The Consequence of Tree Pests and Diseases for Ecosystem Services

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I. L. Boyd *et al.*

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REVIEW SUMMARY

The Consequence of Tree Pests and Diseases for Ecosystem Services

I. L. Boyd,* P. H. Freer-Smith, C. A. Gilligan, H. C. J. Godfray

Background: Trees are major components of many terrestrial ecosystems and are grown in managed plantations and orchards to provide a variety of economically important products, including timber, pulp, fiber, and food. They are subject to a wide range of pests and diseases, of which the most important causative agents are viruses, bacteria, fungi, oomycetes, and insect herbivores. Research on tree pests and diseases has had a historical focus on trees of direct economic importance. However, some epidemics and infestations have damaged and killed common trees that are integral parts of natural ecosystems. These have harmed valuable landscapes and highlighted the wide-ranging consequences arising from tree pests and diseases. There is also growing concern that aspects of globalization—in particular, higher volumes and new forms of trade—may increase the risk of disease spread.

Advances: We review the challenges in maintaining tree health in natural and managed ecosystems. It is argued that it is helpful to consider explicitly the consequences of pests and diseases for the full range of ecosystem services provided by trees. In addition to forest and orchard products, tree pests and diseases can affect the ability of forests to sequester and store carbon, reduce flood risk, and purify water. They can affect the biodiversity supported by trees and the recreational and cultural values accorded to woodland by people. Many of these benefits are uncosted and enjoyed by different classes of stakeholders, which raises difficult questions about who should be responsible for measures to protect tree health. Changes in the risk of pest and disease introduction, the increasing prevalence of genetic reassortment leading to novel disease threats, and the potential role of climate change are all highlighted.

Outlook: Modern pest and disease management is based on an extensive science base that is rapidly developing, spurred in particular by modern molecular technologies. A research priority is to build a better understanding of why certain pathogens and insects become major pests and diseases. This will involve a better understanding of the molecular basis of pathogenicity and herbivory, as will ecological insights into why some species reach epidemic prevalence or abundance. It will also help anticipate which species may become a problem if they are transported to new geographical regions, recombine with other organisms, or experience new climatic conditions. However, identifying all species that may become pests will be impossible, and the Review stresses the importance of risk management at the "pathway of introduction" level, especially when modern trade practices provide potential new routes of entry. Last, when ecosystem services are provided by woods and forests rather than individual tree species, we need to understand better the consequences of pests and diseases that attack or feed on particular species.

READ THE FULL ARTICLE ONLINE
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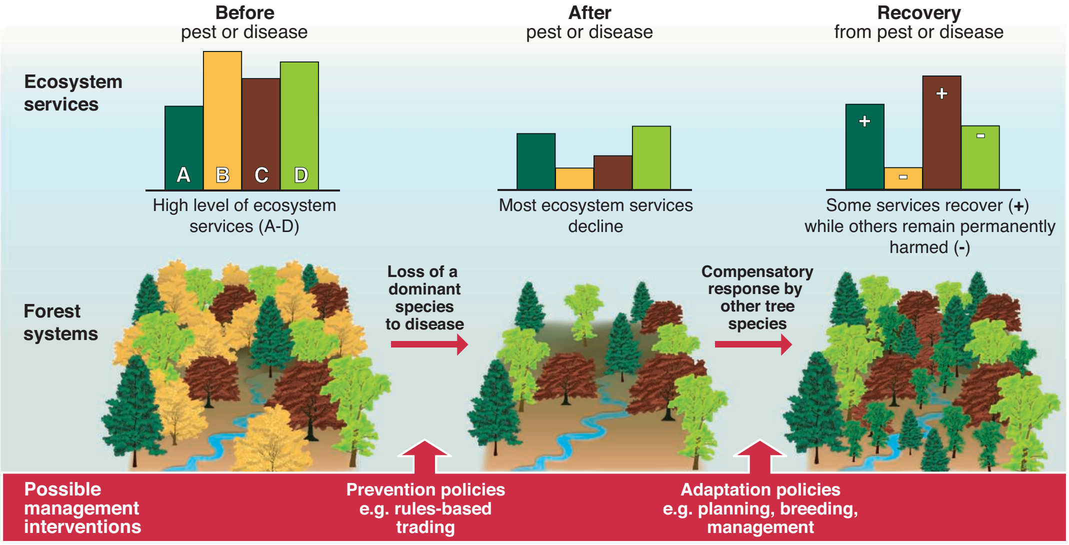
ARTICLE OUTLINE

SUPPLEMENTARY MATERIALS

Supplementary Text
References

A forest providing numerous ecosystem services is subject to a disease epidemic that reduces the abundance of a dominant native species, resulting in a change in forest structure. Initially, a wide range of ecosystem services (**A** to **D**) are harmed. But as trees grow to replace lost species, some (perhaps carbon storage or water purification) are regained, whereas others (perhaps the biodiversity supported by the diseased tree species) are permanently disrupted. Policy measures can both help prevent new diseases being introduced (the first stage) or improve recovery through management practices or planting resistant trees.



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The Consequence of Tree Pests and Diseases for Ecosystem Services

I. L. Boyd,[1]* P. H. Freer-Smith,[2] C. A. Gilligan,[3] H. C. J. Godfray[4]

Trees and forests provide a wide variety of ecosystem services in addition to timber, food, and other provisioning services. New approaches to pest and disease management are needed that take into account these multiple services and the different stakeholders they benefit, as well as the likelihood of greater threats in the future resulting from globalization and climate change. These considerations will affect priorities for both basic and applied research and how trade and phytosanitary regulations are formulated.

