When will we ever learn?
A History of Tree Disease

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The mission statement of BSBI is ‘To advance the study and enjoyment of wild plants and support their conservation in Britain and Ireland’. In recent years it has become apparent that disease is a major threat to the conservation of our native tree species. My aim is to provide a historical perspective on the causes of these diseases and to outline the steps that can be taken to reduce this threat.
Tree disease issues came dramatically to the fore when the presence of Ash dieback was announced in autumn 2012 and prompted the convening of a Cobra meeting.
Ash tree disease threatens British forest, after ministers were 'too slow to act' on news

One vital question that was not addressed at the time was why this disease was so devastating. There was also no historical perspective on tree disease epidemics or any explanation of the factors responsible for such diseases.
Exotic Diseases are the most devastating

Smallpox – ½ of Mexican population
¼ - ½ of Native American population

To understand the causes of major tree disease epidemics, it is important to recognise that pathogens and associated disease are a normal component of natural ecosystems, but their effects are usually not dramatic. A relatively stable pathogen population is generally present, the outcome of long-term co-evolution between hosts and pathogens. However devastating epidemics can occur when exotic pathogens are transported to hosts with which they have not co-evolved. This is illustrated by the catastrophic effects of smallpox transported from Europe to the Americas where the disease had not previously been encountered.
To demonstrate the relevance to trees of this principle, that devastating epidemics arise from import of exotic diseases, I will look at a number of notorious case histories. The first example is concerned with the American chestnut. In the nineteenth century this species formed magnificent stands throughout the eastern US, with a single tree providing enough timber to build a house.
Chestnut provided subsistence for humans and supported a diverse ecosystem that included the passenger pigeon whose numbers at their peak reached some six billion birds.
The demise of the American chestnut was brought about by the importation of seedlings of the related Japanese chestnut from Japan to sites in eastern North America. The purpose was to establish a more efficient production system yielding larger fruits that were more accessible for harvesting.
With the imported Japanese chestnut trees came the chestnut blight fungus. Japanese chestnut had co-evolved with chestnut blight and was resistant to it. However the chestnut blight fungus proved devastating on the highly susceptible American chestnut.
Destruction of the American Chestnut

Within 40 years chestnut blight spread throughout the natural range of American chestnut reducing once magnificent trees to mere sprouting shrubs with consequent collapse of associated biodiversity and dependant communities.
Thus the ultimate cause of the American chestnut blight epidemic was the planting of a related exotic species within the natural distribution of American chestnut.
The second historical example of a devastating tree disease epidemic is one that which continues to affect eastern white pine, a five needled pine native to north eastern America.
A cause of Colonial Friction

Charter of Massachusetts Bay 1691

“For better providing and furnishing of Masts for our Royal Navy wee do hereby reserve to us Our Heires and Successors ALL trees of the diameter of 24 inches and upward of 12 inches from the ground, growing upon any soils or tracts of land within our said Province or Territory not heretofore granted to any private persons.”

From the seventeenth century eastern white pine was recognised as of enormous economic importance for the construction of ship’s masts, and trees of appropriate size were deemed as belonging to the British crown. Grievance over this practice sparked a riot that predated the Boston Tea Party.
Weymouth pine (*Pinus strobus*), emblem of the colonial forces

‘Pine tree flag’

