the US and distributing seeds to farmers (Griesbach, 2013). In 1911, one such USDA plant explorer, David Fairchild, arranged for a gift of 2,000 cherry trees from the people of Japan to be planted along the tidal basin, a prominent garden area in the center of Washington, DC; recognizing the beauty of flowering cherries, Fairchild believed that the planting would demonstrate their use in landscaping. But when the trees arrived from Japan, USDA entomologists and plant pathologists insisted on inspecting the trees, found them to be badly infected by crown gall disease and a variety of insect pests and ordered the entire shipment burned (Liebhold and Griffin, 2016). The following year, a new shipment of trees arrived from Japan with care taken to select clean specimens, they were planted and today the cherry trees are a classic attraction for tourists visiting Washington but they also represent the lurking dangers associated with importing plants.

Pathogen invasions and famines

Invasive pathogen species can be both a consequence and a cause of human migrations. Along with other early written records, the Torah, Bible and Kuran allude to catastrophic crop diseases, interpretable as rusts, mildews, blights, and blast that have caused famine and other drastic changes in the economies and social structures of Empires and nations since the dawn of recorded history. Examples of more recent plant disease outbreaks that trigged mass human migrations include late blight of potato in Ireland (1845–60), powdery and downy mildews of grape in France (1851 and 1878), coffee rust in Ceylon (beginning in the 1870s), Fusarium wilts of cotton and flax, southern bacterial wilt of tobacco (early 1900s), Sigatoka leaf spot and Panama disease of banana in Central America (1900–65), brown spot of rice in Bengal (1942-43), black stem rust of wheat (1916, 1935, 1953–54) and southern corn leaf blight (1970) in the United States.

In the early 1900s, the pathogenic fungus *Cryphonectria parasitica* (Murr.) Bar, causal agent of chestnut blight, was accidentally introduced with chestnut trees imported from Japan and planted in New York City. The disease ultimately drove the previously dominant forest tree, American chestnut, *Castanea dentata,* to near to extinction, and later impacted chestnut stands in Europe. The chestnut blight epidemic in the mountains of southern Europe aggravated food shortages for local human populations and increased migration to urban areas after World War II (Adua, 1999).

The Irish potato famine (1845-1852), resulting from the presence of favourable climatic conditions, which facilitated an epidemic wave of potato blight following the introduction into Europe of the causal Oomycete *Phytophthora infestans*, brought starvation, death, and mass emigration from Ireland. Out of a population of eight million in 1841, approximately one million died of starvation and 1.5 million emigrated, mostly to N. America. Many other regions in Western Europe were also badly affected by potato blight during this same period.

The Bengal rice famine of 1942-43 occurred as a result of unusual climatic conditions combined with the introduction of the plant pathogen *Bipolaris oryzae* (syn.: *Helminthosporium oryzae*) spreading on rice crops and ultimately destroying 50-90% of the most commonly planted rice varieties (Padmanabhan, 1973). The majority of the rural population in the region migrated to cities in the hope of finding employment and food. Finding neither, most slowly died of starvation (Padmanabhan, 1973). At roughtly the same time, Rwanda-Burundi experienced a major famine

(The Ruzagayura famine of 1943-44) initiated by unusually long dry periods in 1942, during which farmers switched to more drought tolerant crops, such as potatoes, cassava and sweet potatoes. In January 1943 an outbreak of *P. infestans* and *Rhizoctonia solani* destroyed the potato and sweet potato crops, leading to mass starvation resulting in large numbers of deaths and a huge population migration out of the territory (Singiza, 2011).

Even to date, rice blast destroys an amount of food that could sustain an estimated 60 million people each year (Ziegler et al. 1994). The 1975 introduction of the groundnut rosette virus pathogen to Africa has resulted in recurrent epidemics (15), seriously limiting groundnut (peanut) production with losses totalling £200 million per epidemic (Olorunju et al., 1992). Rice, maize, wheat and potato, currently provide over 60% of the world's food supply, but invasive plant diseases annually cause losses of 11–16% in these crops worldwide (Oerke, 2006).