Trees support a broad array of organisms that feed on or infect them. When these herbivores or infections are perceived to reduce the value of trees to people, they are termed pests and diseases (*1*, *2*). Recent examples of the near extermination of common tree species over large geographical areas—including that of the American chestnut (*Castanea dentata*) in North America because of chestnut blight (*3*) and elms (*Ulmus* spp.) in Europe and North America because of Dutch elm disease (*4*)—have highlighted the vulnerability of trees to disease and our lack of preparedness to deal with these threats. Current trends in pest and disease outbreaks suggest that greater vigilance and new approaches may be needed.

The management of pests and diseases has historically been concerned with species grown for wood and pulp, for fruit and other food, and to a lesser extent, for their arboricultural and amenity value. Reduction of the direct economic harm of tree pests and disease will continue to be very important, but there is an increasing understanding that trees provide additional benefits to society. Trees can be thought of as key components of natural or artificial ecosystems that provide a wide variety of different ecosystem services (*5*, *6*). Explicit consideration of how pests and diseases affect the multiple services provided by trees can change both research priorities and management strategies (Fig. 1) (*7*).

In this Review, we explore how pests and diseases influence the range of services provided by trees and look at how future trends such as increasing trade and climate change may interact with pests and diseases to affect the benefits we obtain from trees. We use the terms "pest" and "disease" to describe all pathogens and small- to medium-size herbivores that—by causing death, morbidity, or other harm—disrupt the ecosystem services provided by trees. We ask in particular whether the way we research and manage tree pests and diseases, with its historical preoccupation with tree products, is best placed to protect the multiple services we require from trees.

The Pests and Diseases of Trees

Trees are attacked by a wide range of pathogens, including bacteria (*8*), helminths (*9*), viruses (*10*), and many fungi and oomycetes (*11*). Insects and other invertebrates attack all parts of the plant, with defoliators and borers causing most direct damage; other insects may be more evident as disease vectors (*8*, *12*). An illustrated account of some of the most important tree natural enemies is provided in Fig. 2 and the supplementary materials. Pests and pathogens can also interact; for example, trees suffering defoliation by an insect pest are typically more vulnerable to systemic pathogens (*10*). Pest and disease problems may be caused by native organisms attacking native trees, although many of the most pernicious threats arise from introduced species feeding on or infecting trees outside their native range.

In the past 50 years, there have been several major pathogen outbreaks that have drastically reduced the densities of particular tree species. Widespread diebacks have alarmed the public and raised tree health higher on the policy agenda. The most important of these pathogens have been fungi and oomycetes (water molds); the latter are curious organisms once classified as fungi but now recognized as distant relatives of diatoms and algae. The most damaging bacterial disease of trees is probably Citrus greening or huanglongbing caused by *Candidatus Liberibacter asiaticus*, which although of Asian origin is now present in many countries worldwide. The disease was largely ignored until its introduction to the Americas and it is now a substantial challenge in newly infected citrus production areas (*13*). Pine wilt is a problem caused by the nematode *Bursaphelenchus xylophilus*, which is spread by *Monochamus* beetles and with the movement of infested wood. Its native range covers much of Canada, the United States, and Mexico, where it does not kill trees, but it is now present in China, Japan, Korea, Taiwan, and Portugal, where it is causing substantial losses of susceptible trees, especially pines (*9*).

Fungi are behind the devastation of the American chestnut (*Castanea dentata)* in eastern North American forests. The introduced fungus *Cryphonectria parasitica* (chestnut blight) led to a decline in the frequency of this iconic tree from 36% in 1934 to 0.5% in 1993 and its replacement by oak, maple, and hemlock species (*14*, *15*). Dutch elm disease is also a fungal pathogen (*Ophiostoma novo-ulmi*) and is transmitted by bark beetles; it has eliminated mature elms (*Ulmus* spp.) from European and North American landscapes from the late 1960s (*4*, *15*). Today, there is intense concern that another major European tree species, ash (*Fraxinus excelsior*), could suffer a similar fate as an emergent fungal pathogen (*Chalara fraxinea*), first observed to kill trees in Poland in the 1990s, inexorably increases its geographic range (*16*).

The most notable oomycetes are species of *Phytophthora*, which cause disease in both trees and other plants (they include the pathogen responsible for the Irish potato famine). The introduction of *Phytophthora cinnamomi* to Western Australia caused dieback of Jarrah (*Eucalyptus marinata*) over an area of 282,000 ha. *Phytophthora* spp. often have broad host ranges, and in addition to Jarrah, plants in 34 other genera have also been killed by *P. cinnamoni* in Australia (*17*). *Phytophthora ramorum* is another species with a broad host range (*18*). It was probably introduced into North America and Europe from Asia and leads to sudden oak death in the United States (*19*), although in the UK, it unexpectedly causes most problems as a disease of Japanese larch (*Larix kaempferi*).