The species became a symbol of the American colonial forces.
Old growth stands of white pine were of enormous importance for construction timber in northeastern America well into the twentieth century.
In the early eighteenth century Viscount Weymouth recognised the value of eastern white pine and established plantations in Britain. A very productive plantation industry based on the species was also set up in continental Europe in the nineteenth century.
In the mid nineteenth century transfer took place of white pine blister rust from a five needled pine native to eastern Europe to the exotic eastern white pine plantations. A devastating epidemic of blister rust occurred on eastern white pine which had not co-evolved with the rust, making it impossible to grow eastern white pine commercially. The disease epidemic was spread to British plantations via infected nursery stock.
White pine blister rust girdles white pine trees leaving the tree dead from the lesion upwards.
Towards the end of the nineteenth century, American foresters began to restock the white pine sites which had been logged. It was cheaper to buy planting stock from Europe, where there was no longer demand for the species due to the blister rust epidemic. For purely economic reasons infected planting stock was therefore imported from Europe and planted on both coasts of America, bringing with it white pine blister rust and sparking a widespread epidemic.
Attempts to control the epidemic were based on an understanding of the rust’s life cycle. Spores from pine cannot re-infect pine directly. Infection must proceed via secondary hosts, which comprise a wide variety of species of the currant family *Ribes*. A potential control measure is thus the removal of currant bushes from the vicinity of white pines.
A policy of removal of cultivated currant bushes was adopted in the US in order to control the disease. This ran for about 50 years and in today’s currency cost about 1 billion dollars. The professor of plant pathology at the Connecticut Agricultural Experiment Station was not convinced the policy was sound, and protected his own currant bushes at the point of a gun.
ERRADICATION OF CURRANTS FROM PINE FORESTS

“That’s an awfully big garden to weed”

The currant eradication programme extended to the 30+ Ribes species occurring naturally in the native pine forests and involved huge numbers of workers, especially at the time of the great depression in the 1930s. However it was ultimately unsuccessful in curbing the spread of the disease.
White pine blister rust continues to have very serious effects on the many white pine species present in the US, including, most recently, the bristlecone pine, one of the longest lived organisms on earth.
Once again the cause of this devastating tree disease is the transfer of a species into the natural range of a close relative, and the transfer of a pathogen between these relatives.
So far the examples I have highlighted predominantly affect trees native to North America. I now turn to a local example, that of Dutch Elm disease. Bark beetles breed in elm trees, but can only do so if the bark tissue is dead. Beetles chew through bark in canopy twigs, and inject the Dutch elm disease fungus into the xylem. As a result the xylem becomes blocked, the tree limb dies, and the beetle is able to breed in the dead bark. Emerging offspring of the beetle carry fungus on to the next tree to continue the cycle.
1930: EXPORT OF BURL ELM FROM EUROPE TO U.S.A.

Dutch elm disease was known in Europe at the beginning of the twentieth century, but caused relatively little damage, leading to the loss of individual tree limbs rather than death of whole trees. The severity of the disease increased as a consequence of a chain of events involving intercontinental transport of barked logs. A shipment of diseased elm logs with attendant beetle and fungus was sent from France to Ohio to be used in the furniture industry.
TRANSFER OF DUTCH ELM DISEASE FROM EUROPE TO NORTH AMERICA
1930

On arrival Dutch elm disease beetles emerged from the logs and carried the fungus to infect the highly susceptible American elm that had never previously encountered the disease, sparking a catastrophic epidemic.
HIGHLY SUSCEPTIBLE AMERICAN ELM

American elms, one of the most important shade trees in US cities, were completely destroyed by the disease.
Epidemic kills American Elms

Evolution of ‘aggressive’ form

Spread from Ohio was very rapid, and is still continuing today. At the same time natural selection took place favouring those strains of the Dutch elm disease fungus that were most effective in killing trees rapidly, since their rate of reproduction was faster than that of more benign strains. An ‘aggressive’ form of Dutch elm disease evolved.
The next stage of the story involved the shipment of intact, diseased, logs carrying the ‘aggressive’ form of the fungus from North America to Britain. The ‘aggressive’ strain of the fungus was much more damaging than the previous form, and caused destruction of the English elm populations that were previously a prominent feature of the British landscape.
1967: Import to UK of Infected Elm Logs from Canada

“Aggressive” form
Evolved in America

Spread from ports, the sites of entry was very rapid......
Loss of Elm from the English Countryside 1970-