In less developed countries where access to disease-control methods is limited, plant diseases commonly cause annual losses of 30 to 50% to major crops, often resulting in hunger and starvation (Meze-Hausken, 2000). In some years, losses can be much greater, with catastrophic consequences for those who depend on these crops for food and livelihoods. The lives of farmers living in many developing countries are strongly impacted by droughts and pest and disease impacts on agricultural output (Meze-Hausken, 2000). Food shortages, whatever their cause, often trigger famine and waves of migration.

Each of these examples of famine resulted from invasions by non-indigenous diseases, the causal agents of which were plant pathogens, either accidentally introduced with live plant stock or as a consequence of poor agricultural practices, such as the replacement of numerous locally adapted plant varieties with one or two high-yielding cultivars of a given crop in large contiguous areas which are more prone to attack by accidentally introduced pathogens (Swaminathan, 2010).

Literature

1. Adua M, (1999). The sweet chestnut throughout history from the Miocene to the Third Millennium. Acta Horticulturae 494: 29-36.
2. Fry C. (2013). The plant hunters. The University of Chicago Press, Chicago. Pp 63; illustrated. ISBN 9780226093314.

3. Griesbach RJ. (2013). 150 Years of Research at the United States Department of Agriculture: Plant Introduction and Breeding. U.S. Department of Agriculture, Agricultural Research Service, Washington, DC.

4. Liebhold AM, Griffin RL. (2016). The Legacy of Charles Marlatt and Efforts to Limit Plant Pest Invasions. American Entomologist 62: 218-227

5. Meze-Hausken E. (2000). Migration caused by climate change: how vulnerable are people in dryland areas? A Case-study in Northern Ethiopia. Mitigation and Adaptation Strategies for Global Change 5:379–406.

6. Oerke E-C. (2006). Crop losses to pests. Journal of Agricultural Science, 144, 31–43.

7. Olorunju PE, Kuhn CW, Demski JW et al. (1992). Inheritance of resistance in peanut to mixed infections of groundnut rosette virus (GRV) and groundnut rosette assistor virus and a single infection of GRV. Plant Disease, 76:95-100.

8. Osborne MA. (2000). Acclimatizing the world: a history of the paradigmatic colonial science. Osiris. 1:135-51.

9. Padmanabhan SY. (1973). The Great Bengal famine. Annual review of Phytopathology 11:11-24.

10. Singiza D. (2011). La Famine Ruzagayura (Rwanda, 1943-1944): causes, Conséquences et réactions des autorités (in French). Royal Museum of Central Africa, Teveuren (Belgium), 130pp.

11. Swaminathan MS. (2010). Achieving food security in times of crisis. New Biotechnology, 27: 453-460.

12. Tyler-Whittle M. (1970). The Plant hunters. Chilton Book Co., UK, 281 pages

13. Zeigler RS, Leong SA, Teng PS. (1994). Rice Blast Disease. In Rice Blast Disease, pp. 1-626. Cab International, Wallingford.

Table S1. Main famines in the last 200 years.

Country	Year	Name	Phytophthora infestans	Host
Ireland	1845-60	Late potato blight	*Phytophthora infestans*	Potato
France	1851-1878	Powdery and Downy mildew	*Erysiphe necator, Plasmopara viticola*	Grape
Ceylon	1870s	Coffee rust	*Hemileia vastatrix*	Coffee
Central America	early 1900s	Fusarium wilts of cotton and flax	*Fusarium oxysporum*	Cotton and Flax
Central America	early 1900s	Southern bacterial wilt of tobacco	*Ralstonia solanacearum*	Tobacco
Central America	1900-65	Sigatoka leaf spot	*Mycosphaerella musicola*	Banana
Central America	1900-65	Panama disease of banana	*Fusarium oxysporum*	Banana
Bengal	1942-43	Brown spot of rice	*Bipolaris oryzae*	Rice
Rwanda-Burundi	1942-43	Ruzagayura famine	*P. infestans, Rhizoctonia solani*	Potatoes, Cassava and Sweet potatoes
USA	1916, 1935, 1953–54	Black stem rust of wheat	*Puccinia graminis*	Wheat
USA	1970	Southern corn leaf blight	*Bipolaris maydis*	Corn
Africa	1975	Groundnut rosette virus	Groundnut rosette virus (GRV)	Groundnut (peanut)