Insects can also be major tree pests. For example, Asian longhorn beetle (*Anoplophora glabripennis*) is a wood-boring insect that has spread in packaging material from southeast Asia to the United States, Canada, and Europe, with devastating consequences for indigenous broadleaved trees in several countries (*20*). Oak processionary moth (*Thaumetopoea processionea*) is an invasive tree defoliator that can cause local defoliation of oak (*Quercus* spp.), although it is of greater concern because the urticarial hairs shed by its larvae are a threat to human health (*21*). Recent infestations of bark beetles and defoliating insects in North America have been more intense than at any time in recorded history (*22*, *23*). Mountain pine beetle (*Dendroctonus ponderosae*) has a wide tree host range, and outbreaks occur when the beetle experiences several years of favorable weather (*23*). Over 1 million ha of western yellow pine (*Pinus ponderosa*) and 1.5 million ha of piñon pine (*Pinus edulis*) have been killed on the Colorado Plateau and central Rocky Mountains, and over 37 million ha of forest are likely to be affected in British Columbia between 2000 and 2020 (*24*). Emerald ash borer (*Agrilus planipennis*), an insect pest introduced from Asia, is a further threat to ash species in addition to ash dieback in North America and Europe (*7*, *25*).

Tree Health and Ecosystem Services

Thinking about pests and diseases in terms of ecosystem services highlights potential risks that might otherwise be overlooked and reveals who

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benefits from improved tree health and hence who might be expected or required to invest in pest and disease management. A simple classification of the ecosystem services provided by trees includes the direct products used by man (provisioning services), the indirect benefits that occur through modification of the environment (regulating services), and improved human well-being (cultural services).

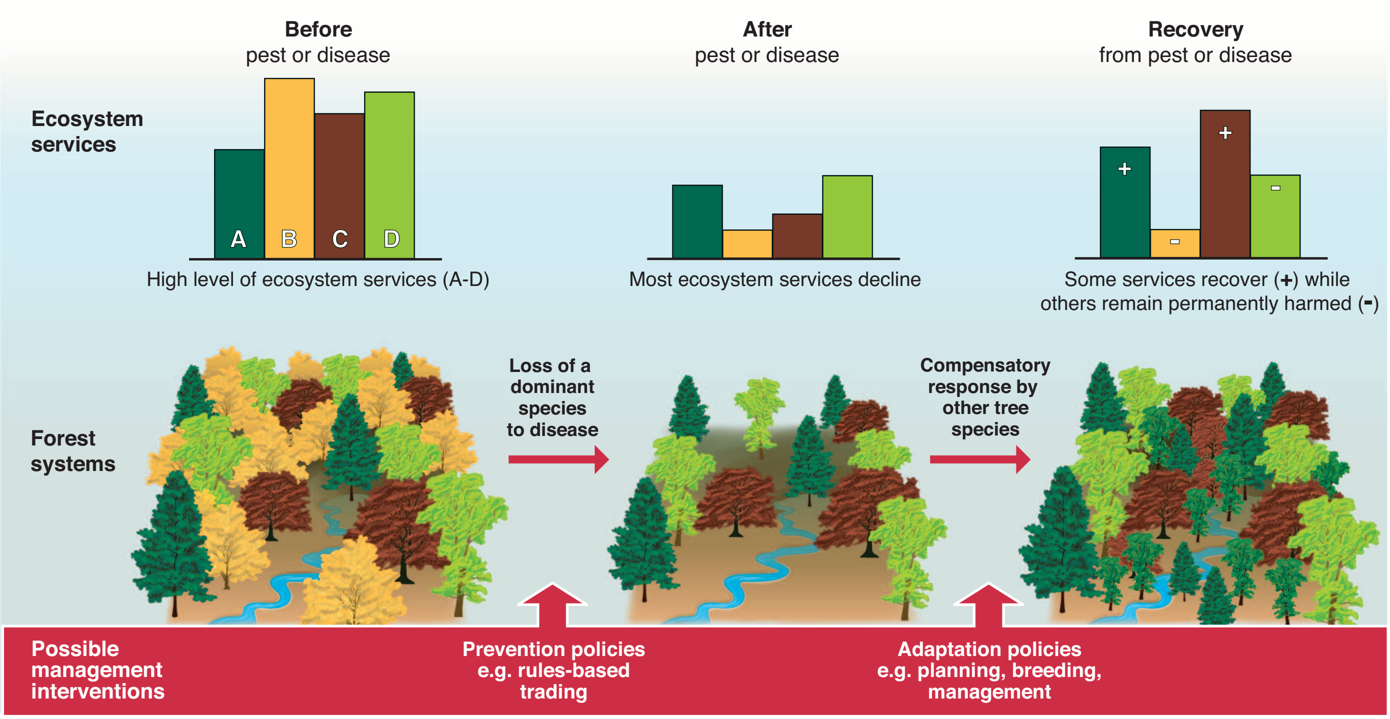

Fig. 1. A forest providing numerous ecosystem services is subject to a disease epidemic that reduces the abundance of a dominant native species, resulting in a change in forest structure. Initially, a wide range of ecosystem services (**A** to **D**) are harmed. But as trees grow to replace lost species, some (perhaps carbon storage or water purification) are regained, whereas others are permanently disrupted (perhaps the biodiversity supported by the diseased tree species). Policy measures can both help prevent new diseases being introduced (the first stage) or improve recovery through management practices or planting resistant trees.