......and the landscape and trees familiar and much loved by Constable were lost.
Effects of Dutch Elm Disease in Scotland – *Ulmus glabra*

Dutch elm disease spread to Wych elm in Scotland, and although some canopy trees can still be found, most have been reduced to shrubs whose rootstocks survive Dutch elm disease, but become re-infected when the suckering stems reach a height of about 4 metres.
Along the Water of Leith
Sanitary felling in Edinburgh, and antibiotic treatment of certain specimen trees in parks has reduced the rate of loss of elms from the city.
However it is only a matter of time before these trees will be lost to the disease.
Once again it is the transport of tree species, in this case in the form of harvested stems, into the range of a related tree species, that has been the ultimate cause of the tree disease epidemic.
One important outcome of the public outcry over ash dieback was that funding became available for research on tree disease. We were thus able to begin a programme of research aimed at understanding the underlying causes of a needle disease of Scots pine which had recently been reported for the first time in the Caledonian pinewoods.
<table>
<thead>
<tr>
<th>Dothistroma needle blight (DNB) is caused by an ascomycete fungus. It has a huge host range on pines. Infection leads to needle loss, growth reduction and, in some circumstance, tree death.</th>
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<td><strong>Dothistroma needle blight of pine DNB (<em>Dothistroma septosporum</em>)</strong></td>
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<tr>
<td>82 host pine species</td>
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<td>Growth reduction α Crown affected</td>
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<td>Epidemics on pine worldwide</td>
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<td>First recorded on Caledonian pine 2010</td>
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In Britain the disease was first recorded on exotic pines in nurseries in southern England. Some 40 years later it was found causing extremely serious damage in exotic Corsican pine plantations, particularly in East Anglia. Outbreaks of DNB were then found on exotic Lodgepole pine planted in Scotland, often close to Caledonian pinewoods. Finally the disease was discovered for the first time on Caledonian Scots pine in 2010. Association of the disease with exotic pine species prompted an investigation of the Dothistroma populations associated with both the exotic pines and the native Caledonian Scots pine.
THREE RACES OF DOTHISTROMA

1. Lodgepole pine race
2. Southern race (Corsican pine)
3. Native Caledonian pine race

A genetic investigation of Dothistroma recognised the existence of three separate races in Scotland. The most distinct race was found only on Lodgepole pine. A race with a predominantly southern distribution was found predominantly on Corsican pine, but also on Lodgepole and Scots pine. The final race was very strongly associated with Native Caledonian pine.
A scenario has been developed to account for the presence of these three races of Dothistroma in Scotland. This proposes that before the planting of exotic pines in Britain, Caledonian Scots pine populations had co-evolved with a Native race of *D. septosporum* which caused little damage, and was therefore overlooked as a pathogen.
SCENARIO TO ACCOUNT FOR MULTIPLE RACES OF DOTHISTROMA

Native Caledonian pine populations in Scotland with native race of *D. septosporum*

Widespread planting of susceptible Corsican pine in England and on coast in Scotland

Widespread planting of highly susceptible Corsican pine then occurred predominantly in England, but extending to coastal sites in Scotland.
SCENARIO TO ACCOUNT FOR MULTIPLE RACES OF DOTHISTROMA

Native Caledonian pine populations in Scotland with native race of *D. septosporum*

Widespread planting of susceptible Corsican pine in England and on coast in Scotland

Introduction of Southern Race from France and build up epidemic on susceptible Corsican pine. Transfer of native race to Corsican pine in north

Transfer of a Southern race of Dothistroma then took place from continental Europe, causing an epidemic on Corsican pine. At the same time spread of the Native race of Dothistroma occurred onto the Corsican pine populations in Scotland.
Native Caledonian pine populations in Scotland with native race of *D. septosporum*

Widespread planting of susceptible Corsican pine in England and on coast in Scotland

Introduction of Southern Race from France and build up epidemic on susceptible Corsican pine. Transfer of native race to Corsican pine in north