Fig. 2. Tree pests and pathogens. In recent years, landscape-scale pest and pathogen problems have drawn attention to the potential threat to trees and forest ecosystems globally. Examples include (**A**) Chestnut blight caused by the fungus (*Cryphonectria parasitica*, top left) on American chestnut (*Castanea dentata*) (bottom left), and European chestnut (*C. sativa*) in Slovakia (main image); (**B**) the oomycete *Phytophthora cinnamomi* (inset) causing mortality in a 4-year-old plantation of sand pine (*Pinus clausa*) in the United States; and (**C**) the mountain pine beetle *Dendroctonus ponderosae* (inset) infesting a lodgepole pine (*Pinus contorta*) plantation in Canada. Illustrated accounts of major tree diseases and outbreaks caused by bacteria, helminths, oomycetes, bark beetles, boring insects and phloem feeders are provided in the supplementary materials. [Photos provided by E. Bush, Virginia Polytechnic Institute and State University; E. L. Barnard, Florida Department of Agriculture and Customer Services; J. O'Brien, U.S. Department of Agriculture (USDA) Forest Services; A. Kunca, National Forest Centre, Slovakia; USDA Forest Service, Region 2, Rocky Mountain Region Archive and R. F. Billings, Texas Forest Service, respectively; all from www.bugwood.org. Top left image, Biodisc/Visuals Unlimited.]

Much of the historical focus on tree pests and diseases has been on the damage they do to provisioning services (*1*, *2*): to timber and pulp or to fruit, nuts, and vegetable oil. Forest products alone are estimated to be worth ~$120 billion annually (*26*). Because many biotic threats cannot be controlled at the level of the individual landholding, state authorities become involved in regulating trade, setting biosanitary standards, and providing information and training to reduce risk. Although it was long assumed in most countries that the state had a direct role in subsidizing provisioning services in agriculture and forestry, many nations now seek to shift the burden to those that benefit financially, a move naturally resisted by industry. Debates about where the balance of responsibility should lie between the different beneficiaries and public good (*27*, *28*) can be very complex. For example, in many countries there is a thriving industry importing saplings, but if this results in the introduction of a new pest or disease, the cost is largely borne not by the industry but by foresters and farmers (*2*). At the international level, a balance has to be struck between the rights of nations to restrict the spread of agents that will harm their tree-based industries and ecosystems and the risk of this being used as a barrier to free trade.

From a societal point of view, major tree health problems reduce the flow of a particular product—pine bark beetles affect the availability of pine wood, for example—leading to a price response. However, in most cases one type of timber or food type can substitute for another without great disruption, especially in a global marketplace, again underlining the point that for provisioning resources, it is the farmer or forester that suffers most in cases of poor tree health. However, forests are a particular asset class with a very delayed return on investment, and the concern that market mechanisms may not always secure long-time supply of forest products (and associated rural economic activity) has led to arguments for state involvement.

Because of the longevity of tree species, threats to tree health are of particular economic importance to provisioning service providers, such as farmers and forest owners, because long-term investment is threatened and it takes time to replace a damaged or destroyed tree. Society may take a view that to encourage assured supply of timber and other tree resources (or associated rural livelihoods), it may want to absorb some component of this risk in order to increase the attractiveness of investing in forestry.

Trees dominate many landscapes and have a major effect on the regulating services provided by these ecosystems. These services include climate regulation, carbon storage (*29*–*31*), carbon sequestration [~30% of global CO_2 emissions are taken up by forests (*32*)], flood control, and water purification (*33*, *34*). The forests and woodlands that provide these services contain individual tree species that typically are the targets of specific pests and diseases. In diverse natural forests, the loss or dramatic reduction in density of one species may be readily compensated by other species filling the gap (*14*, *35*), as was seen by the replacement of American chestnut by other trees after the chestnut blight epidemic. The net effect on carbon stocks or other ecosystem services such as water management may thus be small, although regulating services may be affected during the transition period. The degree to which the functional integrity of the ecosystem is resilient to pests and disease may differ from one place to another. Some North American forests are dominated by foundation or keystone species whose loss to pests and diseases can fundamentally alter the value of the ecosystem services provided by forests (*36*, *37*). For example, much of the northern boreal zone is of low diversity and hence probably reduced functional redundancy, and here a threat to an individual species may have much more impact (*26*, *38*).

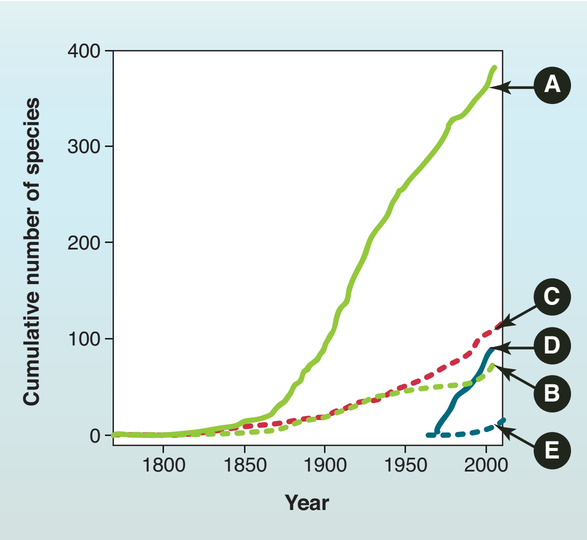

Fig. 3. A composite representation of the increasing number of pests and pathogens affecting different regions. Solid lines indicate the number of introduced species, and dashed lines indicate the number of pests and/or pathogens. Common colors indicate the same geographical region (green, United States; red, Europe; blue, United Kingdom or Great Britain). (**A**) Cumulative number of nonnative insects introduced and found in association with trees to the United States during 1800 to 2006 (*90*). (**B**) Cumulative number of "high-impact" nonnative tree insect pests and pathogens introduced to the United States during 1800 to 2006 (*90*). (**C**) Cumulative number of nonnative tree pathogens introduced to Europe during 1800 to 2009 (*57*). (**D**) Cumulative number of nonnative invertebrates introduced to Great Britain during 1970 to 2004 (*91*). (**E**) Cumulative number tree pests and pathogens introduced to the UK during 1965 to 2012 (*92*). Additional information about the data sources is provided in the supplementary materials.

This Review has excluded discussion of large mammalian herbivores, but their greater polyphagy (deer eat most young saplings) or role as ecosystem engineers (for example, beavers) mean they have a potentially much larger effect on regulating services than do most other pests and diseases.

In many areas of the world, humans largely determine the distribution of forest and woodland. However, pests and diseases can affect regulating services indirectly by influencing land-use decisions. This could happen by reducing the perceived economic returns from forests (including through increased financial risk of return on investment) or by reducing the societal desirability of woodlands.

Regulating services can benefit the landowner (for example, flood control), the region (for example, water management), or everyone (for example, carbon sequestration). Thus, who should pay to reduce the threat from pests and diseases is complex and context-specific and may depend on the scale over which benefits are provided.

Trees and forests are of enormous importance for individuals who cherish particular landscapes, tree species, tree-dominated parks and cityscapes, and even individual trees (*1*, *39*). Attempts to ascribe an economic value to these cultural services are fraught with difficulties. For example, the value of identical woodlands may depend on their proximity to a city or be influenced by an individual's sociocultural background and economic circumstances (*40*, *41*). The mere act of assigning value can influence how a resource is regarded by society, and some have argued for a more explicit ethical, values-driven approach to decisions of this type (*42*).

Tree pests and diseases affect cultural services in different ways (*43*). As with regulating services, we need to understand how a reduction in tree health affects the value placed on these resources—for example, on the importance of woodland and forests to society. This again is complex because it may include how enjoyment of landscapes is transiently affected by the presence of tree pests and diseases. Some of the greatest harm to cultural services occurs when iconic species are severely affected by disease, as noted already for chestnut blight and Dutch elm disease. One concern about the spread of the oak processionary moth is that its larvae's urticarial hairs will affect the amenity value of woodland.

It is often not straightforward to predict which threats to trees will elicit the greatest concern in the general public. The nonmonetary nature of cultural services means it is difficult to track their value, and this can lead to unexpected and apparently rapid shifts in the public value placed on them. Social amplification is a term used to describe dramatic switches in public concern, often caused by positive feedback through new and old media (*44*). Such events can greatly increase the pressure on policy-makers to respond to threats to cultural services (*45*). The nonmonetary nature of most cultural services clearly places a duty on the state to underpin their protection, although other sectors are also involved. In high-income countries, for example, civil society and nongovernmental organizations play a role in protecting forested areas, whereas private individuals owning trees in gardens, as well as the horticultural sector that supports them, have major interests in tree health.

Trees and forests also provide supporting services for other ecosystem components. In particular, they are home to many species of plants and animals that may themselves constitute provisioning services (such as wild honey bees or harvested animals), regulating services (pollinators or the natural enemies of pests), or cultural services [a major fraction of the earth's biodiversity lives in forests, particularly tropical forests (*46*–*48*)]. There are disservices (*49*) as well as services: Forest elephants and deer can cause economic damage in surrounding farmland, and sylvan mosquitoes spread malaria in the Brazilian Amazon (*50*). Some insect herbivores damage both trees and human health through shedding urticarial hairs, or the loss of trees can be associated with increased risk to health (*51*). Native nonpest herbivores that rely on specific tree species are especially vulnerable to disease of their host species; for example, the loss of mature elms in Europe has dramatically decreased the abundance of the white-letter hairstreak butterfly *Satyrium w-album*, which feeds only on this host plant (*52*).

Global Change and Tree Pests and Diseases

Globalization and Pest and Disease Movement

People have moved trees beyond their native range since at least the beginning of agriculture, and international trade has increased greatly over recent decades (*53*). The threat presented by pests and pathogens can be represented by the number of new species of potential pests and pathogens being imported, whether or not they end up becoming pests or causing disease. Based on experience from Great Britain and the United States, there is an apparent constant rate of ingress of new forest invertebrate species (Fig. 3; line A compared with line D), and a similar trend exists for Europe and Africa (*54*). The constant rates illustrated by these data suggest that plant health inspection regimes could be keeping pace with the increased threats from increasing volumes of trade (*55*, *56*).

However, not all of these species cause harm. In contrast to the steady ingress of species that threaten to cause infestations or diseases, there has been a recent acceleration in the occurrence of harmful pests and pathogens in the United States (Fig. 3, line B), Europe (Fig. 3, line C), and the UK (Fig. 3, line E). Santini *et al.* (*57*) found that at least 68% of harmful pathogens introduced to Europe have been assisted in some way by trade. It is also possible that a further proportion of those that have unknown routes of entry (22%) are connected to trade because not all forms of trade can be monitored effectively. This acceleration in the appearance of damaging infestations and disease, especially in recent years, is a cause for concern, and it is not clear why this pattern differs from the relatively constant rate of importation of new species. One possible conclusion is that an increasing proportion of the species that are imported are causing infestations or disease.