Widespread planting of lodgepole pine in Scotland with accidental introduction of lodgepole pine race and resulting epidemics

Finally Lodgepole pine was planted extensively in Scotland, and brought with it a lodgepole pine race of Dothistroma from North America. This flourished on Lodgepole pine and caused serious damage to the Lodgepole pine plantations.
DOTHISTROMA ON CALEDONIAN PINE

Endemic race causing little damage

Planting of two exotic species closely related to Scots pine

Introduction, multiplication and spread of two more virulent races of Dothistroma to Caledonian pinewoods

INTRODUCTION OF EXOTICS CLOSELY RELATED TO NATIVE TREE SPECIES INCREASES THE THREAT POSED BY DISEASE TO THESE NATIVE SPECIES

In Caledonian pine sites there are now three races of Dothistroma: the original Native race; a Southern race capable of infecting and causing damage on Caledonian pine; a Lodgepole pine race affecting the Lodgepole pine planted in close proximity to Caledonian pine. The presence of the two exotic races, introduced as a consequence of planting exotic pines closely related to Caledonian pine, has increased the threat posed by the disease to Scotland’s national tree.
Hundreds of acres of Moray forestry to be felled to prevent spread of infectious disease (Press & Journal, September 2017)

Rothiemurchus harvesting to tackle tree disease and restore natural habitats (Forestry Commission September 2017)

REMOVAL OF LODGEPINE ADJACENT TO CALEDONIAN PINE

Efforts are now being made to remove exotic pines from the vicinity of Caledonian pine populations to reduce the risk of Dothistroma infections from the introduced races.
ASH DIEBACK – AUTUMN 2012

A disease that has the potential to devastate the UK’s ash tree population has been recorded for the first time in the UK’s natural environment.

25/10/12

We can now return to the example with which we began and ask about the ultimate cause of the ash dieback outbreak first announced in 2012.
The importance of ash in Britain is enormous – culturally, commercially and in terms of the huge amount of biodiversity that it supports.

A History of Ash Dieback

10% broadleaved trees in U.K.

Supports >1000 other species

44 species found only on ash
Ash Dieback, *Hymenoscyphus fraxineus*
Known in Continental Europe since 1990

The organism responsible for ash dieback is an ascomycete fungus whose spores infect newly emerging leaves from fruiting bodies on fallen leaves. The fungus grows down the stipe and crosses the barrier into the bark. In the main stem it causes cankers that girdle branches and stems and leads to loss of canopy shoots, whole limbs, and in some cases the death of the entire tree.
Recent research indicates that the ultimate cause of the disease epidemic was the transfer of Manchurian ash trees from eastern to western USSR in the Soviet era. Manchurian ash carried with it, but was not damaged by, the ash dieback fungus. When Manchurian ash came into contact with European ash in western USSR, the ash dieback fungus was transferred, and European ash, which had not encountered the fungus before, proved to be highly susceptible.
Import of Diseased Ash, raised from British seed, from Continental Nurseries into Britain

Although infection of British ash trees has probably taken place as a consequence of spore dispersal across the North sea, the process has been greatly facilitated by the practice of growing planting stock of British ash in nurseries in continental nurseries, and then importing this infected stock for planting in Britain. Ironically many of these plantings were associated with conservation schemes.
Current situation in UK

Ash dieback is now very widespread throughout Britain
Symptoms include leaf spotting...
....wilting of leaves and cankering of stems.......
........snapping of stems above cankers .....
...... basal cankers.......
..... which rapidly kill trees.
Once again the ultimate cause of our problems is the movement of trees into the range of a related species and the transfer of a pathogen between the two species.
FACTORS INCREASING THE RISK OF CATASTROPHIC TREE DISEASE EPIDEMICS

1. Movement of tree species and products across natural biogeographic barriers to exotic locations containing closely related species