Globalization and Genetic Reassortment

Species that may be commensals or only mildly pathogenic within their original tree hosts can become pests or pathogens when moved elsewhere. In some cases, especially among pathogens, new

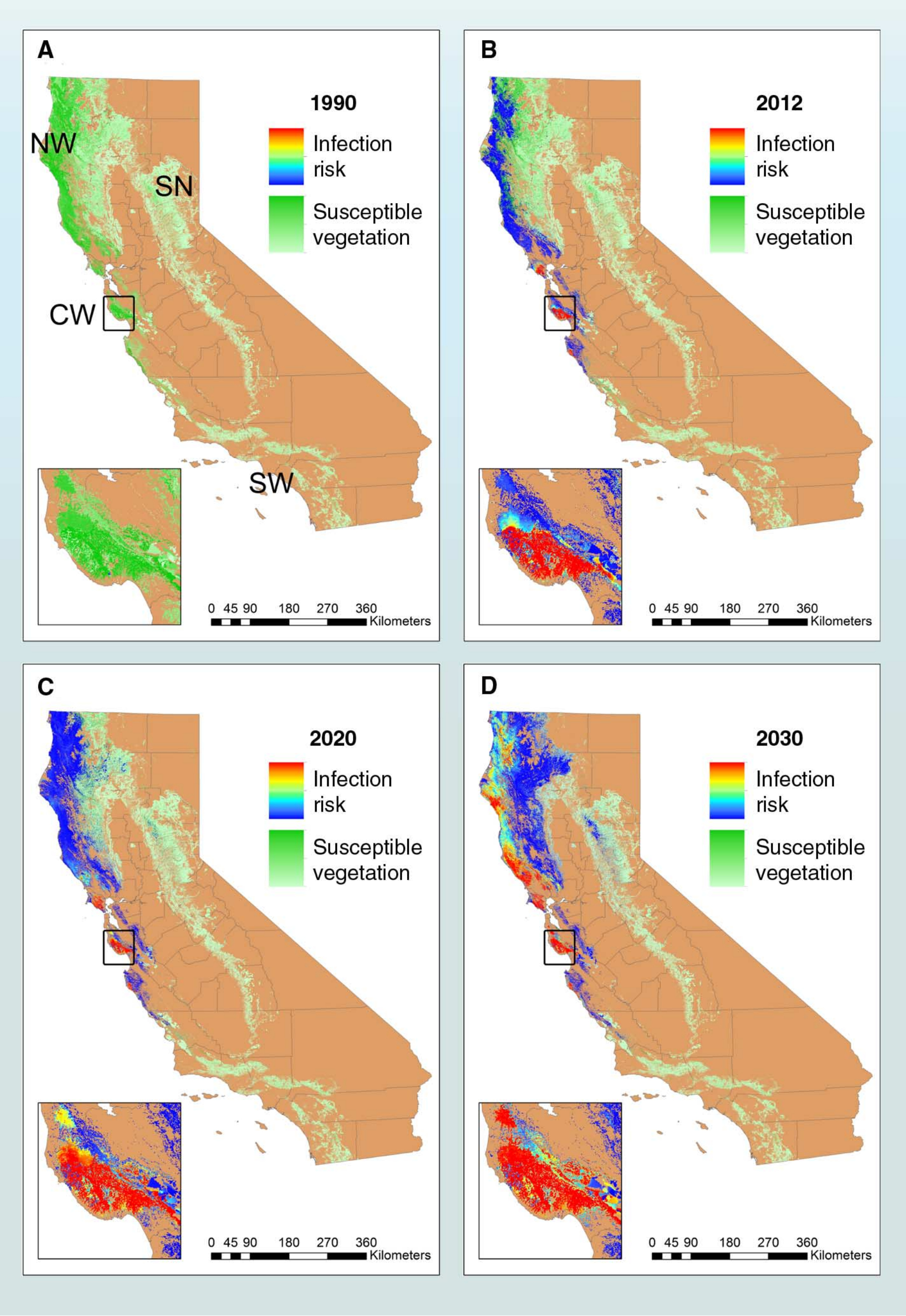

Fig. 4. Predicted spread of sudden oak death (SOD). Shown is from 1990 (putative date of introduction to the San Francisco Bay area) to 2030 in California by using a stochastic, spatially explicit epidemiological model (*79*). The model used two scales of dispersal, involving local spread (~0.1 to 3 km) of *P. ramorum* by spores in rain and wind (*80*) coupled with long-distance movement (~3 to 100 km). Despite its name, SOD has a wide host range (>50 woody species). (**A**) The distribution of susceptible vegetation in California. (**B** to **D**) Model predictions for the risk of spread.

diseases can arise spontaneously because of genetic change in the infecting species. Further problems occur when introduced species escape their own natural enemies or encounter hosts that have no evolved resistance mechanisms.

Several tree diseases have arisen from introduced species that hybridized with or acquired genes from resident species. For example, when the causal agent of Dutch elm disease, *O. novo-ulmi*, spread across the northern hemisphere, it acquired major genes through hybridization with the native species *O. ulmi*. This gene transfer probably prevented the attenuation of infection in elms by *O. novo-ulmi*, which proved to be a very damaging pathogen (*58*). In addition, many invasive pathogens may initially arrive as a single genotype or clone, and sometimes the invasive clone has been a single mating or compatibility type. Some genotypes are more aggressive pathogens than others (*11*), and the presence of compatible mating types and occurrence of sexual reproduction increases the opportunity for the development of pathogenicity. Examples include *Phytophthora cinnamomi*, *P. ramorum*, and *Dothistroma septosporum* (a fungus that causes needle blight on conifers). Genetic reassortment allows introduced pathogens to acquire specific virulence factors that enable them to colonize native hosts. But, genetic exchange may also be facilitated when the nursery trade brings together numerous species and their pathogens in close proximity. The highly aggressive *Phytophthora* of alder arose out of a swarm of new interspecific hybrids, and the spread of the new aggressive subspecies *P. alni* subsp. *Alni* along Bavarian rivers was associated with infested alder nursery stock (*11*).