2. Establishment of exotic plantations within the range of closely related species

3. Movement of planting and harvested material from exotic sites to the native range

The same story is told by all my examples.
FACTORS INCREASING THE RISK OF CATASTROPHIC TREE DISEASE EPIDEMICS

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We can clearly identify the factors that have led to our problems.
PROTECTING NATIVE TREES FROM CATASTROPHIC DISEASE EPIDEMICS

1. **GROW AND SOURCE ALL PLANTING STOCK FROM WITHIN THE UK**

   UK Sourced and Grown (UKSG) Assurance Initiative

   22 Accredited Nurseries

Following a few simple rules can protect our native tree from the devastating consequences of disease caused by exotic pathogens. Firstly, we must source and grow our planting stock within Britain.
PROTECTING NATIVE TREES FROM CATASTROPHIC DISEASE EPIDEMICS

Elm
Ash
Scots pine

2. UNDERTAKE COMPREHENSIVE RISK ASSESSMENT BEFORE INTRODUCTION OF EXOTIC TREE SPECIES

VERY HIGH BIOSECURITY RISK OF SPECIES RELATED TO NATIVE TAXA

Wildlife and Environment Act Scotland 2011

Big leaf maple *Acer macrophyllum*
Red oak *Quercus rubra*

Secondly, we must develop a risk assessment framework for determining the dangers posed by the introduction of any new exotic tree species into Britain. Be should be particularly wary of exotic tree species that are closely related to any of our native tree species. A laissez faire attitude to exotic tree introductions is not acceptable. Two exotic species proposed for planting in response to climate change that would pose particular threats are big leaf maple and red oak.
A very important observation with respect to ash dieback and other introduced exotic diseases is that in the field individuals appear to be differentially affected by the pathogen.
RECOVERY FROM EXOTIC DISEASES – EVOLUTION OF RESISTANCE

Ash dieback

- Damage score
- 5% resistant – phenols in bark

Dothistroma on Caledonian pine

- DNB severity
- Longitude of origin
- Large genetic variation in resistance among families

SPECIES WILL EVOLVE RESISTANCE IF NATURAL REGENERATION CAN TAKE PLACE

Controlled tests of resistance to ash dieback in ash, and Dothistroma in the case of Caledonian pine, indicate that variation in resistance has a genetic basis.
Ash and Caledonian pine both have the potential for copious natural regeneration if managed appropriately.
Where there is genetic variation in resistance and copious natural regeneration in the presence of disease, there is the opportunity for rapid natural selection of more resistant populations of our native tree species.
PROTECTING NATIVE TREES FROM CATASTROPHIC DISEASE EPIDEMICS

Elm  Ash  Scots pine

3. **MANAGE WOODLANDS TO PROMOTE NATURAL REGENERATION**

Condition necessary for natural selection and evolution of resistant populations

Concurrent adaptation to climate change

So the final principle that we should follow to protect our native trees from exotic disease, is to manage for natural regeneration, rather than continue to plant. This will provide the opportunity for adaptation of our native tree species to multiple exotic disease threats, and concurrently provide opportunity for adaptation to climate change.
ACKNOWLEDGEMENTS
Failure of Biosecurity in Australia

Myrtle rust - Disease native to Brazil where it has caused serious damage to Eucalypts planted in exotic plantations

Despite tight Biosecurity Plans Myrtle rust entered Australia 2010

By 2015 established along whole east coast of Australia

After only 4 years exposure mortality rates in two rainforest tree species are 12% and over 50%

![Image of tree affected by Myrtle rust](image-url)
Failure of Biosecurity in Britain

Chestnut blight is an EU quarantine organism – imported plants must have clean passports

2011
Chestnut blight found on >150 sweet chestnut trees *Castanea sativa* planted for nut production – import from French nursery

2011-2017
Further outbreaks in Devon, Dorset, Berkshire, Kent, London, Leicestershire, and Derbyshire