Outside of the major pathogens of commercial trees, we still know relatively little about the diversity of tree pathogens in the field, and frequently a poor understanding of their taxonomy is an impediment to their study. Molecular phylogenetics have allowed the geographic and evolutionary origins of a number of fungal pathogens to be identified (*11*), but taxonomic uncertainty can still be a problem in the diagnosis and response to new diseases. In 2006, the causal agent of ash dieback in Europe, the fungus *Chalara fraxinea*, was wrongly identified as the asexual form of an indigenous saprotrophic fungus, *Hymenoscyphus albidus* (in fungi, sexual and asexual forms of the same species can be given different Linnean binomials, and the asexual form of *C. fraxinea* is now known as *Hymenoscyphus pseudoalbidus*) (*59*). This meant that it was not designated as a controlled organism, and trade in ash was allowed to continue (*60*).

Insect pests can also adapt to new hosts but are less likely to hybridize and acquire new genes. However, many rely on bacterial symbionts, and the acquisition of new associates can give rise to tree disease. The scolytid beetle *Dendroctonus valens* has recently colonized China, where it has acquired novel indigenous isolates of its fungal associate *Leptographium procerum* (*61*). The new symbiosis increases the severity of the pest, partly because the fungus releases volatiles that attract further beetles that help to overwhelm the tree's defenses.

Climate Change

Climate change may influence the susceptibility of trees to pest and disease, which in turn may affect forest ecosystem services such as the regulation of carbon and water cycles (*32*–*34*). Pest and disease outbreaks are often triggered by abiotic stress that weakens trees (*1*), and because climate change is predicted to increase the frequency of drought, flooding, severe gales, and extreme temperature events, it is reasonable to expect more frequent outbreaks. The northern boreal forests of North America are typically carbon sinks but can become sources when severe pest infestations occur (*24*, *62*, *63*), contributing to a positive feedback. Climate warming is possibly the major proximate driver of changes in cover in boreal forests (*64*–*66*), and pests or pathogens are likely to be an important ultimate factor determining tree growth and survival.

There is evidence that climate warming has already resulted in increased tree mortality from disease in boreal Alaska (*66*), where the area damaged by pests and pathogens exceeds that affected by fire (*67*). Spruce beetle outbreaks (*Dendroctonus rufipennis*) occur in Alaska at ~50-year intervals but have increased in frequency and extent in recent years, possibly because of shorter beetle life cycles in a warmer environment (*65*, *68*). Insects such as the mountain pine beetle (*D. ponderosae*) kill large discrete patches of trees and are a major driver of forest disturbance dynamics (*69*). This is a natural element of boreal forest ecology (*70*, *71*) but might make forests more susceptible to the effects of increased fire and wind damage due to a changing climate (*24*).

There is most likely a reporting bias toward the negative effects involving climate change and pests and diseases. Some effects of climate change may be positive. For example, pest insects can overwinter beneath an insulating blanket of snow, and reduced snow cover can increase their exposure to low temperatures, causing the insects to die (*1*). Greater disturbance and hence more dead wood can be positive for those components of biodiversity that require this resource (often rare in managed forests when dead wood is removed). More sophisticated integrated assessments are needed that capture the many different consequences of climate warming in order to understand how the ecosystem services provided by forests will change over the coming decades (*38*).

Priorities for the Future

Research

Parasites and herbivores are both components of natural ecological communities and have the potential to become outbreak pathogens and pests, respectively. Despite substantial advances, there is still much we do not know about tree antagonists in natural communities, including their role in maintaining community diversity (*46*, *72*–*74*), which may be important for the delivery of ecosystem services. Only a small fraction of the many diseases and herbivores affecting any tree species cause major harm to tree health. A better understanding of the natural regulation of herbivores and pathogens and under which circumstances this relationship breaks down and results in the emergence of pest and disease would help improve the management of these threats (*24*, *75*, *76*). Many of the most important recent emergent diseases, as well as some insect pests, have switched to feed on new host plants. Understanding the precise molecular mechanisms that allow successful host plant infection by a pathogen, or that lead an insect to recognize a particular plant species as food, are currently major research themes, with progress greatly facilitated by advances in genomics and other areas of molecular biology (*11*, *77*).

The ability to predict the spatial spread of pests and diseases, especially introduced or emerging species, is critical in managing their damage. The connectivity of the susceptible host population is important in determining the rate and extent of local spread by tree pathogens (*78*). However, many plant pathogens are capable of long-distance dispersal. Daughter foci can occur well ahead of the major region of an invasion, as in the case of the isolated outbreaks of *P. ramorum* in Northern California and Oregon that appeared beyond the main regions of sudden oak death in the central coastal regions of California (*79*). One of the principal challenges in the epidemiology of tree diseases is to characterize dispersal kernels and transmission rates for emerging pathogens, often from limited data such as aerial photographs (*80*) or remote sensing.

Epidemiological modeling can combine an understanding of the disease process with meteorological and detailed geographic data to help predict spread and the optimal design of surveillance programs (Fig. 4). These models can provide generalized predictions of disease spread based on fitting the models to data of historical spread (*81*). The case of sudden oak death in California (Fig. 4) illustrates predicted heterogeneous spread within different regions that reflect interactions of environmental conditions, the density and contiguity of susceptible host vegetation, and the inherent epidemiological scales of dispersal. Outputs from models such as this can be used to help optimize sampling strategies so as to detect disease spread, inform management strategies (*79*, *80*), and predict effects on ecosystem services (*19*).

The longevity of trees and the delay before they reproduce has always been a hindrance to breeding for disease resistance. Today, some of these problems can be mitigated by use of modern genetic techniques, such as marker-assisted selection, which should save several years by allowing rapid identification of resistant genotypes for breeding. The development of resistant hybrids has also proved effective, such as in the case of forest restoration of American chestnut (*3*). However, in *C. dentata* a number of candidate genes for host resistance to chestnut blight fungus (*C. parasitica*) have been identified (*77*), and as for other tree species, understanding the molecular basis of resistance will facilitate the breeding of resistant genotypes. As the full genome sequences of trees become available, progress is likely to accelerate, as will the opportunities to capitalize on genetic modification in countries that permit this technology.

Management

There is considerable scope for both technical and organizational innovation in controlling the spread of tree disease. Risk-based approaches are at the center of the management of tree disease (*82*, *83*) and are governed globally through the World Trade Organization Sanitary and Phytosanitary (WTO SPS) agreement and the International Plant Protection Convention. Regional plant protection organizations (such as the European and Mediterranean Plant Protection Organization) coordinate regional activities. Adoption of risk-based approaches means the acceptance that measures to prevent incursions are implemented in a manner that is proportionate to the severity and likelihood of the hazard. At the moment, however, most assessments of risk focus on direct economic damage to provisioning services rather than on the broader set of ecosystem services explored above. Assessment of risk needs to consider the full range of ecosystem services provided by different host species, including nonmonetary cultural services and their role in supporting other biodiversity. It is also important for all parties to communicate a balanced and realistic assessment of the likely risks of incursions of tree pests and diseases so as to avoid disproportionate public concern (*44*) when infestations do occur.

Current plant health regimes are mainly based on pest risk assessments (PRAs) and control measures against identified, listed organisms, but it is impossible to identify all potential pathogens and to develop risk-based approaches to deal with each on an individual basis. A better approach is to identify different classes of threat defined by (i) type of disease-causing agent (for example, fungal pathogen or insect defoliator); (ii) pathways of movement (for example, natural pathways such as wind, water, animal or man-made pathways, including shipping containers, wood imports, dunnage, and bulk cargos); and (iii) the type of ecosystem service at threat (for example, a tree species valuable for its timber, its keystone role in natural forest, or its conservation importance). It is also critical to anticipate new pathways that may emerge through changing patterns in global trade and the adoption of new technology. For example, recent trends such as the use of containers and refrigeration, the use of wood products as bulk packaging material, as well as the trade in rooted plants in pots with soil provide new potential entry pathways (*55*). In our view, the implementation of voluntary and regulatory measures to address these new pathways has nearly always happened after the fact and are often inadequate.

Biological control—the deliberate release of another organism to control a pest or disease—has had a mixed history for tree pests (*84*) and in managed forests and plantations has to be applied within the context of integrated pest management (*85*). A typical situation in which biological control can be very successful is when a tree is being grown outside its native distribution and an insect from its original range is introduced and becomes a pest. Often, the pest is only an issue because it has escaped its own natural enemies, and their deliberate introduction can solve the problem. Introduction of the Australian predatory Vedalia beetle (*Rodolia cardinalis*) in the late 1800s probably saved the Californian citrus industry, which was being ravaged by a scale insect on which the beetle fed (*86*). The next two decades are likely to see the development of radical new forms of genetics-based biological control: genes that can spread through targeted pest or disease populations despite imposing fitness costs, leading to population suppression (*87*). Whether such approaches will be acceptable to civil society is not yet clear.

Last, increasing resilience to pests and diseases should be a key management goal to help maintain the ecosystem services provided by trees. In orchards and commercial plantations, this is likely to involve greater emphasis on genetic diversity, a move that will be helped by a better understanding of the molecular basis of resistance. For mixed use, amenity, and restored forest, this will require the careful choice of species composition, and for planted forests, improved management practices will be required to restore specific ecosystem services (*88*, *89*). These methods need to be extended to include resilience to possible interactions between climate change and pests and diseases.

Conclusions

There is rising concern that the increase in tree pests and diseases is one of the most tangible manifestations of increasing anthropogenic stresses on life systems. This concern is built on growing evidence that trees, forests, and woodlands are essential parts of sustainable, productive, and safe environments. Trade is an integral part of a modern, globalized economy but, if unregulated, has potentially severe costs for some of the most important ecosystem services involving trees. The evidence suggests that there is likely to be no reduction in this pressure. Although quantifying this cost is likely to be an active research field in the near future, we already know enough to justify substantial investment in novel and practical forms of mitigation. But, science can provide only part of the solution. Policy-makers and civil society need to understand the very many benefits that trees provide beyond timber, fuel, and food and develop and implement evidence-based policies to protect this invaluable component of our natural capital from the extra burdens of pests and diseases to which they are increasingly exposed.

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Supplementary Materials

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Supplementary Text
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